HABITAT USE, DAILY MOVEMENTS, AND BODY SIZE OF THE TEXAS HORNED LIZARD IN AN URBAN ENVIRONMENT IN NORTH-CENTRAL OKLAHOMA

By

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Chapter I

TEXAS HORNED LIZARDS: INTRODUCTION

The Texas horned lizard, Phrynosoma cornutum, was once abundant in Oklahoma and found throughout the state except for the southeastern corner. Over the past several decades, this species has decreased in range and abundance in Oklahoma (Price, 1991; Carpenter et al., 1993) and Texas (Donaldson et al., 1994). Currently, the Texas horned lizard is listed as a species of special concern in Oklahoma (ODWC, 1992) and threatened in Texas (Texas Parks and Wildlife Code, 1987).

Scientific research on this species in Oklahoma has been very limited. In fact, the only study conducted on this species within the state was a population census (Carpenter et al., 1993). Future investigations into the ecology of Texas horned lizards in Oklahoma may be necessary to help conserve this species.

The goal of this study was to gain knowledge of the space and habitat use of Texas horned lizards in Oklahoma and compare Texas horned lizards from northern Oklahoma and southern Texas to look for geographical variation in body size and sexual size dimorphism (SSD). I present my findings here with the hope that they can be used to help conserve this species in Oklahoma and generate additional research ideas. The research is presented as three papers, each in the correct format for submission to a scientific journal. Chapter 2 is in format for submission to the Journal of Herpetology, Chapter 3 is in format for submission to The Southwestern Naturalist, and Chapter 4 is in format for submission to Herpetological Review.

Texas Horned Lizards

Horned lizards belong to the genus *Phrynosoma*, which inhabits semi-arid and arid habitats (Pianka and Parker, 1975). Horned lizards are dorsoventrally flattened, have short limbs and tail, and a spiny integument (Garret and Barker, 1987). Spines are most prominent on the occipital region (Pianka and Parker, 1975). There are 13 species of horned lizards. Seven of these species occur in the western and central regions of the United States (Pianka and Parker, 1975; Sherbrooke, 1981), and two occur in Oklahoma (Conant and Collins, 1991).

The Texas horned lizard varies in color from light yellowish brown to reddish brown (Collins, 1993), depending on the color of the soil of the habitat (Garret and Barker, 1987). Its most notable morphologic feature is several spines on its head, with the two in the center being the most prominent. Dark lines extend down from the eyes and over the top of the head. Two rows of lateral abdominal fringe scales occur on each side of the body. Enlarged spines occur on the entire dorsum. These spines are surrounded by dark spots with rims of yellow or white. A yellow or white middorsal stripe extends from the head to the base of the tail. (Garret and Barker, 1987; Collins, 1993). Snout-vent length for adult Texas horned lizards is 68–130 mm (Brown and Lucchino, 1972; Ballinger, 1974; Pianka and Parker, 1975; Munger 1984b), and adult body weight is 20–90 g (Munger 1984a).

Texas horned lizards are active from April to October (Potter and Glass, 1931; Munger, 1984a; Collins, 1993). They are considered diurnal (Stebbins, 1954; Whitford and Bryant, 1979; Munger, 1984a), although nocturnal activity has been reported (Williams, 1959). Several researchers have reported that

Texas horned lizards are dietary specialists on harvester ants (Pogonomyrmex) (Pianka and Parker, 1975; Whitford and Bryant, 1979; Sherbrooke, 1981; Munger, 1984a, 1984b, 1984c; Whiting et al., 1993). Pianka and Parker (1975) found that harvester ants constituted 69% of the stomach contents of preserved museum specimens. Horned lizards forage near ant mounds and ant foraging trails (Whitford and Bryant, 1979; Munger, 1984a, 1984c). Adult lizards often visit several ant mounds every day (Munger, 1984a, 1984b) and can eat 70–100 ants/day (Whitford and Bryant, 1979; Sherbrooke, 1981). Stomachs of Texas horned lizards are large (13% of body mass) to hold large quantities of ants, which are hard to digest (Carpenter et al., 1993). Lizards also feed on grasshoppers, isopods, other ant species, beetles, and beetle larvae (Davis, 1941; Pianka and Parker, 1979; Whitford and Bryant, 1979; Cohen and Cohen, 1990). They obtain water through ingested food, licking dew from plants, metabolism, and rain harvesting (Sherbrooke, 1981, 1990; Montanucci, 1989).

