ECOLOGY AND DEMOGRAPHY OF THE TEXAS TORTOISE IN A MANAGED THORNSCRUB ECOSYSTEM

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> The Cenozoic came, and with it progressive drought, and the turtles joined in the great hegira of swamp and forest animals to steppe and prairie, and watched again as the mammals rose to heights of evolutionary frenzy reminiscent of the dinosaurs in their day, and swept across the grasslands in an endless cavalcade of restless, warm-blooded types. Turtles went with them, as tortoises now, with high shells and columnar, elephantine feet, but always making as few compromises as possible with the new environment, for by now their architecture and their philosophy had been proved by the eons; and there is no wonder that they just kept on watching as *Eohippus* begat Man o' War and a mob of irresponsible and shifty-eyed little shrews swarmed down out of the trees to chip at stones, and fidget around fires, and build atom bombs.

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CHAPTER I

THE EFFECTS OF GRAZING BY CATTLE ON DEMOGRAPHY AND GROWTH OF TEXAS TORTOISES

ABSTRACT

Within the United States, the state-threatened Texas tortoise (*Gopherus berlandieri)* is primarily restricted to the rangelands of southern Texas. The development of management recommendations for this species is hampered by a lack of information on the effects of land-use practices on Texas tortoises. I evaluated the effects of grazing by cattle (short-duration, winter, rotational grazing regime; 6-28 animal unit days/ha) on this tortoise by comparing 2 grazed and 2 ungrazed sites in the Western Rio Grande Plains, Texas, from April 1994 to August 1997. Capture effort resulted in 132 captures of 106 individuals in the ungrazed pastures and 324 captures of 237 individuals in the grazed pastures. Radiotransmitters were placed on 22 tortoises for 14,619 radio-days in the ungrazed pastures and 25 tortoises for 15,355 radio-days in the grazed pastures. Comparisons of relative abundance, size structure, age structure, body size, size dimorphism index, sex ratio, adult survival, clutch size, proportion of females gravid, proportion of juveniles, and growth rates revealed no differences between tortoises on grazed and ungrazed areas. I suggest that cattle grazing can be compatible with maintenance of robust tortoise populations. My data were consistent with a general model of tortoise biogeography and tolerance of disturbance, with Texas tortoises being adapted to intermediate levels of disturbance.

INTRODUCTION

Approximately 6.7 billion ha of the earth's surface can be classified as rangeland (World Resources Institute 1986). Globally, the dominant land-use practice on rangeland is livestock grazing, particularly in arid and semiarid regions. Although the effects of grazing are ultimately tied to complex interactions among grazing regime, habitat, and climate, use of these rangelands has undergone increasing scrutiny in recent years due to perceived exploitation and degradation of these habitats by livestock grazing. Poorly monitored or uncontrolled grazing regimes have been blamed for reductions of native species richness and diversity, increased dominance of exotic species, alteration of nutrient cycles, perturbation of niche and community structure, deviations from normal successional patterns, and degradation of the landscape through erosion, soil compaction, and damage to riparian corridors (Fleischner 1994, but see Milchunas et al. 1998). In the western United States, livestock grazing has been blamed, either directly or indirectly, for the decline of a number of vertebrate species, including prairie dogs (*Cynomys* spp.) and the desert tortoise (*Gopherus agassizii*; Berry 1978, Fleischner 1994, Miller et al. 1994).

Grazing can be particularly damaging to arid and semi-arid shrublands by enhancing woody plant invasion (Archer 1996). Landscape treatments that exacerbate the effects of shrub encroachment by attempting to reduce woody plant coverage include chaining, roller-chopping, root-plowing, or aeration. Such manipulations, however, can result in less diverse communities that regrow to be more dense in woody vegetation than unmanipulated areas (Ruthven et al. 1993, Nolte et al. 1994).

Tortoises (Order Testudines, Family Testudinidae) are geographically widespread, and a large proportion of the taxa inhabits arid and semi-arid areas traditionally considered rangeland for livestock. These terrestrial chelonians have received much attention due to concerns about declining populations and exploitation by humans on a worldwide basis (Van Abbema 1997). Of the approximately 50 species of tortoise (Ernst and Barbour 1989), 1 is considered "critically endangered", 4 are "endangered", and 18 are listed as "vulnerable" by the IUCN (IUCN/SSC 1996). In North America, the Testudinidae is represented by a single genus (*Gopherus*) with 4 species (Crumly 1994): desert tortoise (*G. agassizii*), Texas tortoise (*G. berlandieri*), Bolson tortoise (*G. flavomarginatus*), and gopher tortoise (*G. polyphemus*). The desert tortoise, Bolson tortoise, and gopher tortoise are listed by the U.S. Fish and Wildlife Service under the Endangered Species Act (Bury and Germano 1994). The Texas tortoise was protected by an act of the Texas Legislature in 1967 and is currently listed as "threatened" in the state (Rose and Judd 1982).

The impact of land-use practices on tortoises is poorly understood despite global concern for the taxon, and much of the information available is largely anecdotal. A switch from a nomadic to a stationary grazing system with camel and sheep in the Turkmen Republic has been implicated with dune destabilization, desertification, and the decline of Horsfield's tortoise (*Testudo horsfieldi*; Makeyev et al. 1997). In the Souss Valley in southern Morocco, Mediterranean spur-thighed tortoises (*Testudo graeca)* are declining as a direct result of changing land-use practices, including dune destabilization and reduced forage availability brought about by overgrazing (Bayley and Highfield 1996). Chaco tortoises (*Geochelone chilensis*) in Argentina rely on annual plants and fruit from a variety of woody species, but unregulated grazing/browsing by free-ranging goats, cattle, and sheep has reduced the availability of both annual vegetation and woody shrubs. Livestock also have been implicated in soil compaction, which further reduces the availability of annual plants, and for trampling of chaco tortoise burrows. Thus, grazing was viewed as negatively impacting chaco tortoises (Waller and Micucci 1997).

North American tortoises, by virtue of their broad distribution, provide a good model taxa to study how grazing effects can vary with grazing regime, habitat, and climate. Considerable debate has raged about the degree to which grazing by livestock might affect these tortoises. In the xeric sand communities of Florida, gopher tortoises prefer rather open habitats that have been maintained historically by periodic fires (Auffenberg and Franz 1982). Due to rapid urbanization and fragmentation of habitats in Florida, fire suppression is now common throughout the state and may be negatively impacting the gopher tortoise as canopies become closed (Auffenberg and Franz 1982). Under such conditions, grazing may benefit tortoises by maintaining more ruderal communities.

The effects of grazing by livestock on the desert tortoise, however, are typically viewed as negative (Berry 1978). Because desert tortoises inhabit regions of extremely low primary productivity, it is arguably the most sensitive species of *Gopherus* to grazing and other disturbances. Evaluation of livestock and desert tortoise interactions, however, has often left the biological arena and entered the realm of emotion and politics (Bostick 1990), and management decisions for desert tortoises often have been made without critically examining the available data (Bury and Corn 1995). Recent research has suggested that dietary overlap between desert tortoises and cattle can be pronounced, particularly during spring in the Mojave Desert in California (Avery and Neibergs 1997). Trampling of burrows and reduction of annual plant germination through soil compaction also might impact desert tortoises (Avery and Neibergs 1997). In reality, little research has specifically addressed livestock and desert tortoise interactions (but see Avery and Neibergs 1997), and much of the potential impacts have been speculative (Oldenmeyer 1994). Because of the widespread lack of comparative studies between grazed and ungrazed areas, much of the literature pertaining to grazing and desert tortoises should be considered suspect (Oldenmeyer 1994).

Because the effects of grazing are dependent upon the primary productivity on a site and the Texas tortoise inhabits an ecoregion intermediate in precipitation and primary productivity to the ranges of the desert and gopher tortoises, the Texas tortoise may be a useful model to investigate grazing effects on populations of this genus. Discussion of grazing concerns relative to the Texas tortoise has been limited to urging against grazing on lomas (coastal clay hills) inhabited by tortoises in the Lower Rio Grande Valley (Bury and Smith 1986). I investigated the ecology of the Texas tortoise in grazed and ungrazed pastures at a site near the northern limit of its range in southern Texas. My primary objectives were to assess the effects of grazing by cattle on the demography of the Texas tortoise by comparing data between grazed and ungrazed pastures and to discuss possible effects of grazing by cattle on the Texas tortoise throughout its range in the Rio Grande Plains (Auffenberg and Weaver 1969, Rose and Judd 1982, Bury and Smith 1986).

STUDY AREA

All research was conducted on the Chaparral Wildlife Management Area (WMA) in Dimmit and La Salle counties, Texas, near the northwestern edge of the geographic range of the Texas tortoise (Fig. I.1). Chaparral WMA is a 6,150-ha facility that has been managed as a research and demonstration area by the Texas Department of Wildlife and

Parks (TPWD) since its acquisition in 1969. Chaparral WMA is currently composed of 15 major pastures ranging from 258 to 750 ha (Fig. I.2). 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).

Climate

Rainfall on Chaparral WMA is bimodally distributed with a primary peak in May-June, a secondary peak in September, and an annual average rainfall of 66 cm (1969-1997; TPWD unpublished data). Quantity and timing of rainfall, however, is extremely variable in this region, and droughts are common. Average annual temperature is 22.3 °C, and average number of days in May, June, July, August, and September with the maximum temperature exceeding 38 °C is 4, 9, 20, 19, and 6, respectively (1984-1997; TPWD unpublished data). Temperatures can remain warm throughout the year and occasionally winters occur with no temperatures below freezing. Length of the frost-free period for the area is typically 275-290 days (Hatch et al. 1990). Relative humidity on Chaparral WMA exhibits a diel pattern of low daytime and high night-time relative humidities throughout the year (TPWD unpublished data).

Floral and Faunal Communities

Vegetation on the area is represented by >475 species (R. T. Kazmaier, unpublished data; botanical nomenclature follows Hatch et al. 1990), but Chaparral WMA is dominated by *Prosopis-Acacia* thornscrub communities. Other communities, such as paloverde (*Parkinsonia texana*)- or ceniza (*Leucophyllum frutescens*)-dominated uplands or whitebrush (*Aloysia gratissima*)-dominated drainages, may be locally significant. There is a clinal tendency to vegetation on Chaparral WMA, with denser thornscrub in the east and more open savannah habitats in the west (TPWD unpublished data). Honey mesquite (*Prosopis glandulosa*), blackbrush acacia (*Acacia rigidula*), guajillo (*Acacia berlandieri*), twisted acacia (*Acacia schaffneri*), granjeno (*Celtis pallida*), brasil (*Condalia hookeri*), Texas persimmon *(Diospyros texana*), coyotillo (*Karwinskia humboldtiana*), hog-plum (*Colubrina texensis*), vine ephedra (*Ephedra antisyphilitica*), ceniza, paloverde, whitebrush, lotebush (*Zizyphus obtusifolia*), and coma (*Bumelia celastrina*) are common woody species. Prickly pear cactus (*Opuntia lindheimeri*) is abundant throughout the area, and tasajillo (*Opuntia leptocaulis*) is locally common.

Dominant native grasses include hooded windmill grass (*Chloris cucullata*), fringed signalgrass (*Brachiaria ciliatissima*), and a variety of species of *Setaria* and *Paspalum*. Much of the graminoid biomass, however, is dominated by two introduced grasses: Lehmann lovegrass (*Eragrostis lehmanniana*) and buffelgrass *(Cenchrus ciliaris*). Forbs are diverse and abundant, and common species include crown coreopsis (*Coreopsis nuecensis*), burridge greenthread (*Thelespermum burridgeanum*), partridge pea (*Chamaecrista fasciculata*), crow poison (*Nothoscordum bivalve*), lazydaisies (*Aphanostephus* spp.), dayflower (*Commelina erecta*), scarlet pea (*Indigofera miniata*), bracted zornia (*Zornia bracteata*), cowpen daisy (*Verbesina encelioides*), indian blanket (*Gaillardia pulchella*), rough nama (*Nama hispidum*), silky evolvulus (*Evolvulus sericeus*), slender evolvulus (*Evolvulus alsinoides*), rough buttonweed (*Diodia teres*), and a variety of verbenas (*Verbena* spp.) and plantains (*Plantago* spp.). Baldy Pasture (Fig. I.2) is somewhat unique for Chaparral WMA, because of a north-south trending, sandstone escarpment that essentially divides the pasture in half. As a result, Baldy

Pasture supports a variety of plant species, including century plant (*Agave scabra*), scented lippia (*Lippia graveolens*), heartleaf hibiscus (*Hibiscus martianus*), and perezia (*Acourtia runcinata*), that are rare or absent from the rest of the area.

The area is also faunistically diverse, with species richnesses of at least 222 birds, 25 mammals, 36 reptiles, and 6 amphibians known from Chaparral WMA (R. T. Kazmaier, unpublished data). Conspicuous members of the vertebrate fauna on Chaparral WMA include greater roadrunner (*Geococcyx californianus*), painted bunting (*Passerina ciris*), vermillion flycatcher (*Pyrocephalus rubinus*), Chihuahuan raven (*Corvus cryptoleucus*), northern bobwhite (*Colinus virginianus*), scaled quail (*Callipepla squamata*), collared peccary (*Tayassu tajacu*), white-tailed deer (*Odocoileus virginiana*), raccoon (*Procyon lotor*), coyote (*Canis latrans*), Merriam's pocket mouse (*Perognathus merriami*), Ord's kangaroo rat (*Dipodomys ordii*), western diamondback rattlesnake (*Crotalus atrox*), coachwhip (*Masticophis flagellum*), longnose snake (*Rhinocheilus lecontei*), Texas spotted whiptail (*Cnemidophorus gularis*), southern prairie lizard (*Sceloporus undulatus consobrinus*), and yellow mud turtle (*Kinosternon flavescens*).

The floristic and faunistic composition in and around Chaparral WMA has elements from Mexico and the Lower Rio Grande Valley (green jay [*Cyanocorax yncas*], Audubon's oriole [*Icterus graduacauda*], least grebe [*Tachybaptus dominicus*], rose-bellied lizard [*Sceloporus variabilis*]), the Edwards Plateau (porcupine [*Erethizon dorsatum*], short-lined skink [*Eumeces tetragrammus*]), and the Trans-Pecos (century plant, verdin [*Auriparus flaviceps*], Harris's hawk [*Parabuteo unicinctus*], Texas banded gecko [*Coleonyx brevis*]). Four species found on the site are classified as threatened by TPWD: Texas tortoise, Texas horned lizard (*Phrynosoma cornutum*), Texas indigo snake

(*Drymarchon corais*), and reticulate collared lizard (*Crotaphytus reticulatus*). This area supports a high diversity and density of potential tortoise predators, including greater roadrunner, crested caracara (*Polyborus plancus*), Harris's hawk, Chihuahuan raven, western diamondback rattlesnake, Texas indigo snake, coyote, bobcat (*Felis rufus*), badger (*Taxidea taxus*), raccoon, striped skunk (*Mephitis mephitis*), feral hog (*Sus scrofa*), and an occasional mountain lion (*Felis concolor*). Established exotic vertebrates on Chaparral WMA are limited to feral hog, house sparrow (*Passer domesticus*), and Mediterranean gecko (*Hemidactylus turcicus*), but European starling (*Sturnus vulgaris*), rock dove (*Columba livia*), and Japanese macaque (*Macaca fuscata*) have occasionally been observed.

Grazing History

Cattle and horses were introduced into Texas by Spanish explorers in the 1500's, but the area remained sparsely inhabited until the late 1800's (TPWD, unpublished report). Before 1900, most grazing operations in the Rio Grande Plains consisted of roaming cattle that did not heavily impact any particular site. Beginning around 1900, however, ranching became more localized and livestock numbers greatly increased. Increased grazing intensity led to overgrazing throughout the Rio Grande Plains and many ranches in the area remain overgrazed today (Lehmann 1969, Crosswhite 1980).

When originally acquired, Chaparral WMA was being continuously grazed with a cow-calf operation at a rate of 750 animal units (AU; 1 AU = 1 cow + 1 calf) on the entire 6,150 ha (0.12 AU/ha/yr; TPWD, unpublished report). In 1971, the grazing program was modified to include 1,673 ha under continuous light grazing (0.06 AU/ha/yr; Ano Nuevo and Guajalote pastures), 1,353 ha under continuous moderate grazing (0.08 AU/ha/yr;

Baldy, Hogue, Headquarters, Rosindo, and Mare pastures), 664 ha under continuous heavy grazing (0.12 AU/ha/yr; Long and Mustang pastures), and 2,284 ha under a 2-herd, 3-pasture rotational grazing regime (166 AU; 0.07 AU/ha/yr; North Jay, South Jay, and Blocker pastures; TPWD, unpublished report). In 1980, the grazing regime was again modified with 3,563 ha receiving continuous light grazing (0.05-0.06 AU/ha/yr; Long, Mustang, Headquarters, Hogue, Rosindo, Cacho, Mare, Ano Nuevo, and Guajalote pastures); the stocking rate for the 2,284 ha under the rotational grazing scheme was reduced to 100 AU (0.04 AU/ha/yr; TPWD, unpublished report). A further modification of the grazing system occurred in 1981 when all grazing was shifted to a rotational regime with one herd rotating through 4 pastures of 1,917 ha (125 AU; 0.07 AU/ha/yr; Guajalote and Blocker pastures) and one herd rotating through 5 pastures of 3,957 ha (175 AU; 0.04 AU/ha/yr; Long, Mustang, Hogue, Rosindo, South Jay, Mare, Cacho, Ano Nuevo, and North Jay; TPWD, unpublished report). Due to continued degradation of range condition, stocking rates were reduced from 125 AU to 75 AU and 175 AU to 100 AU in 1983, but no improvement in range condition was achieved and all cattle were removed by April 1984. At this time, Chaparral WMA was in a severely overgrazed state with little standing herbaceous material (D. R. Synatzske, TPWD, personal communication).

Grazing System

Currently, Chaparral WMA is surrounded by a 2.4-m woven wire fence that was erected in 1983, and the 13 interior pastures are separated by 5-strand barbed-wire cattle fences. A span of 2.4-m woven wire fence also divides the area down the center into the east and west grazing units (Fig. I.2). 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. Cattle grazing was reinitiated in 1991 with a two-herd, dormant-season, short-duration, rotational grazing system. Under this system, each herd was composed of approximately 400 steers (1 AU = 2 steers), and one herd rotated through the 6 western pastures (Mustang, Long, West Blocker, West Guajalote, East Guajalote, East Blocker) while the other herd rotated through the 7 eastern pastures (Headquarters, Hogue, Rosindo, Cacho, Ano Nuevo, North Jay, South Jay). Steers had an average mass of 218 kg on arrival to Chaparral WMA. Grazing was initiated in early October and all cattle were removed in May of the following year. During rotation, a herd grazed a pasture for 3-8 weeks depending on pasture size and forage availability.

For this study, effort was focused on the 2 ungrazed pastures (Baldy [277 ha] and Mare [263 ha]) paired with 2 grazed pastures (East Blocker [372 ha] and South Jay [750 ha]). Pastures were paired by similar vegetation types, as defined by canopy coverages and dominant species of woody plants. Baldy was paired with East Blocker for west side comparisons; Mare was paired with South Jay for east side comparisons. To remain in similar habitat between pasture pairs, search and radiotelemetry effort was skewed toward the eastern half of Baldy (above the escarpment), the eastern two-thirds of East Blocker, the southern half of South Jay, and the southwestern two-thirds of Mare (Fig. I.2).

Grazing intensity by steers in South Jay and East Blocker differed in 1994-1997 (Table I.1), but attempts were made to equalize impacts on herbaceous vegetation in the two pastures each year. A very intense, short-term drought occurred in 1996 (86 mm of rain from 1 December 1995 to 1 July 1996; TPWD unpublished data), and because South Jay is composed of proportionally less open savannah and proportionally more dense thornscrub than East Blocker, South Jay was grazed with less intensity during this period. Timing of grazing for East Blocker and South Jay was during the spring (April-May), when interactions between cattle and tortoises were most likely to occur. Miscommunication with the lessee resulted in South Jay being grazed earlier in the season than East Blocker during the first year of field work (Table I.1).

METHODS

Tortoises were captured by road cruising and during fortuitous encounters and intensive searches throughout the 4 study pastures from 7 April 1994 to 12 October 1997. Data collected at each encounter included sex, straight-line carapace length (SCL; mm; dial calipers), mass (g; Pesola spring scale), and age. Because adult female tortoises retain juvenile characteristics, a carapace length of 120 mm was used as the threshold length for sexing. Tortoises < 120 mm SCL were considered juveniles; tortoises ≥ 120 mm SCL were considered adults. Among adults, tortoises with dimorphic characters (concave plastrons, thickened anal scutes, and enlarged chin glands; Rose and Judd 1982) were considered males; nondimorphic adults were considered females. I estimated age by counting scute annuli (Germano 1988, Zug 1991) on 10 scutes (C2, C3, C6, C7, V1, V2, V3, A1, A2, P1 and P2; scute nomenclature follows Kazmaier 1994) and the mode was used to indicate age. Several recent studies have been critical of annuli techniques for aging turtles (Brooks et al. 1997, Bjorndal et al. 1988, Litzgus and Brooks 1998). However, data from recaptures over the 4 years of this study verified that Texas tortoises on Chaparral WMA accumulate 1 annulus per year and the scute annuli technique is a useful indicator of age for this population (Table I.2).

Distance and time driven were periodically recorded along with number of tortoises captured along roads. This information was used to develop relative abundance estimates (tortoises/km; tortoises/hr) for each year within each pasture. Road densities (km road/km^2) were high and similar among pastures (Baldy: 4.5 km/km^2; East Blocker: 4.4 km./km^2; South Jay: 4.6 km/km^2; and Mare: 4.8 km/km^2) and only interior roads (*i.e.*, not along fencelines) were sampled. Relative abundances were compared between treatments using a repeated-measures analysis of variance procedure, with the experimental unit being the relative abundance within each pasture for each year. Only data from the active season of tortoises (15 April-15 October) were used for analysis. Type I error rate for this and all subsequent statistical tests was set at $\alpha = 0.05$. Data recorded from relative abundance estimates amounted to 37.6% (ungrazed) and 40.5% (grazed) of total captures resulting from road cruising during the active season in the study pastures over all 4 years.

Sex and Age Structure

Frequency distributions of ages and sizes were compared between treatments using Chi-square tests of homogeneity. Data were pooled between pastures within each treatment for these analyses. If individuals were encountered more than once, captures were randomly chosen for inclusion in the analyses such that each individual was only represented once. Size distributions were created based on 10-mm size classes. Due to low cell counts, I pooled ages ≤ 3 and ≥ 12 into age classes 0-3 and 12+ for analysis. Size classes also were pooled before analysis where necessary due to low cell counts (<70 mm and >160 mm). Adult sex ratios and proportion of juveniles (<120 mm SCL) were compared between treatments using Chi-square analyses.

Sizes (SCL) of adults were compared between treatments using pooled data and between pasture pairs (east and west tested separately) by sex using analysis of variance. To allow comparison of the degree of sexual size dimorphism (SSD) of Chaparral WMA tortoises to other turtles, I calculated a sexual dimorphism index (SDI) following Lovich and Gibbons (1992):

$$SDI = -\frac{Male\ SCL}{Female\ SCL} + 1$$

With this SDI, positive values indicate females are larger than males and negative values indicate males are larger than females. Within Chaparral WMA, I compared SSD between treatments by analysis of variance of the raw data for carapace length in a 2 x 2 factorial design (sex x treatment). Significance of the sex by treatment interaction term from analysis of variance indicates different SSD between areas (Thorpe 1989, Ritke and Kennedy 1993, Lovich et al. 1998).

Reproduction and Survival

I attempted to monitor 6 female and 4 male tortoises using radiotelemetry in each study pasture. Radiotransmitters (~20 g; L. L. Electronics, Mahomet, Illinois, USA) were attached to adults >500 g and mounted to the anterior portion of the carapace using silicon rubber. While the silicon was still tacky, radiotransmitters were coated with a layer of sand from the area of collection to help camouflage the transmitter bundle. I relocated radiotransmittered tortoises using a 2-element, hand-held yagi antenna and a TR-4 receiver (Telonics Inc., Mesa, Arizona, USA) at least once weekly during the active season (15 April-15 October) and once monthly during the inactive season (16 October-14 April). All relocations were carried out by walking in and visually observing tortoises. Tortoises were monitored by radiotelemetry from 15 June 1994 to 1 September 1997.

Telemetry data were adjusted to a single year and survival estimates were obtained using the Kaplan-Meier staggered entry procedure (Pollock et al. 1989). For each sex, shapes of annual survival curves were compared between treatments using log-rank tests and annual survival end-point estimates were compared between treatments using *Z*-tests (Pollock et al. 1989). Analyses were conducted with SAS code from White and Garrott (1990). Survival rates also were calculated from log(frequency) distributions (Hellgren et al. 2000) of ages (ages 5-12) from grazed and ungrazed areas. Survival rates from ln(frequency) analysis were compared between treatments by testing for equal slopes. Sexes were combined for these analyses due to low cell counts in the higher ages.

I used ultrasound (Robeck et al. 1990, Rostal et al. 1990, 1994) and X-ray (Gibbons and Greene 1979) techniques to assess reproduction. For part of 1996 and most of 1997, all females from the study areas >130 mm in carapace length were scanned with an Echo Camera SSD-500v ultrasound unit (Aloka Ltd., Wallingford, Connecticut, USA) by placing a 7.5 MHZ probe (model UST-932-7.5, Aloka Ltd.) lubricated with Sonotrack ultrasound transmission gel (Echo Ultrasound, Reedsville, Pennsylvania, USA) in each rear leg opening. To test the validity of the ultrasound, a subset of females was submitted for radiography (Wintergarden Veterinary Clinic, Dilley, Texas, USA) in 1997. For radiography, rare earth film (3M Rare Earth System 400 green) and a Porta Ray MT Super 8020 X-ray unit (Med-Tec Inc., St. Joseph, Missouri) were used at settings of 15 MA, 70 KVP, and 0.2 sec. Comparison of clutch sizes obtained from X-ray (mean ± 1 SE = 2.0 ± 0.3) and ultrasound (1.7 ± 0.4) of the same females using a paired t-test showed that the ultrasound was a reliable technique (*n* = 14, t = 0.773, *P* = 0.453) for assessing clutch size in Chaparral WMA tortoises. Clutch sizes were compared between grazed and ungrazed areas using a Mann-Whitney rank sum test due to nonnormal data (*P* = 0.024). Proportion females gravid was compared between treatments using Chi-square analysis.

Growth

Growth curves were developed by plotting carapace length and mass vs. age (e.g., number of annuli) separately for males and females by treatment. I included data on juveniles by randomly assigning a sex to each individual assuming a 1:1 sex ratio. Data were pooled between each of the pasture pairs for each treatment. I used PROC NLIN (SAS Institute, 1989) to fit logistic and von Bertalanffy growth curves to the data. The resulting curve parameters were compared between treatments using a Z-test with the level of significance being adjusted for multiple comparisons using the Bonferroni inequality (Manly 1992). Parameters were not constrained during the nonlinear regression procedures.

Because juvenile growth was likely to be more susceptible to impacts of grazing, I assessed growth separately for young tortoises. Growth curves were developed using simple linear regressions of carapace lengths and age for ages 0-5 only. Slopes of regressions were compared between grazed and ungrazed treatments to determine if differences in growth existed between treatments for juveniles.

RESULTS

Recorded road cruising effort during the active season amounted to 197.0 hr and 900.8 km in the ungrazed pastures and 244.6 hr and 2337.7 km in the grazed pastures.

Relative abundances based on distance averaged (mean ± 1 SE; $n = 8$ for each treatment) 4.6 ± 1.7 tortoises/100 km for the grazed treatment and 3.4 ± 1.0 tortoises/100 km in the ungrazed treatment across pastures and years. Relative abundances based on time averaged (mean ± 1 SE; $n = 8$ for each treatment) 4.2 ± 1.3 tortoises/10 hr for the grazed treatment and 1.7 ± 0.5 tortoises/10 hr in the ungrazed treatment across pastures and years. Tests for normality for both types of relative abundance measures indicated that the data were not normally distributed ($P = 0.024$ for distance abundances; $P = 0.026$ for time abundances); thus analyses were performed on ranks (Conover and Iman 1981, Hora and Conover 1984). Repeated-measures ANOVA indicated that relative abundance did not vary between treatments for either tortoises/km ($P = 0.289$) or tortoises/hr ($P = 0.727$).

Sex and Age Structure

Ages were obtained from 228 tortoises in the grazed pastures and 106 tortoises in the ungrazed pastures (Fig. I.3). The distribution of ages did not differ between treatments ($\chi^2_9 = 9.74$, $P = 0.372$). Carapace length measurements were available from 237 tortoises in the grazed pastures and 105 tortoises in the ungrazed pastures (Fig. I.4). Chi-square analysis suggested no difference in the distribution of size classes between treatments ($\chi^2_{10} = 9.78$, $P = 0.460$).

Adult sex ratios (F:M) were 1:0.93 ($n = 212$) for the grazed pastures and 1:1.19 ($n = 81$) for the ungrazed pastures, with no difference between treatments ($\chi^2_1 = 0.672$, $P = 0.412$). If data were partitioned into east and west pasture pairs, sex ratios were 1:0.88 ($n = 124$) for grazed west, 1:1.56 ($n = 41$) for ungrazed west, 1:1 for grazed east ($n = 88$), and 1:0.90 (*n* = 40) for ungrazed east. East and west pasture pairs also did not differ between treatments ($\chi^2_1 = 1.95$, $P = 0.163$ for west; $\chi^2_1 = 0.0051$, $P = 0.943$ for east).

Proportion of juveniles was 0.321 (*n* = 312) for the grazed pastures and 0.372 (*n* = 129) for the ungrazed pastures, and did not differ between treatments ($\chi^2_1 = 0.870$, $P = 0.351$). After partitioning data into east and west pasture pairs, comparisons between treatments also were nonsignificant ($\chi^2_1 = 0.226$, $P = 0.635$ for west; $\chi^2_1 = 0.292$, $P = 0.589$ for east).

Carapace lengths averaged (mean ± 1 SE) 149.4 ± 1.8 (*n* = 102) and 152.6 ± 2.7 (*n* = 43) for grazed and ungrazed male tortoises, respectively. Carapace length data for males passed tests of normality ($P = 0.099$) and homogeneity of variance ($P = 0.891$). For females, carapace lengths averaged 138.3 ± 0.9 (*n* = 110) and 141.7 ± 2.0 (*n* = 36) for grazed and ungrazed treatments, respectively. Carapace length data for females passed tests of normality ($P = 0.339$) and homogeneity of variance ($P = 0.191$). Comparisons between treatments revealed no differences ($P = 0.320$ for males; $P = 0.094$ for females) in length between grazed and ungrazed areas.

Calculated SDIs were -0.0769 and -0.0803 for grazed tortoises and ungrazed tortoises, respectively. Analysis of variance on carapace lengths revealed no interaction between sex and treatment ($P = 0.507$), suggesting that sexual size dimorphism was not different between grazed and ungrazed areas. When data were partitioned into individual pastures (SDI = -0.0806 for East Blocker, -0.0886 for Baldy; -0.0758 for South Jay, -0.0736 for Mare), the sex by site interaction term from analysis of variance remained nonsignificant ($P = 0.905$).

Reproduction and Survival

Radiotelemetry effort for females amounted to 15 tortoises and 10,013 radiodays (1 radioday = 1 radiotransmitter on 1 tortoise for 1 day) in the grazed pastures and 13 tortoises and 7,732 radiodays in the ungrazed pastures. Female mortalities numbered 5 and 8 in the grazed and ungrazed areas, respectively. Annual survival rates (± SE) for females derived from the Kaplan-Meier staggered entry procedure were 0.84 ± 0.06 for the grazed treatment and 0.70 ± 0.09 for the ungrazed treatment (Fig. I.5).

Radiotelemetry effort for males amounted to 10 tortoises and 5,342 radiodays in the grazed pastures and 9 tortoises and 6,887 radiodays in the ungrazed pastures. Male mortalities numbered 5 and 4 in the grazed and ungrazed areas, respectively. Annual survival rates for males derived from the Kaplan-Meier staggered entry procedure were 0.73 ± 0.10 for the grazed treatment and 0.83 ± 0.08 for the ungrazed treatment (Fig. I.6). Annual survival estimates did not vary by treatment for females ($P = 0.101$) or males ($P = 0.223$). Curve shapes did not differ between treatments for females ($\chi^2 = 0.299$, $P = 0.584$) or males ($\chi^2 = 0.0006$, $P = 0.981$).

Annual survival rates (ages 5-12) from ln(frequency) analysis were 0.79 and 0.82 for the ungrazed and grazed treatments, respectively (Fig. I.7). Slopes of regression lines were not different ($P = 0.673$), indicating no difference in survival between treatments. If age 10 tortoises are excluded from analysis, survival rates become identical (0.82) for each treatment ($y = -0.193x + 3.70$, $r^2 = 0.85$ for ungrazed; $y = -0.193x + 4.44$, $r^2 = 0.68$ for grazed). Survival rates estimated by ln(frequency) and Kaplan-Meier methods were similar and suggested no differences in adult survival between treatments.

Mortalities of radiotransmittered tortoises were restricted to the active season and were concentrated in late summer (Figs. I.5, I.6). All mortalities of radiotransmittered tortoises appeared to be due to predation events, but direct evidence of type of predator was usually lacking. Dead tortoises were typically encountered with the head and one or more legs removed.

Although 7 of the radiotransmitter antennas were pulled from the silicon mounting medium and had damage consistent with being chewed upon by a mammal, no radio-tagged mortalities had tooth marks or other damage to the shell. Predation of Texas tortoises was not observed on Chaparral WMA, but I have observed raccoons killing and eating sliders (*Trachemys scripta*) on Chaparral WMA. Due to the similarity in appearance between dead sliders known to have been killed by raccoons and some of the radiotransmittered tortoise mortalities, I believe that 9 of the recovered mortalities were the result of raccoon predation. A single raccoon hair was recovered from one of these mortalities.

Five of the radiotransmittered tortoise mortalities had damage consistent with being eaten by an avian predator with a raptorial beak and I believe these are most likely the result of predation by crested caracaras. On 4 occasions, I observed crested caracaras standing over live tortoises on Chaparral WMA that had been flipped over on their backs. Circumstantial evidence of the remaining transmitter mortalities was not sufficient to speculate on cause of mortality. Thus, of the 17 radiotransmittered mortalities, 9 were attributable to mammalian carnivores, probably raccoons, and 5 were attributable to avian predators, probably crested caracaras.

Totals of 28 and 11 female tortoises from grazed and ungrazed pastures, respectively, were scanned with the ultrasound unit. Clutch size averaged (mean ± SE) 1.9 ± 0.3 ($n = 10$) from the grazed pastures and 2.0 ± 0.6 ($n = 4$) from the ungrazed pastures, and did not vary between treatments ($P = 0.943$). Proportion gravid did not differ by treatment ($\chi^2_1 = 0.111, P = 0.739$).

Growth

Nonlinear regression of growth using logistic models resulted in coefficients of determination (r^2) values ranging from 0.64 to 0.89 (Tables I.3, I.4), while von Bertalanffy models resulted in r^2 values ranging from 0.63-0.89 (Tables I.5, I.6). Values of r^2 for logistic and von Bertalanffy curve types were similar, with mean differences in r^2 between curve types of 0.0054 ± 0.0018 for SCL ($n = 4$), 0.0135 ± 0.0045 for mass ($n = 4$), and 0.0094 ± 0.0027 overall ($n = 8$). In general, growth curves were similar between grazed and ungrazed areas (Figs. I.8-11), although there was a slight tendency for larger asymptotic size of females in ungrazed areas relative to grazed areas (Figs. I.8-9). Parameter values for the logistic growth models did not vary between treatments (Table I.7). With the exception of k for female carapace length ($Z = 3.203$) and female mass ($Z = 3.283$), comparisons between treatments of regression parameter values for the von Bertalanffy growth models also lacked significance (Table I.8). However, nonlinear regression using von Bertalanffy growth models for females resulted in unrealistic asymptotes for both mass and carapace length for the ungrazed treatment (Tables I.5, I.6; Figs. I.8, I.9). Y-intercepts from curves for grazed female carapace length and all mass regressions using the von Bertalanffy model were negative and, thus, also unrealistic

(Figs. I.8, I.9, I.11). Thus, with these data sets, a logistic growth model described growth in Texas tortoises better than a von Bertallanffy growth model.

For examination of young tortoise growth rates, 48 and 111 tortoises with 0-5 annuli were captured from ungrazed pastures and grazed pastures, respectively. Linear relationships between carapace length and age (e.g., number of annuli) for these tortoises were very similar ($y = 14.5x + 53.1$ for ungrazed and $y = 14.7x + 54.5$ for grazed; Fig. I.12). Slopes were not different between grazed and ungrazed areas ($P = 0.8949$), suggesting identical growth rates for young tortoises.

DISCUSSION

Interpopulation Comparisons of Demography

Although published demographic data are scant, life history characteristics of the Texas tortoise population on Chaparral WMA appear quite different from populations previously studied in the Lower Rio Grande Valley of Texas. In coastal populations, mean carapace lengths of 141 to 170 mm for females and 167 to 189 mm for males have been reported (Auffenberg and Weaver 1969, Rose and Judd 1982, Bury and Smith 1986) compared to 138-142 mm for females and 149-153 mm for males in my study. Size distributions are skewed toward larger size classes in Cameron County, particularly at the Laguna Atascosa National Wildlife Refuge (Bury and Smith 1986), and proportion of juveniles appears to be higher on Chaparral WMA (0.32-0.37 for Chaparral WMA compared to 0.01-0.27 for coastal tortoises; Auffenberg and Weaver 1969, Judd and Rose 1983, Bury and Smith 1986). Although sex ratios on Chaparral WMA are not different from 1:1, coastal populations tend to be male-biased with ratios (F:M) up to 1:1.7 (Bury and Smith 1986). Coastal tortoises also appear to be more sexually dimorphic with SDIs up to -0.18 (Auffenberg and Weaver 1969) and have larger clutches ($\overline{x}$ = 2.65, range 1-5; Judd and Rose 1989). Thus, the Chaparral WMA population appears to have a high proportion of juveniles and be made up of smaller adults that are less sexually dimorphic, produce smaller clutches of eggs, and have a sex ratio nearer to equality than conspecifics in Cameron County.

Juvenile tortoises are notoriously difficult to sample (Morafka 1994), and differences in proportion of juveniles between Chaparral WMA and coastal sites could be the result of higher recruitment on Chaparral WMA, variation in juvenile tortoise activity or detectability between sites, or differences in sampling methodology between studies. Texas tortoises have been sampled by intensively searching grids (Judd and Rose 1983), walking roads (Bury and Smith 1986), fortuitous encounters during off-road searches (Auffenberg and Weaver 1969), and road-cruising (present study). Although grid searches are appealing because they sample defined areas, efforts to use such searches on Chaparral WMA were abandoned due to lack of captures (no tortoises were found during 4 10-ha grid searches during peak tortoise activity; R. T. Kazmaier, unpublished data). Subsequent observations using radiotelemetry revealed that adult tortoises easily detected approaching observers and typically took refuge under dense cover where they were difficult to observe (R. T. Kazmaier, personal observation). If juvenile Texas tortoises are equally shy, low estimates of proportion of juveniles in a population are expected from searches that involve walking observers. The magnitude of this effect could, however, be somewhat dependent on habitat and available cover. When adequate road systems are available, road-cruising may be desirable because it allows detection of tortoises before they have the opportunity to seek cover.