Texas horned lizards tend to have bimodal activity patterns in summer. They are usually most active during mid-morning and late afternoon. Peak feeding activity of the lizards coincides with the peak feeding activity of harvester ants (Whitford and Bryant, 1979; Munger, 1984a). Texas horned lizards seek shelter and remain inactive during the hottest parts of the day by climbing into shrubs, burrowing beneath the soil, and resting in shaded areas (Whitford and Bryant, 1979; Sherbrooke, 1981). Mean critical thermal minimum is 9.5° C, mean critical thermal maximum is 47.9° C, and mean preferred body temperature is 38.5° C (Prieto and Whitford, 1971). Horned lizards hibernate under the soil surface, rocks, or wood or in abandoned animal burrows during autumn and winter (Peslak, 1985; Garret and Barker, 1987). Most Texas horned lizards have begun hibernation by October (Munger, 1984a).

Texas horned lizards have restricted home ranges (Munger, 1984a). They can move an average of 46.8 m/day (Whitford and Bryant, 1979). Socially, a horned lizard generally is considered non-territorial and non-aggressive (Carpenter et al., 1993), although several authors have reported social interactions that involve dominance displays (Lynn, 1965; Sherbrooke, 1987) and even combat (Whitford and Whitford, 1973; Peslak, 1986).

Despite their spiny defenses, Texas horned lizards have numerous predators, including mammals, birds, snakes, and other lizards (Miller, 1948; Milne and Milne, 1950; Sherbrooke, 1981; Munger, 1986). Juveniles are more vulnerable to predation than adults (Pianka and Parker, 1975) because of their small size and undeveloped spines (Sherbrooke, 1981). Unlike most phrynosomatid lizards, Texas horned lizards usually remain still when approached by a predator, relying on their cryptic coloration and spines to avoid predation (Pianka and Parker, 1975; Munger, 1984a, 1986). Other methods used to avoid detection include retreat, burrowing into the soil, inflation of the torso, and defensive stances (Sherbrooke, 1981, 1990; Peslak, 1985). Defensive stances include arching the back and rocking back and forth on all limbs while facing the predator and standing perpendicular to the predator and then raising the side of the body closest to the predator and lowering the opposite side while the body is dorsoventrally flattened. Additional predator-avoiding tactics include hissing, lunging toward the predator, biting, jabbing with the occipital spines, and ejecting blood from orbital sinuses (Burleson, 1942;

Heath, 1966; Milne and Milne, 1950; Stebbins, 1954; Sherbrooke, 1981; Lambert and Ferguson, 1985; Peslak, 1985).

Texas horned lizards mate soon after they emerge from their winter burrows. Females excavate slanted holes 12–17 cm deep (Garret and Barker, 1987) and lay a mean clutch of 26.5 eggs (Pianka and Parker, 1975). The female deposits eggs in 2–3 layers and covers each layer with soil (Reeve, 1952; Sherbrooke, 1981). The female covers the excavated hole with soil after all eggs are deposited (Hewatt, 1937) and then rakes the soil surface to help hide the nest. She may stay at the nest overnight but leaves and never returns by the next day (Ramsey, 1956; Sherbrooke, 1981). Incubation is 5–9 weeks, depending on ground temperature, cloud cover, and soil moisture (Ramsey, 1956; Sherbrooke, 1981; Peslak, 1985; Garret and Barker, 1987).

Texas horned lizards have decreased in range and abundance in Oklahoma over the past several decades. Although exact causes for the decline of Texas horned lizards in Oklahoma are not known, several possible factors have been identified. These include 1) habitat alteration, 2) urban expansion, 3) use of insecticides, which kill their main food supply (harvester ants) and may be toxic to the lizards and their eggs, 4) heavy lawn watering and agricultural irrigation, 5) collection of lizards for pets, 6) predation by feral cats and cattle egrets, and 7) death caused by automobiles (Carpenter et al., 1993).

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Chapter II

HABITAT USE OF THE TEXAS HORNED LIZARD IN NORTH-CENTRAL OKLAHOMA

HABITAT USE OF THE TEXAS HORNED LIZARD IN NORTH-CENTRAL OKLAHOMA

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ABSTRACT. — Habitat use of Texas horned lizards (Phrynosma cornutum) at two study sites (AF and SF) in north-central Oklahoma was examined at the macro- and microhabitat levels during summer 1998 (at AF) and 1999 (at AF and SF) using compositional analysis. Texas horned lizards were sensitive (use and availability differed significantly) to patches of macrohabitat at AF in 1998 and indifferent to patches of macrohabitat in 1999 at AF and SF. The summer of 1998 was the fourth hottest summer on record for Oklahoma, and lizards actively selected patches of vegetation to take cover from the heat of the day. Microhabitats were used significantly different than available in all cases (AF 1998 and 1999; SF 1999), and bare ground, grass, herbaceous vegetation, leaf litter, and gravel were used most. Bare ground provided basking sites and areas to forage for ants, their main prey source, vegetation offered refuge from environmental stresses and predators, and a gravelly substrate helped conceal the lizards from predators.

Keywords: Phrynosoma cornutum; habitat selection; compositional analysis; availability; microhabitat; macrohabitat

The Texas horned lizard, Phrynosoma cornutum, was once abundant in Oklahoma and found throughout the state except for the southeastern corner. Over the past several decades, this species has decreased in range and abundance in Oklahoma (Price, 1990; Carpenter et al., 1993) and Texas (Donaldson et al., 1994). Numerous possible causes for its decline have been identified, including habitat alteration and urban expansion (Carpenter et al., 1993; Donaldson et al., 1994). Scientific research on this species in Oklahoma has been limited to a population census (Carpenter et al., 1993), so studies of the ecology of Texas horned lizards in Oklahoma are necessary to help conserve this species.

Knowledge of habitat use is a prerequisite for the effective conservation of any species. An adequate understanding of habitat use by a species requires researchers to identify and quantify possible habitat selection. An animal's use of a particular habitat is the result of habitat selection at more than one level (Wiens, 1973; Johnson, 1980). For example, a lizard may choose to forage in one habitat rather than three others nearby, but first has to choose the general area that includes all four habitats. Johnson (1980) identified an ordering of habitat selection processes. He defined first-order selection as the selection of the geographic range of the species. Second-order selection occurs next and is defined as the selection of the home range of an individual or a social group. Third-order selection is the selection of sub-areas within the home range, and fourth-order selection is the selection of food items within the sub-areas.

I examined habitat use of Texas horned lizards in north-central Oklahoma at the second and third-orders of selection. Here, I use the terms macrohabitat selection and microhabitat selection rather than second-order selection and third-order selection, respectively, because my definitions of levels of habitat selection differ slightly from those of Johnson (1980). I define macrohabitat selection as the selection of broad habitat categories such as large (> 2 m^2) areas of grassy and herbaceous vegetation and large areas of open, bare ground; and microhabitat selection as the selection of specific habitat sub-areas such as patches of embedded rock or gravel within the broader macrohabitat category. Field methods to assess both levels of habitat selection were different and specific to that level.

Gathering data on habitat use first requires information about the exact locations of the study animals. In the past, researchers have used methods such as direct observation, trailing methods, radioactive tags, and radiotelemetry to track reptiles (Fellers and Drost, 1989). Each of these methods, although useful for many species, has disadvantages if used to track Texas horned lizards. Direct observation does not work well for very cryptic animals (Fellers and Drost, 1989) such as the Texas horned lizard. Additionally, it is labor-intensive and presence of the researcher may affect the behavior of the animal (Blankenship et al., 1990). Trailing methods, such as the spool-and-line method, are useful only for larger animals (Fellers and Drost, 1989) such as turtles, and they are limited by the amount of string on the spool (Blankenship et al., 1990). Use of radioactive tags does not provide the researcher with information on the exact movements of the animal between points of recapture (Fellers and Drost, 1989). Furthermore, use of radioactive tags requires the researcher to attain special equipment, licensing, and special training. Radioactive tags also may be hazardous to animals and the researcher (Butler and Graham, 1993). Radiotelemetry is expensive and, like radioactive tags, is not precise in determining exact movements of lizards (Blankenship et al., 1990). Attached radio transmitters also may affect natural behavior of lizards (Butler and Graham, 1993).

An alternative method to assess movement is fluorescent powder. Researchers have successfully used fluorescent powder to track small mammals (Lemen and Freeman, 1985), tortoises (Blankenship et al. 1990; Butler and Graham 1993; Keller 1993), and lizards (Fellers and Drost 1989; Stark and Fox, in press). I used fluorescent powder to track Texas horned lizards because this method provided advantages over the other tracking methods. The fluorescent powder method allowed me to obtain exact locations of lizards by providing a continuous record of their daily movements (Stark and Fox, in press) and was relatively inexpensive.

My objectives were to (1) test for nonrandom habitat use by Texas horned lizards at the macro- and microhabitat levels, (2) rank macro- and microhabitats in order of relative use, (3) test for differences in habitat use between sexes and age classes, and (4) provide information that may help conserve this species in Oklahoma and generate additional research.