Juveniles are also likely to be seasonally variable in their activity and short-term studies may result in biased estimates. Intrasite variation from published studies is available only from Judd and Rose (1983), where juveniles composed 9-27% of the population over 5 years. Juveniles on Chaparral WMA, however, consistently make up a large proportion of the tortoises captured on Chaparral WMA each year (24-40%; 1994-1997; Hellgren et al. 2000), suggesting high recruitment on Chaparral WMA.

Comparison of body size and SSD across the range of the Texas tortoise reveals a high degree of regional variation, with larger, more sexually dimorphic tortoises in Cameron County and smaller, less sexually dimorphic tortoises on Chaparral WMA. Larger clutch sizes for Texas tortoises in Cameron County are likely tied to the larger body sizes of females found at the coastal sites. Variation in body size and SSD is less easily explained. Larger body sizes for Cameron County tortoises might be the result of longer seasons of activity that allow for higher growth rates during the years before sexual maturity is reached. Tortoises on Chaparral WMA are rarely active after early October (R. T. Kazmaier, unpublished data), but tortoises in Cameron County are often observed to be active through early December (S. F. Patten, TPWD, personal communication). Longer activity seasons in Cameron County might also contribute to higher SSD, because female growth rates slow more dramatically than male growth rates once sexual maturity is reached (present study). Similar patterns could exist if the more productive and equitable coastal climate provides better nutrition than the more arid interior.

Alternatively, differences in body size and SSD, could be the result of differential selection pressures between the sites. Male Texas tortoises are highly aggressive towards other males and male-male combat for access to females is considered common (Weaver 1970). Densities of tortoises from coastal populations appear to be much higher than the Chaparral WMA population (Judd and Rose 1983; Hellgren et al. 2000). Under higher densities, increased male-male interaction and combat for access to females may select for larger-sized males. Because female-female aggression is rare (Weaver 1970), a similar selection pressure would not act to increase female size. Male-male combat was never observed on Chaparral WMA (R. T. Kazmaier, unpublished data) and densities may be low enough on Chaparral WMA that increased male body size provides little selective advantage.

Age distributions for other populations of Texas tortoises have not been published, but growth curves developed based upon annuli lengths suggested that mean age at maturity for this species was 13.3 years (Germano 1994). Inspection of Chaparral WMA age distributions and growth curves (based on a validated aging technique) indicates that the 13.3 year estimate of attainment of sexual maturity cannot be considered valid for the Chaparral WMA population. On average, tortoises on Chaparral WMA reach sexual maturity at 5-6 years of age (Hellgren et al. 2000), closer to estimates of Auffenberg and Weaver (1969). Unfortunately, the lack of collection of age data by researchers from other sites hampers my ability to determine if differences in body size between sites are influenced by variation in age distributions. Although Germano (1994) found no consistent relationship between climate and growth or age at maturity for the 4 *Gopherus*, the Chaparral WMA population of Texas tortoises clearly does not conform to

Germano's growth model for *G. berlandieri* and regional variation in climate might contribute to regional variation in demography or growth for this species.

Grazing and the Texas Tortoise

The grazing system employed by Chaparral WMA has had no detectable effect on the demography of the Texas tortoise for the parameters examined. Degree of disturbance has been suggested as a driving force in the structuring of many communities, and under the intermediate disturbance hypothesis, diversity is often highest at intermediate levels of disturbance (Connell 1978; Fig. I.13). For example, diversity measures of several taxa in the shortgrass steppe display the bell-shaped curve proposed by the intermediate disturbance hypothesis in response to increasing grazing intensity in the long-term (Milchunas et al. 1998). Many herbaceous species either require or thrive under moderate levels of disturbance (Hobbs and Huenneke 1992). The rotational grazing regime employed by Chaparral WMA is designed to provide such moderate rates of disturbance. My data from Chaparral WMA and the available literature on other tortoise species allows some speculation about how grazing might affect the Texas tortoise under other grazing regimes.

The genus *Gopherus* occupies the southern tier of North America, with annual precipitation ranging from 150 cm in the east to 10 cm in the west (Germano 1994). In turn, tortoises appear to tolerate a level of disturbance in proportion to the primary productivity of their distributional range. As a result of habitat and effective precipitation, gopher tortoises thrive under conditions of relatively high disturbance that maintain more ruderal vegetation communities (Auffenberg and Franz 1982). However, desert tortoises in arid regions of the southwestern United States appear to require more undisturbed or climax communities (Luckenbach 1982). Because Texas tortoises evolved in a region that is intermediate in precipitation and primary productivity compared to areas inhabited by other *Gopherus* (Germano 1994), this species may be more adapted to intermediate levels of disturbance.

Positive effects of grazing disturbance on tortoise demography and ecology include germination of forbs, changes in the dispersion and density of woody cover, and encroachment of prickly pear cactus. For example, one objective of the winter-spring grazing on Chaparral WMA is to enhance germination of seed producing forbs, such as *Croton* spp., for the benefit of seed-eating birds. If winter and early springs rains occur, timing of Chaparral WMA grazing also allows plants to respond to the grazing disturbance and be available as forage when tortoises emerge from hibernation.

It is generally believed that cattle grazing cannot be decoupled from the rapid increase in woody plant cover in southern Texas (Scifres 1980, Brown and Archer 1987, Archer et al. 1988, Archer 1989). Rapid expansion of woody cover can reduce herbaceous cover through shading and competition for water and nutrients. The contribution of other factors, such as fire suppression, to the woody plant invasion in southern Texas, however, is poorly understood (Brown and Archer 1989). Nevertheless, because tortoise nutrient requirements are fairly low (Nagy and Medica 1986), it is expected that the woody plant increase would need to be extremely severe to impact herbaceous species enough to affect tortoises. The wide range of woody cover used by tortoises in this study, coupled with avoidance of extremes of woody cover (old-field and dense riparian areas, Chapter II), is consistent with this view.

Benefits to tortoises associated with increases in woody cover include increased number of available pallet (= sleeping) sites, reduced probability of hyperthermia, increased availability of fruit, and increased protection from predators, particularly avian predators. Without better quantification of the nutritional requirements of Texas tortoises, the extent to which increased fruit availability would be helpful is unknown. On Chaparral WMA, tortoises consume >12 species of fruit from woody species, and at certain times of the year, fruit composes >50% of the overall diet (R. T. Kazmaier, unpublished data).

Prickly pear cactus appears to be increasing in many areas with brush encroachment (Archer et al. 1988). Increased availability of prickly pear cactus has all the possible benefits of increases in other woody species, and the added enhancement of increased water availability. Thus, increased cactus availability might allow tortoises to better withstand periods of drought. Because of high acidity and the presence of oxalates in cactus, however, the effects of increased or prolonged consumption of prickly pear cactus on Texas tortoises needs to be quantified (Hellgren et al. 2000). The costs and benefits of brush encroachment (particularly prickly pear) in southern Texas need to be better evaluated to determine possible impacts on the Texas tortoise.

The squat, lumbering gait of tortoises makes it difficult for them to maneuver in areas of dense grass. Removal of excess litter by cattle may allow tortoises to navigate in the landscape more easily. Such removal also might expose uncommon, but highly nutritious, herbaceous vegetation for tortoises to consume. Grazing by cattle encourages regrowth in many species of plants, particularly grasses, and regrowth is often of higher nutritional quality than older growth (Detling 1988, McNaughton 1985). If tortoises have access to regrowing vegetation, their nutritional needs might be more easily met.

Negative effects of cattle grazing on Texas tortoises include direct effects of cattle on tortoise mortality, trampling and biomass removal, and the cascading effects of soil compaction. The former effects are unlikely. Burrow trampling is commonly cited as a cause of concern for a variety of tortoises (Berry 1978, Waller and Micucci 1997). Collapsed burrows could lead to problems associated with increased energetic expenditure to rebuild the burrows, increased risk of predation due to exposure, or increased thermal stress due to an inability to find suitable shelter. Texas tortoises, however, do not normally construct burrows (Auffenberg and Weaver 1969); thus, burrow destruction is not expected to be a problem for this species.

Direct mortality due to trampling by livestock has been cited as a cause for concern for the desert tortoise (Berry 1978). Because of the rather secretive nature of active Texas tortoises, such cattle-tortoise interactions are undoubtedly rare in Texas. Texas tortoises create shallow depressions, called pallets, for loafing sites (Auffenberg and Weaver 1969), and on Chaparral WMA, pallets are typically situated against the bases of prickly pear cacti, adjacent to the trunks of woody plants, or within dense shrub clumps (R. T. Kazmaier, unpublished data). Placement of pallets in such locations is probably important for shading and thermoregulation, but it is unlikely that cattle could trample tortoises while they are using such protected pallets. Because the grazing regime used on Chaparral WMA consists mostly of grazing during the inactive season for tortoises (October-April), direct encounters between tortoises and cattle are even less likely.

The ecological impacts of grazing potentially have greater effects on tortoise populations. Soil compaction can lead to reduced water infiltration and increased runoff, resulting in a change in the long-term moisture status of the soil (Alderfer and Robinson 1947, Naeth et al. 1991). Reduced water availability leads to less reliable germination and a reduction in primary production. Soil compaction also leads to the development of a hard pan that is physically difficult for seedlings to germinate through (Willatt and Pullar 1984, Proffitt et al. 1993). Thus, soil compaction could reduce the availability of forage for tortoises. The extent to which grazing in the western Rio Grande Plains causes soil compaction has, apparently, not been addressed. Likelihood and degree of soil compaction tends to increase with the amount of clay in the soil (Hanson et al. 1970, Wood and Blackburn 1984). Because most of the soils in the western Rio Grande Plains are sandy (Stevens and Arriaga 1985), soil compaction is less likely to lead to problems for the Texas tortoise in this region.

The "herd effect", whereby trampling of the soil by large numbers of livestock (i.e., extreme disturbance) increases germination rates, water infiltration, and plant productivity, is believed to function in some ecosystems (Savory and Parsons 1980). Such effects would be beneficial to tortoises through enhanced forage availability. The extent to which the "herd effect" operates in the Rio Grande Plains, however, is unknown, and studies in other North American arid and semiarid grasslands suggest either negligible or negative effects (McCalla et al. 1984, Kirby et al. 1986, Bryant et al. 1989, Taylor 1989), as discussed in the preceding paragraph.

Disturbance can increase invasion of exotic species (Hobbs and Huenneke 1992) that may be detrimental to tortoises. The exotic grass *Eragrostis lehmanniana* is increasing rapidly in southern Texas, but does not appear to be readily used by tortoises (R. T. Kazmaier, unpublished data). Areas dominated by *E. lehmanniana* or other introduced African lovegrasses typically support lower native forb and grass diversities (Bock et al. 1986). If a grazing regime results in increases in undesirable exotics at the expense of desirable species, tortoises could ultimately be impacted.

Competition with cattle for forage could result in declines in tortoise density, but the nutritional ecology of Texas tortoises needs to be evaluated before precise predictions can be made. Without knowledge of nutritional demands, it is difficult to speculate on whether forage remaining after cattle grazing is sufficient to sustain tortoises (Oldemeyer 1994). However, because of the small size and ectothermic nature of the Texas tortoise, it is probable that overall nutrient requirements are rather low for these tortoises (averaged across the entire year, estimated dry matter intake for desert tortoises is only $4.52\ g \cdot kg^{-1} \cdot day^{-1}$; Nagy and Medica 1986). The impact of forage competition between tortoises and cattle on tortoise reproduction and survival is dependent upon the complex interaction between tortoise nutritional status and nutrient demands, climate, available forage, and intensity and duration of grazing.

It is possible that I failed to detect a grazing effect because of inadequate statistical power. However, even with the large number of variables examined, there were no general tendencies or trends in the parameters examined, except perhaps for female growth. My analyses of female growth showed a consistent trend for larger sizes of females on ungrazed areas compared to grazed areas. Because female turtle growth slows dramatically at the onset of reproduction (Gibbons and Lovich 1990), the growth curves suggest that females began allocating energy to reproduction slightly earlier in grazed areas. Thus, tortoises in ungrazed areas may be larger because of delayed reproduction relative to the grazed areas.

Causes of delayed reproduction might be based on either predation or nutrition. Predation pressure can vary with body size in turtles (Tucker et al. 1999), and differential predation pressure between grazed and ungrazed areas could drive selection for differential body size. Thus, tortoises in ungrazed pastures may be experiencing heavier predation pressure at smaller sizes, leading to selection for females that delay reproduction and grow larger.

Alternatively, acquisition of sufficient resources to meet the demands of reproduction might be easier in grazed areas through enhanced availability of forage or particular nutrients by the actions of cattle. Due to egg development, calcium is an important component of reproduction in tortoises and there is compelling evidence that female tortoises on Chaparral WMA may have problems acquiring or mobilizing this mineral (Hellgren et al. 2000). The presence of prickly pear cactus in the diet of tortoises may reduce calcium availability, because of the large amount of calcium binding oxalates in cactus. If calcium rich forage is less available or if cactus utilization is higher in ungrazed areas, more time may be needed to acquire sufficient calcium for egg development. Such a delay in reproduction could explain the differences in growth curves observed.

Thus, there is limited evidence to suggest that there may be differences in growth and age at reproduction between the grazed and ungrazed areas. Differences in growth, however, may be an artifact of my inability to adequately pair grazed and ungrazed study areas (see Chapter II) instead of a treatment difference. More detailed research focusing on growth and reproduction, particularly of 4-8-year-old tortoises, is certainly warranted to determine if these apparent trends in differential growth are real and the extent to which these differences are related to grazing treatment.

CONCLUSIONS

State-and-Transition models of succession suggest that in certain systems, natural or anthropogenic perturbations may alter the trajectory of succession into transitions that lead to different stable states (Westoby et al. 1989). Once the trajectory is altered across a threshold, it can be difficult, if not impossible, for succession to proceed towards the state of the pre-disturbance community (Friedel 1991). The transition from a grass or herbaceous state to a woody state following a perturbation is a common feature of arid and semiarid regions (Archer 1989, Friedel 1991). Historical accounts of habitats in the Rio Grande Plains before they were impacted by livestock grazing are scant, but there is a general belief that the region was more savannah-like than it is today (Archer 1989). Because habitats in the Rio Grande Plains have been so dramatically and uniformly altered by anthropogenic disturbance, it may be impossible to evaluate the demography of the Texas tortoise under the conditions in which it evolved and current characteristics of tortoises may reflect adaptations to ecologically recent modifications of habitat. It is possible, however, that historical grazing has modified the trajectory of succession on Chaparral WMA into a state that is demographically-neutral for Texas tortoises.

This study provides a framework to address the effects of grazing on the ecology of the Texas tortoise and is a substantive addition to available data sets concerning grazing effects on this protected taxa. Although additional research is needed to better evaluate the potential interactions between tortoises and cattle, my data suggest that grazing by cattle can be compatible with robust Texas tortoise populations. The grazing regime employed by Chaparral WMA appears to have had no immediate impact on tortoise demography. Even within southern Texas, however, a single grazing regime might impact populations differently as habitat and effective precipitation vary across the landscape. For example, in the Rio Grande Plains, northern bobwhites on more productive sites had highest densities under early seral stages (i.e., more disturbance), whereas bobwhites on less productive sites were unaffected by seral stage (Spears et al. 1993). In addition, the Chaparral WMA grazing regime is somewhat atypical for the western Rio Grande Plains. Ranchers in this region typically graze at higher intensities for longer durations, and grazing is not restricted to the winter (D. C. Ruthven, TPWD, personal communication).

The potential effects on tortoises of grazing by cattle involves complex interactions among climate, tortoise ecology, livestock ecology, and the plant communities at a site. Obviously, any potential impact of grazing by cattle on the Texas tortoise will be dependent upon the intensity, timing, and duration of grazing. Evaluation of livestock-tortoise (or other herbivore) interactions should not underestimate the importance of temporal and spatial variation on the impact of grazing on vegetation biomass. Species responses to grazing can depend on productivity of the system (Milchunas et al. 1998), with range-adapted species exhibiting greater compatibility with grazing as system productivity increases. Accordingly, generalities about the impact of cattle grazing on the 4 North American tortoises should be avoided unless they can be placed in the context of grazing regime, effective precipitation, habitat quality, and tortoise requirements.

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Table I.1. Grazing periods, stocking rates[a], and stocking densities[a] for the two pastures used as grazing treatments to examine the effects of cattle grazing on Texas Tortoises at Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas.

		Days of	Number	Stocking rate		Stocking density
Pasture	Grazing period	grazing	of steers	AUD/ha	AU/ha/yr	AU/ha
South Jay (750 ha)	16 Dec 94-10 Feb 95	56	400	14.9	0.04	0.27
	29 Mar 96- 6 May 96	38	347	5.9[b]	0.02	0.23
	2 Mar 97-25 May 97	84	448	21.6[b]	0.07	0.30
East Blocker (372 ha)	9 Apr 95- 1 May 95	22	400	11.8	0.03	0.54
	3 Apr 96- 7 May 96	34	341	13.8	0.04	0.46
	27 Mar 97-13 May 97	47	440	27.8	0.08	0.59

[a] Stocking rate refers to annual grazing pressure. Stocking density refers to instantaneous grazing pressure.

[b] Stocking rate is lower than expected from days of grazing and number of animals because of extended period of entry to and exit from the pasture.

Table I.2. Expected (assuming 1 annulus per year) and actual differences in the number of scute annuli of Texas tortoises based upon recaptures at Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas, from April 1994 to September 1997.

Expected difference in annuli counts	Actual difference in annuli counts		Number of recaptures	Proportion ± 1 annulus of expected
	Mean	SE		
0[a]	0.37	0.08	43	1.0
1	1.00	0.07	61	1.0
2	1.97	0.10	36	0.94
3	3.07	0.20	14	0.93

[a] Tortoises recaptured within the same year. Tortoises captured very early in the year (before much growth has occurred) and then recaptured later in the same year occasionally show an additional annulus because of the timing of captures and growth between captures.

Table I.3. Sample sizes (*n*), coefficients of detemination (r^2), and parameter estimates derived from nonlinear regression analysis of growth based on fitting carapace length to a logistic model for female and male Texas tortoises from grazed and ungrazed areas on Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas.

Sex	Treatment	*n*	r^2	Parameter	Estimate ± SE
Female	Grazed	107	0.73	k	0.53 ± 0.07
				a	148.30 ± 2.36
				b	2.33 ± 0.49
	Ungrazed	52	0.89	k	0.40 ± 0.05
				a	161.04 ± 5.35
				b	2.16 ± 0.23
Male	Grazed	126	0.84	k	0.32 ± 0.03
				a	177.73 ± 4.52
				b	2.08 ± 0.19
	Ungrazed	53	0.72	k	0.40 ± 0.08
				a	166.35 ± 6.02
				b	2.28 ± 0.58

Table I.4. Sample sizes (*n*), coefficients of determination (r^2), and parameter estimates derived from nonlinear regression analysis of growth based on fitting mass to a logistic model for female and male Texas tortoises from grazed and ungrazed areas on Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas.

Sex	Treatment	*n*	r^2	Parameter	Estimate ± SE
Female	Grazed	107	0.64	k	0.69 ± 0.11
				a	772.94 ± 30.80
				b	16.36 ± 7.33
	Ungrazed	52	0.87	k	0.68 ± 0.09
				a	862.57 ± 43.00
				b	21.91 ± 7.47
Male	Grazed	125	0.80	k	0.45 ± 0.05
				a	1144.60 ± 53.80
				b	13.96 ± 2.98
	Ungrazed	54	0.67	k	0.35 ± 0.08
				a	1220.63 ± 140.33
				b	8.53 ± 3.20

Table I.5. Sample sizes (*n*), coefficients of determination (r^2), and parameter estimates derived from nonlinear regression analysis of growth based on fitting carapace length to a von Bertalanffy model for female and male Texas tortoises from grazed and ungrazed areas on Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas.

Sex	Treatment	*n*	r^2	Parameter	Estimate ± SE
Female	Grazed	107	0.73	k	0.37 ± 0.05
				a	150.36 ± 2.91
				b	1.01 ± 0.15
	Ungrazed	52	0.89	k	0.17 ± 0.03
				a	181.73 ± 12.31
				b	0.76 ± 0.03
Male	Grazed	126	0.84	k	0.18 ± 0.03
				a	187.53 ± 7.08
				b	0.82 ± 0.04
	Ungrazed	53	0.73	k	0.24 ± 0.06
				a	172.37 ± 8.56
				b	0.89 ± 0.14

Table I.6. Sample sizes (*n*), regression coefficients (r^2), and parameter estimates derived from nonlinear regression analysis of growth based on fitting mass to a von Bertalanffy model for female and male Texas tortoises from grazed and ungrazed areas on Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas.

Sex	Treatment	*n*	r^2	Parameter	Estimate ± SE
Female	Grazed	107	0.63	k	0.31 ± 0.06
				a	826.65 ± 50.52
				b	1.74 ± 0.33
	Ungrazed	52	0.86	k	0.07 ± 0.04
				a	1835.76 ± 660.16
				b	1.05 ± 0.05
Male	Grazed	125	0.80	k	0.12 ± 0.03
				a	1503.79 ± 184.24
				b	1.20 ± 0.08
	Ungrazed	54	0.69	k	0.09 ± 0.05
				a	1726.35 ± 572.12
				b	1.11 ± 0.13

Table I.7. Treatment comparisons of parameters fitted to logistic growth models for carapace length (SCL) and mass for Texas tortoises from Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas. No values of *Z* were significant at $\alpha = 0.05$ following Bonferroni adjustments for multiple comparisons.

Comparison	Variable	Parameter	*Z*
Grazed female x ungrazed female	SCL	k	1.572
		a	2.179
		b	0.306
	Mass	k	0.051
		a	1.694
		b	0.530
Grazed male x ungrazed male	SCL	k	0.917
		a	1.513
		b	0.320
	Mass	k	1.105
		a	0.506
		b	1.241

Table I.8. Treatment comparisons of parameters fitted to von Bertalanffy growth models for carapace length (SCL) and mass for Texas tortoises from Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas. Values of *Z* that are significant at $\alpha = 0.05$ following Bonferroni adjustments for multiple comparisons are marked with '*'.

Comparison	Variable	Parameter	*Z*
Grazed female x ungrazed female	SCL	k	3.203*
		a	2.481
		b	1.625
	Mass	k	3.283*
		a	1.524
		b	2.058
Grazed male x ungrazed male	SCL	k	0.935
		a	1.365
		b	0.493
	Mass	k	0.526
		a	0.370
		b	0.623

Fig. I.1. Location of Chaparral Wildlife Management Area in relation to Texas and Mexico and the geographic range of the Texas tortoise (stippled area).

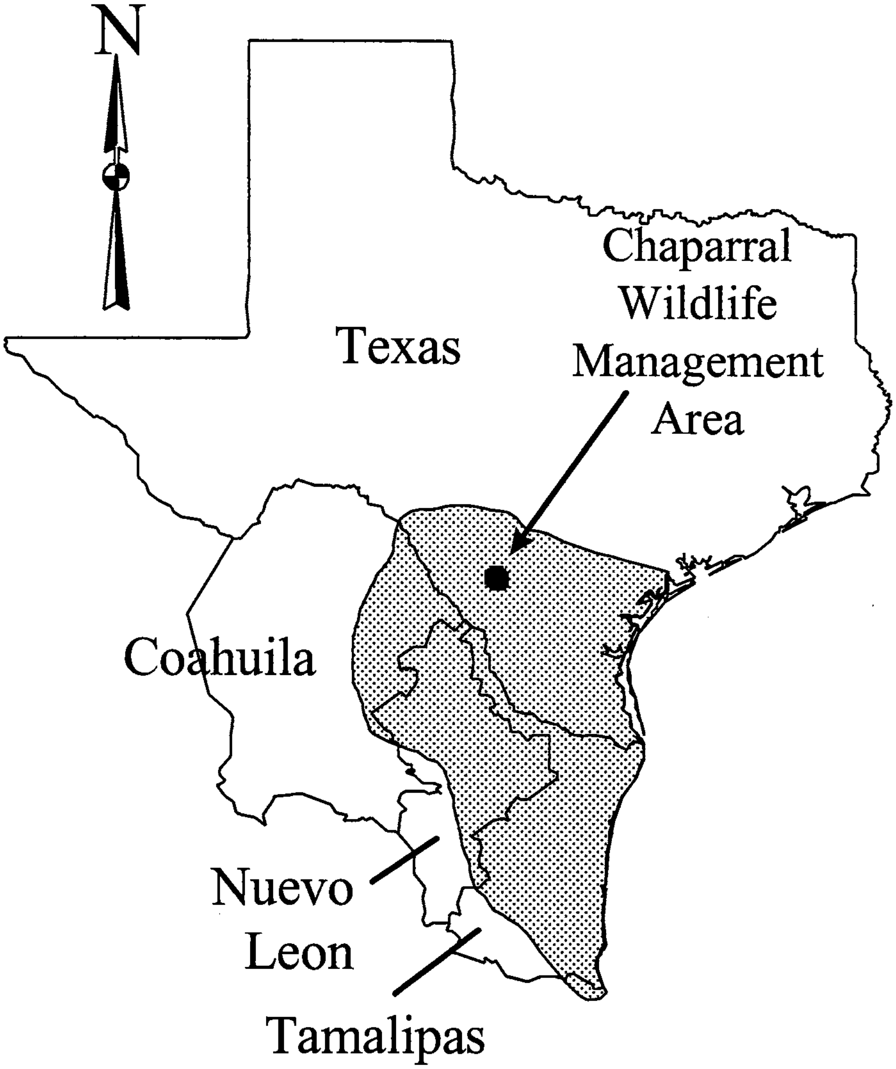

N
Texas
Chaparral Wildlife Management Area
Coahuila
Nuevo Leon
Tamalipas

Fig. I.2. Pasture arrangement and fencing types on Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas, 1994-1997. Stippled areas indicate primary study areas and arrows indicate direction of movement of cattle between rotations.

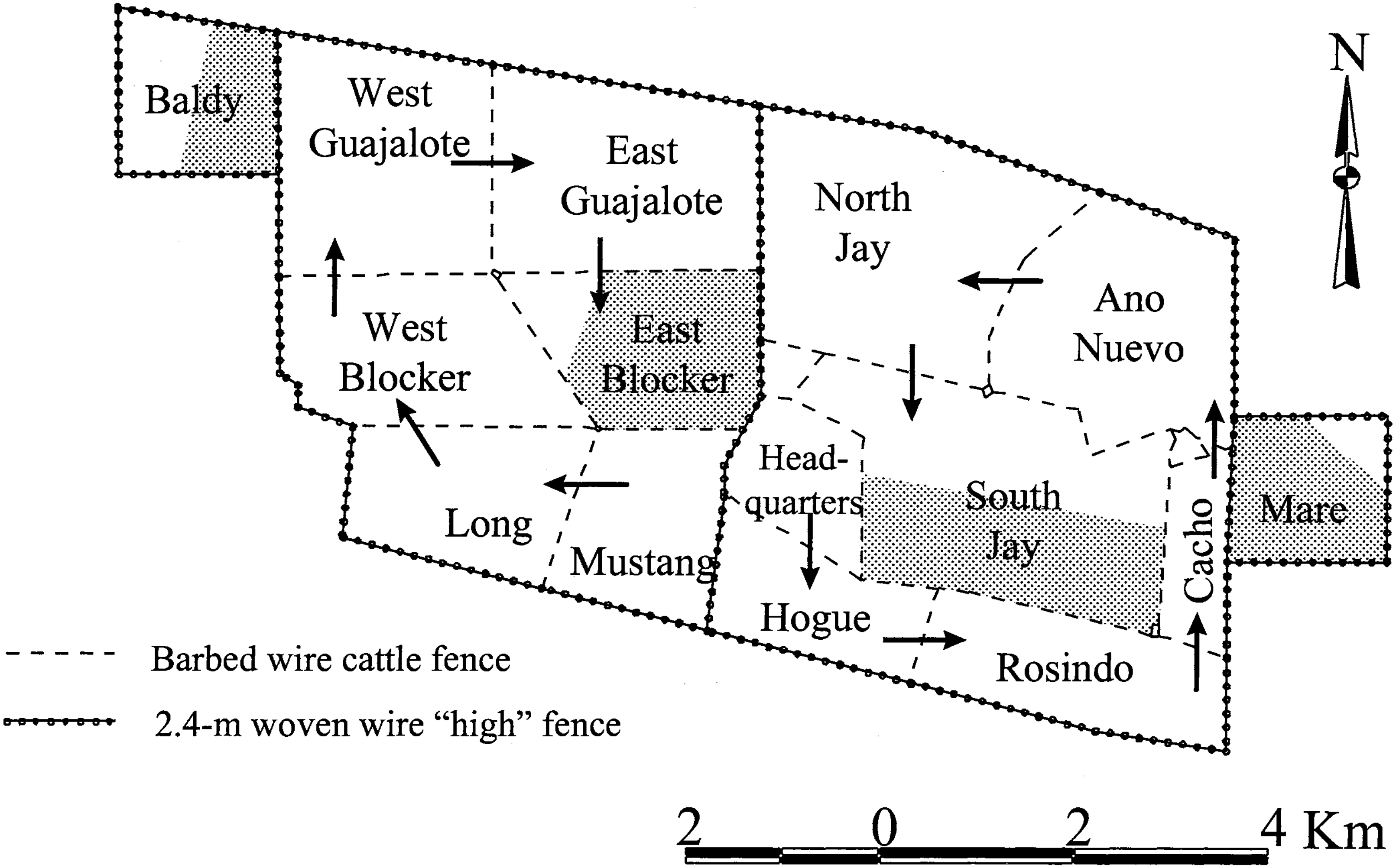

N
Baldy
West Guajalote
East Guajalote
North Jay
Ano Nuevo
West Blocker
East Blocker
Head-quarters
South Jay
Cacho
Mare
Long
Mustang
Hogue
Rosindo
Barbed wire cattle fence
2.4-m woven wire “high” fence
2 0 2 4 Km

Fig. I.3. Proportional distribution of age classes (number of annuli) of Texas tortoises from grazed ($n = 228$) and ungrazed ($n = 106$) areas on Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas, 1994-1997.

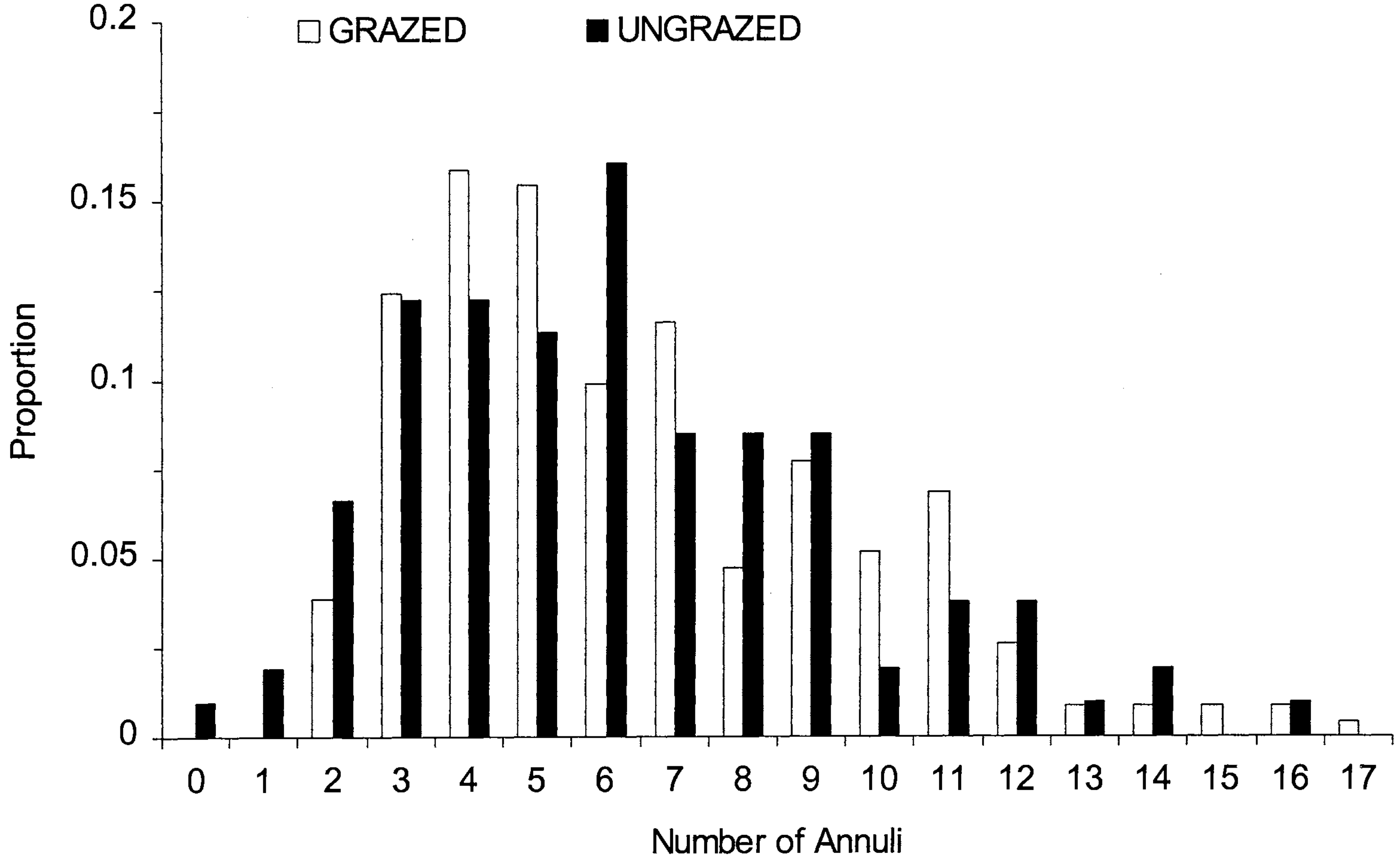

□ GRAZED
■ UNGRAZED
Proportion
0.2
0.15
0.1
0.05
0
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
Number of Annuli

Fig. I.4. Proportional distribution of size classes based on carapace length of Texas tortoises from grazed (*n* = 237) and ungrazed areas (*n* = 105) on Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas, 1994-1997.

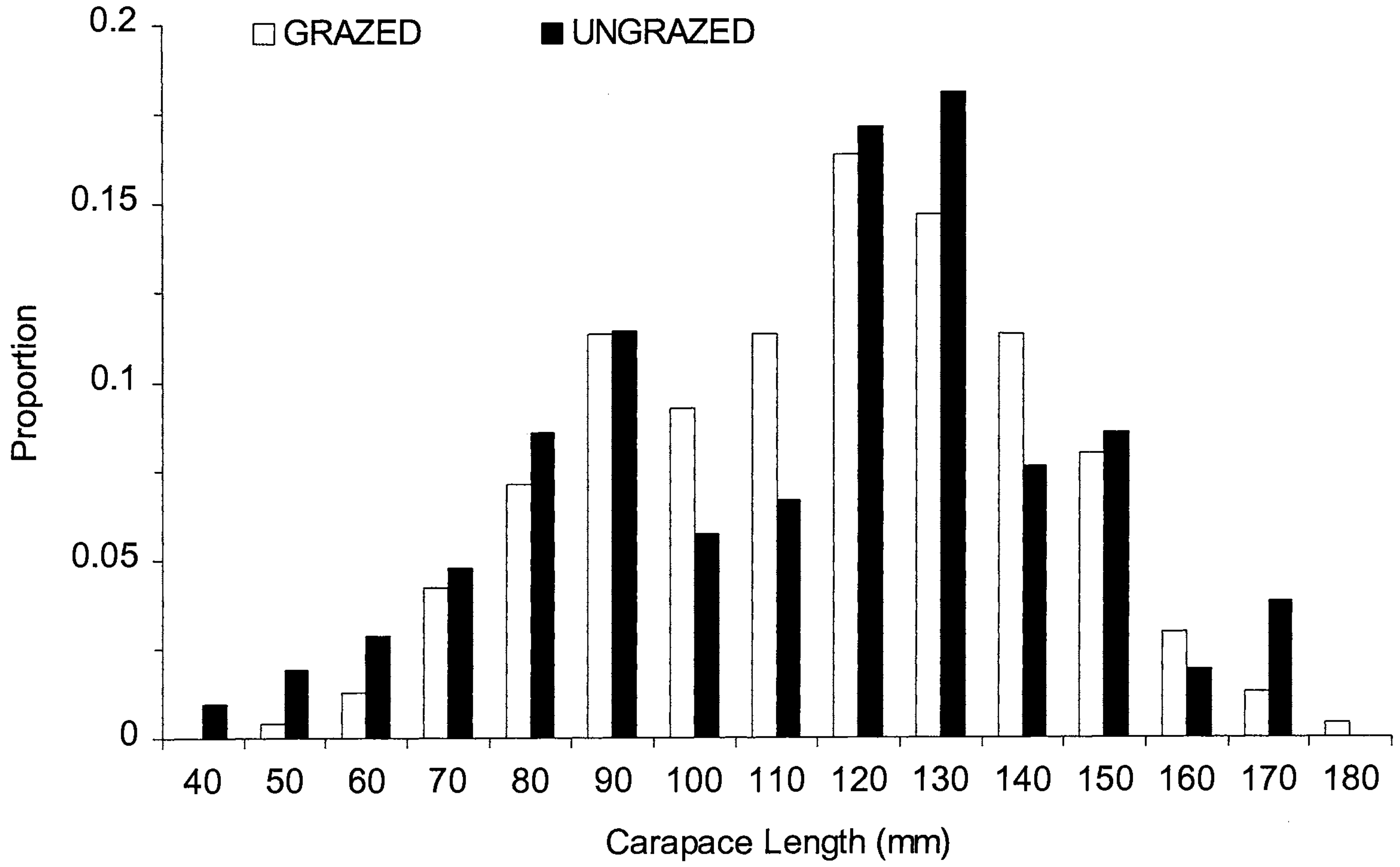

□ GRAZED
■ UNGRAZED
Proportion
0.2
0.15
0.1
0.05
0
40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
Carapace Length (mm)

Fig. I.5. Kaplan-Meier survival rates for female Texas tortoises that were radio-tagged in grazed and ungrazed areas on Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas, 1994-1997.