MATERIALS AND METHODS

I used fluorescent powder (Stark and Fox, in press) to track Texas horned lizards on two urban study sites in Payne County, Oklahoma (36° 06' 30" N and 97° 01' 30" W) which I named Antique Field (AF) and South Field (SF) (Figures 1 and 2). AF was a 2-ha site with flat terrain that contained areas of dense grassy and herbaceous vegetation (substrate was not visible through the vegetation), open areas of bare ground and sparse vegetation, and a small area of sand with sparse vegetation (Table 1 and Figure 1). The dominant grasses at AF were little bluestem (Schizachyrium scoparium), silver bluestem (Bothriochloa saccharoides), and switchgrass (Panicum virgatum), and the dominant forbs were Himalayan bush clover (Lespedeza cuneata), Illinois bundleflower (Desmanthus illinoensis), and western ragweed (Ambrosia psilostachya). SF was 4.4 ha with flat terrain located about 0.40 km southwest of AF. This site consisted mostly of dense grassy and herbaceous vegetation but also contained open areas of sparse vegetation (Table 1 and Figure 2). Dominant grasses at SF were little bluestem (Schizachyrium scoparium), Japanese brome (Bromus japonicus), and tall dropseed (Sporobolus asper). The dominant forbs were annual broomweed (Gutierrezia dracunculoides), Himalayan bush clover (Lespedeza cuneata), and western ragweed (Ambrosia psilostachya). Lizards were tracked at AF over two field seasons: 2 May - 6 August 1998 and 8 May - 25 July 1999. At SF, lizards were tracked only during the second field season: 28 May - 25 July 1999.

I used visual searches to locate lizards that consisted of 1–3 researchers walking parallel lines until the entire study area was searched. I located 24 horned lizards at AF in 1998 (4 females, 12 males, 8 juveniles; mean adult female mass, 16.0 g; mean adult male mass, 11.4 g; mean juvenile mass, 1.4 g; mean adult female snout-vent length, 60.0 mm; mean adult male snout-vent length, 57.2 mm; mean juvenile snout-vent length, 29.5 mm) and 25 in 1999 (10 females, 6 males, 9 juveniles; mean adult female mass, 13.9 g; mean adult male mass, 13.3 g; mean juvenile mass, 2.4 g; mean adult female snout-vent length, 54.3 mm; mean adult male snout-vent length, 57.2 mm; mean juvenile snout-vent length, 34.4 mm). At SF, I located 15 horned lizards (6 females, 7 males, 2 juveniles; mean adult female mass, 23.2 g; mean adult male mass, 15.0 g; mean juvenile mass, 3.0 g; mean adult female snout-vent length, 64.7 mm; mean adult male snout-vent length, 59.3 mm; mean juvenile snout-vent length, 38.3 mm). After capture, a lizard was toe clipped for future identification, dipped in the flourescent powder, and released at the place of capture (Figure 3). The trail of powder was tracked that night with a portable ultra-violet lamp. Every 5 m along the trail of powder, a marker flag was placed in the ground.

The following day, I used a 0.25-m^2 quadrat to estimate microhabitat use. The quadrat was placed over a flag so that the flag was in the center of the quadrat and I estimated the percentages of microhabitat categories within the quadrat. (It is important to note that although this method allowed me to determine the exact movements of lizards, I could not determine how long a lizard spent at a particular location.) I then estimated percentages of microhabitat categories within the quadrat at a location 5 m from the trail for every flag on the trail to get a measure of microhabitat availability. I determined the direction I would pace from the trail to get a measure of availability by looking at the second hand on my watch and pacing in the direction that the second hand was pointing. Microhabitat categories included: bare ground, grass, gravel (< 10 mm diameter), cobble (10 - 50 mm diameter), boulder (> 50 mm diameter), embedded rock, herbaceous vegetation, leaf litter, ant mound, woody vegetation, and sand.

A macrohabitat was an area of dense vegetation, sand, or sparse vegetation that was greater than about 2 m^2. Macrohabitat use was measured using aerial photography and a geographic information system (GIS) at AF in 1998 and in the field at both sites during the1999 field season. I also used a GIS and aerial photography to determine availability of macrohabitats at both study sites. Before the aerial photographs were taken, I set up a grid system on each study site using survey equipment so that the X-Y coordinates of all lizard locations could be determined. I painted a large symbol at four outer posts of each grid system and used those markers to reference aerial photographs of each site to its grid system using ArcView and the Spatial Analyst extension (ESRI Inc., Redlands, California). I digitized photographs of the study sites on screen in ArcView to create habitat maps. Three macrohabitats were available at AF: open or sparsely vegetated, densely vegetated, and sand (Figure 1 and Table 1). Two macrohabitats were available at SF: open and densely vegetated (Figure 2 and Table 1). To obtain macrohabitat availability at the sites during both years, the XTOOLS extension was used to calculate the area of each site and each macrohabitat category. To obtain proportional macrohabitat use of individual lizards during the 1998 field season at AF, the X-Y coordinate data file of the lizard locations was brought in as an event theme and overlayed on the habitat map, and the observed number of instances in each macrohabitat was determined by querying lizard locations by individual toe-clip numbers. I obtained macrohabitat use at both sites during 1999 by recording the macrohabitat at each flag.

Macro- and microhabitat use was analyzed using compositional analysis (Aebischer et al., 1993), the log-ratio analysis of compositions, because it has advantages over other resource-use analyses (Aebischer et al., 1993; Friedman, 1937; Neu et al., 1974; Johnson, 1980). Compositional analysis uses the number of animals rather than locations as the sampling unit, so the apparent number of degrees of freedom is not inflated (increase in Type I error), and the independence of sequentially collected animal locations is not required (Aebischer et al., 1993). Log ratios of use and availability data are used to avoid the unit-sum constraint (proportional use must sum to 100% over all habitats) so that use of each habitat is independent of use of other habitats (Aitchison, 1986; Aebischer et al., 1993).

Compositional analysis uses a multivariate analysis of variance (MANOVA) procedure to test, simultaneously, over all habitat types at a study site if differences in log-transformed use and availability data are different than zero ($P < 0.05$), indicating habitat selection. We used proportional habitat use by individual horned lizards for the analyses. If horned lizards selected habitats differently from their availability, compositional analysis ranked habitats in order of relative use using a matrix of pair-wise differences between matching log-ratios of use and availability data averaged over all lizards, where the habitat of the row was the numerator and the habitat of the column was the denominator.

The number of positive values occurring in each row was used to rank habitats in order of relative use, a 0 indicating the least relatively used habitat. For each matrix element, a *t*-value was calculated from the ratio mean and standard error so that significant differences in use among habitats was determined (Aebischer et al., 1993). We also used MANOVA to test for differences in macro- and microhabitat use among males, females, and juveniles, between males and females, and between adults and juveniles at AF, and in microhabitat use among age/sex classes at SF. We performed ANOVAs to test for differences in macrohabitat use among age/sex classes at SF because only two macrohabitats were available.

RESULTS

Macrohabitat Use.— Macrohabitat use of Texas horned lizards was nonrandom at AF in 1998 (Lambda = 0.55, $X^2 = 11.27$, $P < 0.05$), and macrohabitats were ranked in the following order of relative use: densely vegetated > open > sand. No differences were found in use of densely vegetated and open ($P = 0.14$), densely vegetated and sand ($P = 0.10$), or open and sand ($P = 0.14$). There were no differences in macrohabitat use between females, males, and juveniles (Lambda = 0.77, $F = 1.04$, $P = 0.40$), females and males (Lambda = 0.91, $F = 0.63$, $P = 0.55$), or adults and juveniles (Lambda = 0.84, $F = 1.50$, $P = 0.25$).

We did not find a difference in macrohabitat use and availability in 1999 at AF (Lambda = 0.91, $X^2 = 2.18$, $P = 0.34$) or SF (Lambda = 0.94, $X^2 = 0.94$, $P = 0.33$). No differences were found at AF in macrohabitat use between females, males, and juveniles (Lambda = 0.90, $F = 0.54$, $P = 0.71$), females and males

(Lambda = 1.0, $F = 0.01$, $P = 1.0$), or adults and juveniles (Lambda = 0.90, $F = 1.16$, $P = 0.33$), and macrohabitat use at SF did not differ between females, males, and juveniles ($F = 1.07$, $P = 0.38$), females and males ($F = 0.963$, $P = 0.35$), or adults and juveniles ($F = 1.15$, $P = 0.30$).

Microhabitat Use.— Microhabitat use by Texas horned lizards was nonrandom at AF in 1998 (Lambda = 0.04, $X^2 = 54.38$, $P < 0.0001$), AF in 1999 (Lambda = 0.08, $X^2 = 59.46$, $P < 0.0001$), and SF in 1999 (Lambda = 0.13, $X^2 = 26.23$, $P < 0.001$). Microhabitats not used and/or available during a field season were not used in analyses. These microhabitats included boulder at AF in 1999, and boulder, ant mound, and woody vegetation at SF in 1999. The five highest ranking microhabitats (most used) were bare ground, leaf litter, grass, herbaceous vegetation, and gravel in all three cases, although not always in the same order (Table 2).