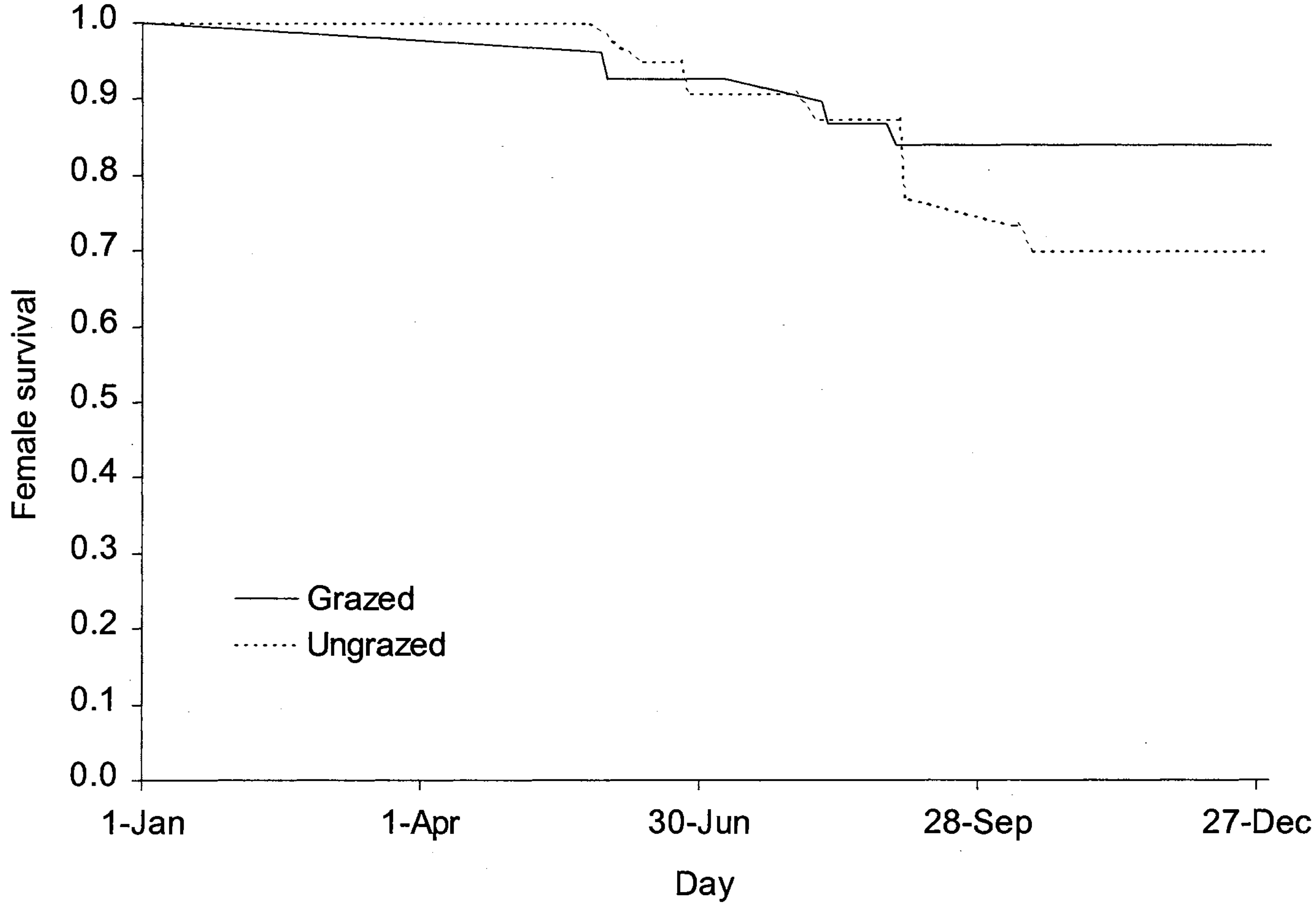

1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Female survival
Grazed
Ungrazed
1-Jan
1-Apr
30-Jun
28-Sep
27-Dec
Day

Fig. I.6. Kaplan-Meier survival rates for male Texas tortoises that were radio-tagged in grazed and ungrazed areas on Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas, 1994-1997.

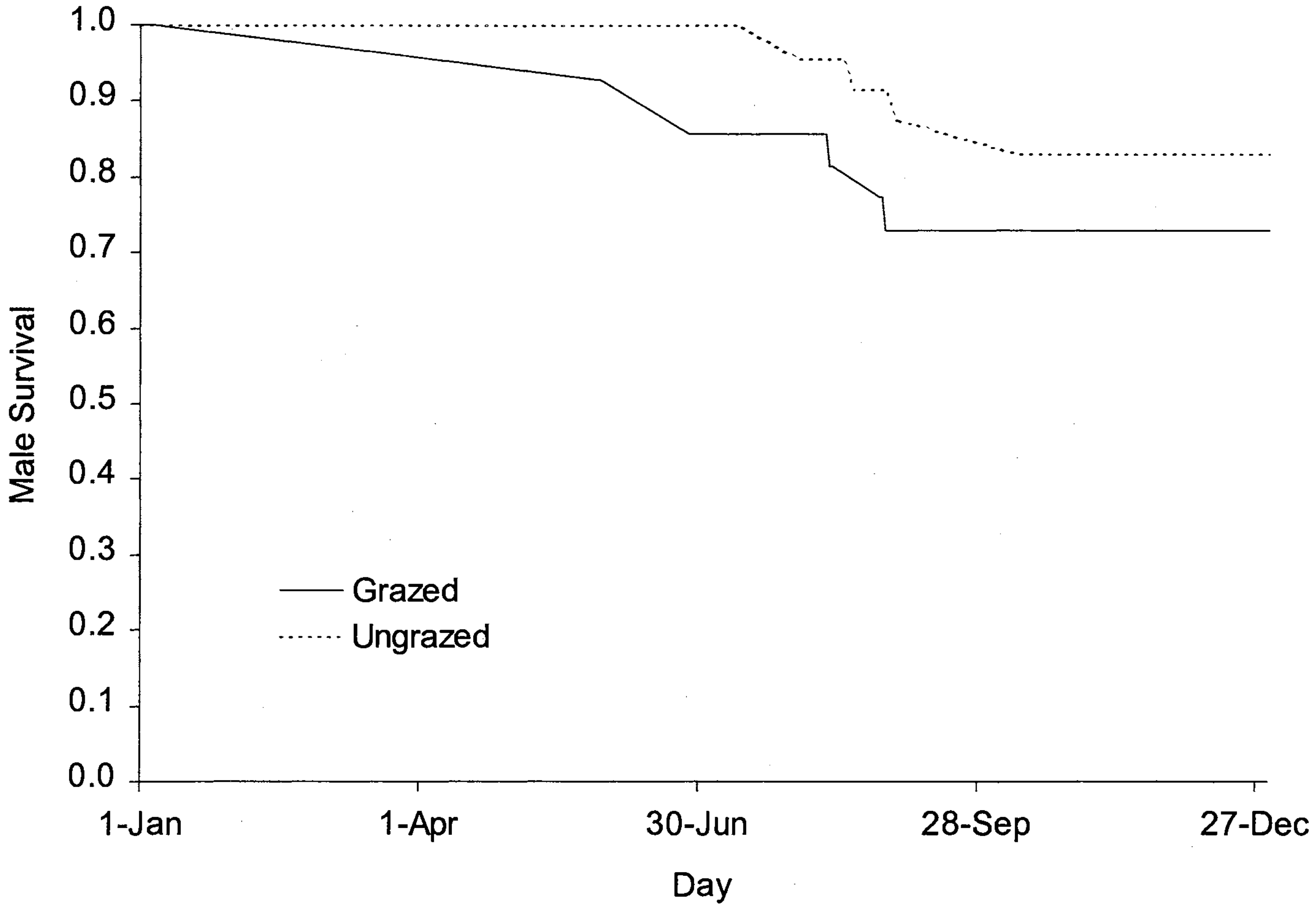

1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Male Survival
1-Jan
1-Apr
30-Jun
28-Sep
27-Dec
Day
Grazed
Ungrazed

Fig. I.7. Ln(frequency)-age distribution for calculation of annual survival of adults (ages 5-12) from grazed and ungrazed areas on Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas, 1994-1997.

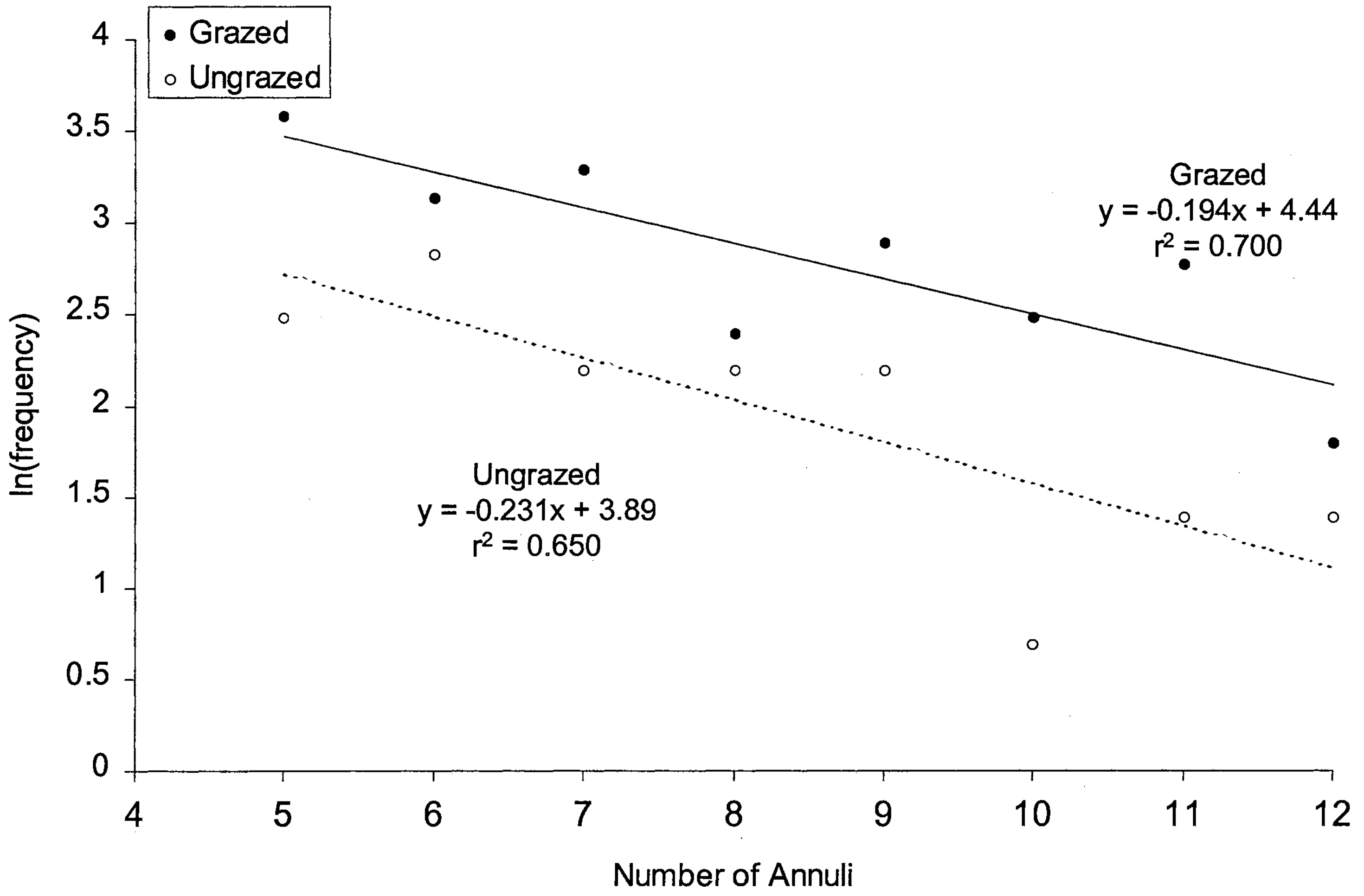
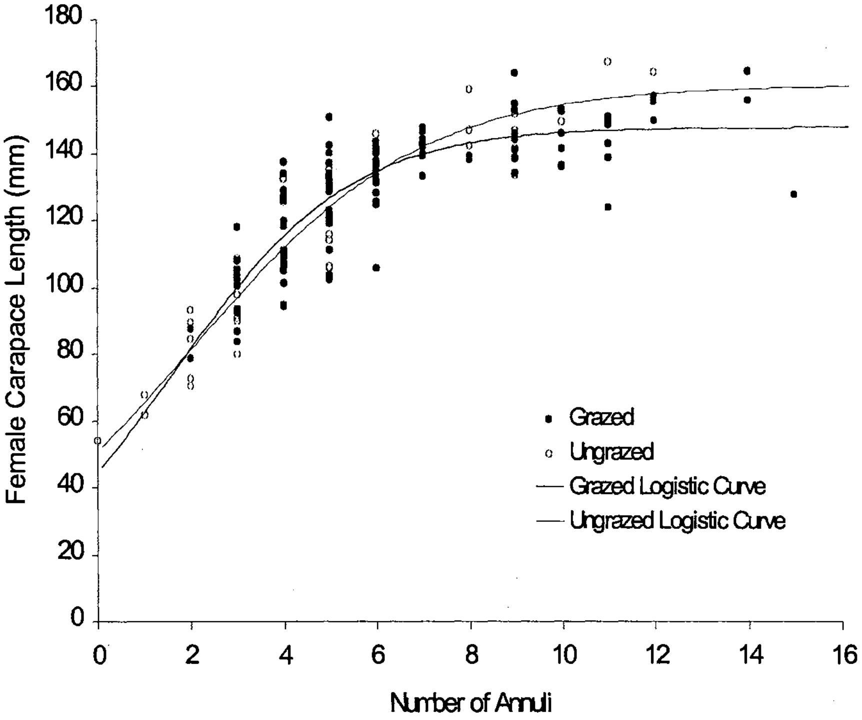
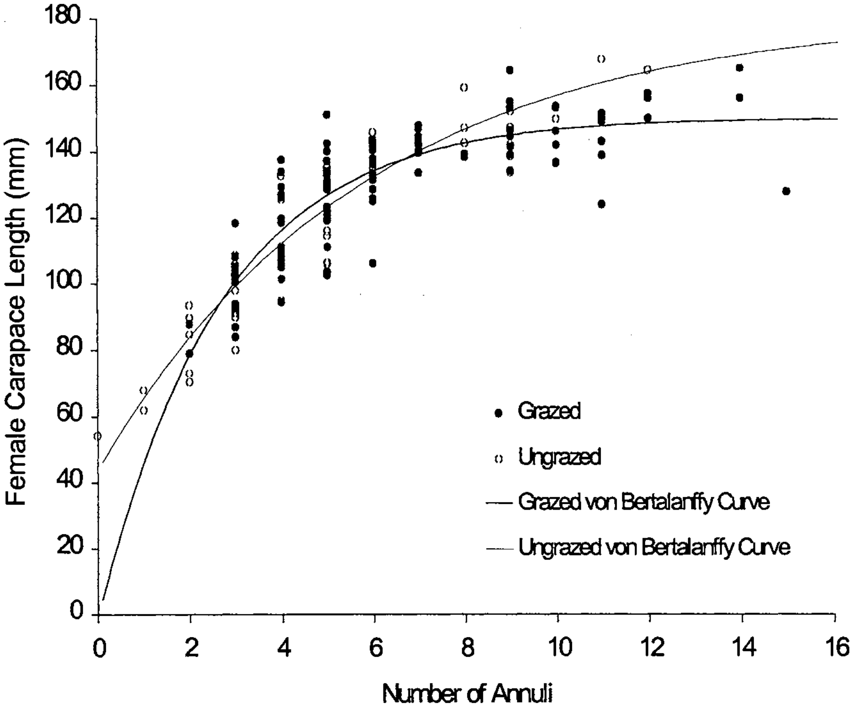

● Grazed
○ Ungrazed
Grazed
y = -0.194x + 4.44
r^2 = 0.700
Ungrazed
y = -0.231x + 3.89
r^2 = 0.650
ln(frequency)
0
0.5
1
1.5
2
2.5
3
3.5
4
4
5
6
7
8
9
10
11
12
Number of Annuli

Fig. I.8. Logistic and von Bertalanffy growth curves for carapace length of female Texas tortoises from grazed and ungrazed areas on Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas, 1994-1997.

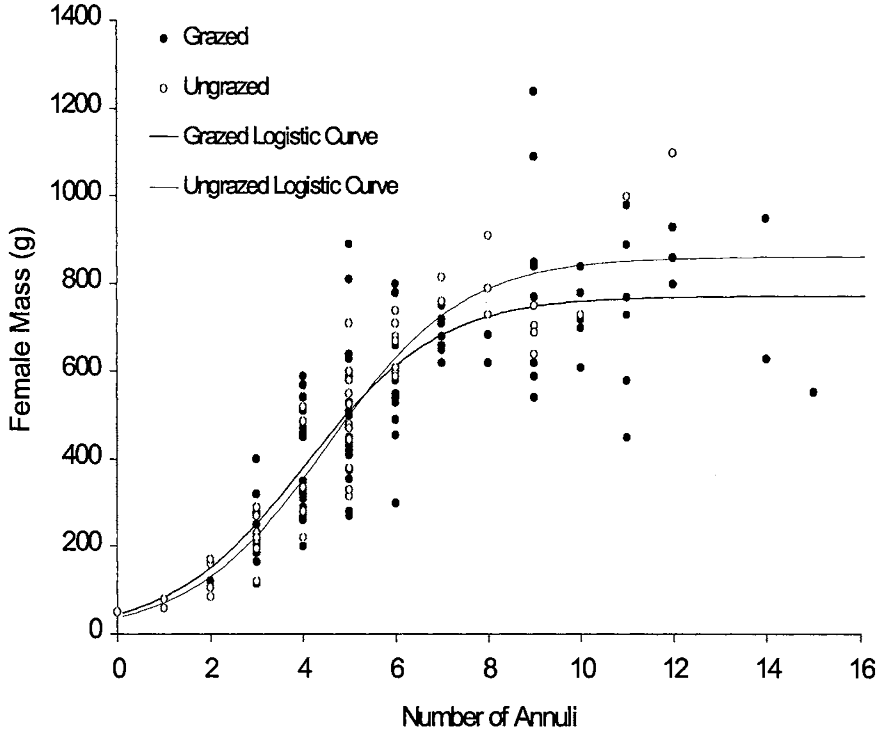


180
160
140
120
100
80
60
40
20
0
Female Carapace Length (mm)
0
2
4
6
8
10
12
14
16
Number of Annuli
• Grazed
○ Ungrazed
— Grazed Logistic Curve
— Ungrazed Logistic Curve

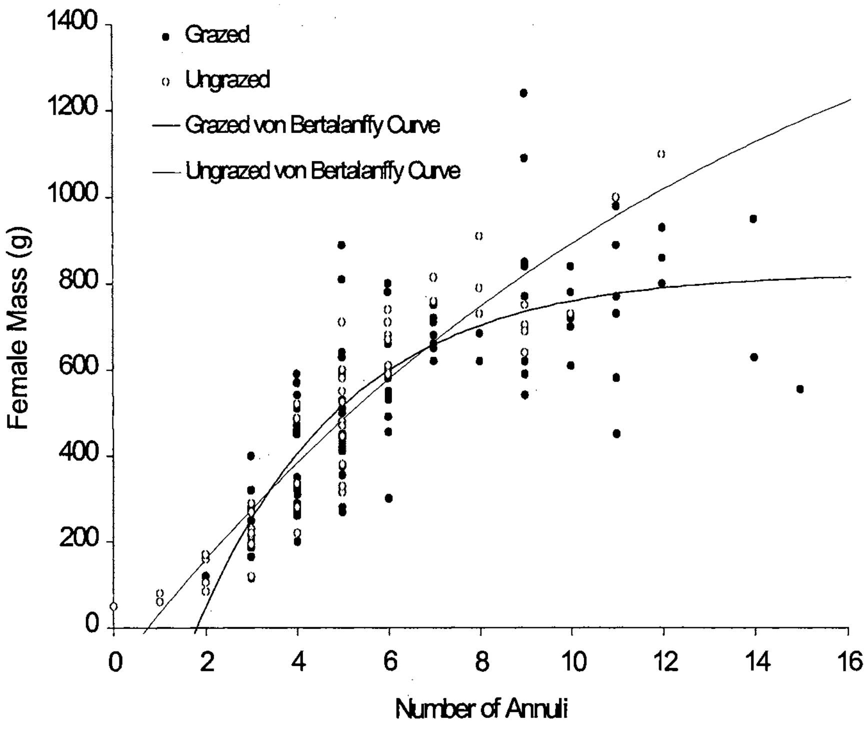


180
160
140
120
100
80
60
40
20
0
Female Carapace Length (mm)
0
2
4
6
8
10
12
14
16
Number of Annuli
• Grazed
○ Ungrazed
— Grazed von Bertalanffy Curve
— Ungrazed von Bertalanffy Curve

Fig. I.9. Logistic and von Bertalanffy growth curves for mass of female Texas tortoises from grazed and ungrazed areas on Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas, 1994-1997.

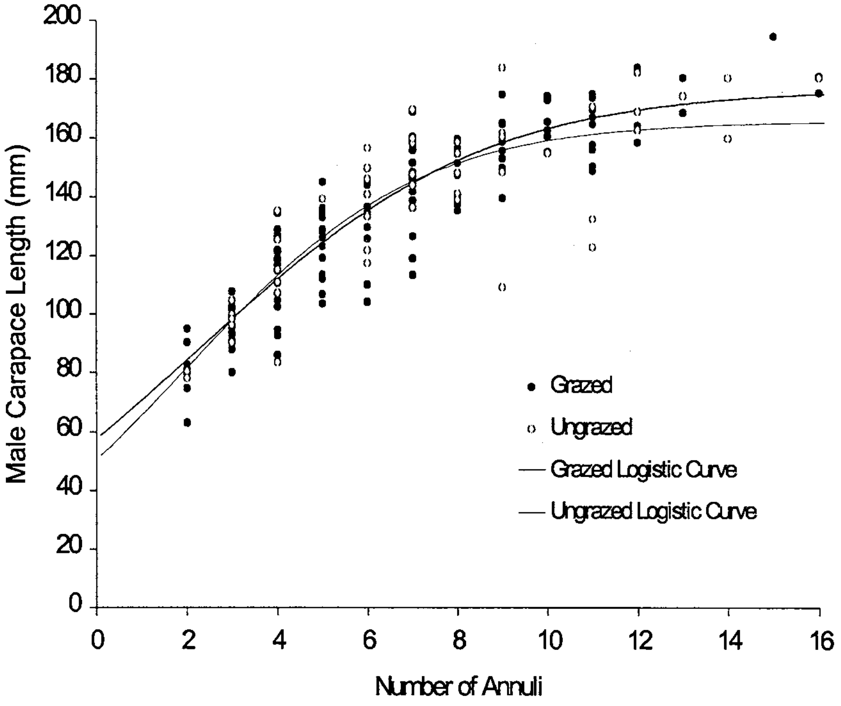


Grazed
Ungrazed
Grazed Logistic Curve
Ungrazed Logistic Curve
Female Mass (g)
0
200
400
600
800
1000
1200
1400
0
2
4
6
8
10
12
14
16
Number of Annuli

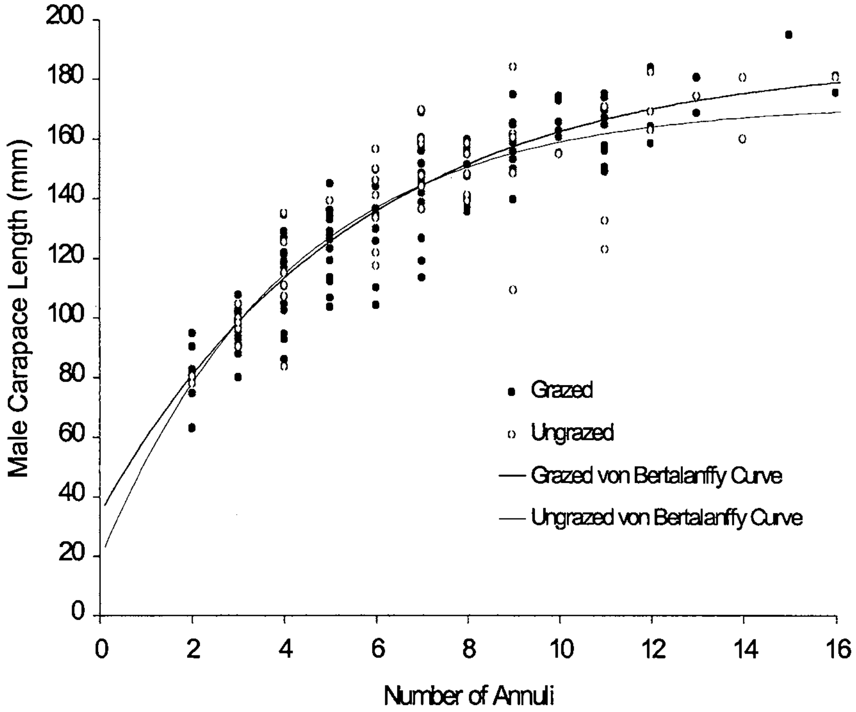


Grazed
Ungrazed
Grazed von Bertalanffy Curve
Ungrazed von Bertalanffy Curve
Female Mass (g)
0
200
400
600
800
1000
1200
1400
0
2
4
6
8
10
12
14
16
Number of Annuli

Fig. I.10. Logistic and von Bertalanffy growth curves for carapace length of male Texas tortoises from grazed and ungrazed areas on Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas, 1994-1997.

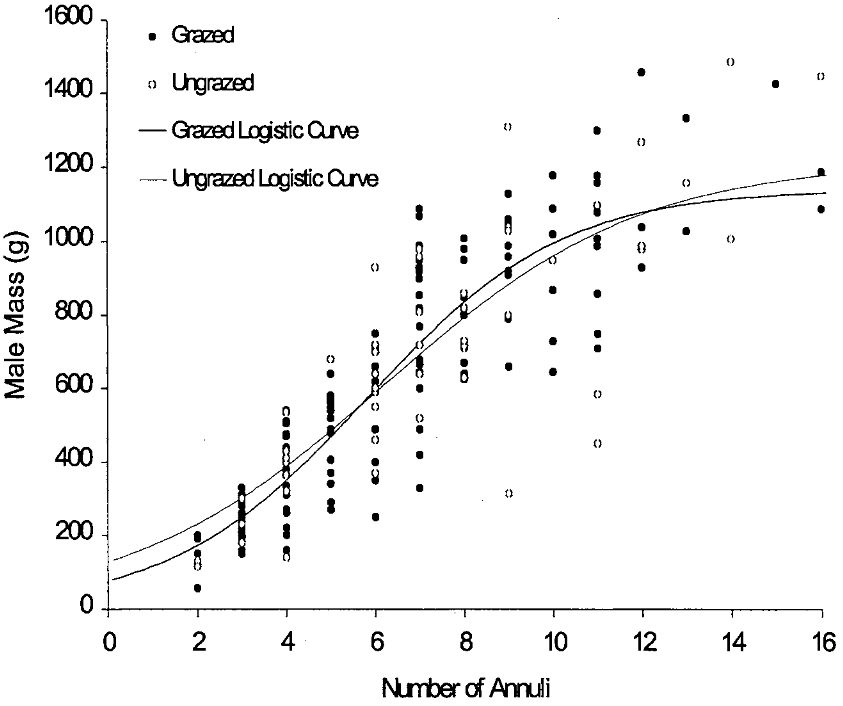


200
180
160
140
120
100
80
60
40
20
0
Male Carapace Length (mm)
0
2
4
6
8
10
12
14
16
Number of Annuli
● Grazed
○ Ungrazed
Grazed Logistic Curve
Ungrazed Logistic Curve



200
180
160
140
120
100
80
60
40
20
0
Male Carapace Length (mm)
0
2
4
6
8
10
12
14
16
Number of Annuli
● Grazed
○ Ungrazed
Grazed von Bertalanffy Curve
Ungrazed von Bertalanffy Curve

Fig. I.11. Logistic and von Bertalanffy growth curves for mass of male Texas tortoises from grazed and ungrazed areas on Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas, 1994-1997.


Grazed
Ungrazed
Grazed Logistic Curve
Ungrazed Logistic Curve
Male Mass (g)
0
200
400
600
800
1000
1200
1400
1600
0
2
4
6
8
10
12
14
16
Number of Annuli

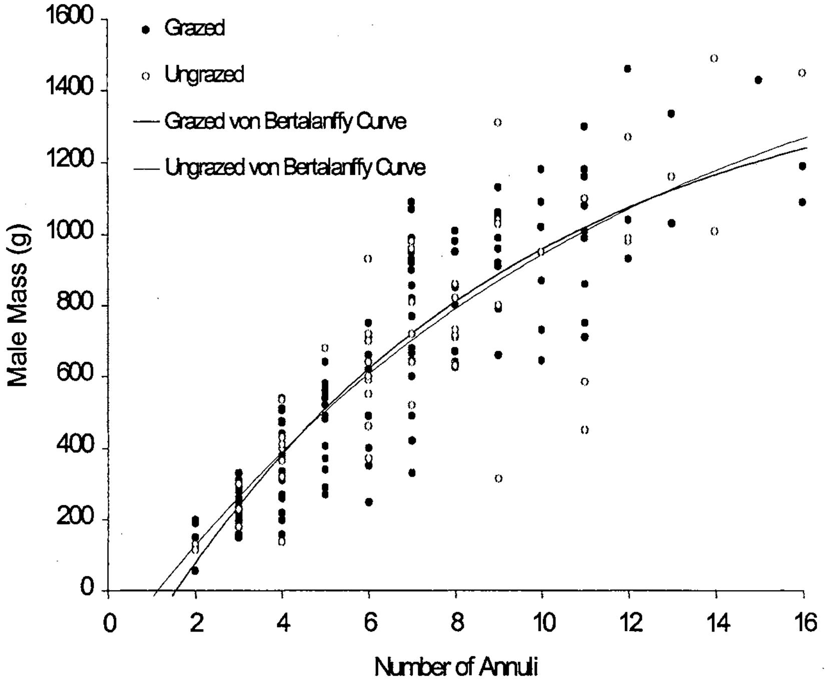

Grazed
Ungrazed
Grazed von Bertalanffy Curve
Ungrazed von Bertalanffy Curve
Male Mass (g)
0
200
400
600
800
1000
1200
1400
1600
0
2
4
6
8
10
12
14
16
Number of Annuli

Fig. I.12. Simple linear regressions of carapace length on age for young tortoises (0-5 annuli) from grazed and ungrazed areas on Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas, 1994-1997.

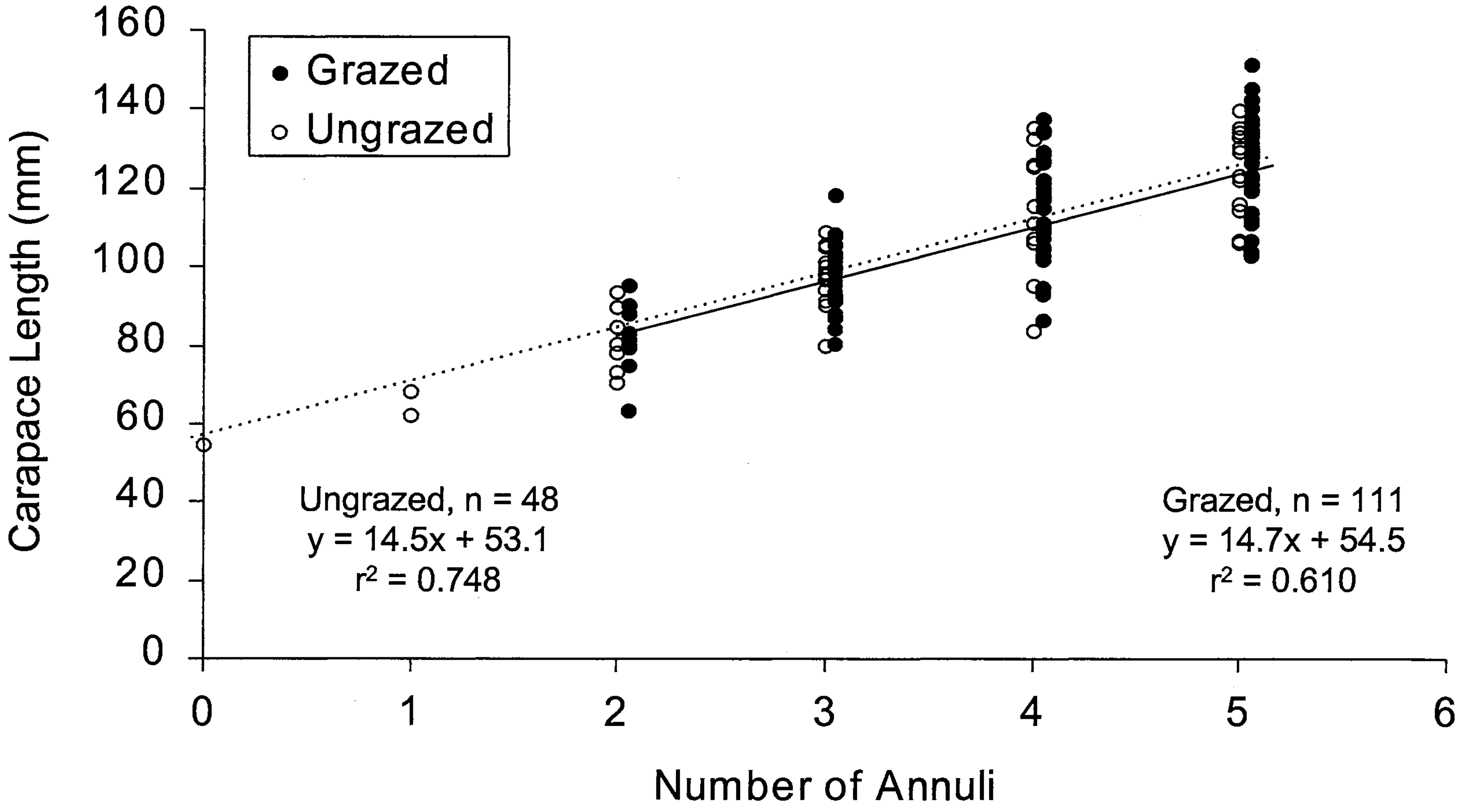
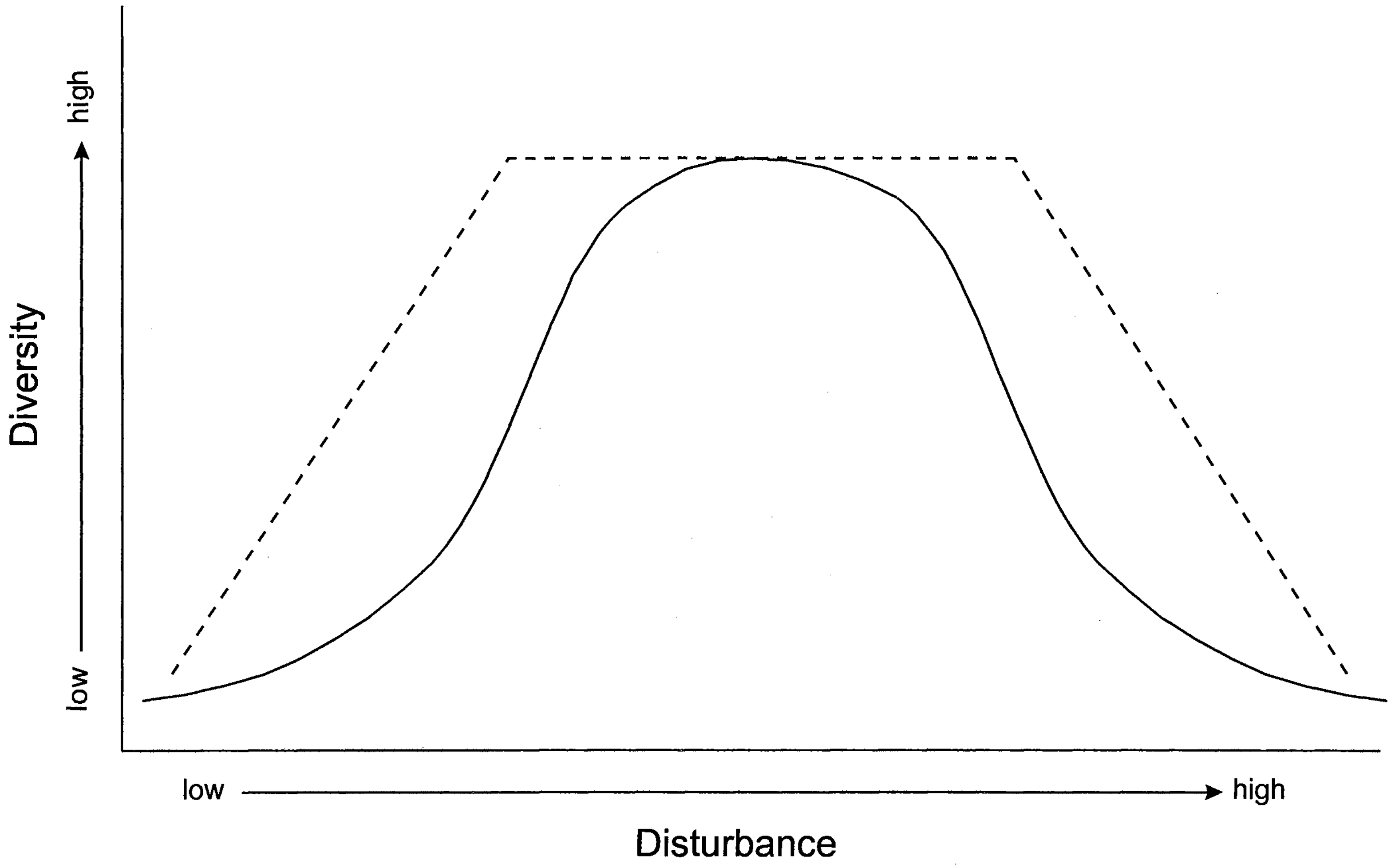

Grazed
Ungrazed
Carapace Length (mm)
160
140
120
100
80
60
40
20
0
Number of Annuli
0
1
2
3
4
5
6
Ungrazed, n = 48
y = 14.5x + 53.1
r² = 0.748
Grazed, n = 111
y = 14.7x + 54.5
r² = 0.610

Fig. I.13. Two possible relationships between diversity and disturbance following the assumptions of the intermediate disturbance hypothesis.


Diversity
high
low
low
high
Disturbance

CHAPTER II

HABITAT SELECTION BY THE TEXAS TORTOISE IN A MANAGED THORNSCRUB ECOSYSTEM

ABSTRACT

Increases in brush encroachment, which are coupled to livestock grazing on semiarid shrublands, have created global concern. 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 the perceived threat to Texas tortoises due to habitat change brought about by brush encroachment, I monitored 36 Texas tortoises by radiotelemetry in 1994-1996 to assess habitat selection on a site containing grazed and ungrazed pastures. Tortoises did not exhibit habitat selection at the level of points within home ranges. Differential habitat selection at the level of home ranges within study areas was not apparent for sex, but was evident for treatment (grazed or ungrazed) and side (east or west). Analysis of pooled data suggested that tortoises selected home ranges within study areas throughout the study site. Selection was expressed as preferential avoidance of extreme habitats (oldfield and riparian), although tortoises tolerated the broad continuum of other brush communities on the study site. Apparent treatment differences may be an artifact of an inability to adequately pair study areas given the scale of tortoise movement. My data suggest that grazing-induced brush encroachment will not be detrimental to Texas

tortoises, but large-scale range improvement practices, such as root-plowing, create unsuitable habitats for this species.