At AF in 1998, bare ground was used significantly more than all other microhabitats. Boulder was used less than all other microhabitats and significantly less than bare ground, grass, herbaceous vegetation, leaf litter, and ant mound (Table 3). At AF in 1999, bare ground was used more than all other microhabitats but not significantly more than grass, herbaceous vegetation, and leaf litter. Ant mounds were used significantly less than all microhabitats except sand and embedded rock (Table 4). At SF in 1999, grass was used relatively more than the other microhabitats, but only significantly more than sand and leaf litter. Sand was used significantly less than all other microhabitats (Table 5).

At AF in 1998 and AF and SF in 1999, I did not find any differences in

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microhabitat use between females, males, and juveniles (Lambda = 0.11, F = 1.42, P = 0.25; Lambda = 0.38, F = 0.97, P = 0.52; Lambda = 0.14, F = 1.23, P = 0.38), females and males (Lambda = 0.21, F = 1.14, P = 0.52; Lambda = 0.59, F = 0.54, P = 0.81; Lambda = 0.21, F = 2.16, P = 0.24), or adults and juveniles (Lambda = 0.33, F = 1.64, P = 0.25; Lambda = 0.56, F = 1.34, P = 0.30; Lambda = 0.39, F = 1.34, P = 0.37). Adult horned lizards tended to bed in dense vegetation only; juveniles bedded in both vegetation and in small indentations in the ground. Only one lizard that we tracked to a sleeping spot had burrowed into the substrate.

DISCUSSION

Organisms respond to a hierarchy of patches (areas that differ from their surroundings in some manner and contain interior patches that exist at a finer scale) when selecting habitats. This hierarchy of patches ranges from the finest "grain" to the largest "extent," and extremes of a hierarchical mosaic of patches vary from species to species. A species is patch sensitive when it responds to a patch of a certain scale, and patch indifferent when it does not respond (Kotliar and Weins, 1990). Texas horned lizards were sensitive to patches of macrohabitat at AF in 1998 and indifferent to patches of macrohabitat in 1999 at AF and SF.

Oklahoma experienced a heat wave during summer 1998, resulting in the fourth hottest summer on record. There were 40 days when the temperature exceeded 38 ^{0} C, and 16 of these days occurred consecutively. By way of comparison, summer 1999 experienced only 16 days > 38 ^{0} C, few of which were

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consecutive. The patch level that I defined as macrohabitat was significant to the Texas horned lizards only during the warmer-than-average year, and dense vegetation was the relatively most used macrohabitat. Dense vegetation provides horned lizards refuge from the heat of the day, whereas open and sandy areas do not. Temperatures hotter than average may have forced lizards to select at this scale of habitat when they would otherwise be sensitive to only a finer scale. I suggest that during a normal summer, Texas horned lizards may be indifferent to the macrohabitat level because temperatures are not high enough to necessitate refuging into dense vegetation. Thus, lizards can select habitat at a finer scale.

It is likely that many organisms adjust their scale of habitat selection along the hierarchy of patches available to them, especially so during episodes of abnormal weather, such as a drought or hot spell. Likewise, this hierarchy probably differs among populations of a species with a broad geographic range. Thus, it is important to study habitat needs of a species over multiple years so that a range of climatic factors is observed and to study habitat needs of intraspecific populations that occur in distinct eco-regions.

Patches that I defined as microhabitats existed within the hierarchy of habitat patches used by Texas horned lizards in north-cental Oklahoma because microhabitat use was significantly different than available in all three instances (AF 1998, AF 1999, and SF 1999). Bare ground, grass, herbaceous vegetation, leaf litter, and gravel were used most, although they did not always rank in the same order.

Bare ground was the most used microhabitat at AF during both years and

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the third highest category at SF. Texas horned lizards emerge in mid-morning to bask, and areas of bare ground provide basking habitat. Also, horned lizards are sit-and-wait foragers that prefer to use open areas (Pianka, 1966). Basking and foraging are not mutually exclusive activities; horned lizards are known to forage while they are basking (Whitford and Bryant, 1979; Munger, 1984c).

Texas horned lizards are primarily myrmecophagous and may have a dietary preference for harvester ants (Pogonomyrmex sp.) (Pianka and Parker, 1975; Whitford and Bryant, 1979; Sherbrooke, 1981; Munger, 1984a, 1984b, 1984c; Whiting et al., 1993). Munger (1984c) found that Texas horned lizards obtained most of their ants by foraging at or near colony entrances. However, Whitford and Bryant (1979) found that Texas horned lizards took few ants at mound entrances. Ant mounds ranked low at AF in 1998 and 1999 and were never used at SF. Foraging away from ant mounds, and at several ant trails, may help ensure that ants of any mound are not reduced below the level that would cause the mound to stop outside activity, and hence, reduce prey availability (Whitford and Bryant, 1979).

Boulder was the least used microhabitat at AF in 1998 and was not used in the analysis at AF or SF in 1999 because the category was used only once by a single lizard at both sites and was never located as available when measuring microhabitat availability. Boulders are likely unimportant for Texas horned lizards, unlike many other phrynosomatids, and use of boulders may even be disadvantageous for this species. As ant specialists, horned lizards must consume large numbers of their prey because ants are small and contain copious undigestible chitin. This diet requires lizards to have a large stomach for

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their body size, resulting in reduced sprint performance (Pianka, 1994). Because horned lizards lack the sprint speed needed to quickly escape to cover that is seen in many other lizards with slender body forms, natural selection has favored phenotypes that possess cryptic characteristics that allow them to blend in with the substrate while foraging for ants (Pianka, 1994). A lizard perched on top of a boulder may lose the benefit of a body shape and coloration that has been selected for such crypsis.

Vegetative categories of microhabitat (grass, herbaceous vegetation, leaf litter) can provide cover from stressful environmental conditions and predators. Although it has been predicted that the shape of a Texas horned lizard's body would make travel through dense vegetation difficult (Whiting et al., 1993; Fair and Henke, 1997), I found that Texas horned lizards often traveled through areas of dense vegetation for extended distances rather than just entering vegetation and taking refuge near an open area. Traveling through dense vegetation may, at times, be advantageous for a cryptic sit-and-wait forager because movement in the open is more likely to attract the attention of a predator. Plus, food may be available in dense vegetation. Although harvester ants were not present at AF, several other small species of ants did inhabit AF, and these ants were found both in the open and in dense vegetation. Hence, it is possible that the horned lizards used dense vegetation to forage and to take refuge. Harvester ants were abundant at SF and were not found in dense vegetation. Nevertheless, horned lizards still traveled extensively through dense vegetation even at this site. Grass also was used more than bare ground at SF, although not significantly more.

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Gravel was the fifth most used microhabitat in all cases and always ranked higher than cobble or embedded rock. Texas horned lizards have dark spots with rims of yellow or white and small spines on their dorsum, a pattern that resembles a substrate of small grains of gravel more so than ground covered with cobble or embedded rock. Hence, it may be advantageous for a Texas horned lizard to select a gravelly substrate rather than ground covered by small stones or embedded rock. Also, food may be less plentiful in these latter microhabitats.

My results indicate that areas of dense vegetation are as important as open areas of bare ground and sparse vegetation for Texas horned lizards. I suggest that habitat suitable for this species should contain an abundant source of ants and a patchwork of bare ground and dense vegetation. However, because loss of habitat is likely a contributing factor to the decline of Texas horned lizards, quantitative information on the preferred ratio of bare ground and dense vegetation (and absolute amounts of each) would be helpful if restoration efforts for this species are attempted.

Acknowledgments.– This work was part of a study on the space and habitat use of Texas horned lizards in Oklahoma. Financial support was provided by the Wildlife Diversity Program of the Oklahoma Department of Wildlife Conservation, the Department of Zoology at Oklahoma State University, and the Oklahoma Cooperative Fish and Wildlife Research Unit (Okla. State Univ., Okla. Dep. Wildl. Conserv., U.S.G.S. Biol. Resour. Div., and Wildl. Manag. Inst., cooperating). I thank ARC Communities and Lambert Construction for allowing me to conduct

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TABLE 1. Area (ha) and percentage of macrohabitats available to Texas horned lizards at AF in 1998 and 1999 and SF in 1999.

Site	Macrohabitat	Area (ha)	Percent
AF	Open/sparse vegetation	0.90	45.45
	Dense vegetation	1.06	53.54
	Sandy	0.02	1.01
SF	Open/sparse vegetation	0.54	12.40
	Dense vegetation	3.86	87.60

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TABLE 2. Rankings of microhabitats used by Texas horned lizards at AF in 1998 and 1999 and SF in 1999. BG = Bare Ground, HV = Herbaceous Vegetation, ER = Embedded Rock, LL = Leaf Litter, AM = Ant Mound, WV = Woody Vegetation; >>> indicates a significant difference between two consecutive microhabitats.