INTRODUCTION

Shrubland habitats are common in semiarid regions throughout the world. The dominant land management practice on these habitats involves grazing by livestock, because aridity and climatic variability make them unsuitable for farming (Archer 1996). Globally, concern has been mounting due to perceived increases in woody plant coverage in these habitats at the expense of herbaceous species utilized by livestock (Archer 1996, Milchunas and Lauenroth 1993). Although causes of brush encroachment are still debated, domestic livestock are often implicated as a contributing factor through competitive release of woody species by removal of herbaceous species (Archer 1989, 1990, 1996), increased woody plant germination due to disturbance or preparation of the seed bed (Williams and Ashton 1987), or by enhanced seed dispersal (Kramp et al. 1998).

The genus *Gopherus* is composed of small- to medium-sized (0.5-5 kg) herbivorous testudinids found in the southern United States and northern Mexico (Bury and Germano 1994). These North American tortoises are generally restricted to arid and semi-arid regions. In the southeastern United States, the gopher tortoise (*Gopherus polyphemus*) may be an exception to this generality, but even in this region it tends to prefer more xeric sand plain or hammock communities (Auffenberg and Franz 1982). All members of the genus *Gopherus* receive some form of protection from state or federal governments due to concerns over declining populations (Bury and Germano 1994).

Gopher tortoises appear to thrive in relatively open-canopied or early successional habitats with high light intensities at ground level and high herbaceous plant diversities

(Auffenberg and Franz 1982). In Mexico, Bolson tortoises (*G. flavomarginatus*) inhabit flatland desert areas dominated by tobosa grass (*Hilaria mutica;* Morafka 1982), whereas desert tortoises (*G. agassizii*) seem to prefer arroyos, slopes, and bajadas in habitats ranging from relatively open Sonoran savanna grassland to closed-canopied Sinaloan deciduous forest (Fritts and Jennings 1994). In contrast, desert tortoises in the Mojave desert of California and Nevada, frequently occupy flatlands (Bury et al. 1994, Germano et al. 1994). Desert tortoises are thought to be affected by livestock grazing through changes in habitat (Berry 1978). However, data to support the impacts of grazing, either positive or negative, on desert tortoises are lacking (Oldemeyer 1994). Nevertheless, there seems to be an opinion that desert tortoises are relatively intolerant of habitat change.

The Texas tortoise (*G. berlandieri*) is significant, because it exists in a climatic regime intermediate to that of the other *Gopherus* (Germano 1994). In the United States, Texas tortoises are restricted to thornscrub and coastal prairie habitats in southern Texas (Rose and Judd 1982). Auffenberg and Weaver (1969) suggested that a shift in land-use practices, particularly in the Lower Rio Grande Valley, from livestock grazing to agricultural crops has created unusable habitat for tortoises. Bury and Smith (1986) urged against grazing on lomas (coastal clay ridges) inhabited by Texas tortoises, but suggested that small-scale burning of dense brushland could be beneficial by creating patches of high-quality, herbaceous vegetation. However, empirical evidence is not available to assess the impacts of land-use practices on Texas tortoises other than the disappearance of tortoises from lands urbanized or converted to agriculture.

The region of southern Texas and northeastern Mexico characterized as the Tamaulipan Biotic Province (Blair 1950) or the Rio Grande Plains Ecoregion (Correl and Johnston 1979) is dominated by a *Prosopis-Acacia* thornscrub community. This shrubland community encompasses approximately 8 million ha in Texas that have experienced extensive grazing by domestic livestock (primarily cattle) since the early to mid 1800s (Crosswaite 1980). Brush invasion has been viewed as a persistent problem within this region (Archer 1989, 1995). Throughout southern Texas, ranchers have responded to the perceived threat of brush encroachment with management practices geared toward "range improvement." Reductions in woody plant coverages through chaining, roller-chopping, root-plowing, or aeration are designed to increase herbaceous forage at the expense of woody species. Such manipulations, however, typically result in only short-term increases in herbaceous cover and, ultimately, in woody habitats that are both denser and less diverse than initial woody habitats (Archer 1990).

The boundaries of the geographic range of the Texas tortoise are nearly identical to the boundaries of the Tamaulipan Biotic Province (Iverson 1992, Blair 1950). In light of perceived changes in woody plant cover and predominance of livestock grazing in this region, I investigated the ecology of the Texas tortoise in grazed and ungrazed pastures at a site near the northern limit of its range in southern Texas. My primary objective was to evaluate habitat selection as a prelude for making predictions regarding the impact of livestock-influenced brush encroachment on this species.

STUDY AREA

All research was conducted on the Chaparral Wildlife Management Area (WMA) in Dimmit and La Salle counties, Texas. Chaparral WMA is a 6,150-ha facility that has been managed as a research and demonstration area by the Texas Parks and Wildlife Department (TPWD) since its acquisition in 1969. During my research, Chaparral WMA was composed of 15 major 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, and the 13 interior pastures are separated by 5-strand barbed-wire cattle fences. A span of 2.4-m woven wire fence also divides the area down the center into the 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 removal of all cattle on Chaparral WMA in 1984, cattle grazing was reinitiated in 1991 with a one-herd, dormant-season (Oct-May), short-duration, rotational grazing system on each side (east and west) of the area. Under this system, herds composed of 341-448 steers grazed pastures for 3-8 weeks each year depending on pasture size and forage availability.

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 (1969-1997; TPWD unpublished data). Quantity and timing of rainfall, however, are extremely variable in this region, and droughts are common. Although woody vegetation on Chaparral WMA is dominated by *Prosopis-Acacia* thornscrub communities, other communities, such as paloverde (*Parkinsonia texana*)- or ceniza (*Leucophyllum frutescens*)-dominated uplands or whitebrush (*Aloysia gratissima*)-dominated drainages, may be locally significant. There is a clinal tendency to vegetation on Chaparral WMA, with denser thornscrub in the east and more open savannah habitats in the west (TPWD unpublished data).

METHODS

For this study, effort was focused on the 2 ungrazed pastures (Baldy [277 ha] and Mare [263 ha]) paired with 2 grazed pastures (East Blocker [372 ha] and South Jay [750 ha]; Fig. II.1). Pastures were paired by similar vegetation types, as defined by canopy and dominant species of woody plants. Baldy pasture was paired with East Blocker pasture for west-side comparisons; Mare pasture was paired with South Jay pasture for east-side comparisons. To remain in similar habitat types between pasture pairs, search and radiotelemetry effort was skewed toward the eastern half of Baldy pasture (above a rocky escarpment), the eastern two-thirds of East Blocker pasture, the southern half of South Jay pasture, and the southwestern two-thirds of Mare pasture (Fig. II.1). Grazing in South Jay and East Blocker pastures occurred during the spring (Apr-May), when interactions between cattle and tortoises were most likely to occur.

Tortoise Monitoring

I attempted to monitor 6 female and 4 male tortoises using radiotelemetry in each study pasture. Radiotransmitters (~20 g; L. L. Electronics, Mahomet, Illinois, USA) were attached to adults >500 g by mounting them to the anterior portion of the carapace using silicon rubber. Transmitter bundles were coated with a layer of sand from the area of collection before the silicon hardened to help camouflage the transmitter bundle. I relocated radiotransmittered tortoises using a 2-element, hand-held yagi antenna and a TR-4 receiver (Telonics, Mesa, Arizona, USA) once weekly during the active season (15 Apr-15 Oct) and once monthly during the inactive season (16 Oct-14 Apr). All relocations were carried out by homing to and visually observing tortoises. Locations 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 for each location were computed from pacing distances using a Geographical Information System (GIS) with layers for roads and landmarks. Tortoises were monitored by radiotelemetry from 15 June 1994 to 15 October 1996.

Assessment of Habitat Types and Habitat Selection

A habitat type map was developed for each study pasture and incorporated into a GIS using black and white aerial photography of Chaparral WMA taken on 29 April 1997. Aerial photographs were taken at a nominal scale of 1 cm = 48 m and combined into a composite image of the entire Chaparral WMA. This composite black and white image was scanned at a resolution of 600 dpi on a drum scanner, resampled at 2-m resolution, and georeferenced using control points. I used on-screen digitizing in ArcView version 3.0 (Environmental Systems Research Institute, Redlands, California, USA) to delineate habitat types. Habitats were delineated into 9 major types based on generalized canopy closure, canopy coverage, and dominant woody species (Table II.1).

Second- and third-order habitat selection were assessed using compositional analysis (Aebischer et al. 1993). Compositional analysis uses log-ratios of use and availability in a multivariate approach to evaluate selection among habitats. This approach alleviates some of the statistical problems of other habitat selection methods and allows for the testing of differential selection between effects (*e.g.*, treatment or sex). By using compositional analysis, tortoises, not radiolocations as in Neu et al. (1974), were considered replicates. Second-order selection (Johnson 1980) compares the habitat composition within a tortoise's home range (*i.e.*, used habitat) to the habitat composition of the study area (*i.e.*, available habitat), whereas third-order selection (Johnson 1980) involves comparison of habitat composition of an individual tortoise's radiolocations (*i.e.*, used habitat) with the habitat composition of its home range (*i.e.*, available habitat).

Home ranges were calculated at the 100% level using the minimum convex polygon method with the program CALHOME (Kie et al. 1994). I only used locations collected during the active season for analyses and only calculated home ranges for tortoises that had >20 locations. To maximize use of location data while reducing the effects of variable durations of monitoring, home ranges were calculated over 2 years for each tortoise. Thus, home ranges used for analyses encompassed either 1994-1995 or 1995-1996.

Study areas were defined for each pasture as the area enclosed by the smallest rectangle that included all tortoise home ranges (Warrick et al. 1998). Due to differences in size of home ranges between males and females (Kazmaier, unpublished data), study areas were defined separately for the sexes. Habitat types of points, home ranges, and study areas were determined by intersecting GIS coverages for each tortoise's relocations, 100% minimum convex polygon home range, and the study areas with the habitat coverage using PC Arc/Info version 3.5 (Environmental Systems Research Institute, Redlands, California, USA).

Separate analyses were performed to evaluate sex (male, female), treatment (grazed, ungrazed), and side (east, west) effects on habitat selection. Small sample sizes precluded a complete factorial approach. Main effects (sex, treatment, or side), habitat selection, and the interaction of each main effect and selection were tested using

MANOVAs in SAS (SAS Institute Inc. 1989). With this approach, significance of the selection factor indicated overall selection of at least 1 habitat type by both groups of the main effect, whereas significance of the interaction between the selection factor and the main effect indicated differential selection by the groups of the main effect. I did not report levels of significance for main effects, because differences between sexes, treatments, or sides indicated only that use or availability varied between the main effects, but these differences were confounded. An analysis also was conducted by pooling data across all effects to evaluate overall habitat selection by the Texas tortoise. Analyses of selection were considered significant at $P < 0.1$.

RESULTS

I monitored 36 tortoises (13F:7M on grazed sites; 9F:7M on ungrazed sites) for sufficient time to calculate home ranges. No selection ($P > 0.97$ for all interactions) was apparent at the level of points within home ranges (third-order selection), regardless of comparison (Table II.2). At the level of home ranges within study areas (second-order selection), there was no effect of sex on habitat selection ($P = 0.37$), but differential selection was apparent based on grazing ($P = 0.04$) and side ($P = 0.002$; Table II.2). Comparison of the pooled data suggested that Texas tortoises made broad-scale habitat selection at the level of home ranges within study areas ($P = 0.0001$; Table II.2).

Comparisons of habitat rankings indicated that second-order selection differed primarily for PARKLAND, WOODLAND, and WHITEBRUSH habitats between grazed and ungrazed areas (Table II.3). PARKLAND was avoided in the grazed study sites relative to the ungrazed sites, where it was selected. WOODLAND showed the converse result. WHITEBRUSH was selected to a greater degree in ungrazed pastures relative to grazed pastures. RIPARIAN and OLDFIELD habitats were avoided in both treatments (Table II.3).

Pooling grazed and ungrazed sites on each side of the overall study area and comparing the east and west sides of Chaparral WMA revealed that PARKLAND, WOODLAND, and WHITEBRUSH habitats were selected differentially between sides (Table II.3). Relative to other habitats, PARKLAND was most preferred on the west side, but ranked as one of the least preferred habitats on the east side. Again, this result was mirrored by differential selection for WOODLAND. Similar to the treatment effects, OLDFIELD and RIPARIAN habitats were consistently avoided on both sides. When data were pooled for all tortoises, habitat selection was detectable as preferential avoidance of RIPARIAN and OLDFIELD habitats (Table II.3).

Across all analyses, Texas tortoises appeared to select more open habitats, such as PARKLAND. There was some variation in habitat rankings depending on comparison (Table II.3), with a tendency for tortoises in grazed pastures and tortoises on the east side of Chaparral WMA to select WOODLAND. However, OLDFIELD and RIPARIAN habitats were consistently avoided in all analyses (Table II.3).

DISCUSSION

Habitats avoided by tortoises represented the vegetational extremes in the continuum of habitat types on Chaparral WMA, with OLDFIELD being dense grassland with no woody component and RIPARIAN being the densest woodland with very low herbaceous and cactus densities. OLDFIELD might be avoided due to difficulties in moving through the habitat, low forb (*i.e.*, forage) and cactus availabilities, increased susceptibility to predators (*e.g.*, crested caracaras [*Polyborus plancus*]) in open habitats, or reduced ability to thermoregulate due to the absence of shade provided by woody species. In a coastal population of Texas tortoises, Bury and Smith (1986) suggested that certain shrub and tall grassland conditions may be too dense for tortoise movement. RIPARIAN habitat might be avoided due to low forb and cactus availabilities, increased susceptibility to predators (*e.g.*, raccoons [*Procyon lotor*]) along drainages, or reduced ability to thermoregulate due to excessive shade provided by the woody canopy. Relative to other tortoises, Texas tortoises on Chaparral WMA have low adult survival rates, and raccoons and crested caracaras are believed to be the 2 most important predators of tortoises on Chaparral WMA (Hellgren et al. 2000). Thus, avoidance of predation may be an important advantage to avoiding OLDFIELD and RIPARIAN habitats.

Texas tortoises avoided extreme habitats while tolerating the broad continuum of other shrubland communities present on Chaparral WMA. Thus, management practices that involve large-scale manipulations of woody communities that essentially produce OLDFIELD habitats for cattle are probably detrimental to tortoises, because they avoid such habitat. If source populations are available, tortoises might recolonize manipulated areas after acceptable levels of woody vegetation regrow. Auffenberg and Weaver (1969) suggested that some level of brush manipulation, such as small prescribed burns (Bury and Smith 1986), might be beneficial to tortoises by encouraging a grassland-shrubland mosaic. In the long-term, manipulated shrublands in southern Texas typically regenerate into dense woodland (Archer 1989), but RIPARIAN habitat would remain restricted to drainages. Tortoises in South Jay Pasture, portions of which have experienced brush manipulation in the past, apparently preferred WOODLAND habitat. Thus, dense woodlands that regenerate after brush manipulation can remain viable tortoise habitat.

However, regenerated woodlands can have lower plant diversity than natural woodlands (Nolte et al. 1996, Ruthven et al. 1993) and the extent to which this might affect tortoise habitat selection is unknown.

Among other habitats, there was an overall tendency for Texas tortoises to select more open-canopy habitats, particularly ESCARPMENT, HOGPLUM, and PARKLAND, to a greater degree than closed-canopy habitats, particularly BLACKBRUSH and WHITEBRUSH. When data were partitioned by treatment or side, however, patterns in selection were less distinct. Variability in selection due to side or treatment is mostly the result of South Jay Pasture, where tortoises tended to prefer more closed canopy habitats like WOODLAND and WHITEBRUSH. Ecologically, it is difficult to explain why tortoises in South Jay Pasture preferred closed-canopy habitats while tortoises in the other 3 pastures preferred more open-canopy sites. Statistically, such differences in second-order selection might be an artifact of the arbitrary nature in which habitat availability of the study area is defined (Aebischer et al. 1993). Because study areas were defined by the smallest rectangle that included all tortoise home ranges, the presence of "outlier" home ranges resulted in the inclusion of a substantial amount of habitat within the study area that was actually not available to monitored tortoises. For example, an outlying home range in South Jay resulted in a large amount of PARKLAND being included in the study area while the areas immediately around home ranges were predominantly WOODLAND.

Differences in habitat selection 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 (Judd and Rose 1983, Rose and Judd 1975). However, Chaparral WMA tortoises had home ranges 15-70 times larger than Cameron County tortoises (Chapter III). As a result, original study areas had to be increased in area as radioed tortoises ranged, and tortoises used habitats that differed between the paired sites. This effect was notable on the west side where ESCARPMENT and BLACKBRUSH habitats were frequently utilized in Baldy Pasture (ungrazed), but were unavailable in the paired grazed pasture (East Blocker). A similar problem occurred on the east side where HOGPLUM became an important habitat in Mare Pasture (ungrazed), but was absent from the paired grazed pasture (South Jay). Thus, differences in habitat selection may actually be an artifact of differential availability of habitats instead of an effect of grazing.

The demonstrated tolerance for a wide range of habitats is consistent with the view that Texas tortoises are adapted to more intermediate levels of disturbance relative to other North American tortoises (Chapter I). In the mesic southeastern United States, gopher tortoises apparently require a relatively high degree of disturbance to maintain open canopies necessary for forage production (Auffenberg and Franz 1982, Aresco and Guyer 1999). High plant productivity in the southeastern United States also reduces the likelihood of forage competition between tortoises and cattle on grazed sites. In the more xeric and less productive southwestern United States, desert tortoises are apparently negatively impacted by relatively low levels of disturbance and forage competition with cattle, particularly during droughts, becomes a more likely phenomenon. In arid Mexico, any disturbance that alters tobosa grass flatlands may negatively impact Bolson tortoises, because of their reliance on this habitat (Morafka 1982).

I proffer that the scale at which I examined habitat selection by the Texas tortoise might have been too large to detect third-order selection. However, I believe some selection might be occurring at the level of points within home ranges because of my observations of tortoises on Chaparral WMA. In East Blocker Pasture, for example, tortoises often seemed to concentrate activity around PALOVERDE habitat and seemed to move through surrounding PARKLAND habitat to preferentially exploit PALOVERDE areas (R. T. Kazmaier, unpublished data). In East Blocker Pasture, PALOVERDE areas tend to have high forb diversities while PARKLAND areas tend to be dominated by the introduced grass *Eragrostis lehmanniana* (R. T. Kazmaier, unpublished data). Thus, tortoises might be selecting PALOVERDE habitat due to increased forage availability. Failure to detect this third-order habitat selection might be due to inadequate sampling or a consequence of the scale at which habitats were defined.

Detailed analyses of habitat selection at finer scales, perhaps at the level of individual shrub clumps (mottes) or herbaceous communities, might be more meaningful for exploring how tortoises select habitats across the variable shrubland landscape. Dispersal distances of >10 km have been recorded for juvenile tortoises on Chaparral WMA (R. T. Kazmaier, unpublished data) and an exploration of habitat selection by juvenile tortoises, particularly during times of dispersal, would help address why tortoises eventually choose the locations in which they reside as adults.

MANAGEMENT IMPLICATIONS

My data suggest that managed manipulations of woody plant communities in southern Texas will have negligible effects on habitat selection by Texas tortoises as long as extremes in woody plant canopy cover are avoided. However, because different brush manipulation techniques ultimately result in potentially different types of woody communities in terms of vegetation diversity and density, more research is warranted, particularly at different spatial scales, to address the impacts of type of brush manipulation on habitat selection by this state-threatened species. In the broader context of the dynamic nature of shrubland communities in southern Texas, it appears that brush encroachment and managed grazing will have little effect on the Texas tortoise.

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Table II.1. Delineation of major habitat categories used for analysis of second- and third-order habitat selection by Texas tortoises on Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas, 1994-1996.

Habitat category	Canopy closure	Canopy cover (%)	Dominant woody plants	Comments
BLACKBRUSH	closed	>50	blackbrush	restricted to shallow soils; ceniza locally common, but other woody plants rarely important
ESCARPMENT	open	<10	none	restricted to Baldy Pasture; eroded sandstone surface; includes zone of prickly pear cactus immediately down slope of rocky escarpment; herbaceous vegetation scarce on rocky escarpment, but typically abundant in prickly pear cactus zone
HOGPLUM	open	<50	hogplum	restricted to Mare Pasture; coyotillo locally common, but other woody plants unimportant

PALOVERDE	open	<50	paloverde	typically on shallow soils; other woody species rarely important
PARKLAND	open	<60	honey mesquite, guajillo	Highly diverse and many other woody species serve as local codominants; prickly pear cactus density variable, but tending to be high
WOODLAND	closed	>60	honey mesquite, guajillo	Highly diverse and many other woody species serve as local codominants; typically high prickly pear cactus density
RIPARIAN	closed	>60	granjeno, Texas persimmon, sugarberry, brasil	honey mesquite and guajillo rare; typically low prickly pear cactus density; restricted to drainages
WHITEBRUSH	closed	80-100	whitebrush	other woody species and cactus rare or absent; restricted to drainages

OLDFIELD	open	<10	none	includes regrown food plots, recently root-plowed areas, old oil well pads, and areas immediately around ponds; dominated by very dense graminoid vegetation

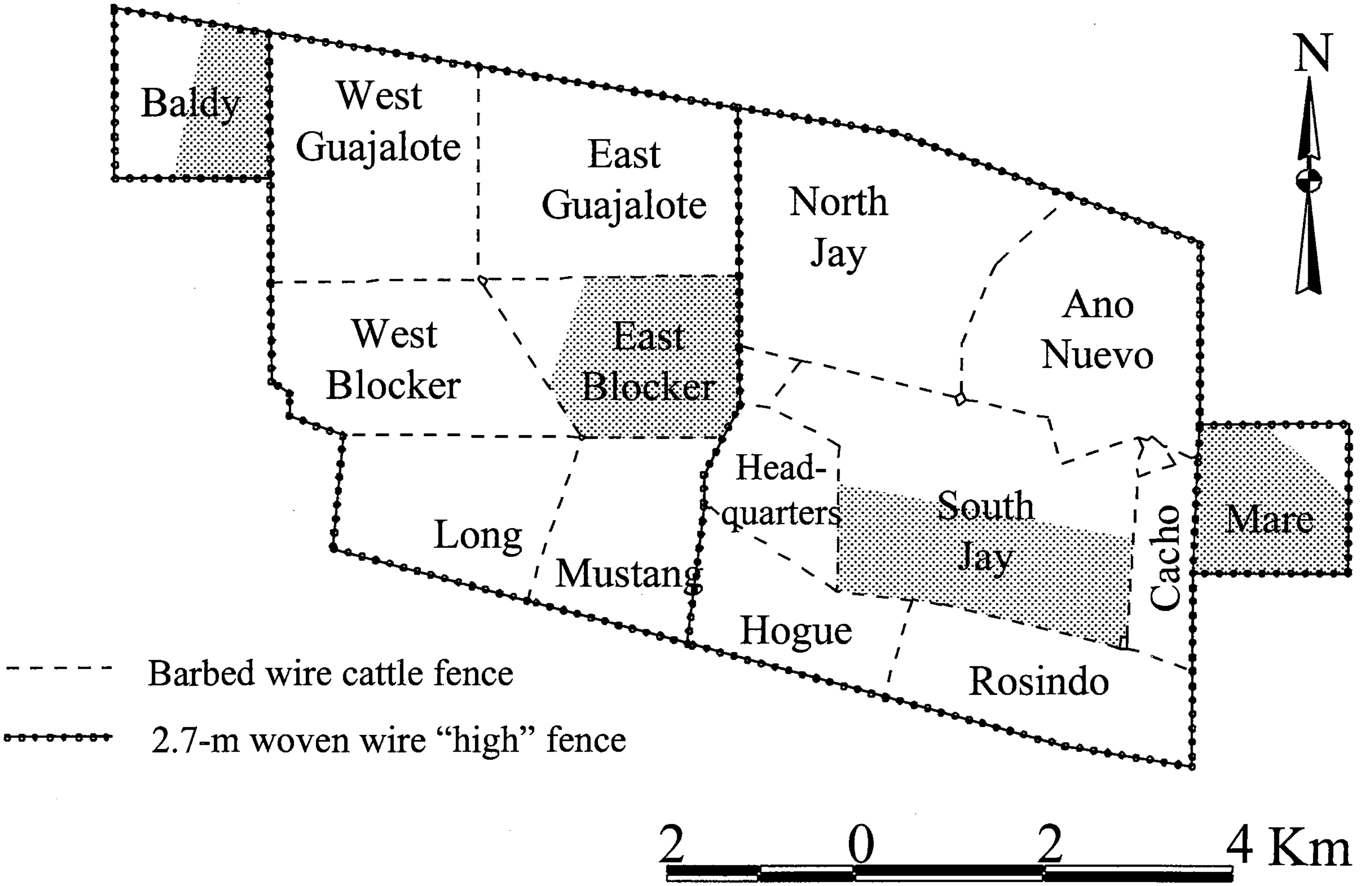
Table II.2. Test statistics and *P*-values for second-order (home ranges within study areas) and third-order (points within home ranges) habitat selection based on compositional analysis for Texas tortoises on Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas.

		Third-order selection		Second-order selection	
Analysis	Parameter	Wilks' λ	*P*	Wilks' λ	*P*
Treatment	Selection	0.977	0.993	0.477	0.0001
(grazing)	Treatment*selection	0.980	0.996	0.779	0.044
Sex	Selection	0.989	0.999	0.487	0.0001
	Sex*selection	0.976	0.992	0.874	0.374
Side	Selection	0.982	0.997	0.480	0.0001
	Side*selection	0.971	0.984	0.675	0.002
Pooled	Selection	0.985	0.999	0.471	0.0001

Table II.3. Ordered rankings of habitat preferences determined by second-order compositional analysis for Texas tortoises in east ($n = 21$) and west ($n = 15$) or grazed ($n = 20$) and ungrazed ($n = 16$) study sites and pooled across study sites ($n = 36$) on Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas.

Analysis	Factor	Habitat Selection
Treatment	grazed	Woodland > Paloverde > Parkland > Oldfield > Whitebrush > Riparian
	ungrazed	Parkland > Escarpment > Whitebrush > Hogplum > Paloverde > Woodland > Blackbrush > Oldfield > Riparian
Side	East	Woodland > Whitebrush > Hogplum > Blackbrush > Parkland > Oldfield > Riparian
	West	Parkland > Escarpment > Blackbrush > Woodland > Paloverde > Oldfield > Whitebrush > Riparian
Pooled		Escarpment > Hogplum > Parkland > Woodland > Paloverde > Blackbrush > Whitebrush > Oldfield > Riparian

Fig. II.1. Pasture arrangement, fencing types, and primary study areas (stippled areas) for Chaparral Wildlife Management Area, Dimmit and La Salle counties, Texas


Baldy
West Guajalote
East Guajalote
North Jay
Ano Nuevo
West Blocker
East Blocker
Head-quarters
South Jay
Cacho
Mare
Long
Mustang
Hogue
Rosindo
N
Barbed wire cattle fence
2.7-m woven wire “high” fence
2
0
2
4 Km

CHAPTER III

RANGE USE AND DISPERSAL OF THE TEXAS TORTOISE IN A MANAGED THORNSCRUB ECOSYSTEM

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, I assessed range use, movements, and dispersal of Texas tortoises at a managed site near the northern limit of its range. Home ranges were larger for males than females regardless of method of home range calculation. Home range sizes determined by minimum convex polygon and bivariate normal methods were larger for tortoises in grazed pastures relative to ungrazed pastures, 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 locations suggested that males moved more than females, but I did not detect differences in movement due to grazing. Texas tortoises appear to exhibit male-biased natal dispersal based on recapture distances. My 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 due to dispersal losses.

INTRODUCTION

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 (e.g. the Rio Grande Plains Ecoregion of Correl and Johnston 1979) grades from *Prosopis-Acacia* savannas in the northwest to dense chaparral woodlands in the southeast. Historically, the more western portions of the region have been utilized extensively for grazing by livestock, whereas the more coastal and southern portions have undergone modification for agriculture. Brush invasion has been viewed 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. 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).

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 (Iverson 1992, Blair 1950). All 4 North American tortoises (genus *Gopherus*) are of considerable conservation interest due to perceived reductions in abundance. The Texas tortoise is considered threatened within the state of Texas and the other 3 *Gopherus* receive some form of governmental protection due to concerns over declining populations (Bury and Germano 1994). From ecological and conservation standpoints, range use and dispersal are important characteristics of populations. Little information has been published on movements and home ranges of Texas tortoises and knowledge of dispersal in reptiles is universally poor. In light of extensive human-induced modifications of thornscrub communities in southern Texas, I investigated the ecology of the Texas tortoise on a managed site near the northern limit of its range in southern Texas. My objectives were (1) to assess home range size, movements, and dispersal of the Texas tortoise at a site composed of contiguous habitat in the western portion of the Rio Grande Plains; and (2) to discuss conservation implications of these aspects of life history in light of livestock grazing, brush manipulation, and habitat fragmentation within the distribution of this protected species.

STUDY AREA

All research was conducted on the Chaparral Wildlife Management Area (WMA) in Dimmit and La Salle counties, Texas. Chaparral WMA is a 6,150-ha facility that has been managed as a research and demonstration area by the Texas Parks and Wildlife Department (TPWD) since its acquisition in 1969. During my research, Chaparral WMA was composed of 15 major 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, and the 13 interior pastures are separated by 5-strand barbed-wire cattle fences. A span of 2.4-m woven wire fence also divides the area down the center into the 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 are not sufficient to 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 (Oct-May), short-duration, rotational grazing system on each side (east and west)of the area. Under this system, herds composed of 341-448 steers grazed pastures for 3-8 weeks each year depending on pasture size and forage availability.

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 (1969-1997; TPWD, unpublished data). Quantity and timing of rainfall, however, are extremely variable in this region, and droughts are common. Soils on the area are predominately red sandy loams (Hatch et al. 1990). 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, unpublished data).

METHODS

Tortoise telemetry

I focused effort on the 2 ungrazed pastures (Baldy [277 ha] and Mare [263 ha]) paired with 2 grazed pastures (East Blocker [372 ha] and South Jay [750 ha]; Fig. III.1) for movement and home range analyses. Pastures were paired by similar vegetation types, as defined by canopy and dominant species of woody plants. Baldy pasture was paired with East Blocker pasture for west side comparisons; Mare pasture was paired with South Jay pasture for east side comparisons. To remain in similar habitat types between pasture pairs, search and radiotelemetry effort was skewed toward the eastern half of Baldy pasture (above a rocky escarpment), the eastern two-thirds of East Blocker pasture, the southern half of South Jay pasture, and the southwestern two-thirds of Mare pasture (Fig. III.1). Because tortoises are relatively inactive from mid-October to mid-April, grazing in South Jay and East Blocker pastures occurred during the spring (Apr-May) when interactions between cattle and tortoises were most likely to occur.

I attempted to monitor 6 female and 4 male tortoises using radiotelemetry in each study pasture. Radiotransmitters (~20 g; L. L. Electronics, Mahomet, Illinois, USA) were attached to adults >500 g by mounting them 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. I relocated radiotransmittered tortoises using a 2-element, hand-held yagi antenna and a TR-4 receiver (Telonics, Mesa, Arizona, USA) at least once weekly during the active season (15 Apr-15 Oct) and once monthly during the inactive season (16 Oct-14 Apr). Tortoises were monitored by radiotelemetry from 15 June 1994 to 1 September 1997. All relocations were carried out by homing to 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 and Dispersal

Average distance between locations of radiotransmittered 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 version 3.0 (Environmental Systems Research Institute, Redlands, California, USA). This method compares the movement patterns of an individual with pathways derived from distances between sequential locations at randomized angles in a Monte Carlo simulation.

From June 1990 to August 1999, tortoises were captured by road-cruising throughout the 6,150-ha area. Upon capture, location was recorded on a map and straight-line carapace length (SCL) was measured using dial calipers. Tortoises < 120 mm SCL tortoises were unsexable by external characters and were considered juveniles. All tortoises > 120 mm SCL were considered adults. Adults with thickened anal scutes, concave plastrons, and/or enlarged sublingual glands were considered males; adults without these characters were considered females. Tortoises on Chaparral WMA generally reach adult size by 5 years of age (Hellgren et al. 2000). After measuring and sexing, tortoises 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 version 3.0 (Environmental Systems Research Institute, Redlands, California, USA). When multiple recaptures were reported for a single individual, only first and last captures were used for calculating distances. 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). Distances moved between recaptures was compared among recapture categories using analysis of variance. Number of years between recaptures was used as a covariate in order to reduce the influence of differential time between recaptures on movement distances. I conducted analysis of variance on ranks due to non-normality in the data (Conover and Iman 1981, Hora and Conover 1984).

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 version 3.0 (Environmental Systems Research Institute, Redlands, California, USA). 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). I used only locations collected during the active season for analyses and calculated home ranges only for tortoises that had >20 locations. To reduce effects of variable durations of monitoring, home ranges were calculated over 2 active seasons for each tortoise. Thus, home ranges used for analyses encompassed either 1994-1995 or 1995-1996. Home ranges were compared between treatments and sexes using ANOVA with side (east or west) as a blocking variable. Home ranges were compared between methods using a repeated-measures ANOVA. Analysis of variance was performed on ranks due to 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 (SAS Institute Inc. 1989) and comparisons were considered significant when $P < 0.05$.

RESULTS

Movement and Dispersal

Distances between relocations of adult radioed tortoises were normally distributed ($P = 0.07$) and were not different between grazed and ungrazed areas ($F_{1,31} = 1.86$, $P = 0.156$). However, movements were greater for males than females ($F_{1,31} = 24.79$, $P = 0.001$; Table III.1). Site fidelity tests indicated that all radioed tortoises exhibited movements that were more constrained than random ($P \geq 0.644$ for all individuals).

Distance between recaptures from the 10-yr dataset varied by recapture category ($F_{5,347} = 2.73$, $P = 0.0241$). Juvenile males recaptured as adults had larger recapture distances than the other 4 recapture groups ($P \leq 0.029$; Table III.2). Median movement distance for the JAM group (551 m) was greater than twice as far as all other recapture classes (176-261 m; Table III.2). Although not included in the JA categories, 2 of the 3 longest movements between recaptures approached inclusion in that category. The longest movement recorded was 11.3 km after 368 days for a JJ individual. This movement occurred when the tortoise was 3-4 yrs of age and the individual was only 1 mm shorter than the minimum adult size 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 interval when movements were made. Comparison of frequency distributions across the 5 recapture classes indicated no differences among movement directions of the groups ($X^2_{12} = 4.75$, $P = 0.97$). Within each recapture class, movement directions were not different from random ($P > 0.72$; Table III.2).

Home Range

I monitored 36 tortoises (13F:7M on grazed sites; 9F:7M on ungrazed sites) for sufficient time to calculate home ranges. Although the number of points used to calculate home ranges varied from 20-64, regressions within each sex and treatment indicated no relationship between number of points 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 points 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 III.1).

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 III.3; Figs. III.2-13). Comparisons between methods indicated differences in home range size based on methodology (F = 5.0, $P = 0.0008$). 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 ($P = 0.0001$ for 95% adaptive kernel and both MCP methods, $P = 0.0007$ for fixed kernels, $P = 0.030$ for bivariate normals; Table III.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%; Figs. III.2-5) and bivariate normal ($P = 0.029$; Figs. III.6-7) methods, but this relationship was weaker for home ranges calculated by adaptive kernel ($P = 0.103$; Figs. III.8-9) and fixed ($P = 0.077$; Figs. III.10-13) methods (Table III.3). Interactions between treatment and sex were not significant ($P > 0.20$) for any home range method.

DISCUSSION

I 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 towards female-biased dispersal (Greenwood 1980). Dispersal has been poorly addressed for reptiles, and I found 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 by individuals that were 3-5 years of age. Female Texas tortoises on Chaparral WMA typically become sexually mature at age 5 (Hellgren et al. 2000). Although I 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 years of age (R. T. Kazmaier, unpublished 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 consistent with dispersal patterns exhibited by many birds and mammals (Greenwood 1980).

Dispersal data derived from mark-recapture data suffers from constraints imposed by the size of the study area. I report 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 axis. Clearly, tortoises are capable of moving beyond the boundaries of the study area and my measurement of dispersal distance should not be considered to include maximum movement distances. Further research involving intensive monitoring of juvenile tortoises is necessary to determine actual movement distances between natal and adult home ranges, and to determine the proportion of juveniles that undergo natal dispersal.

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. Thus, various utilization distribution tests (i.e., kernel methods) are being increasingly used to describe home range (Worton 1989, Harris et al. 1990). However, the 95% MCP method consistently produced smaller home ranges than bivariate normal or adaptive kernel methods. In some cases, the bivariate normal and both kernel methods produced home ranges that incorporated pastures that were not used by tortoises (Figs. III.6-10, III.12). Because development of kernel home ranges is dependent upon designation of a smoothing parameter, 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 delineating core areas within home ranges, I believe that MCPs provide the most useful estimate of the areal extent of home range size. This is particularly true for comparisons with other studies where differences in the designation of a smoothing parameter and variable sample sizes cloud interpretations of the kernel methods.

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 tortoises on ungrazed areas compared to grazed areas. Calculation of home ranges using fixed or adaptive kernel methods suggested no relationship between grazing and home range size. Decreased home range size in grazed pastures could be a response to increased resource availability (*i.e.*, forage) due to the activity of cattle. Increased vegetation diversities and abundances of certain species are common under intermediate levels of disturbance (Collins and Barber 1985, Gibson 1989). 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 (Judd and Rose 1983, Rose and Judd 1975). However, Chaparral WMA tortoises had much larger home ranges. As a result, original study areas had to be increased in size as radioed tortoises ranged, and tortoises used 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, the paired grazed pasture. A similar problem occurred on the east side where a region dominated by hogplum (*Colubrina texensis*) became an important habitat in Mare Pasture (ungrazed), but was absent from South Jay, 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. However, robust tortoise populations exist in the LRGV without the presence of cactus (Kazmaier, unpublished data). Regardless, differences in home range size may be an artifact of differential availability of habitats instead of an effect of grazing.

Texas tortoises on Chaparral WMA had much larger home ranges and movement distances than animals in previous work. 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 loma 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 home 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 methodology. 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 inland sites. Additionally, the population studied in Cameron County existed on a loma (*i.e.,* coastal clay hill). It is suspected that tortoises do not voluntarily leave lomas due to unsuitable 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 8-22 tortoises/ha for their Cameron County site, while densities on Chaparral WMA were <1 tortoise/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. Tortoises on Chaparral WMA were monitored by radiotelemetry, but tortoises in Cameron County were relocated using grid searches (Judd and Rose 1983, Rose and Judd 1975). Because grid searches by definition are conducted over a specified area, maximum possible size of home ranges was constrained 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 points 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 my 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 very large home ranges relative to their body size (<180 mm carapace length) 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), 2.0-53.0 ha in Arizona (Barrett 1990, Vaughan 1984), 5.9-46.0 ha in Nevada (Burge 1977, O'Connor et al. 1994), and 0.4-34.0 ha in California (Vaughan 1983).

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 (see Chapter IV), 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 with a female (R. T. Kazmaier, personal observation). However, female tortoises also made occasional forays for distances of up to 0.8 km in

May-June. I interpret the long-distance male movements as mate seeking and female movements as nesting movements. While 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.

The difference in home range size for male tortoises between treatments suggests that sex ratios or densities might differ between treatment areas, and males exhibit greater activity while searching for females in ungrazed areas. However, I found no evidence for different sex ratios or relative abundances between treatments (see Chapter I).

Male gopher tortoises tend to have larger home ranges than females (Diemer 1992, McRae et al. 1981). Similarly, there is a tendency for male desert tortoises to have larger home ranges than females (Ernst et al. 1994, O'Connor et al. 1994), but Vaughan (1983) reported larger home ranges for females ($\overline{x} = 7.0$ ha) than males ($\overline{x} = 5.5$ ha). In addition, both Barrett (1990) and O'Connor et al. (1994) found no differences in home range size between the sexes for the populations they studied.

Mechanisms causing variation in space use patterns among and within the 4 *Gopherus* are not understood and deserve further attention. Gopher tortoises presumably have small home ranges because of their obligatory reliance on burrow systems. Although desert tortoises also use burrows, they rely on them to a lesser extent than gopher tortoises, 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 very large home ranges relative to other *Gopherus*, do not normally use burrows (Rose and Judd 1982; R. T. Kazmaier, unpublished data) and they exist in a region intermediate in productivity between the other North American tortoises (Germano 1994).

Despite an inability to decouple differences in the apparent effects of cattle grazing on range use by tortoises from differences in habitat availability in my study, I feel the grazing regime utilized by Chaparral WMA has had no effect on the Texas tortoises. It is obvious, however, that the effects of grazing are ultimately tied to the intensity and duration of grazing, and potential exists for other grazing systems used in southern Texas to affect tortoises. As a result, examination of Texas tortoise populations exposed to different grazing regimes is certainly warranted.

Range use and dispersal by Texas tortoises has 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 (see Chapter 2). 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 impact 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 more skewed to older age classes than tortoises on Chaparral WMA (R. T. Kazmaier, unpublished data), and this difference could be 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, this could be an artifact of methodology. If tortoises in the LRGV actually require larger than reported home ranges (Rose and Judd 1975, Judd and Rose 1983) 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 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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Table III.1. Sample sizes (*n*), number of points used in analysis, and average distances (m) moved between relocations for 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	
Number 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

Table III.2. Comparison of movements between recaptures for Texas tortoises on Chaparral Wildlife Management Area, Dimmit and La Salle counties, Texas, from 1990-1999. Recapture history relates to the status (J = juvenile, A = adult) of the individual at its initial capture and at its final recapture.

			Distance between first and last capture (m)			Test for randomness of direction	
Sex	Recapture history	*n*	median	$\bar{x}$	SE	X^2	P
Unknown	JJ	106	176	673	146	1.340	0.72
Females	JA	58	210	870	184	0.316	0.96
	AA	133	239	555	81	0.854	0.84
Males	JA	27	511	1478	347	0.356	0.95
	AA	155	261	759	108	0.922	0.82

Table III.3. Home ranges (ha) calculated by minimum convex polygon (MCP), bivariate normal (BV), adaptive kernel (ADK), and fixed kernel (FK) methods for female and male Texas tortoises in grazed and ungrazed areas on Chaparral WMA, Dimmit and La Salle Counties, Texas.

		Grazed				Ungrazed			
Sex	Method	$\bar{x}$	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

Fig. III.1. Arrangement of study areas (stippled areas) within pastures for examination of range use by Texas tortoises on Chaparral WMA, Dimmit and La Salle counties, Texas.

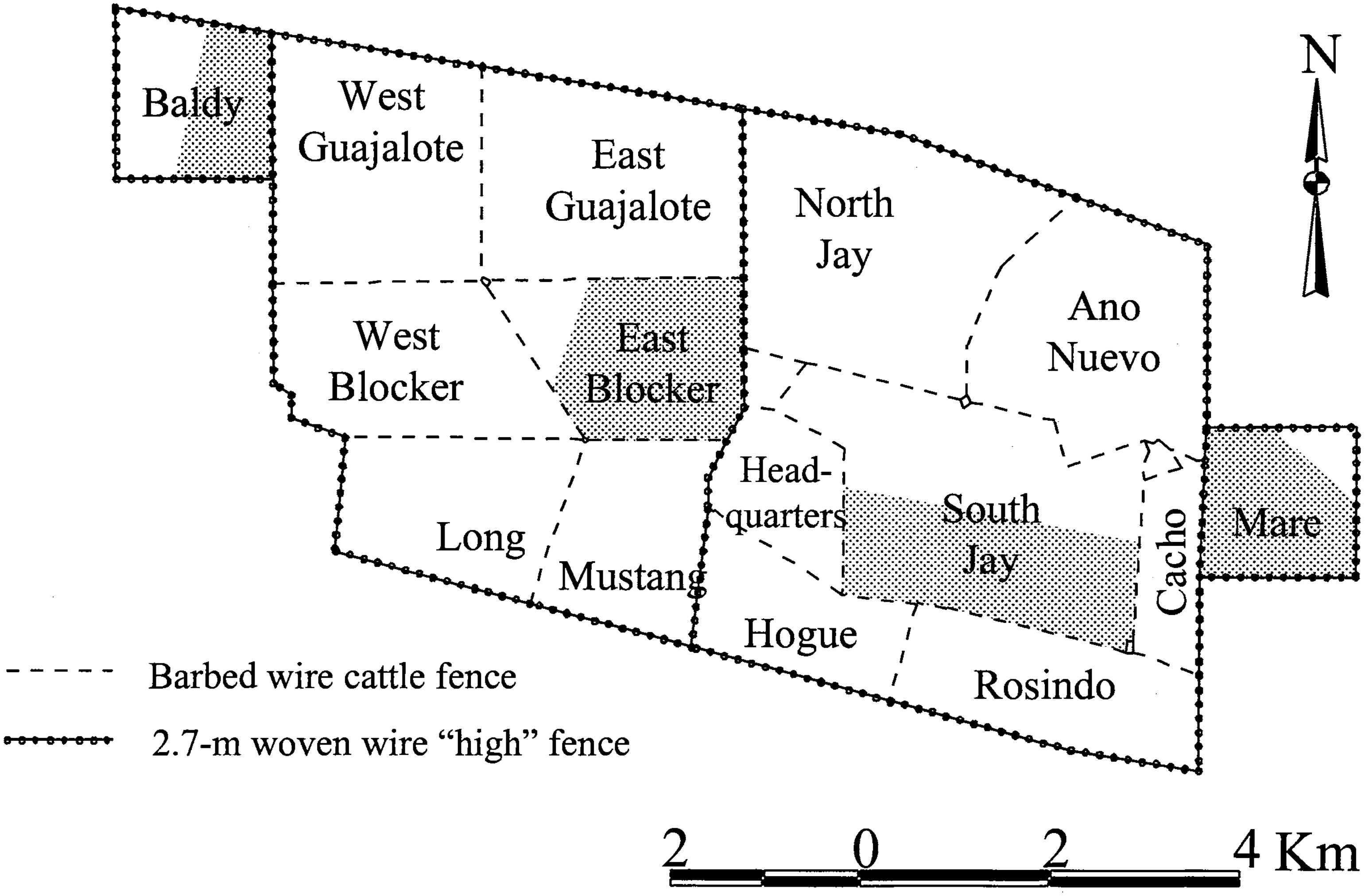
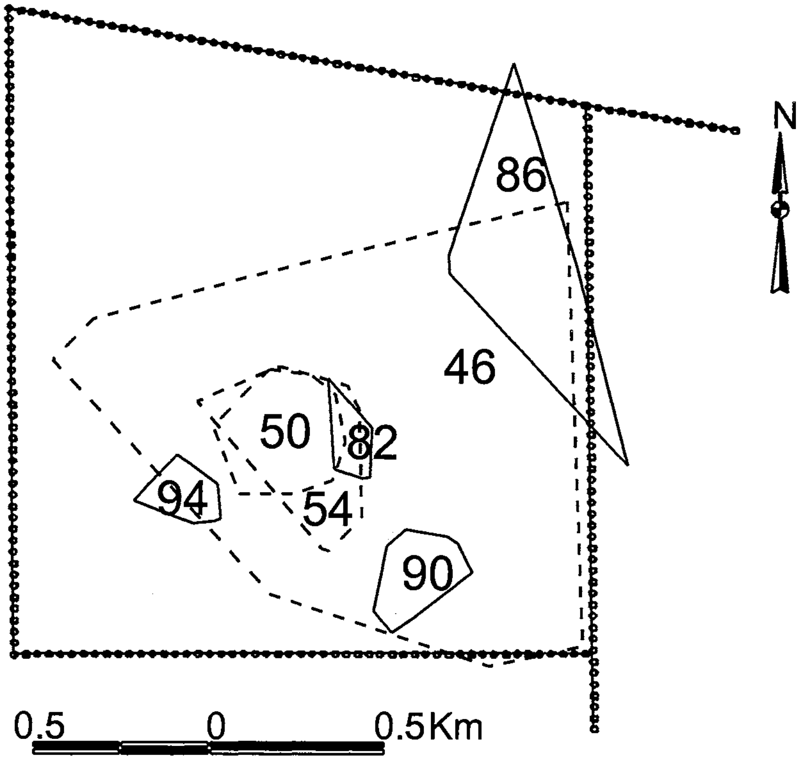

Baldy
West Guajalote
East Guajalote
North Jay
Ano Nuevo
West Blocker
East Blocker
Head-quarters
South Jay
Cacho
Mare
Long
Mustang
Hogue
Rosindo
N
Barbed wire cattle fence
2.7-m woven wire "high" fence
2
0
2
4 Km

Fig. III.2. Home ranges using the minimum convex polygon method (100%) for female (solid lines) and male (dashed lines) Texas tortoises on the paired pastures from the west side (Baldy pasture [ungrazed] on top; East Blocker [grazed] pasture on bottom) of Chaparral WMA. Numbers within home range boundaries refer to tortoise identification numbers.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86
46
50
82
94
54
90
0.5
0
0.5Km

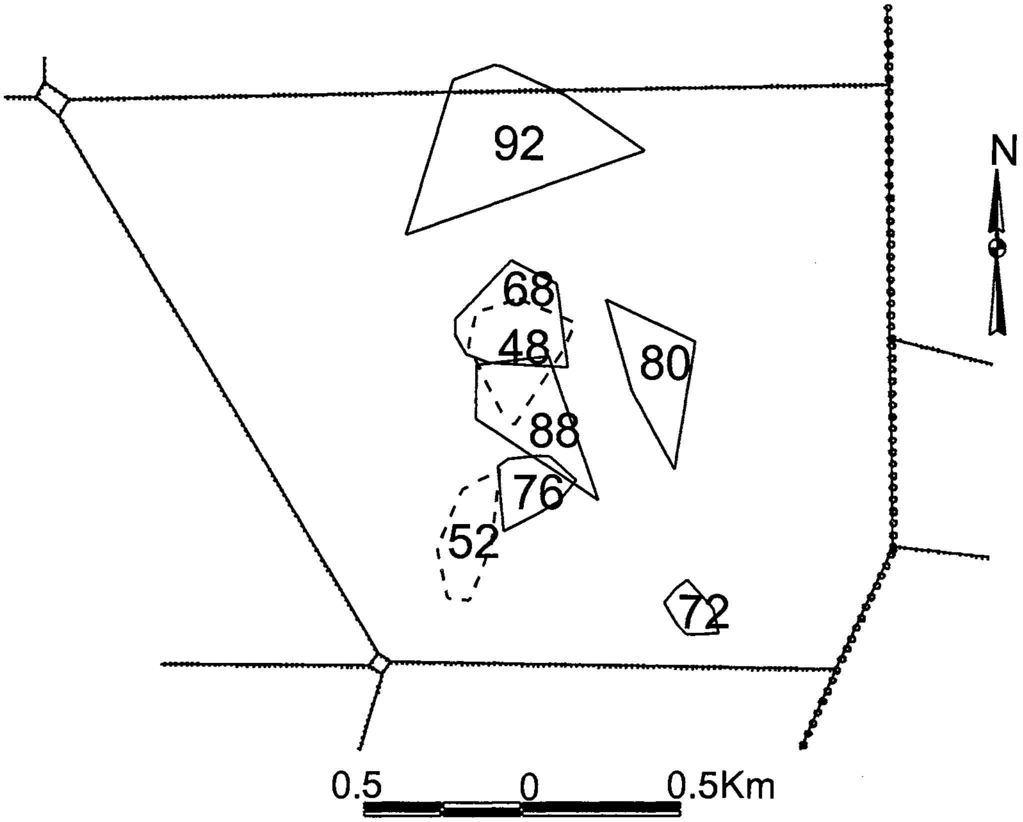
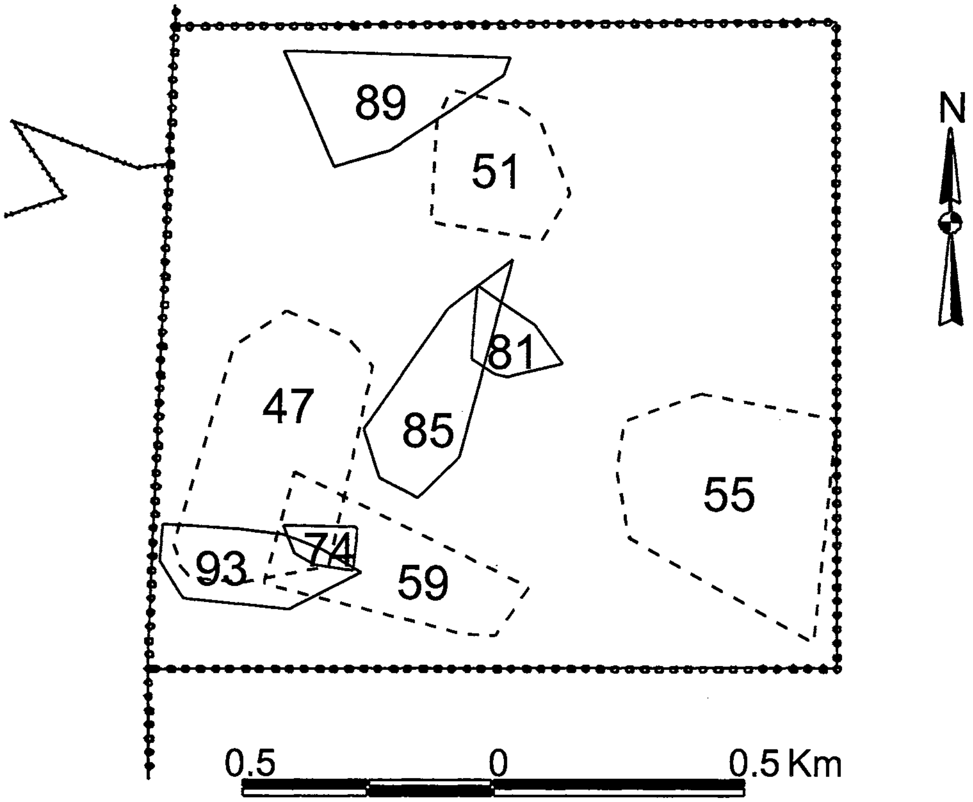

N
92
68
48
80
88
76
52
72
0.5
0
0.5Km

Fig. III.3. Home ranges using the minimum convex polygon method (100%) for female (solid lines) and male (dashed lines) Texas tortoises on the paired pastures from the east side (Mare pasture [ungrazed] on top; South Jay pasture [grazed] on bottom) of Chaparral WMA. Numbers within home range boundaries refer to tortoise identification numbers.


89
51
81
47
85
55
74
93
59
N
0.5
0
0.5 Km

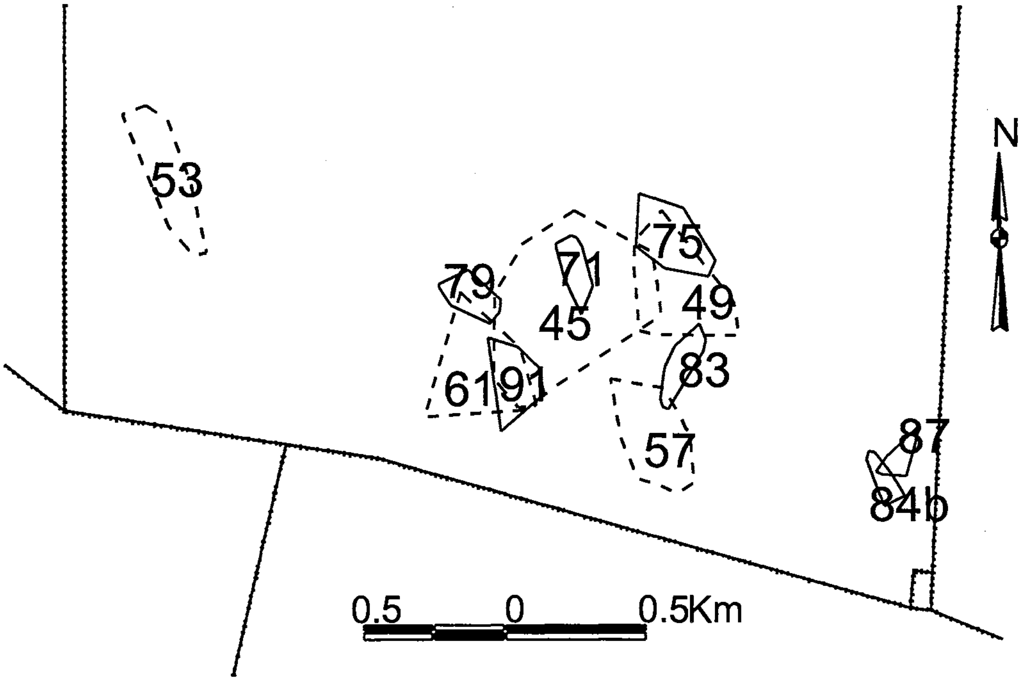
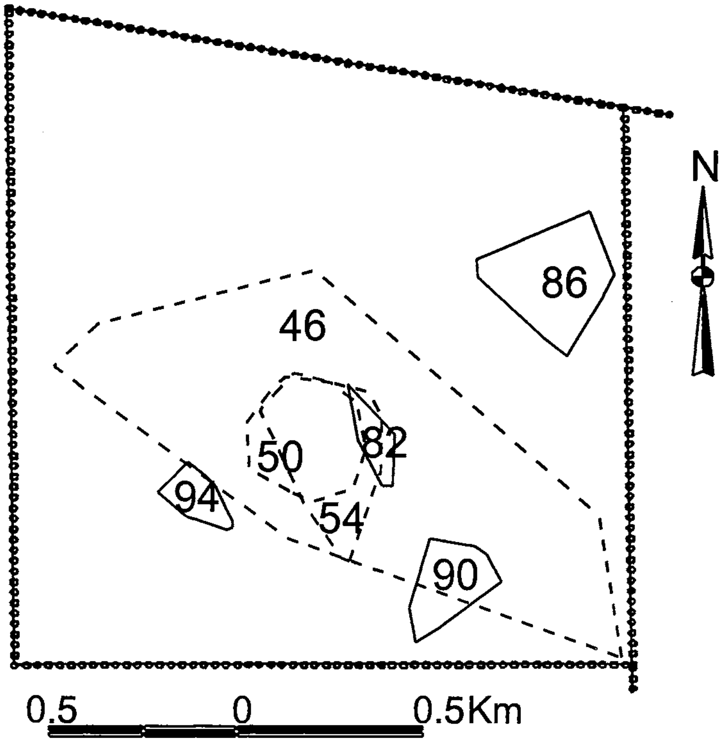

53
75
71
79
49
45
83
61
91
57
87
84b
N
0.5
0
0.5Km

Fig. III.4. Home ranges using the minimum convex polygon method (95%) for female (solid lines) and male (dashed lines) Texas tortoises on the paired pastures from the west side (Baldy pasture [ungrazed] on top; East Blocker [grazed] pasture on bottom) of Chaparral WMA. Numbers within home range boundaries refer to tortoise identification numbers.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86
46
50
82
54
94
90
0.5
0
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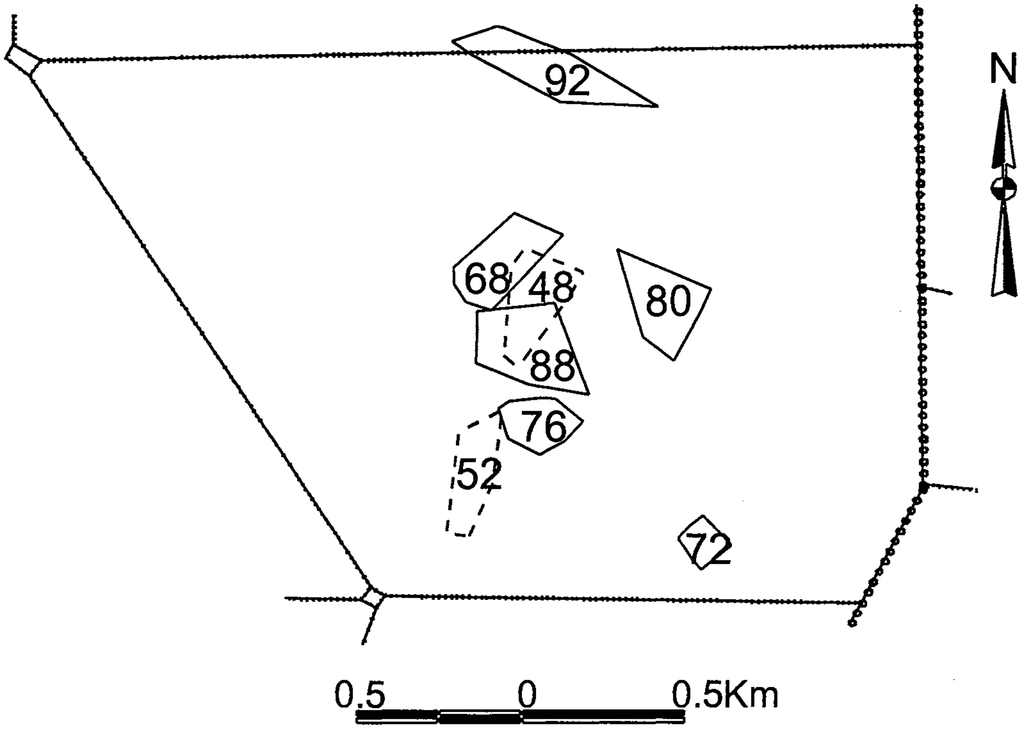
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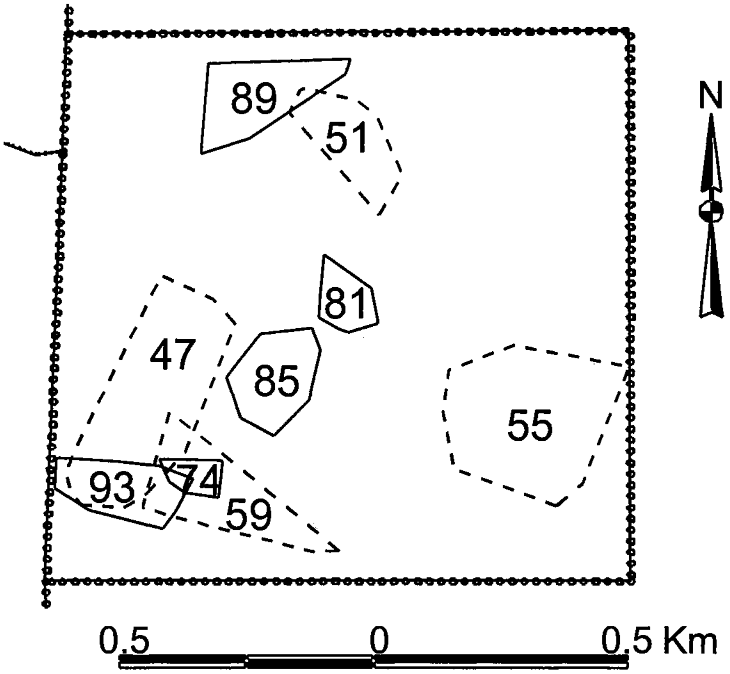
92
68
48
80
88
76
52
72
0.5
0
0.5Km

Fig. III.5. Home ranges using the minimum convex polygon method (95%) for female (solid lines) and male (dashed lines) Texas tortoises on the paired pastures from the east side (Mare pasture [ungrazed] on top; South Jay pasture [grazed] on bottom) of Chaparral WMA. Numbers within home range boundaries refer to tortoise identification numbers.


N
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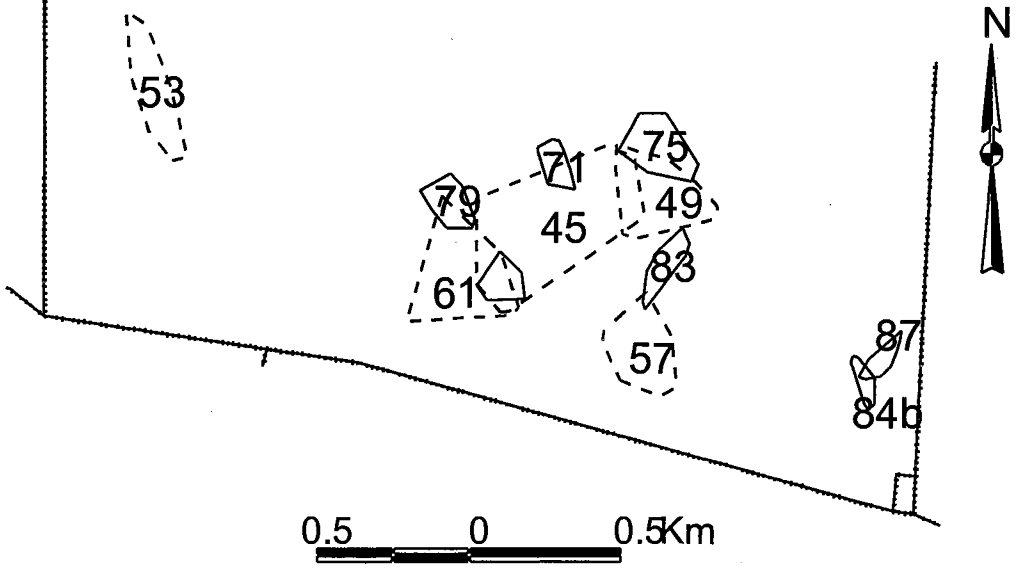
51
81
47
85
55
93
74
59
0.5
0
0.5 Km


N
53
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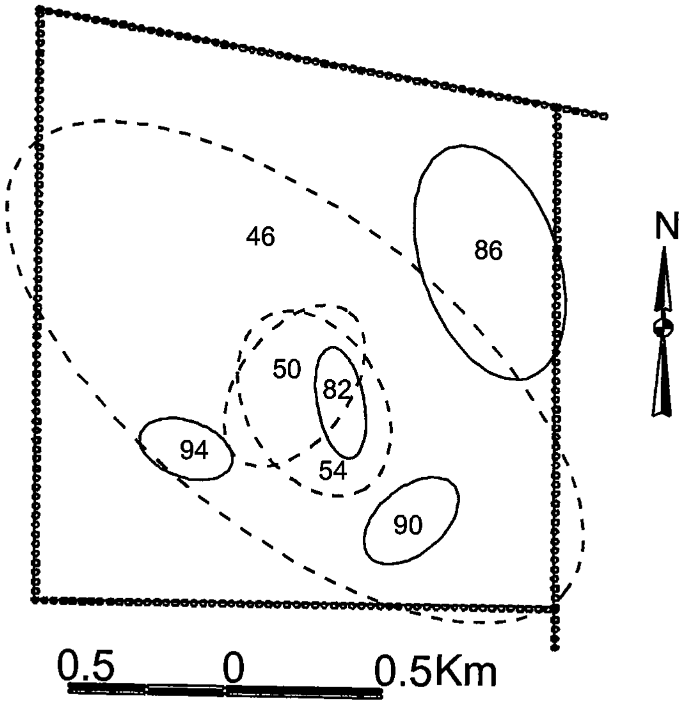
71
79
49
45
83
61
87
57
84b
0.5
0
0.5Km

Fig. III.6. Home ranges using the bivariate normal method (95%) for female (solid lines) and male (dashed lines) Texas tortoises on the paired pastures from the west side (Baldy pasture [ungrazed] on top; East Blocker [grazed] pasture on bottom) of Chaparral WMA. Numbers within home range boundaries refer to tortoise identification numbers.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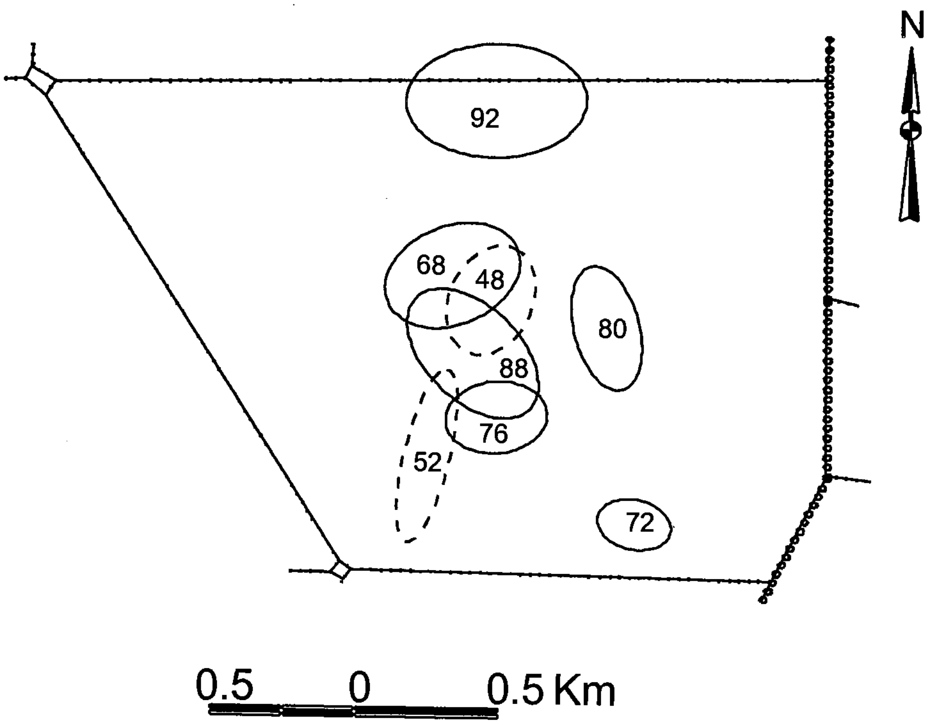
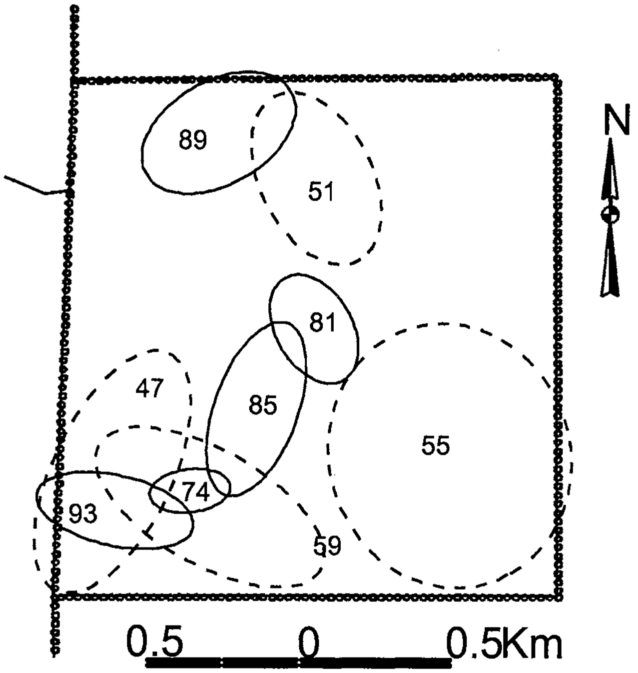

N
92
68
48
80
88
76
52
72
0.5
0
0.5 Km

Fig. III.7. Home ranges using the bivariate normal method (95%) for female (solid lines) and male (dashed lines) Texas tortoises on the paired pastures from the east side (Mare pasture [ungrazed] on top; South Jay pasture [grazed] on bottom) of Chaparral WMA. Numbers within home range boundaries refer to tortoise identification numbers.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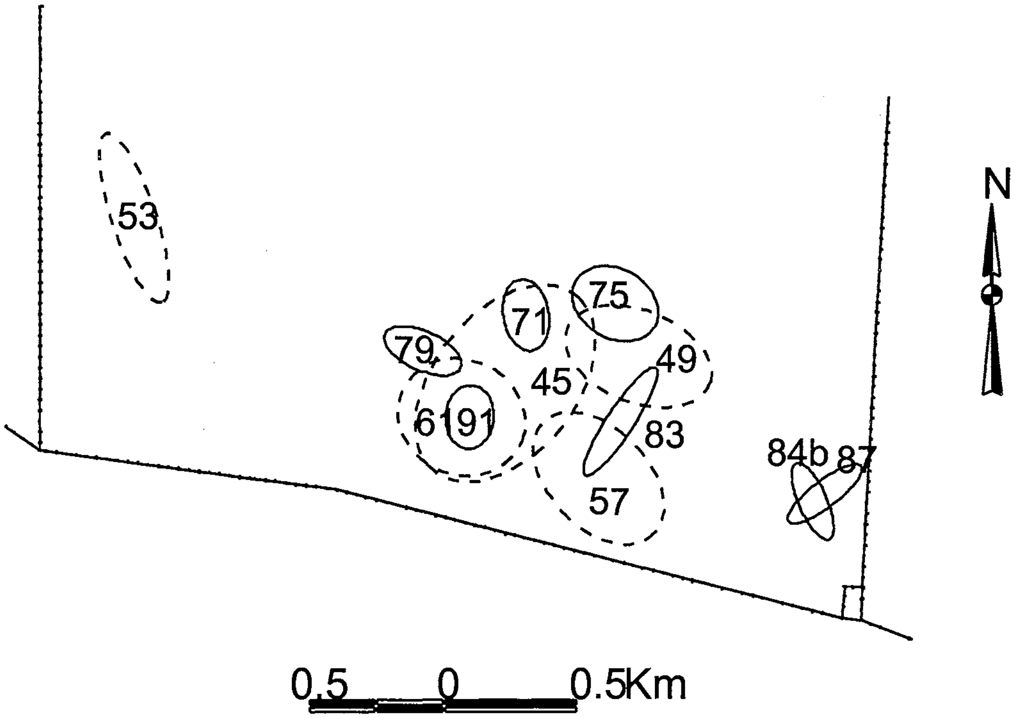
74
93
59
0.5
0
0.5Km


N
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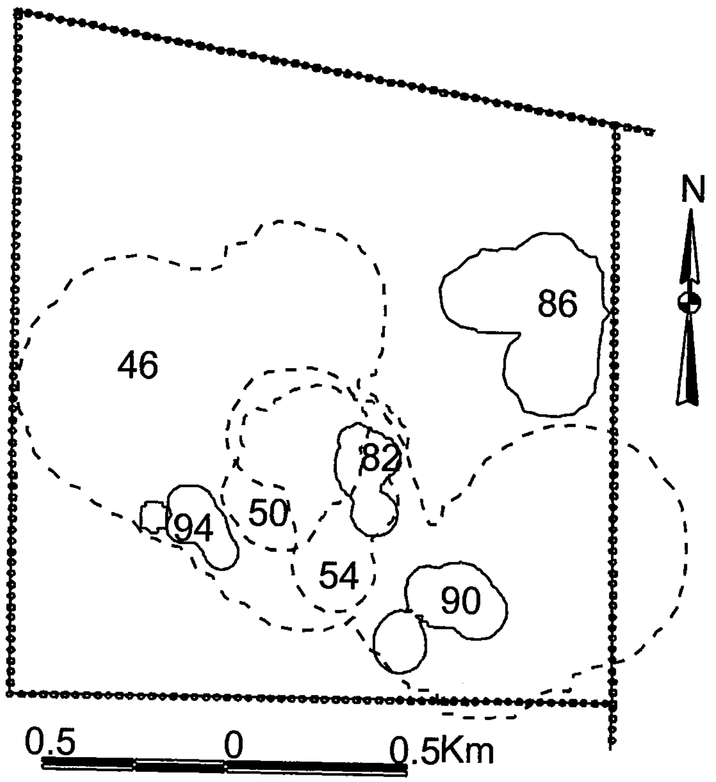
75
71
79
45
49
61
91
83
84b
87
57
0.5
0
0.5Km

Fig. III.8. Home ranges using the adaptive kernel method (95%) for female (solid lines) and male (dashed lines) Texas tortoises on the paired pastures from the west side (Baldy pasture [ungrazed] on top; East Blocker [grazed] pasture on bottom) of Chaparral WMA. Numbers within home range boundaries refer to tortoise identification numbers.


N
46
86
82
50
94
54
90
0.5
0
0.5Km

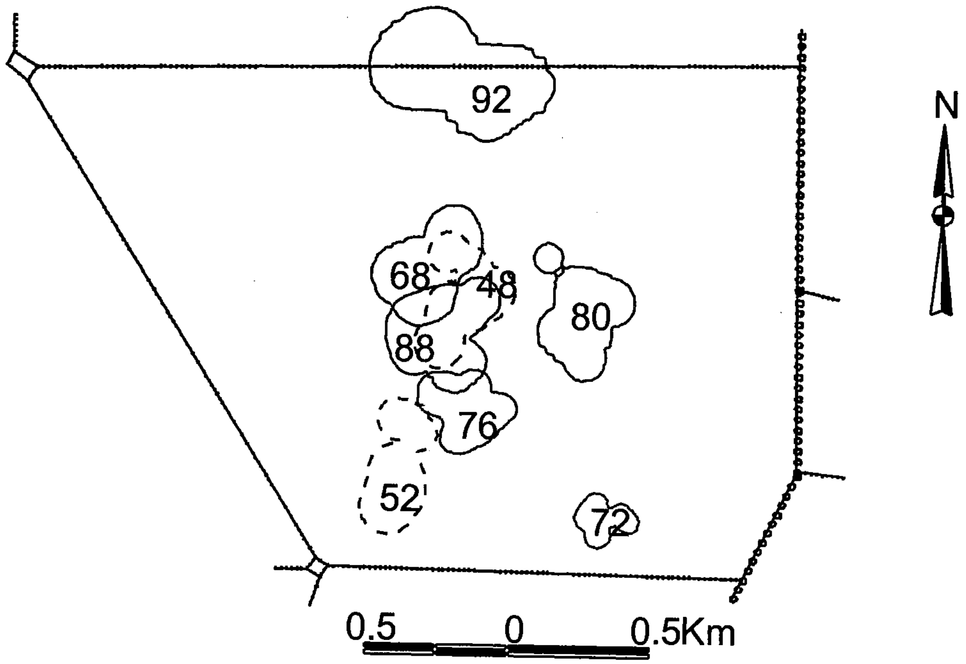
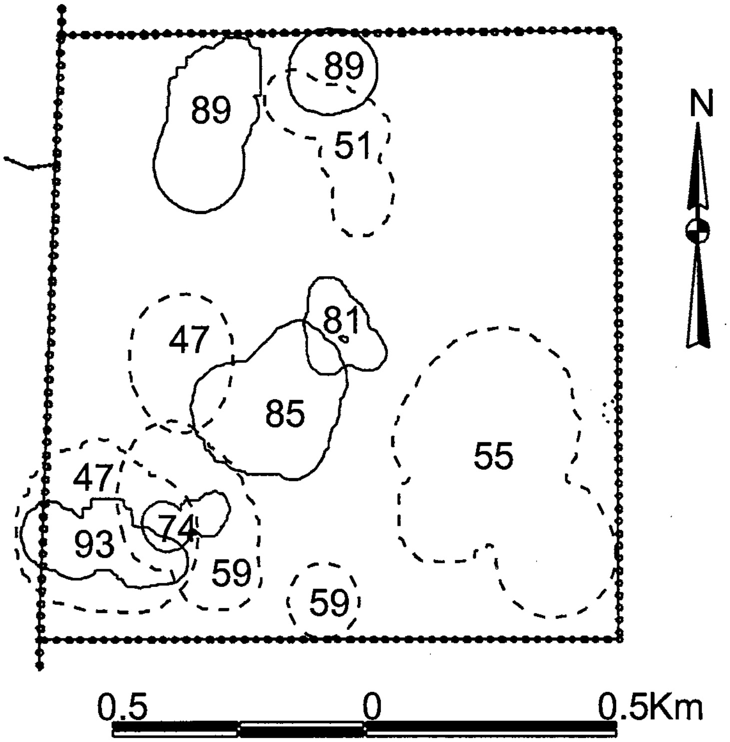

92
N
68
48
80
88
76
52
72
0.5
0
0.5Km

Fig. III.9. Home ranges using the adaptive kernel method (95%) for female (solid lines) and male (dashed lines) Texas tortoises on the paired pastures from the east side (Mare pasture [ungrazed] on top; South Jay pasture [grazed] on bottom) of Chaparral WMA. Numbers within home range boundaries refer to tortoise identification numbers.


89
89
51
81
47
85
55
47
74
93
59
59
N
0.5
0
0.5Km

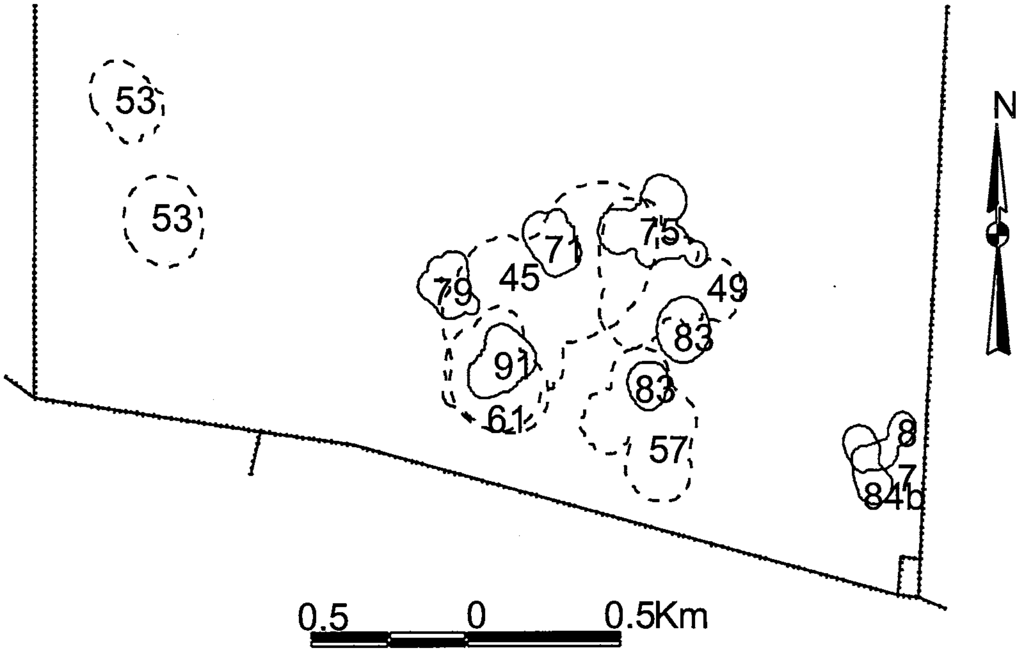
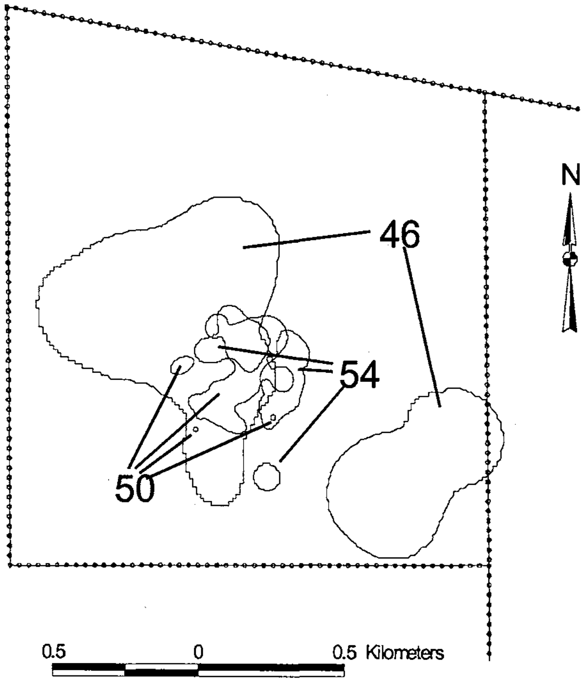

53
53
N
75
71
45
79
49
83
91
83
61
57
8
7
84b
0.5
0
0.5Km

Fig. III.10. Home ranges using the fixed kernel method (95%) for male (top) and female (bottom) Texas tortoises from Baldy pasture (ungrazed; west side) of Chaparral WMA. Numbers associated with home range boundaries refer to tortoise identification numbers; solid lines tie disjunct regions of the home range to the identification numbers.


46
54
50
N
0.5
0
0.5 Kilometers

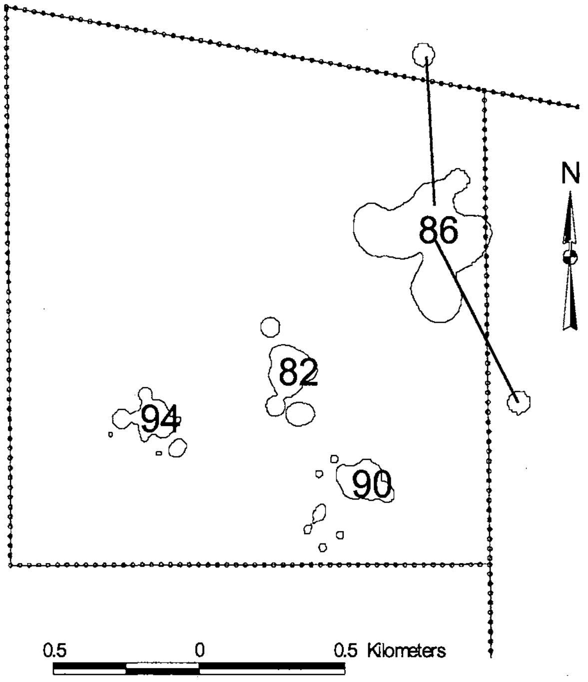
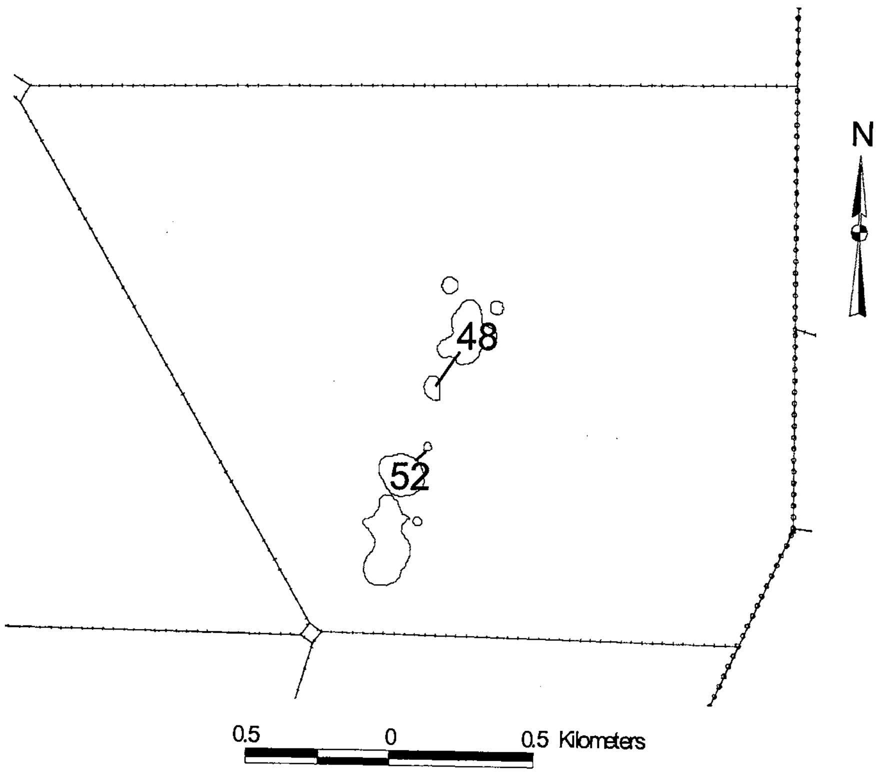

86
82
94
90
N
0.5
0
0.5 Kilometers

Fig. III.11. Home ranges using the fixed kernel method (95%) for male (top) and female (bottom) Texas tortoises from East Blocker pasture (grazed; west side) of Chaparral WMA. Numbers associated with home range boundaries refer to tortoise identification numbers; solid lines tie disjunct regions of the home range to the identification numbers.


N
48
52
0.5
0
0.5 Kilometers

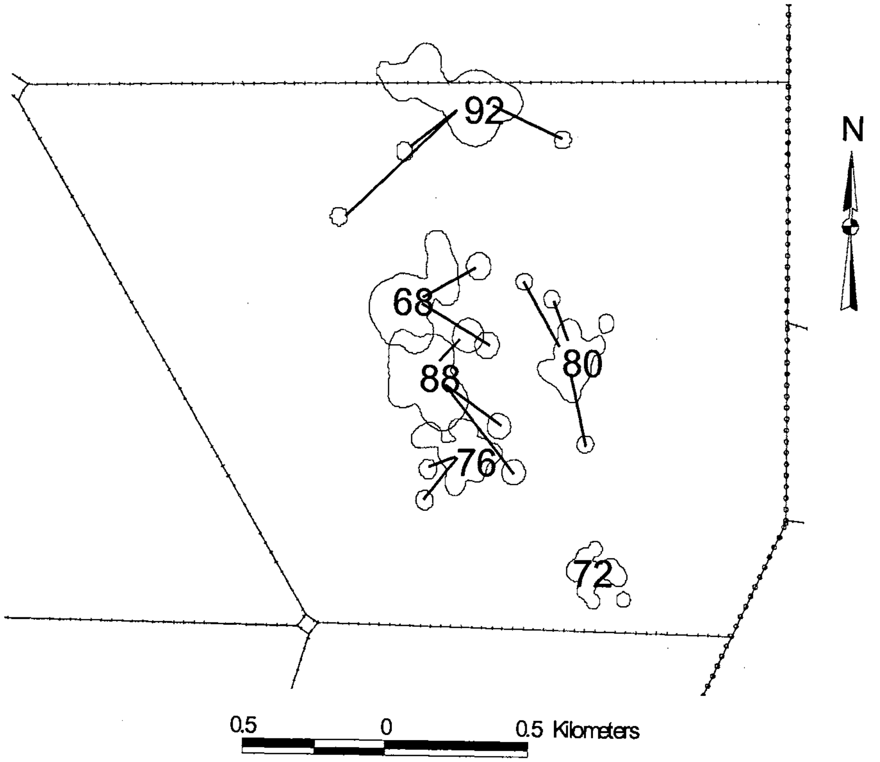
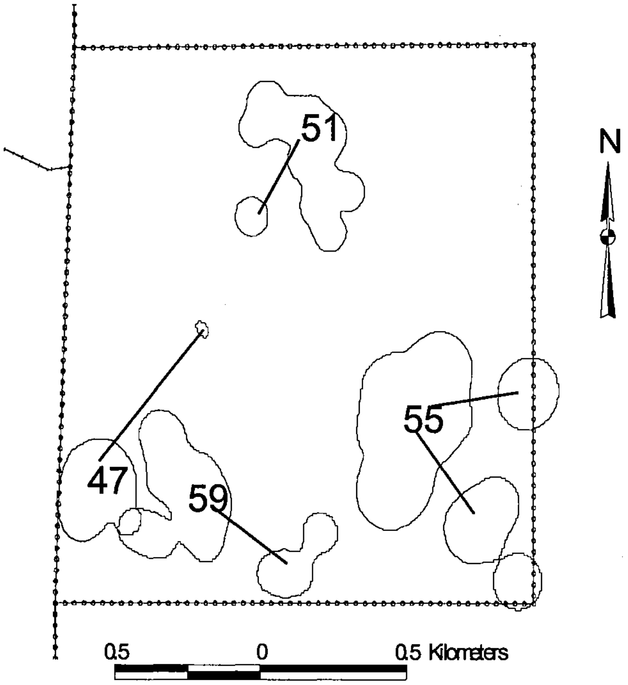

N
92
68
80
88
76
72
0.5
0
0.5 Kilometers

Fig. III.12. Home ranges using the fixed kernel method (95%) for male (top) and female (bottom) Texas tortoises from Mare pasture (ungrazed; east side) of Chaparral WMA. Numbers associated with home range boundaries refer to tortoise identification numbers; solid lines tie disjunct regions of the home range to the identification numbers.


51
N
47
59
55
0.5
0
0.5 Kilometers

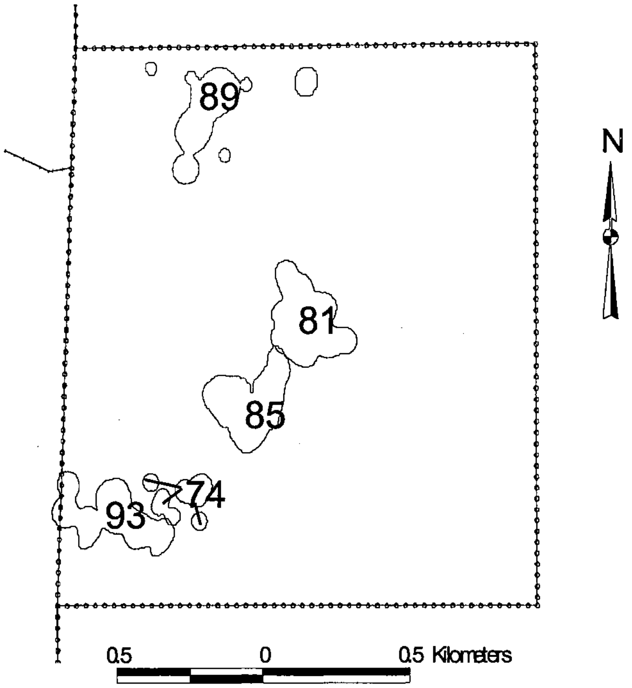
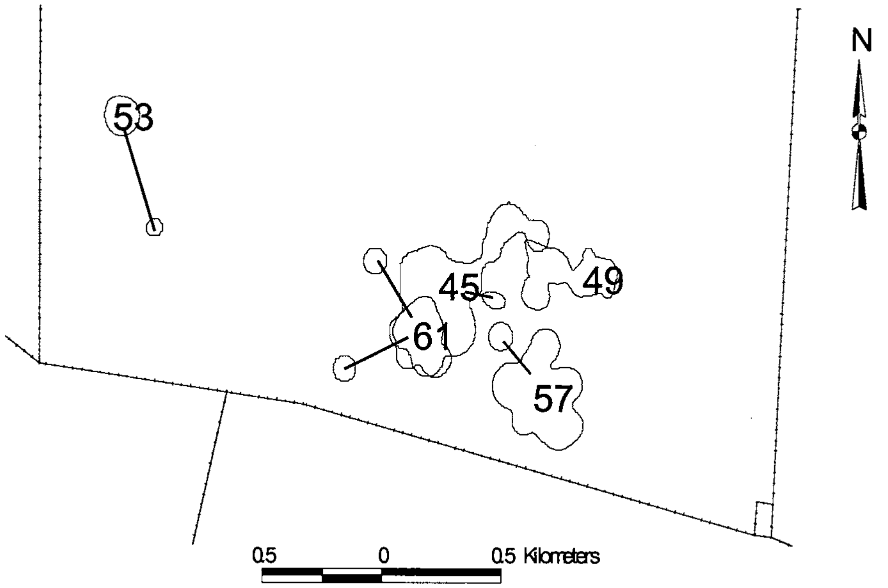
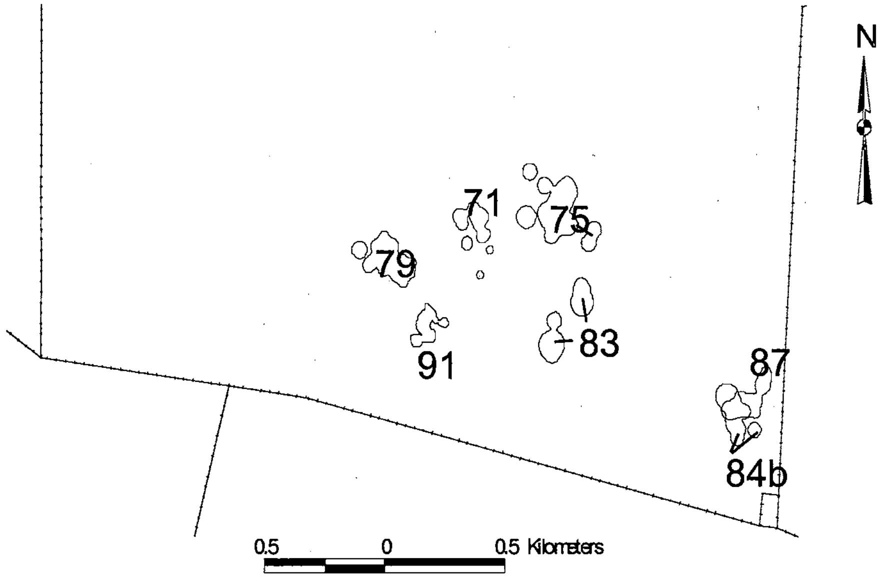

89
N
81
85
74
93
0.5
0
0.5 Kilometers

Fig. III.13. Home ranges using the fixed kernel method (95%) for male (top) and female (bottom) Texas tortoises from South Jay pasture (grazed; east side) of Chaparral WMA. Numbers associated with home range boundaries refer to tortoise identification numbers; solid lines tie disjunct regions of the home range to the identification numbers.


N
53
45
49
61
57
0.5 0 0.5 Kilometers


N
71
75
79
91
83
87
84b
0.5 0 0.5 Kilometers

CHAPTER IV

PATTERNS OF BEHAVIOR IN ADULT *GOPHERUS BERLANDIERI*: A MULTIVARIATE ORDINATION APPROACH

ABSTRACT

I compared the distribution of 19 categories of behavior exhibited by 47 adult Texas tortoises (*Gopherus berlandieri*) over three years with the use of Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA). DCA revealed a gradient from passive to active behavior along axis 1. Tortoises were more active in 1994 and less active in 1996, likely due to the extremely hot and dry conditions in 1996. With sex, age, size, year, and grazing treatment (grazed vs. ungrazed) as environmental variables in CCA, year was the most significant variable in explaining variability in behavior. Age, size, and grazing treatment were not significant variables in CCA. Tortoises used proportionally more burrows, surface pallets, and cavity pallets, and ate more cactus in 1996. More foraging and active behaviors, like courtship, were observed in 1994. After controlling for the effects of year, sex was a significant variable in explaining behavioral variability. Males tended to exhibit more active behaviors than females. My analyses suggested that grazing regime did not affect the patterns of behavior exhibited by this protected tortoise.

INTRODUCTION

Concern exists about the status of the four North American species of tortoises. The desert tortoise (*Gopherus agassizii*), gopher tortoise (*G. polyphemus*), and bolson tortoise (*G. flavomarginatus*) receive some form of federal protection (Bury and Germano

1994) whereas the Texas tortoise (*G. berlandieri*) is currently listed as threatened by the state of Texas (Rose and Judd 1982). Despite protection, the Texas tortoise remains the least known of the four species (Bury and Germano 1994). While several studies have been conducted on the basic biology of this species (Auffenberg and Weaver 1969, Rose and Judd 1975, Judd and Rose 1983, Bury and Smith 1986), analyses of behavior of free-ranging Texas tortoises are lacking. In particular, little is known about how this species responds to variations in climate or land management practices (Bury and Smith 1986).

This lack of information on behavior is a common element in the literature on turtles. Efforts to characterize behavior in turtles have focused on particular types of behavior, such as courtship (Weaver 1970, Bels and Crama 1994), nesting (Jackson 1991), thermoregulation (Hailey and Coulson 1996), or aggression (Weaver 1970). Little attention has been given to the entire suite of behavior exhibited by turtles in natural conditions, although Ruby and Niblick (1994) and Ruby et al. (1994) explored behavior patterns of desert tortoises in enclosures. Investigation of variability in the pattern of behavior and attempts to explain why such variation occurs are necessary to better understand these organisms. Such knowledge, particularly as it pertains to land management practices, is becoming more important as more species or populations are considered in need of conservation.

My objective was to evaluate the entire suite of behaviors observed in Texas tortoises with respect to five variables: sex, age, size, year, and treatment (grazed or ungrazed). In other words, could I detect variation in the pattern of tortoise behavior associated with these five factors? I employed a novel approach for this analysis, namely multivariate ordination analyses, normally used in community ecology, to detect and explain patterns in tortoise behavior. The ability to identify patterns in behavior will be useful to understand better the ecology of the Texas tortoise and aid with the development of management plans for this poorly known, but protected, species.

MATERIALS AND METHODS

Study Site

The data used for these behavioral analyses were collected as part of a larger study examining the effects of grazing by cattle on the demography and ecology of the Texas tortoise on the 6,150-ha Chaparral Wildlife Management Area (Chaparral WMA) in Dimmit and La Salle Counties, Texas. Acquired by the Texas Parks and Wildlife Department (TPWD) in 1969, Chaparral WMA is in the Western Rio Grande Plains ecological region. The area is dominated by the *Prosopis-Acacia* mixed brush community typical of the Tamaulipan biotic province (Blair 1950, Jahrsdoerfer and Leslie 1988). The climate of Chaparral WMA is semi-arid with average annual rainfall of 65 cm, but year-to-year variation in climate can be extreme (TPWD, unpublished data).

Cattle grazing occurred from October to May in a short-duration, rotational grazing system during this study. Grazing intensity was considered light to moderate at a rate of 340-440 animal units (AU; 1 AU = 2 steers) on 5,500 ha. Two pastures on Chaparral WMA have remained ungrazed since the early 1980s and served as controls. A marking and monitoring program for the Texas tortoise was initiated on this site in 1990, and the site supports a robust tortoise population (Kazmaier 1995).

Field Methods

I monitored tortoises in four pastures (two grazed, two ungrazed) from 20 June 1994 to 15 October 1996. Grazed pastures were paired with the ungrazed pastures by habitat type. I used radiotelemetry to observe the same tortoises repeatedly throughout the study. I attached 20-g radiotransmitters (L.L. Electronics, Mahomet, Illinois) to the anterior portion of the carapace of adult tortoises using silicon rubber. Radiotagged individuals were relocated at least once weekly during the active season (15 April-15 October) and once monthly during the inactive season (16 October-14 April). All relocations by radiotelemetry were completed by walking in and visually observing the subject. Although relocations were made at all times of the day in 1994, effort was skewed to periods of highest tortoise activity (morning and late afternoon) during the active season. In 1995-1996, relocations only occurred during morning and late afternoon periods. At each relocation, I scored the behavior of the tortoise to a predefined code (see below). The dense brush of Chaparral WMA can make visual observations difficult, and behavior was not scored if tortoises were disturbed by the presence of the observer.

Behavioral Categories

I evaluated 19 different behavioral categories for the Texas tortoise (Table IV.1). These categories were not intended to develop a comprehensive ethogram for the Texas tortoise, but were intended to provide some reasonably simplified groupings for analysis. Inactive behavior was mostly categorized by the type of loafing site at which the tortoise was relocated. Texas tortoises, unlike other North American tortoises, do not normally construct burrows (an excavated cavity longer than the carapace length of the tortoises;

Auffenberg and Weaver 1969). When Texas tortoises used the burrows of other animals, particularly those of the American badger (*Taxidea taxus*) and the nine-banded armadillo (*Dasypus novemcinctus*), for loafing sites, the behavior was coded as BURROW. More often, however, Texas tortoises excavated shallow depressions, termed pallets (Auffenberg and Weaver 1969), for sleeping. Pallets were usually constructed against some object, such as a cactus, or underneath dense forb or grass cover. Tortoises on Chaparral WMA rarely reuse pallets (R. Kazmaier, unpublished data). Because tortoises apparently chose what type of pallet they constructed, I coded pallet types differently in an attempt to detect why variability in pallet type occurs. ANGLED described a pallet excavated at an angle relative to the surface. Tortoises using angled pallets typically had 10-50% of their carapace in contact with the substrate. VERTICAL indicated a pallet in which the long axis of the carapace was nearly perpendicular to the substrate surface. Vertical pallets required more excavation than other pallet types and 40-90% of the carapace was usually in contact with the substrate. CAVITY involved the excavation into the side of a mound of soil or debris pile of a cavity similar to a tortoise-made burrow (see Auffenberg and Weaver 1969 for a photograph of this type of pallet), although cavities were never longer than the carapace length of the tortoise using them. BURIED was a special case of inactivity in which the long axis of the carapace remained parallel with the surface of the substrate, but excavation was such that 80-100% of the carapace was covered by soil. BURIED was most often a characteristic of hibernation, but tortoises occasionally returned to the BURIED state after periods of post-hibernation activity. SURFACE was characterized by a tortoise sleeping on the surface with no excavation of the substrate.

To explore the variability in types of foraging behavior with respect to environmental variables, consumption of different types of foods was divided into categories. GRASS and FORB indicated foraging of grass and forbs, respectively. Tortoises eating fruits, most notably *Opuntia engellmanii* and *Diospyros texana*, were scored as FRUIT. SOIL describes consumption of soil, small stones, or bones. CACTUS was indicated by eating the cladodes of *Opuntia*. RAPID FORAGING MOVEMENT (RFM) consisted of rapid, frenetic movements in which multiple food items were sampled. RAPID FORAGING MOVEMENT was easily distinguishable from other foraging codes, because tortoises did not focus on any particular type of food in RFM.

WALKING involved normal movement activity. RAPID LINEAR MOVEMENT (RLM) was characterized as a very rapid, directed, linear movement. WALKING and RLM were easily distinguished due to the speed and directionality of RLM. When males were actively attentive towards females, the behavior was coded COURTSHIP. COURTSHIP included tending behavior and active courtship. CLEANING was used to describe the active construction or cleaning of a pallet. ALERT indicated a tortoise that was awake, but in a pallet. Texas tortoises have a fairly narrow activity temperature range (Judd and Rose 1977), thus thermoregulation is important. BASKING was indicated by an alert tortoise resting in full sun or a sun fleck, usually with the long axis of the carapace perpendicular to the incoming sunlight. BASKING typically occurred in the morning as tortoises attempted to raise their temperatures after emerging from a sleeping pallet (Voigt and Johnson 1976). In contrast, RESTING described an active tortoise resting in shade, typically after a period of activity, in an apparent effort to lower body temperature. Tortoises classified as BASKING and RESTING were not associated with pallets.

Statistical Methods

I defined a sampling unit as the frequency distribution of behavioral categories for a tortoise within a year (active season only). Any sampling units that contained fewer than 20 observations was excluded from analysis.

I used Detrended Correspondence Analysis (DCA) as a method to detect gradients in behavior. DCA is an analysis technique in which gradients are predicted from the distributions of species and sample scores in multivariate space (Hill and Gauch 1980, Gauch 1982). In DCA, sample scores are arbitrary numbers assigned to each sample and species scores are the average (weighted by species abundances) of these initial sample scores. New sample scores are then assigned as averages (weighted by the species abundances) of the species scores. After standardizing scores, detrending axes, and repeated iterations, a stable solution of sample and species scores results (Palmer 1993). For my purposes, individual behaviors were analogous to species and samples were the annual collection of behavioral for each tortoise. Because DCA is an indirect gradient analysis technique, the influence of environmental variables in patterning behavior cannot be statistically tested; instead, such influences are inferred from the pattern of species and sample scores.

Canonical Correspondence Analysis (CCA)(ter Braak 1986, ter Braak and Prentice 1988, Palmer 1993) was used as a direct gradient analysis technique. CCA is similar to DCA, however, the initially assigned sample scores are linear combinations of environmental data. Thus, species (= behavioral categories) composition is directly related to environmental variables, and CCA can be used to test the influence of environmental variables on the distribution of species (= behavioral categories). For this analysis, environmental variables were defined as year, sex, treatment (grazed or ungrazed), age (number of scute annuli; Hellgren et al. 2000), and size (carapace length in mm). Monte Carlo analyses using 1000 permutations were used to test each CCA model at a significance level of 0.05. Because DCA simply searches for pattern in a sample by species data matrix, and the results of CCA are constrained by those environmental variables chosen for analysis, the two techniques are fundamentally different. Thus, I chose to use both ordination methods. All ordination analyses were computed using CANOCO version 3.12 (ter Braak 1987) on untransformed data.

RESULTS

Field Effort

I monitored 47 adult tortoises (28F:19M) throughout the study. After calculating frequency distributions of behavioral categories for each tortoise within each year, 78 samples (2,023 observations) from 37 tortoises (22F:15M) met the criteria of having ≥20 observations. Across the study, 20 samples were from 1994, 35 were from 1995, and 23 were from 1996. Because some tortoises were monitored for more than one year, samples were distributed such that 11 tortoises had 3 samples, 19 had 2 samples, and 7 had 1 sample. Radiotelemetry effort was similar between the grazing treatments; total radio-days (defined as a tortoise carrying a radiotransmitter for 1 day) from the start of the study until 31 December 1996 were 12,225 radio-days in grazed pastures and 12,227 radio-days in the ungrazed pastures.

Rainfall patterns varied dramatically during the 3 years of the study, with 1994 having a very wet spring and 1996 having a very dry spring (Fig. IV.1). Although total annual rainfall was similar in 1994 (82.8 cm) and 1995 (82.2 cm), the pattern of rainfall events was considerably different between the years. In 1995, precipitation occurred in fewer, but heavier rainfall events relative to 1994. Because of this precipitation pattern, drying between the more dispersed rainfall events in 1995 resulted in drier overall conditions relative to 1994. Total rainfall in 1996 (38.2 cm) was only 59% of the longterm annual average (64.9 cm; 1969-1996; TPWD unpublished data). Average high monthly temperatures during May and June of 1996 were much higher than temperature in 1994, 1995, or the longterm average (1984-1996) for those months (Fig. IV.2).

Statistical Analyses

The sum of all unconstrained eigenvalues for the DCA was 1.340, and the first four axes explained 39.3% of the variance in the data. DCA produced a pattern on the first two axes that suggested an activity gradient (Fig. IV.3), with codes corresponding to active behavior ("active codes") clustered toward the left and inactive codes clustered toward the right of DCA axis 1. In particular, foraging behavior was concentrated to the left of DCA axis 1. A notable exception to this pattern is foraging on cactus, which was grouped with the inactive behavioral codes. I could not interpret DCA axes 2, 3, and 4. Examination of sample scores classified by year strongly suggested that activity varied by year (Fig. IV.4). According to the distribution of behavior scores and sample scores, tortoises exhibited more active behavior in 1994 and more inactive behavior in 1996.

Monte Carlo analysis of the full CCA model indicated that the pattern of behaviors was significantly different from random (*P*=0.001 for CCA axis 1 and *P*=0.001

for all axes). The ratio of sum of canonical eigenvalues (0.314) to sum of unconstrained eigenvalues (1.340) suggested that the environmental variables used in the full CCA model accounted for 23.4% of the variation explainable by the ordination. The pattern of behavior produced by CCA was similar to that produced by DCA, with inactive behavioral codes skewed toward one side of CCA axis 1 and active behavioral codes skewed toward the other side of the axis (Fig. IV.5A). As in DCA, foraging on cactus grouped with inactive behavioral codes. Position of the centroids for years indicated a strong influence of year along CCA axes 1 and 2 (Fig. IV.5B); thus, a partial CCA was computed using year as a covariable.

Monte Carlo analysis of the partial CCA indicated that a pattern significantly different from random was still apparent when the effects of year were controlled (P=0.044 for CCA axis 1 and P=0.001 for all axes). The ratio of sum of canonical eigenvalues (0.170) to sum of unconstrained eigenvalues (1.197) suggested only 14.2% of the explainable variation in the ordination was attributable to sex, age, size, and grazing treatment. Positions of the centroids indicated that sex was the most important variable in this analysis, and position and relative length of biplot arrows indicated that age and size had little effect in explaining variation along CCA axes 1 and 2 (Fig. IV.6B). When the position of centroids for male and female were compared with the distribution of behavior scores, the pattern suggested that males were more active than females (Fig. IV.6).

To control for the effects of sex, a second partial CCA was computed using year and sex as covariables. Monte Carlo analysis of this second partial CCA was not significant (P=0.16 for CCA axis 1 and P=0.07 for all axes). Thus, these ordination techniques were unable to detect an influence of grazing treatment, age, or size on the distribution of behavior exhibited by the tortoises.

DISCUSSION

Texas tortoises exhibited behavioral plasticity to changes in climatic and environmental conditions. Multivariate ordination analyses used the entire repertoire of tortoise behavior to depict this plasticity. Demonstration of such annual or gender-related variation in behavior under more traditional approaches would have required multiple univariate tests, often resulting in problems associated with multiple comparisons or small sample sizes. In addition, the use of canonical analyses allowed for interpretation of variation in rare events (such as cactus foraging) that would not have been possible with univariate tests. Multivariate ordination methods in ecology have traditionally been applied to community analyses (Gauch 1982), but because these methods have the ability to examine relationships and detect patterns between many variables simultaneously, I believe such techniques are ideal for detecting patterns in other complex phenomena, such as behavior.

Climatic effects likely influenced the interannual pattern of behavior exhibited by the tortoises, which were more active in 1994 than in 1996. This hypothesis is supported by weather data. Rainfall was above average and temperatures were moderate in 1994, while 1996 had one of the hottest and driest spring-early summer periods recorded for Chaparral WMA. These weather trends were particularly pronounced during May and June, the months of typically highest tortoise activity on Chaparral WMA (TPWD, unpublished data). Because of their fairly narrow range of activity temperatures (Judd and Rose 1977), Texas tortoises remain inactive in sleeping pallets when temperatures are extreme. Hailey and Coulson (1996) suggested that small tortoises may remain inactive during droughts due to their inability to find adequate food. Similarly, water and temperature conditions interacted to limit desert tortoise activity in experimental enclosures (Ruby et al. 1994).

Rainfall on Chaparral WMA is bimodally distributed, with a primary peak in April-May and a secondary peak in September-October (Fig. IV.1). April-May rains are responsible for the production of spring forbs, which are an important food source for tortoises. Emergence of tortoises from hibernation on Chaparral WMA is often triggered by spring rains (R. Kazmaier, unpublished data). Chaparral WMA received very little rain from November 1995 until mid-July 1996 (Fig. IV.1). This lack of winter and spring rainfall was coupled with excessively high temperatures in the spring of 1996. Associated with this brief but intense drought, emergence from winter pallets was delayed. Once tortoises did emerge, succulent forbs were unavailable for food, and tortoises responded to the shortage of forbs by consuming more cactus. This shift in diet explains the location of the behavioral score for foraging on cactus in the DCA, which was skewed to the extreme right of DCA axis 1 amongst the behavioral scores for inactive behavior.

Despite that I skewed my field effort to periods of expected activity, tortoises exhibited active behavior for only 13% of relocations. Less than 50% of tortoise activity, or about 6% of all behavior, was associated with foraging. During periods of excessive heat and drought, tortoises were less active, consumed more cactus, and reduced the amount of courtship behavior. Decreased activity and increased cactus consumption also were observed for desert tortoises during a drought year in the Mojave desert (Peterson 1996).

Type of loafing site also may be influenced by year. Behavioral scores for surface pallet, cavity pallet, and burrow were located to the extreme right of DCA axis 1. Sample scores for 1996 were also skewed to the right of DCA axis 1, suggesting increased use of burrows, surface pallets, and cavity pallets in 1996 relative to the other two years. Increased burrow use may have reflected an effort to avoid extreme temperatures by refuging underground. Cavity pallets were uncommon, but their construction may be a way for tortoises to establish a more equable microclimate, similar to a burrow. Surface pallets minimize a tortoise's contact with the substrate surface. Thus, when temperatures are high, surface pallets may reduce conductance of heat from the substrate to the tortoise.

Canonical Correspondence Analysis supported the results of DCA. Monte Carlo analyses indicated that both year and sex were important in explaining the variation in behavior observed, whereas grazing treatment, age, and size were unimportant. The distribution of behavior scores from the CCA suggested the same pattern related to year as in the DCA. When the effects of year were controlled, CCA suggested that male tortoises were more active than females. In particular, rapid linear movement sorts out near the male centroid. The reason that males, more than females, used rapid linear movements is unknown, but it may be associated with attempts by males to track females for courtship and mating. Texas tortoises have chin glands that may provide olfactory clues related to reproduction (Rose et al. 1969), and males on Chaparral WMA are known to travel over 0.5 km to court females (R. Kazmaier, personal observation). Calculation of tortoise home range size for the Chaparral WMA population indicates that males have home ranges 2-10 times the size of home ranges for females (R. T. Kazmaier, Chapter II). These differences in home range size also support conclusions drawn from CCA that males are more active than females, and are consistent with sex-based differences in movements among other *Gopherus* (Rose and Judd 1975, McRae et al. 1981, O'Connor et al. 1994; but see Rose and Judd 1983).

Because of the ability of multivariate ordination methods to reveal patterns in complex data sets with many variables, I believe their use for behavioral analyses is very promising. Ordination of the frequency distributions of behavioral categories for the Texas tortoise indicated that tortoise behavior was influenced by year and sex. Annual variation in behavior was likely tied to climate. Males were more active than females, and rapid linear movements appeared to be a character mostly of males. Age and size did not appear to influence the pattern of behavior. However, all tortoises monitored by radiotelemetry were adults within a fairly narrow age range (6-12 years). Thus, the pattern of juvenile behavior and any effect of year, sex, or treatment on that pattern remains unknown. Despite the belief that grazing may be detrimental to desert tortoises (Berry 1978), these analyses suggested that the light to moderate, short-duration, rotational, winter grazing regime employed by Chaparral WMA does not affect the pattern of behavior exhibited by adult Texas tortoises.

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Table IV.1. Behavioral codes, type of code (active, inactive, or intermediate), and frequency of occurrence of behaviors from 2,023 observations of Texas tortoises on Chaparral Wildlife Management Area, Dimmit and La Salle counties, Texas, 1994-1996. See text for detailed descriptions of behavior codes.

		Frequency			
Code	Type	1994	1995	1996	Total
ANGLED	Inactive	151	333	157	641
SURFACE	Inactive	96	223	204	523
RESTING	Intermediate	32	153	77	262
WALKING	Active	63	39	19	121
BASKING	Intermediate	52	36	12	100
BURROW	Inactive	26	33	41	100
RFM	Active	36	28	0	64
BURIED	Inactive	13	30	10	53
ALERT	Intermediate	4	34	8	46
CAVITY	Inactive	3	14	3	20
COURTSHIP	Active	10	3	2	15
FORB	Active	6	6	3	15
FRUIT	Active	7	6	0	13
CACTUS	Active	0	3	9	12
VERTICAL	Inactive	6	4	1	11
SOIL	Active	4	5	0	9
CLEANING	Active	3	5	0	8
GRASS	Active	3	1	2	6
RLM	Active	4	0	0	4
TOTAL		519	956	548	2023

Fig. IV.1. Pattern of monthly precipitation during the active season (April-October) of Texas tortoises on Chaparral Wildlife Management Area for the years of collection of behavioral data (1994-1996) on tortoises and the longterm average (1969-1996).

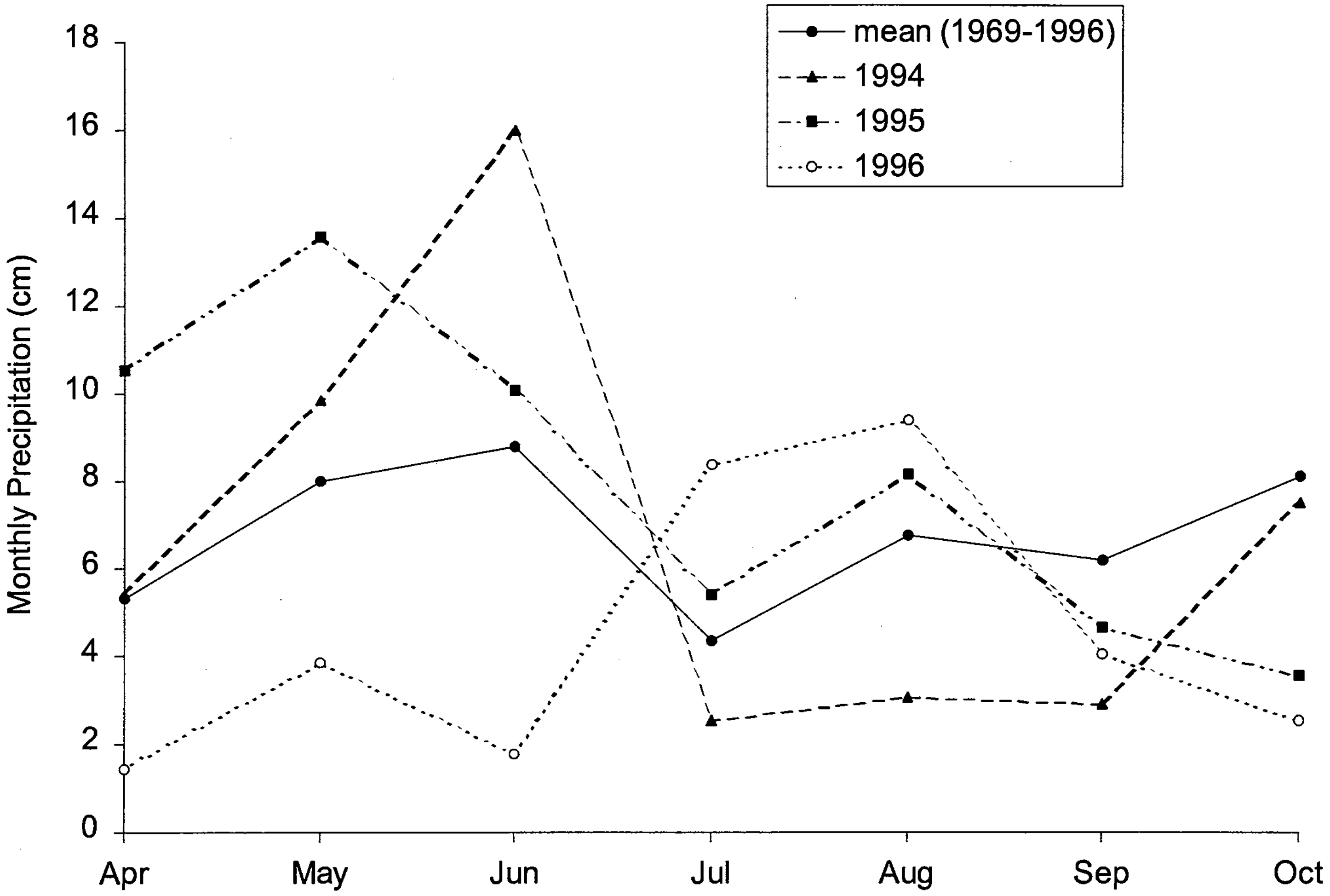

mean (1969-1996)
1994
1995
1996
Monthly Precipitation (cm)
0
2
4
6
8
10
12
14
16
18
Apr
May
Jun
Jul
Aug
Sep
Oct

Fig. IV.2. Pattern of mean monthly high temperatures during 1994-1996 and the longterm average (1984-1996) for the active season (April-October) of Texas tortoises on Chaparral Wildlife Management Area.

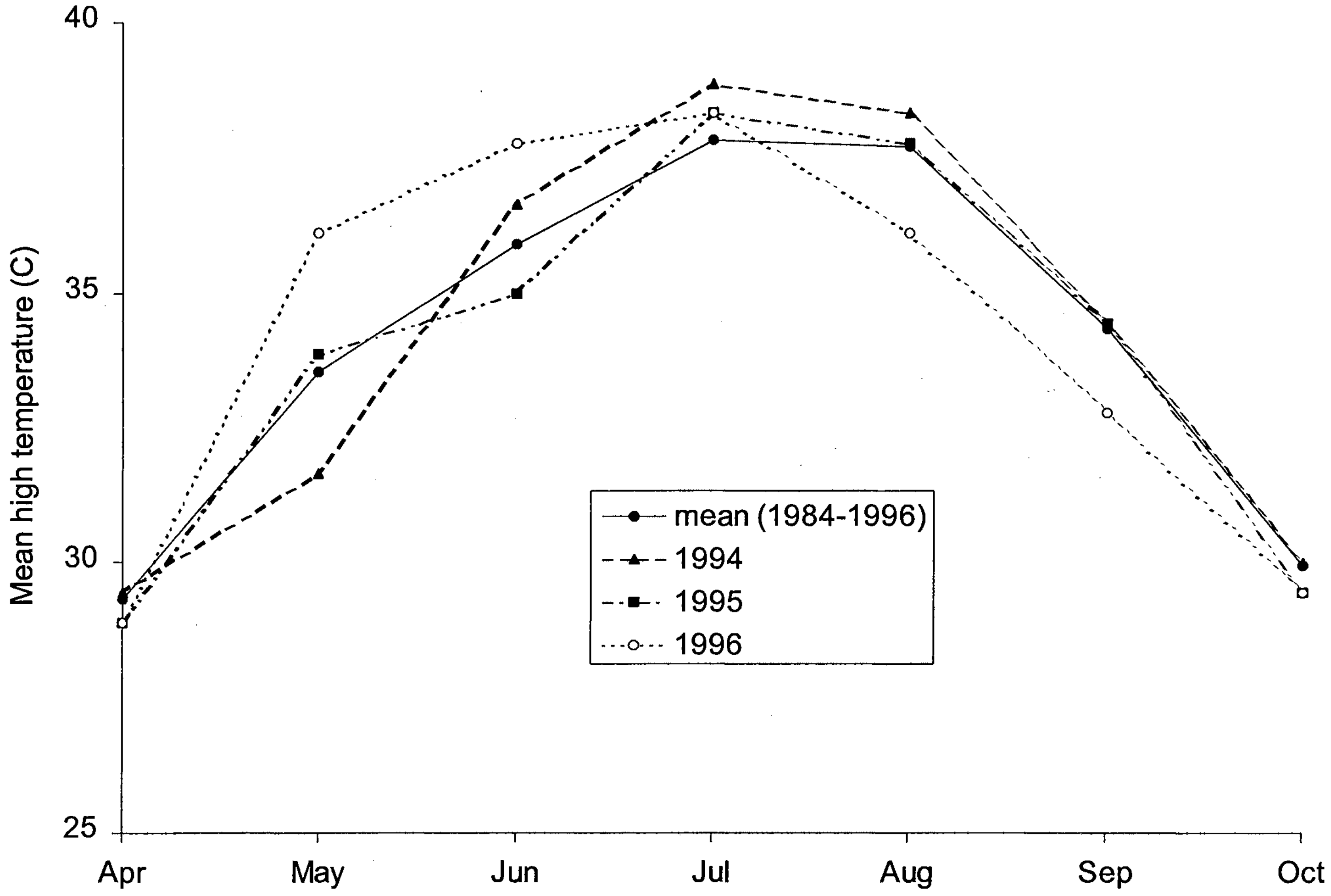

Mean high temperature (C)
40
35
30
25
Apr
May
Jun
Jul
Aug
Sep
Oct
mean (1984-1996)
1994
1995
1996

Fig. IV.3. Distribution of behavioral scores from Detrended Correspondence Analysis for Texas tortoises at Chaparral Wildlife Management Area, Dimmit and La Salle counties, Texas. Open circles refer to behavior associated with pallets; stars indicate foraging behavior; closed circles indicate other behavior.

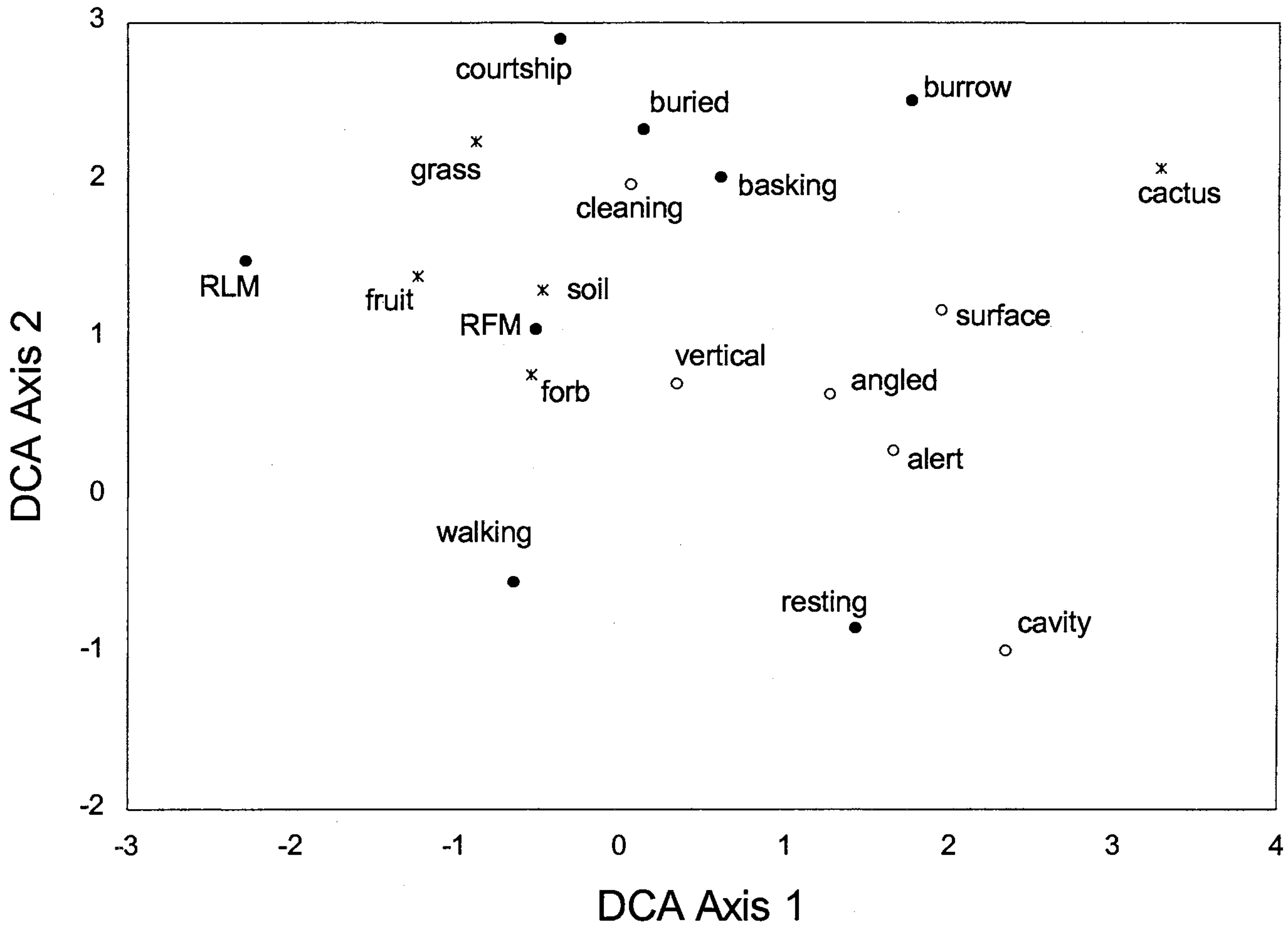

3
2
1
0
-1
-2
-3
-2
-1
0
1
2
3
4
DCA Axis 1
DCA Axis 2
courtship
buried
burrow
grass
basking
cleaning
cactus
RLM
fruit
soil
RFM
surface
vertical
forb
angled
alert
walking
resting
cavity

Fig. IV.4. Distribution of sample scores from Detrended Correspondence Analysis for Texas tortoises at Chaparral Wildlife Management Area, Dimmit and La Salle counties, Texas. Open circles are samples from 1994; stars are samples from 1995; closed circles are samples from 1996.

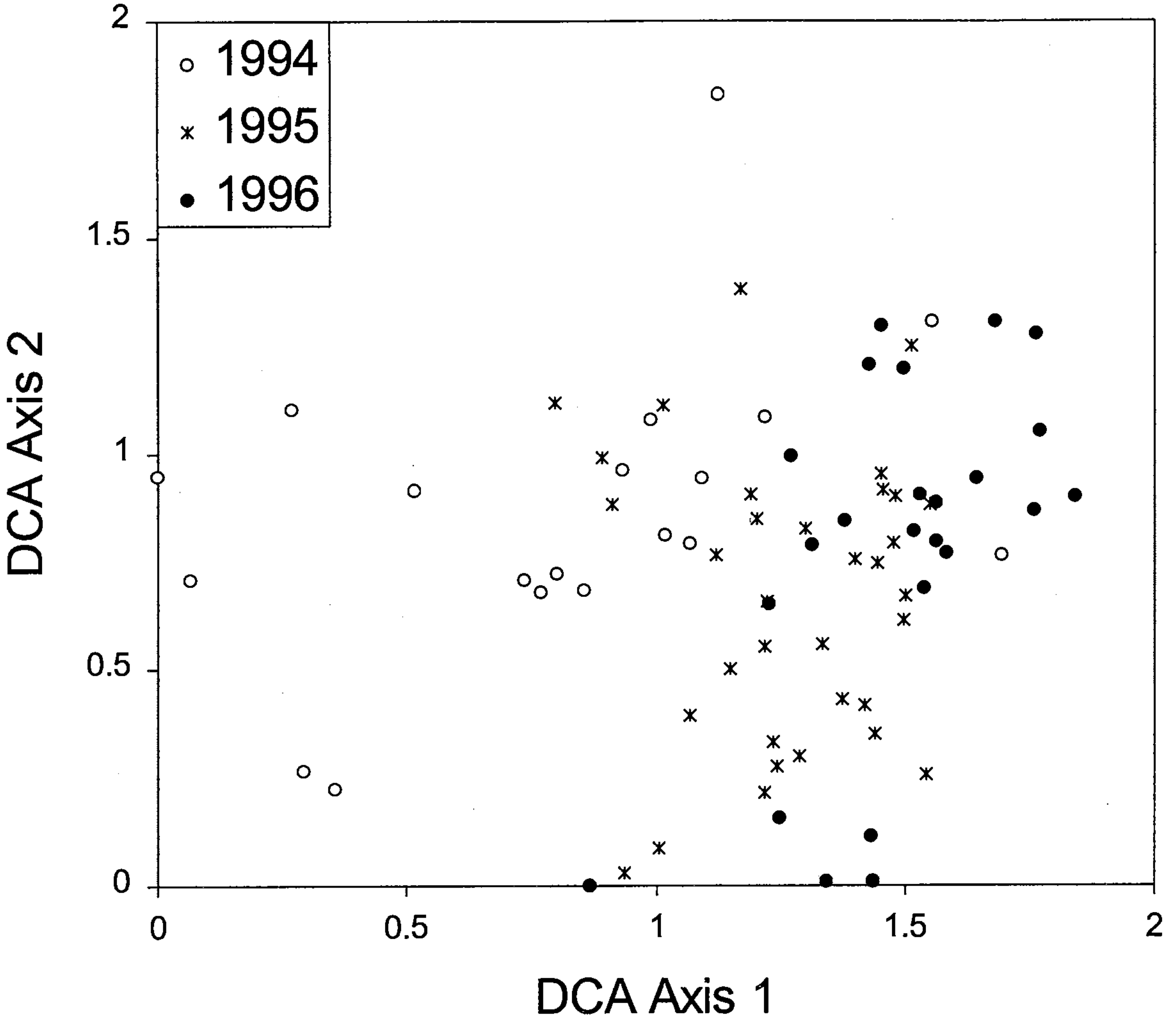

○ 1994
✱ 1995
● 1996
DCA Axis 2
2
1.5
1
0.5
0
0
0.5
1
1.5
2
DCA Axis 1

Fig. IV.5. Distribution of behavioral scores (A) and environmental variables (B) derived from the full Canonical Correspondence Analysis CCA model (see text) for Texas tortoises at Chaparral Wildlife Management Area, Dimmit and La Salle counties, Texas. In A, open circles refer to behavior associated with pallets; stars indicate foraging behavior; closed circles indicate other behavior. In B, arrows indicate biplot arrows for the continuous variables age and size; closed circles indicate centroids for the dummy variables year, sex, and treatment.

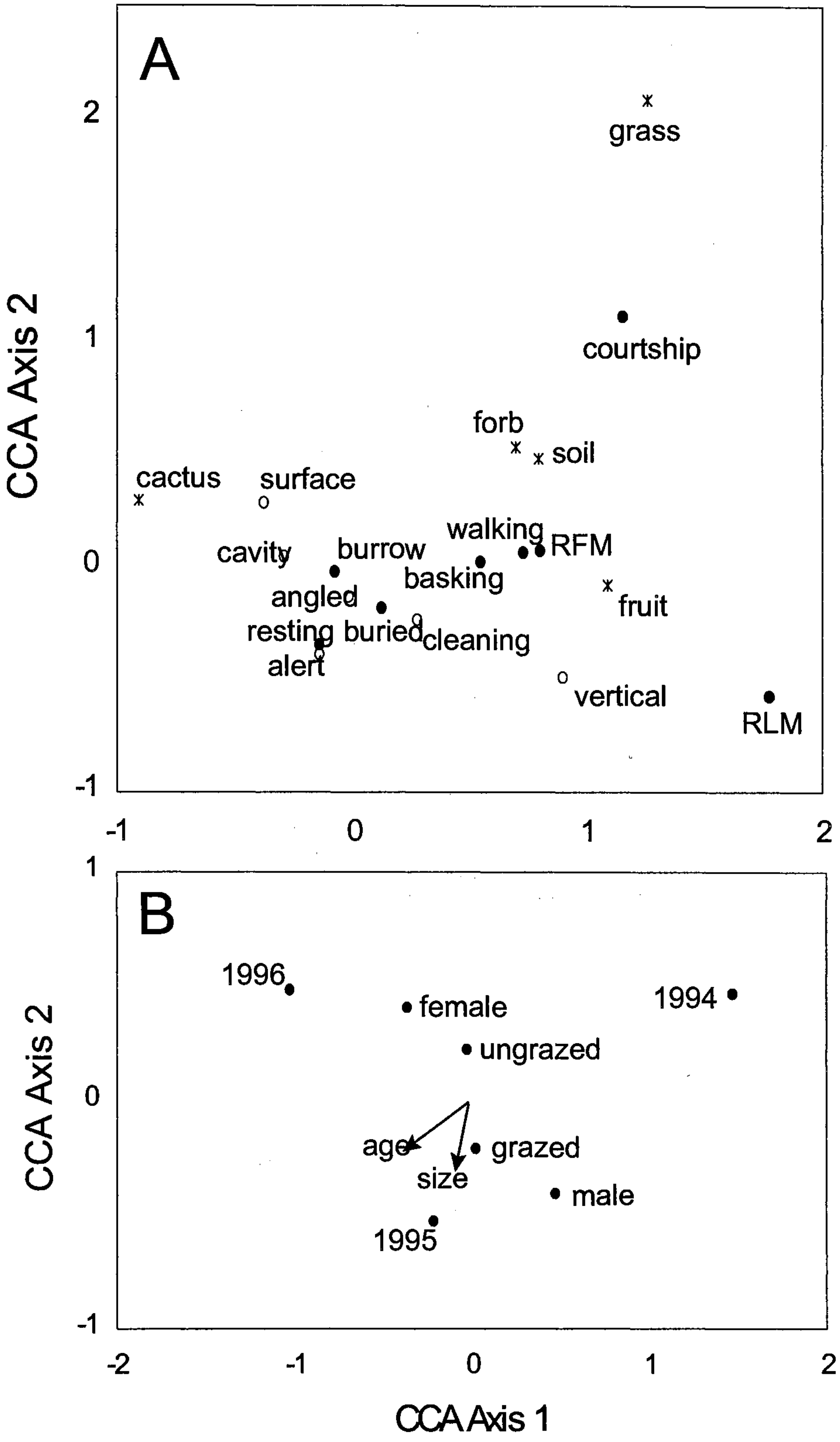
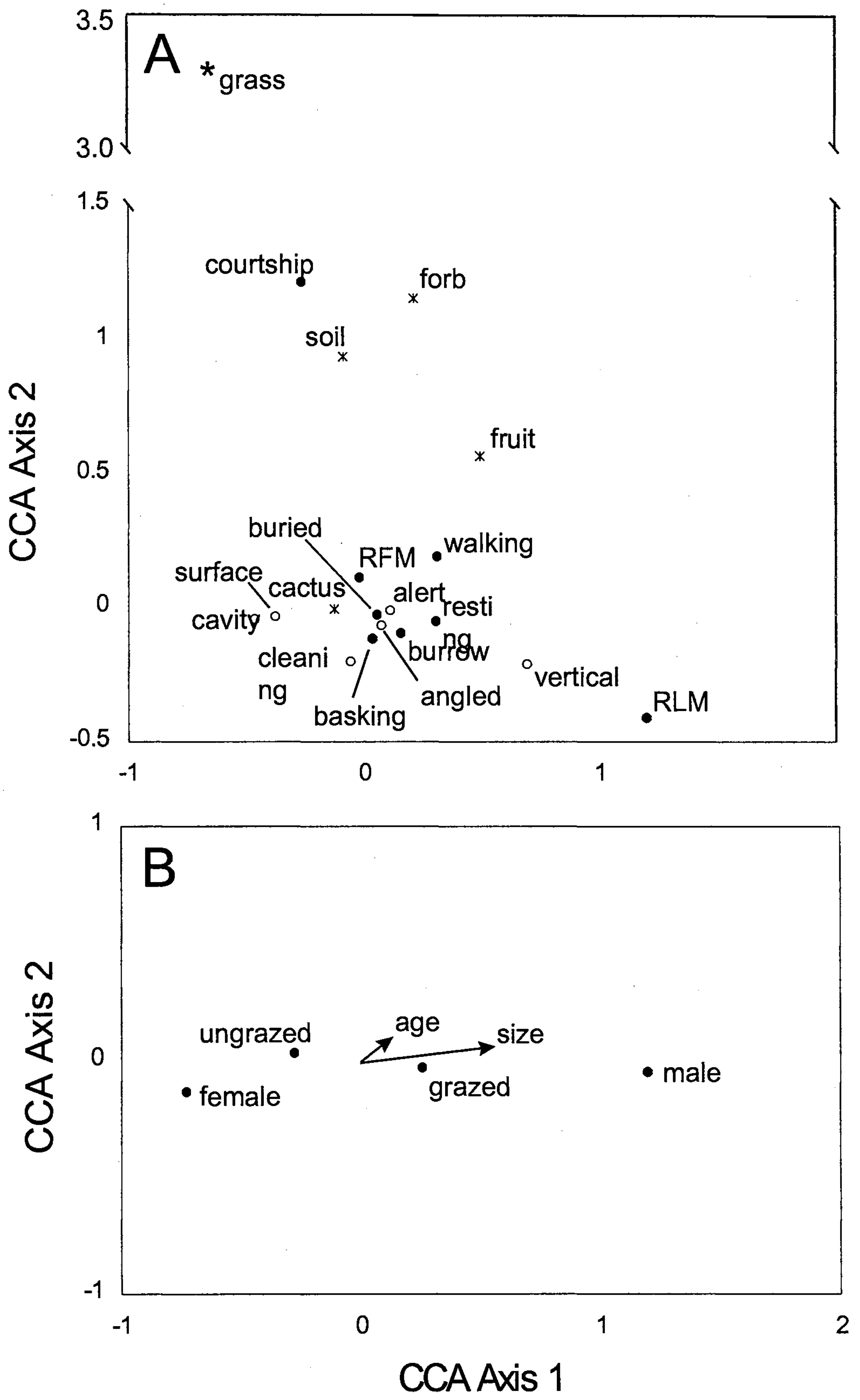

A
CCA Axis 2
2
1
0
-1
-1
0
1
2
grass
courtship
forb
soil
cactus
surface
walking
RFM
cavity
burrow
basking
fruit
angled
resting
buried
cleaning
alert
vertical
RLM
B
1
0
-1
-2
-1
0
1
2
CCA Axis 2
CCA Axis 1
1996
female
1994
ungrazed
age
grazed
size
male
1995

Fig. IV.6. Distribution of behavioral scores (A) and environmental variables (B) derived from the partial Canonical Correspondence Analysis model using year as a covariable (see text) for Texas tortoises at Chaparral Wildlife Management Area, Dimmit and La Salle counties, Texas. In A, open circles refer to behavior associated with pallets; stars indicate foraging behavior; closed circles indicate other behavior. In B, arrows indicate biplot arrows for the continuous variables age and size; closed circles indicate centroids for the dummy variables sex and treatment.


A
grass
courtship
forb
soil
fruit
buried
walking
RFM
surface
cactus
alert
resti
ng
cavity
burrow
cleani
ng
vertical
angled
basking
RLM
3.5
3.0
1.5
1
0.5
0
-0.5
-1
0
1
CCA Axis 2
B
ungrazed
age
size
female
grazed
male
1
0
-1
-1
0
1
2
CCA Axis 2
CCA Axis 1

APPENDICES

APPENDIX A

HABITAT MAPS FOR STUDY PASTURES

Figure A.1. Habitat map for Baldy Pasture on Chaparral Wildlife Management Area, Dimmit County, Texas. Dotted and solid lines indicate boundaries of male and female study areas, respectively.

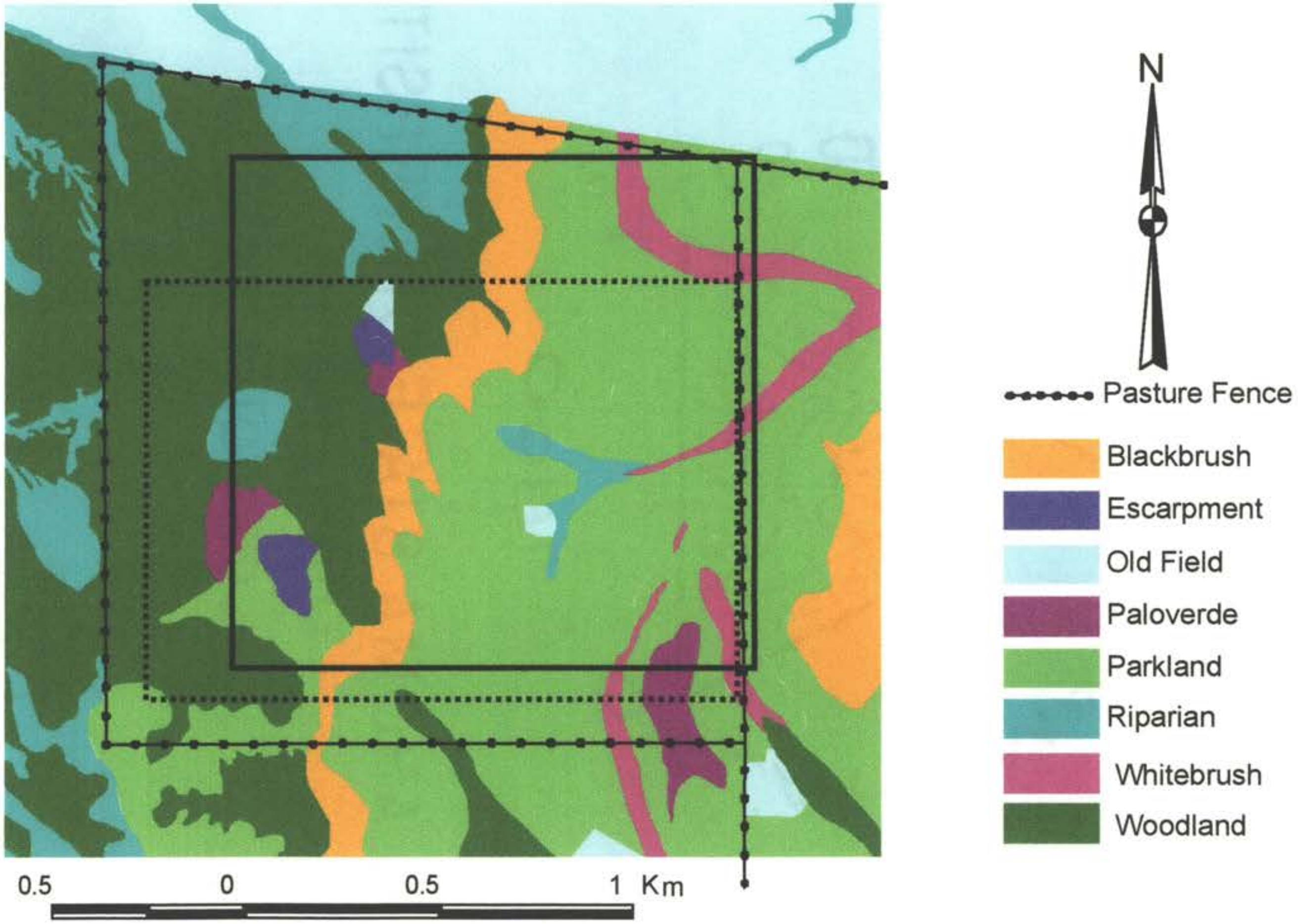

N
Pasture Fence
Blackbrush
Escarpment
Old Field
Paloverde
Parkland
Riparian
Whitebrush
Woodland
0.5
0
0.5
1 Km

Figure A.2. Habitat map for East Blocker Pasture on Chaparral Wildlife Management Area, Dimmit County, Texas. Dotted and solid lines indicate boundaries of male and female study areas, respectively.

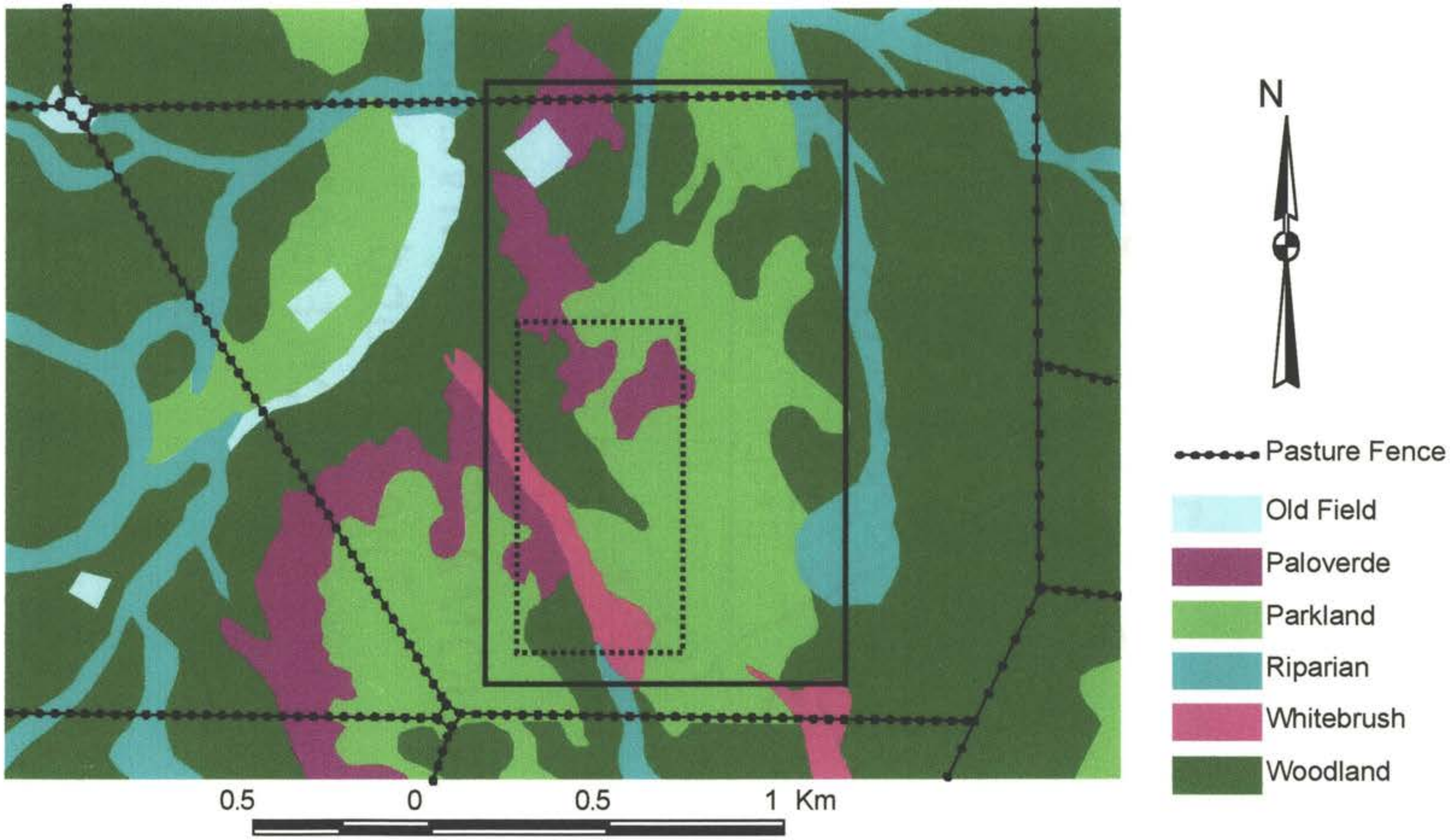

N
Pasture Fence
Old Field
Paloverde
Parkland
Riparian
Whitebrush
Woodland
0.5
0
0.5
1 Km

Figure A.3. Habitat map for South Jay Pasture on Chaparral Wildlife Management Area, Dimmit and La Salle counties, Texas. Dotted and solid lines indicate boundaries of male and female study areas, respectively.

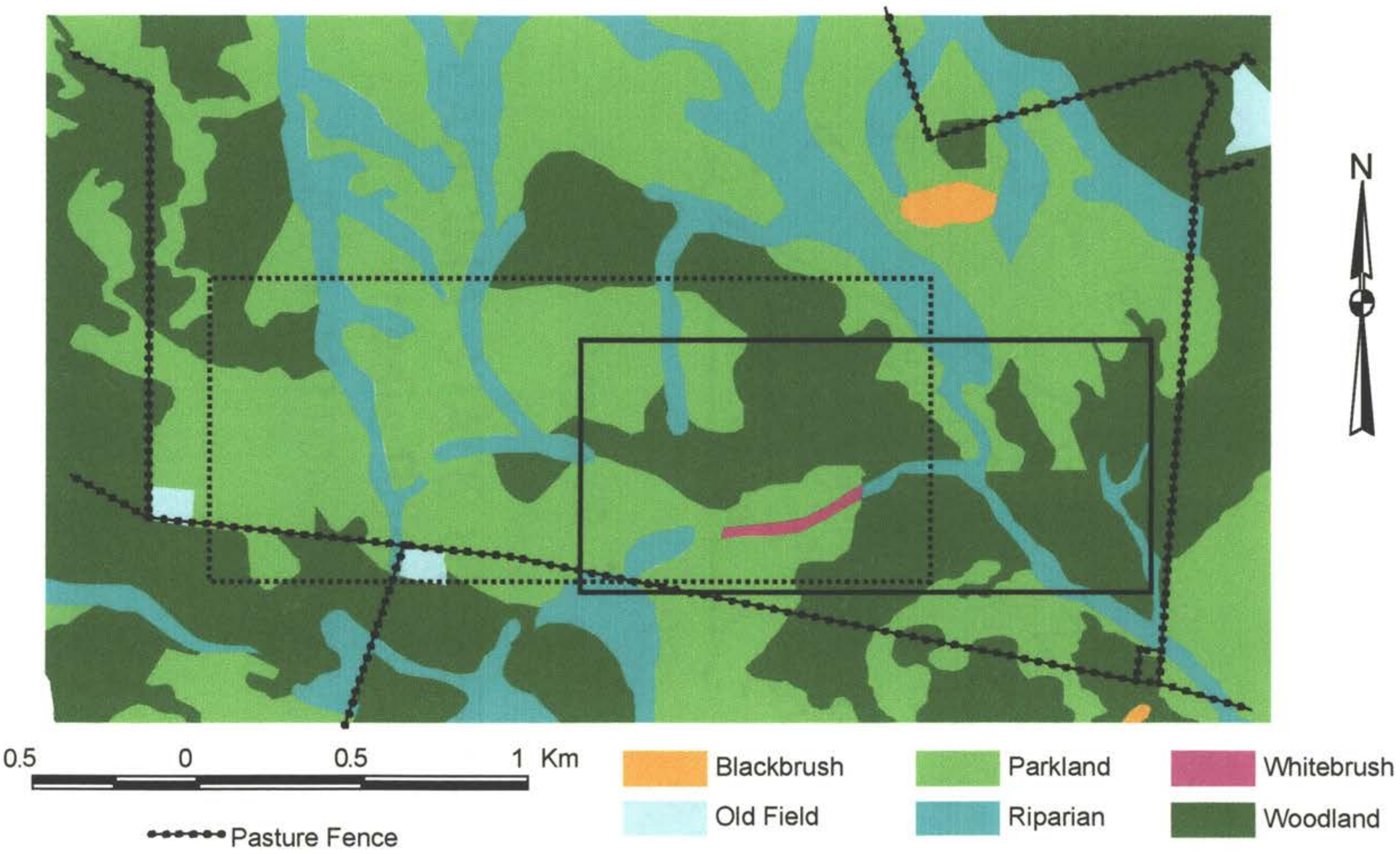
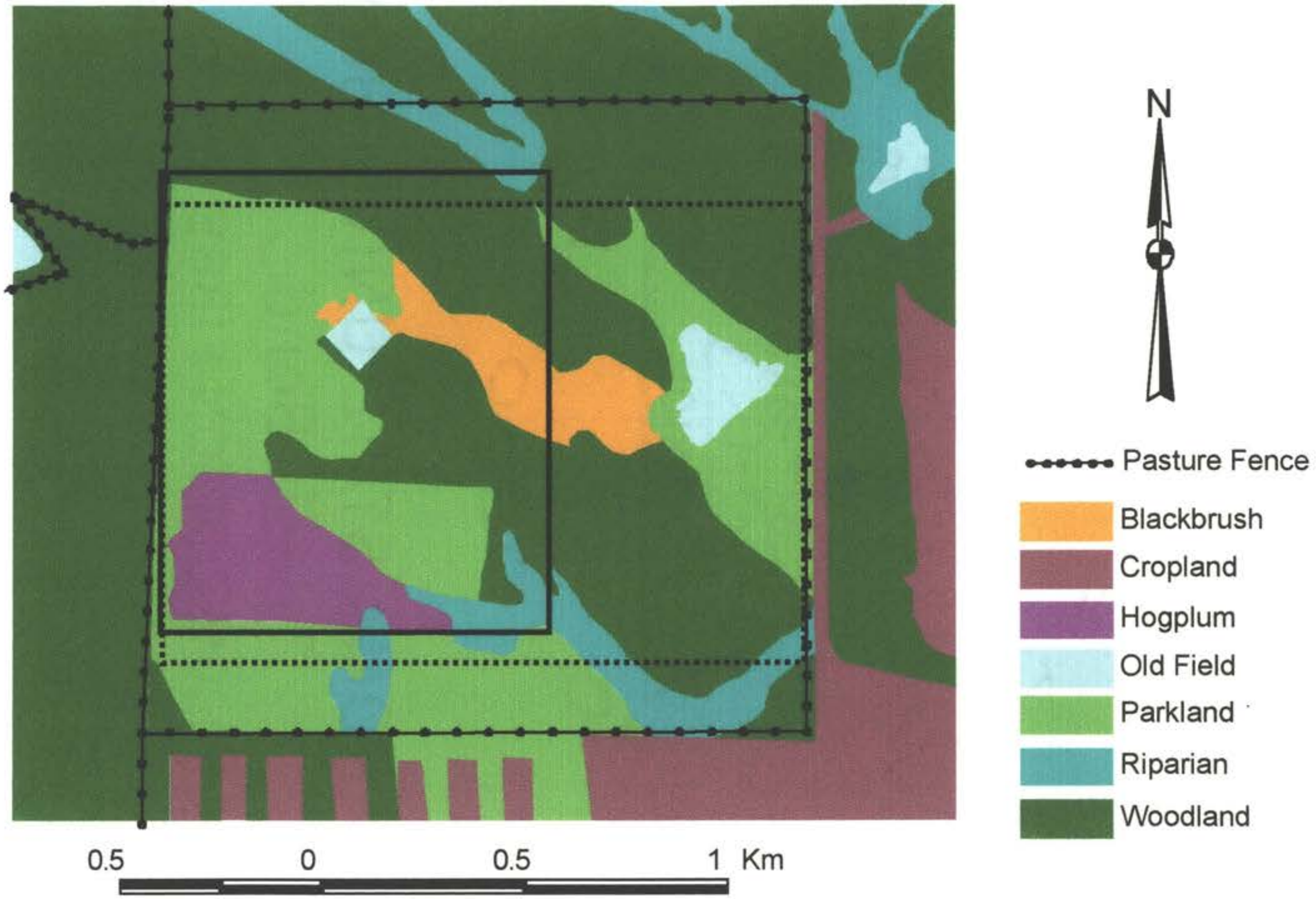

N
0.5
0
0.5
1 Km
Pasture Fence
Blackbrush
Parkland
Whitebrush
Old Field
Riparian
Woodland

Figure A.4. Habitat map for Mare Pasture on Chaparral Wildlife Management Area, La Salle County, Texas. Dotted and solid lines indicate boundaries of male and female study areas, respectively.


N
Pasture Fence
Blackbrush
Cropland
Hogplum
Old Field
Parkland
Riparian
Woodland
0.5
0
0.5
1 Km

APPENDIX B

PROPORTIONS OF USE AND AVAILABILITY

Appendix B.1. Averages of proportional use (points) and availability (100% minimum convex polygon home ranges cumulative over 2 seasons [1994-1995 or 1995-1996]) of habitats by female (n = 22) and male (n = 14) Texas tortoises on Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas.

	Female				Male			
	Proportion Available		Proportion Used		Proportion Available		Proportion Used	
Habitat	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Blackbrush	0.016	0.014	0.013	0.012	0.049	0.029	0.036	0.021
Escarpment	0.027	0.027	0.028	0.028	0.001	0.001	0.001	0.001
Hogplum	0.049	0.038	0.057	0.043	0.067	0.046	0.097	0.066
Paloverde	0.041	0.023	0.033	0.021	0.062	0.042	0.035	0.023
Parkland	0.411	0.070	0.461	0.074	0.352	0.057	0.330	0.074
Woodland	0.418	0.075	0.371	0.076	0.425	0.093	0.437	0.100
Riparian	0.020	0.010	0.032	0.017	0.019	0.010	0.012	0.007
Whitebrush	0.014	0.008	0.004	0.003	0.023	0.015	0.050	0.036
Old Field	0.005	0.004	0.0009	0.0009	0.0003	0.0003	0	

Appendix B.2. Averages of proportional use (points) and availability (100% minimum convex polygon home ranges cumulative over 2 seasons [1994-1995 or 1995-1996]) of habitats by Texas tortoises in east (*n* = 21) and west (*n* = 15) study sites on Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas.

	East				West			
	Proportion Available		Proportion Used		Proportion Available		Proportion Used	
Habitat	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Blackbrush	0.017	0.015	0.016	0.012	0.045	0.027	0.031	0.020
Escarpment	0		0		0.041	0.040	0.042	0.041
Hogplum	0.096	0.048	0.125	0.061	0		0	
Paloverde	0		0		0.117	0.047	0.081	0.033
Parkland	0.269	0.051	0.312	0.064	0.555	0.074	0.547	0.085
Woodland	0.579	0.074	0.517	0.086	0.200	0.053	0.229	0.056
Riparian	0.028	0.012	0.022	0.009	0.008	0.006	0.028	0.023
Whitebrush	0.011	0.008	0.009	0.007	0.026	0.015	0.040	0.033
Old Field	0		0		0.007	0.006	0.001	0.001

Appendix B.3. Averages of proportional use (points) and availability (100% minimum convex polygon home ranges cumulative over 2 seasons [1994-1995 or 1995-1996]) of habitats by Texas tortoises in grazed (n = 20) and ungrazed (n = 16) study sites on Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas.

	Grazed				Ungrazed			
	Proportion Available		Proportion Used		Proportion Available		Proportion Used	
Habitat	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Blackbrush	0		0		0.065	0.030	0.050	0.023
Escarpment	0		0		0.038	0.037	0.040	0.038
Hogplum	0		0		0.126	0.062	0.163	0.077
Paloverde	0.086	0.037	0.058	0.026	0.002	0.002	0.003	0.003
Parkland	0.336	0.057	0.344	0.065	0.454	0.081	0.492	0.089
Woodland	0.529	0.068	0.525	0.067	0.286	0.089	0.237	0.092
Riparian	0.022	0.011	0.038	0.018	0.018	0.009	0.008	0.004
Whitebrush	0.023	0.012	0.035	0.025	0.010	0.009	0.006	0.005
Old Field	0.005	0.005	0		0.001	0.0003	0.001	0.001

Appendix B. 4. Averages of proportional use (100% minimum convex polygon home ranges cumulative over 2 seasons [1994-1995 or 1995-1996]) and availability (study areas) of habitats by female (n = 22) and male (n = 14) Texas tortoises on Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas.

	Female				Male			
	Proportion Available		Proportion Used		Proportion Available		Proportion Used	
Habitat	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Blackbrush	0.028	0.008	0.016	0.014	0.033	0.009	0.049	0.029
Escarpment	0.003	0.001	0.027	0.027	0.004	0.002	0.001	0.001
Hogplum	0.028	0.011	0.049	0.038	0.021	0.009	0.067	0.046
Paloverde	0.036	0.012	0.041	0.023	0.034	0.019	0.062	0.042
Parkland	0.427	0.012	0.411	0.070	0.472	0.022	0.352	0.057
Woodland	0.367	0.024	0.418	0.075	0.335	0.015	0.425	0.093
Riparian	0.077	0.005	0.020	0.010	0.067	0.012	0.019	0.010
Whitebrush	0.024	0.004	0.014	0.008	0.023	0.012	0.023	0.015
Old Field	0.010	0.002	0.005	0.004	0.011	0.003	0.0003	0.0003

Appendix B.5. Averages of proportional use (100% minimum convex polygon home ranges cumulative over 2 seasons [1994-1995 or 1995-1996]) and availability (study areas) of habitats by Texas tortoises in east (*n* = 21) and west (*n* = 15) study sites on Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas.

	East				West			
	Proportion Available		Proportion Used		Proportion Available		Proportion Used	
Habitat	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Blackbrush	0.023	0.006	0.017	0.015	0.039	0.011	0.045	0.027
Escarpment	0		0		0.007	0.002	0.041	0.040
Hogplum	0.043	0.012	0.096	0.048	0		0	
Paloverde	0		0		0.084	0.018	0.117	0.047
Parkland	0.421	0.016	0.269	0.051	0.477	0.013	0.555	0.074
Woodland	0.409	0.017	0.579	0.074	0.279	0.013	0.200	0.053
Riparian	0.091	0.006	0.028	0.012	0.049	0.006	0.008	0.006
Whitebrush	0.004	0.001	0.011	0.008	0.052	0.008	0.026	0.015
Old Field	0.009	0.002	0		0.012	0.002	0.007	0.006

Appendix B.6. Averages of proportional use (100% minimum convex polygon home ranges cumulative over 2 seasons [1994-1995 or 1995-1996]) and availability (study areas) of habitats by Texas tortoises in grazed (n = 20) and ungrazed (n = 16) study sites on Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas.

	Grazed				Ungrazed			
	Proportion Available		Proportion Used		Proportion Available		Proportion Used	
Habitat	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Blackbrush	0		0		0.067	0.004	0.065	0.030
Escarpment	0		0		0.007	0.002	0.038	0.037
Hogplum	0		0		0.057	0.014	0.126	0.062
Paloverde	0.058	0.017	0.086	0.037	0.008	0.002	0.002	0.002
Parkland	0.439	0.016	0.336	0.057	0.452	0.017	0.454	0.081
Woodland	0.384	0.022	0.529	0.068	0.318	0.019	0.286	0.089
Riparian	0.086	0.009	0.022	0.011	0.058	0.004	0.018	0.009
Whitebrush	0.030	0.008	0.023	0.012	0.016	0.005	0.010	0.009
Old Field	0.005	0.001	0.005	0.005	0.017	0.002	0.001	0.000

Appendix B.7. Averages of proportions of habitats for points used by tortoises, within home ranges (100% minimum convex polygon home ranges cumulative over 2 seasons [1994-1995 or 1995-1996]), and within study areas for all Texas tortoises ($n = 36$) examined on Chaparral Wildlife Management Area, Dimmit and La Salle Counties, Texas.

	Proportion					
	Points		Home range		Study area	
Habitat	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Blackbrush	0.022	0.011	0.029	0.014	0.030	0.006
Escarpment	0.018	0.017	0.017	0.017	0.003	0.001
Hogplum	0.072	0.036	0.056	0.029	0.025	0.008
Paloverde	0.034	0.015	0.049	0.021	0.035	0.010
Parkland	0.410	0.054	0.388	0.048	0.445	0.012
Woodland	0.397	0.060	0.421	0.058	0.355	0.016
Riparian	0.025	0.011	0.020	0.007	0.073	0.006
Whitebrush	0.022	0.014	0.017	0.008	0.023	0.005
Old Field	0.001	0.001	0.003	0.003	0.010	0.002

APPENDIX C

RECAPTURE DISTANCES AND DIRECTIONS

Figure C.1. Spider diagram of distances and distances and directions between recaptures for juvenile tortoises recaptured as juveniles on Chaparral Wildlife Management Area, 1990-1999.

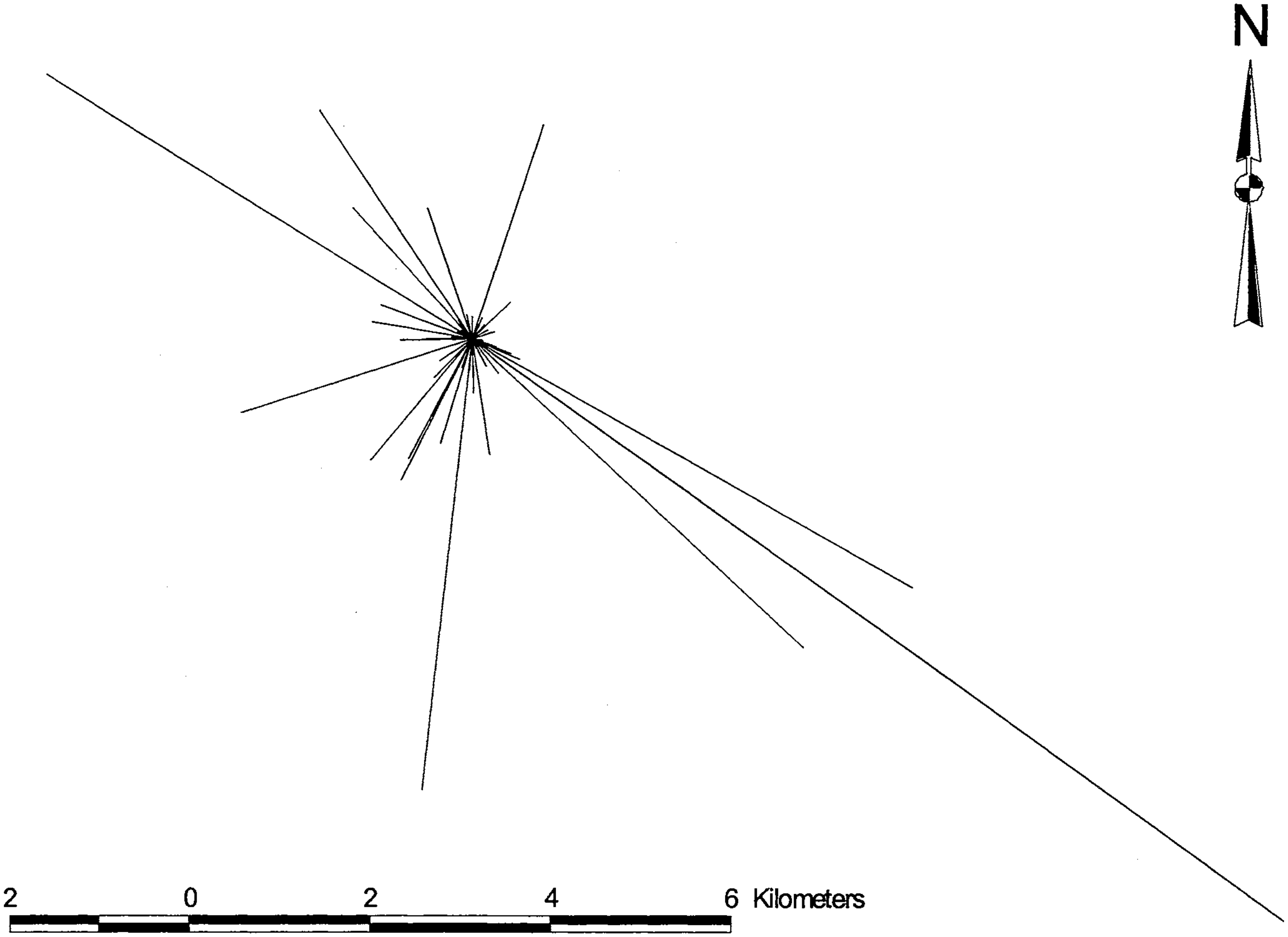

N
2
0
2
4
6 Kilometers

Figure C.2. Spider diagram of distances and distances and directions between recaptures for juvenile female tortoises recaptured as adults on Chaparral Wildlife Management Area, 1990-1999.

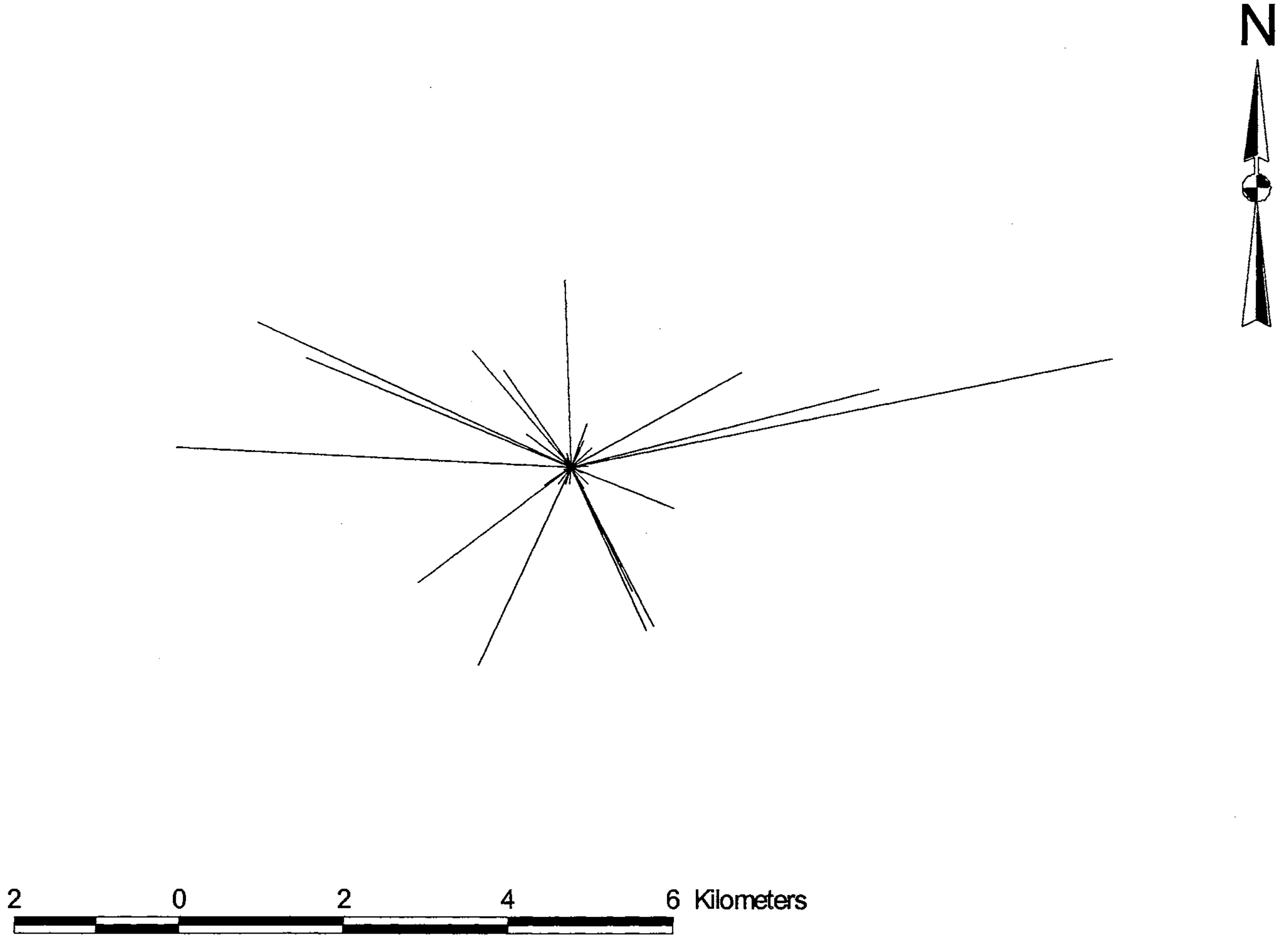

N
2
0
2
4
6 Kilometers

Figure C.3. Spider diagram of distances and distances and directions between recaptures for juvenile male tortoises recaptured as adults on Chaparral Wildlife Management Area, 1990-1999.

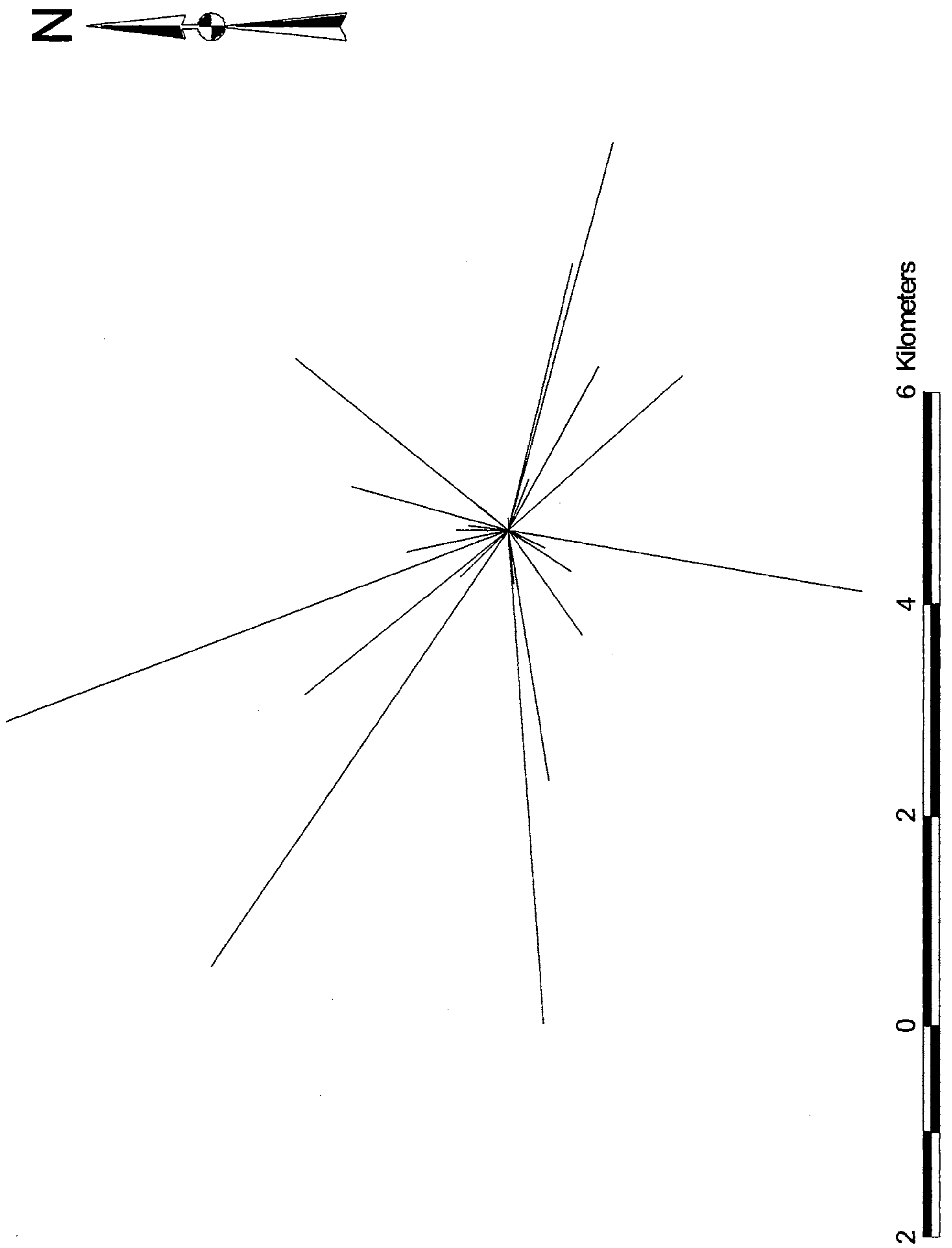

N
2
0
2
4
6 Kilometers

Figure C.4. Spider diagram of distances and distances and directions between recaptures for adult female tortoises recaptured as adults on Chaparral Wildlife Management Area, 1990-1999.

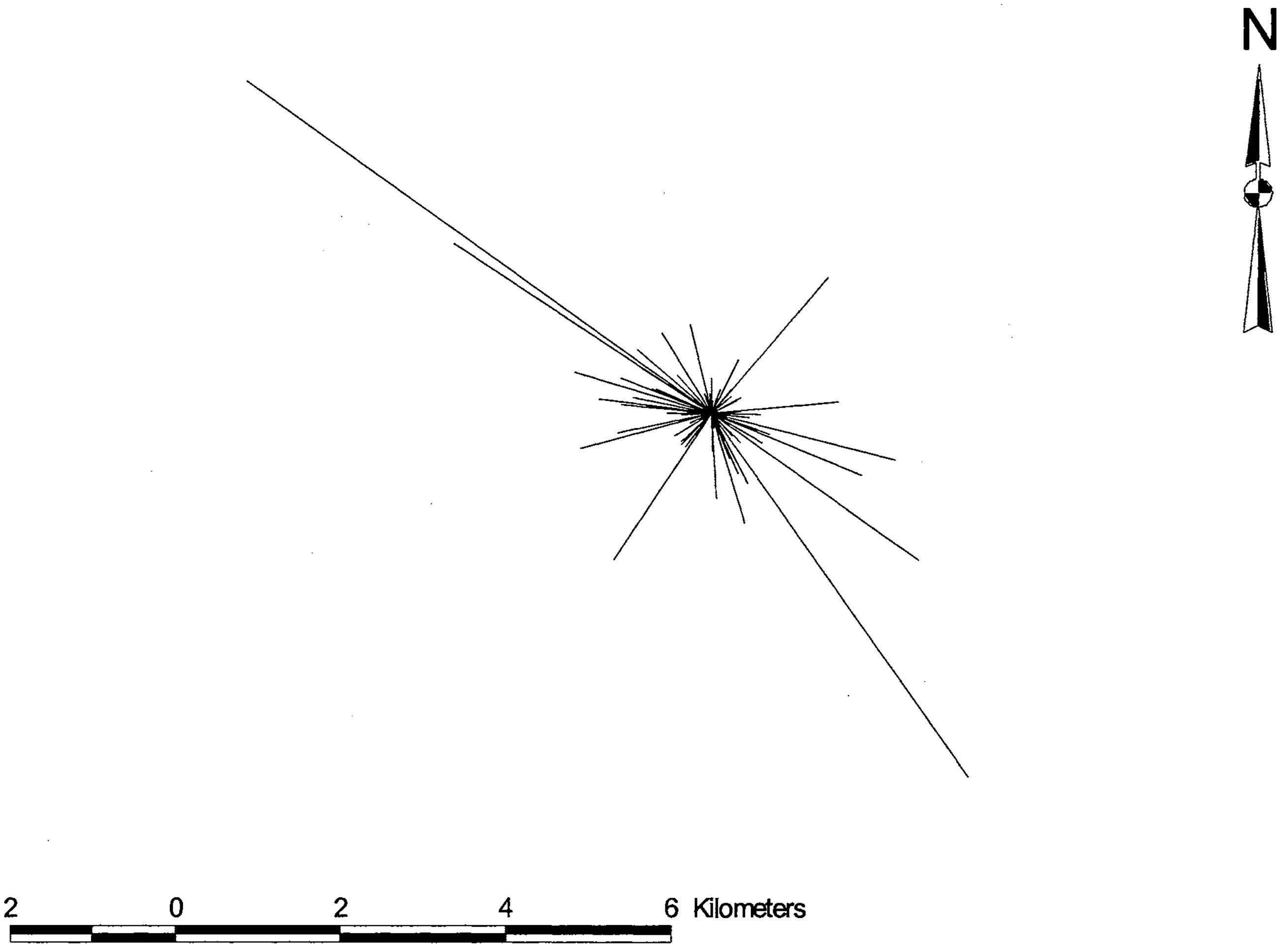
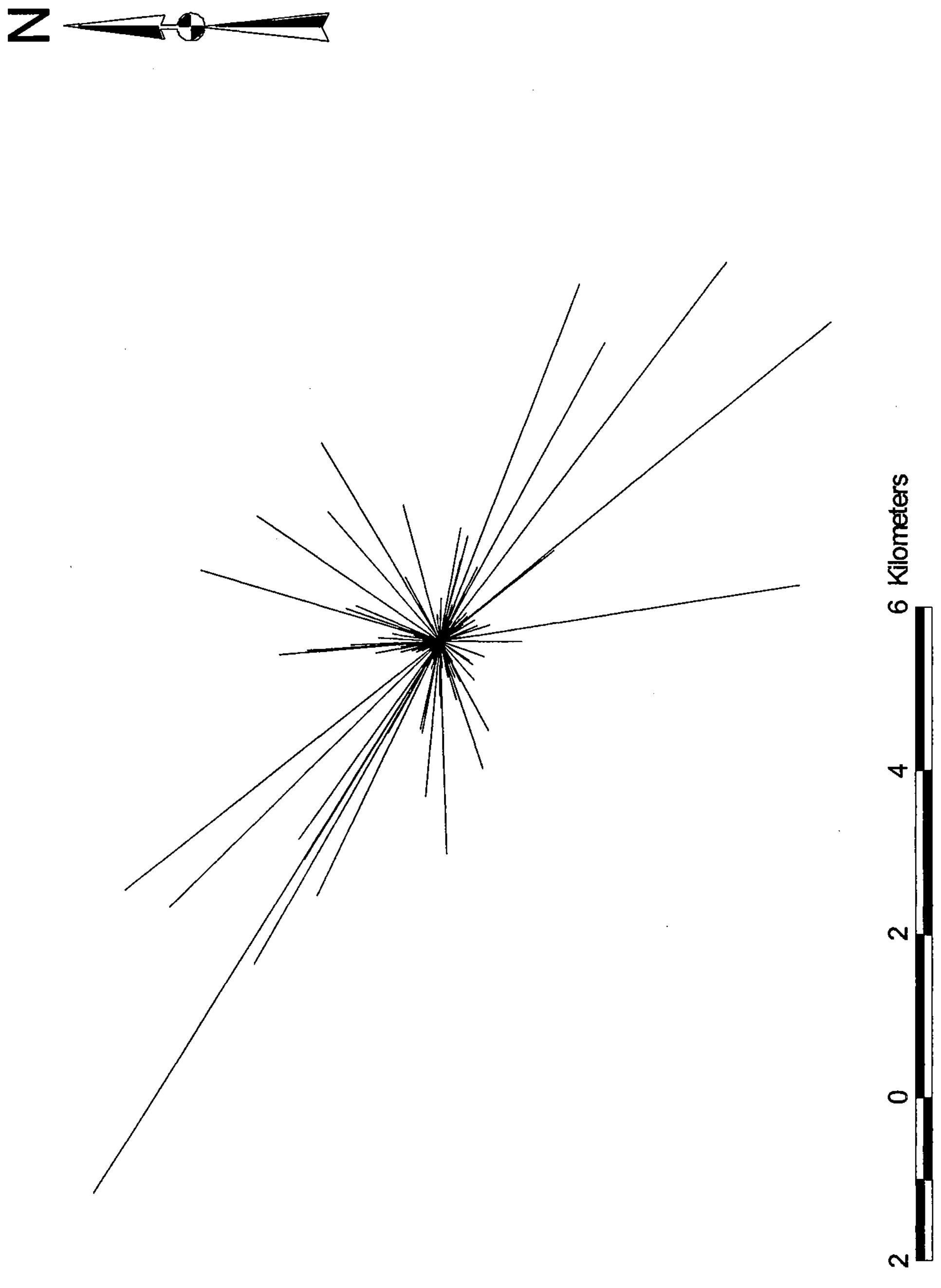

N
2
0
2
4
6
Kilometers

Figure C.5. Spider diagram of distances and distances and directions between recaptures for adult male tortoises recaptured as adults on Chaparral Wildlife Management Area, 1990-1999.


N
2
0
2
4
6 Kilometers

APPENDIX D

PRELIMINARY COMPARISONS OF TORTOISE AND CATTLE DIETS

INTRODUCTION

The Family Testudinidae (tortoises) is restricted to 4 species in North America, and there is considerable concern about the conservation status of all 4 species. The desert tortoise (*Gopherus agassizii*), Bolson tortoise (*G. flavomarginatus*), and gopher tortoise (*G. polyphemus*) all receive some form of protection from the federal government under the Endangered Species Act. The Texas tortoise (*G. berlandieri*) was protected by an act of the Texas legislature in 1967 and is currently listed as threatened in the state.

Studies of Texas tortoises have concentrated on the basic ecology and natural history of this species in costal populations, primarily in Cameron county, Texas (Auffenberg and Weaver 1969, Rose and Judd 1975, Rose and Judd 1982, Judd and Rose 1983, Bury and Smith 1986). Despite these studies, however, the Texas tortoise remains the least known of the 4 *Gopherus* (Bury and Germano 1994). In particular, inferences about how various land use practices affect tortoises have been largely anecdotal or inconclusive.

There is concern that cattle grazing may adversely affect desert tortoise populations (Berry 1978, Medica et al. 1982), but Bostick (1990) suggested that cattle have a beneficial effect on desert tortoises. Auffenberg and Franz (1982) considered moderate grazing to be beneficial for the gopher tortoise in the absence of fire. Oldenmeyer (1994), however, admitted that no data has been collected to adequately quantify tortoise-cattle interactions. To address one aspect of potential interaction between tortoises and cattle, we compared diet between Texas tortoises and cattle during the time period of a grazing regime with the highest probability of interaction between tortoises and cattle. This report concerns part of a much larger study designed to address how grazing by cattle affects the demographic, spatial, and dietary dimensions of the realized niche of a population of Texas tortoises in the western Rio Grande Plains, Texas.

METHODS

Research was conducted on the Chaparral Wildlife Management Area (CWMA) in Dimmit and LaSalle counties, Texas. CWMA was acquired by the Texas Parks and Wildlife Department in 1969 and is currently managed as a research and demonstration facility for the South Texas Plains ecoregion. CWMA consists of a series of grazed and ungrazed pastures, with a rotational grazing system consisting of a light to moderate stocking rate from October to May. Fieldwork was initiated in April 1994 and completed in August 1997. Research efforts focused on 2 ungrazed pastures paired by dominant plant communities with 2 grazed pastures.

To obtain information on tortoise diets, observations of foraging were recorded during fortuitous encounters and by relocations of up to 10 radiotransmittered tortoises in each study pasture. Whenever possible, fecal samples were collected from tortoises and frozen for determination of diet by both macro- and microhistological methods. Whole plant and seed vouchers were collected to assist with identification of food items from fecal material. To assess cattle diets, 10 fecal samples were collected in each grazed pasture during both April and May, 1996. Samples were collected in April and May, because that represented the period of the grazing regime with the highest tortoise activity (Kazmaier, unpublished data). Cattle fecal samples were dried in a drying oven and then lightly ground. Samples were then homogenized for each pasture and month (N=4) and submitted to a laboratory (Wildlife Habitat Lab, Washington State University, Pullman, WA) for microhistological determination of plant composition. Microhistological examination of cattle diets resulted in percentages of taxa (usually genus) observed in each sample. Taxa were combined into major vegetation categories (grass, sedge, forb, cactus, fruit, shrub) and percentages from the 4 homogenized samples were averaged for comparison with tortoise diets. Frequency distributions for major vegetation categories derived from direct observation of tortoises were converted to percentages for comparisons derived from microhistological analysis of cattle samples.

RESULTS

Tortoises were seen foraging on plant material during 79 observations. An additional 49 foraging observations were not used in the comparison with cattle diets, because they involved consumption of items (soil, bone, snail shells, scat) not identifiable by microhistology. Collection of tortoise fecal material resulted in 132 samples, but these samples are awaiting macro- and microhistological analysis.

Grasses and shrubs accounted for 92% of the diet of cattle and only 28% of the tortoise foraging observations (Table D.1). Forbs, cactus, and fruit made up 72% of the tortoise foraging observations, but only 7% of the cattle diet consisted of forbs, cactus, or fruit (Table D.1). Comparison of presence and absence of plant species by genus revealed only 2 genera in common between cattle and tortoise diets: *Eragrostis* and *Opuntia* (Table D.2).

DISCUSSION

Analysis of major vegetation categories between cattle and tortoises suggested that tortoises relied more heavily on forbs, fruit, and cactus, and cattle relied more heavily on grasses and shrubs. Only 2 genera were found in common between tortoise and cattle diets. Thus, comparisons of either presence/absence of genera or proportion of the diet by major vegetation categories suggested that there is little dietary overlap between cattle and Texas tortoises.

These results, however, should be interpreted cautiously. Data used to establish frequency distributions from direct observations of tortoises were collected at all times of the year and during all 4 years of the study, but because of the cost of microhistological analysis, cattle fecal samples could only be examined in April-May, 1996. In addition, an intense short-term drought occurred during this study, as CWMA did not receive a significant rain between November 1995 and July 1996. Due to the lack of rain, forb production was very low during the winter and cattle did not have access to many forbs during the April-May, 1996, sampling period. Thus, forb consumption may have been low in the cattle diets not because they did not select forbs, but because forbs were unavailable. Frequencies of foraging observations were too low to allow comparison of diets by season or year.

The degree of annual and seasonal variability common in arid and semi-arid regions like the Rio Grande Plains makes long-term studies invaluable for drawing conclusions about the effects of management practices on a species. Thus, examination of cattle samples during other seasons and years would allow better interpretation. Forthcoming analyses of tortoise fecal samples should give a better indication of tortoise diets and allow better interpretations and hypotheses concerning potential tortoise-cattle dietary interactions.

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Table D.1. Percentage of major vegetation categories in diets of cattle and Texas tortoises from Chaparral Wildlife Management Area, Dimmit and La Salle counties, Texas. Cattle diet determined from microhistological analysis of fecal material from April-May 1996. Tortoise diet determined from direct observation of tortoises from April 1994-August 1997.

Vegetation category	Percentage of cattle diet	Percentage of tortoise diet
grass	78	28
sedge	1	0
forb	6	47
cactus	1	14
fruit	0	11
shrub	14	0

Table D.2. Presence of genera in the diets of cattle and Texas tortoises on Chaparral Wildlife Management Area, Dimmit and La Salle counties, Texas. Cattle diet determined from microhistological analysis of fecal material from April-May 1996. Tortoise diet determined from direct observation of tortoises from April 1994-August 1997.

Vegetation category	Genus	Cattle diet	Tortoise diet
Grass	*Agrostis*	*	
	Aristida	*	
	Bouteloua	*	
	Cenchrus	*	
	Chloris	*	
	Digitaria	*	
	Eragrostis	*	*
	Panicum	*	
	Paspalum	*	
	Setaria	*	
	Sporobolus	*	
	Stipa	*	
	Tridens	*	
Sedge	*Eleocharis*	*	
Forb	*Aclesianthes*		*
	Allionia		*
	Ambrosia	*	
	Chamaecrista		*
	Commelina		*
	Evolvulus		*
	Mollugo		*
	Nama		*
	Oenothera	*	
	Sida	*	
	Simsia		*

	Solanum	*	
	Sphaeralcea	*	
	Talinum		*
	Zornia		*
Cactus	*Opuntia*	*	*
Fruit	*Diospyros*		*
	Opuntia		*
Shrub	*Acacia*	*	
	Ephedra	*	
	Leucophyllum	*	
	Parkinsonia	*	
	Prosopis	*	

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