Site and year	Microhabitat Rankings
AF 1998	BG >>> LL > Grass > HV > Gravel > Cobble > AM > Sand > ER > WV > Boulder
AF 1999	BG > HV > Grass > LL > Gravel > Cobble > WV > ER > Sand > AM
SF 1999	Grass > HV > BG > LL > Gravel > ER > Cobble >>> Sand

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TABLE 3. Matrix of microhabitat rankings for AF 1998 where 10 is the highest ranking habitat. A positive value indicates the habitat of the row was used relatively more than the habitat of the column and a negative value indicates that habitat was used relatively less. A 3 indicates a significant difference in use between habitats. BG = Bare Ground, HV = Herbaceous Vegetation, ER = Embedded Rock, LL = Leaf Litter, AM = Ant Mound, WV = Woody Vegetation.

Resource	Rank	BG	Grass	Sand	HV	ER	Gravel	Cobble	Boulder	LL	AM	WV
BG	10		3	3	3	3	3	3	3	3	3	3
Grass	8	-3		3	1	3	1	3	3	-1	3	3
Sand	3	-3	-3		-3	1	-1	-1	1	-3	-1	1
HV	7	-3	-1	3		3	1	3	3	-1	3	3
ER	2	-3	-3	-1	-3		-3	-1	1	-3	-1	1
Gravel	6	-3	-1	1	-1	3		1	1	-1	1	1
Cobble	5	-3	-3	1	-3	1	-1		1	-3	-3	-1
Boulder	0	-3	-3	-1	-3	-1	-1	-1		-3	-3	-1
LL	9	-3	1	3	1	3	1	3	3		3	3
AM	4	-3	-3	1	-3	1	-1	-1	3	-3		1
WV	1	-3	-3	-1	-3	-1	-1	-1	1	-3	-1	

TABLE 4. Matrix of microhabitat rankings for AF 1999 where 9 is the highest ranking habitat. A positive value indicates the habitat of the row was used relatively more than the habitat of the column and a negative value indicates that habitat was used relatively less. A 3 indicates a significant difference in use between habitats. BG = Bare Ground, HV = Herbaceous Vegetation, ER = Embedded Rock, LL = Leaf Litter, AM = Ant Mound, WV = Woody Vegetation.

Microhabitat	Rank	BG	Grass	Sand	HV	ER	Gravel	Cobble	LL	AM	WV
BG	9		1	3	1	3	3	3	1	3	3
Grass	7	-1		3	-1	3	1	3	1	3	3
Sand	1	-3	-3		-3	-1	-3	-1	-3	1	-1
HV	8	-1	1	3		3	1	3	1	3	3
ER	2	-3	-3	1	-3		-3	-1	-3	1	-1
Gravel	5	-3	-1	3	-1	3		1	-1	3	3
Cobble	4	-3	-3	1	-3	1	-1		-1	3	1
LL	6	-1	-1	3	-1	3	1	1		3	3
AM	0	-3	-3	-1	-3	-1	-3	-3	-3		-3
WV	3	-3	-3	1	-3	1	-3	-1	-3	3	

TABLE 5. Matrix of microhabitat rankings for SF 1999 where 7 is the highest ranking habitat. A positive value indicates the habitat of the row was used relatively more than the habitat of the column and a negative value indicates that habitat was used relatively less. A 3 indicates a significant difference in use between habitats. BG = Bare Ground, HV = Herbaceous Vegetation, ER = Embedded Rock, LL = Leaf Litter, AM = Ant Mound, WV = Woody Vegetation.

Microhabitat	Rank	BG	Grass	Sand	HV	ER	Gravel	Cobble	LL
BG	5		-1	3	-1	1	1	1	1
Grass	7	1		3	1	1	1	1	3
Sand	0	-3	-3		-3	-3	-3	-3	-3
HV	6	1	-1	3		1	1	1	1
ER	2	-1	-1	3	-1		-1	1	-1
Gravel	3	-1	-1	3	-1	1		1	-1
Cobble	1	-1	-1	3	-1	-1	-1		-1
LL	4	-1	-3	3	-1	1	1	1	

Figure Legends

FIG. 1. Available macrohabitat at AF, Stillwater, Payne County, Oklahoma. Open refers to areas of bare ground and sparse vegetation; Sand refers to a small area of sparsely vegetated sand; Trees refers to a small wooded area never used by the lizards; and Veg refers to areas of dense vegetation.

FIG. 2. Available macrohabitat at SF, Stillwater, Payne County, Oklahoma. Building refers to a small storage building; Veg refers to areas of dense vegetation; and Open refers to areas of bare ground and sparse vegetation.

FIG. 3. Photograph of a Texas horned lizard dipped in Fluorescent powder. I held the lizards by the head while dipping them to keep powder out of their eyes, nares, and ear openings.

Figure 1

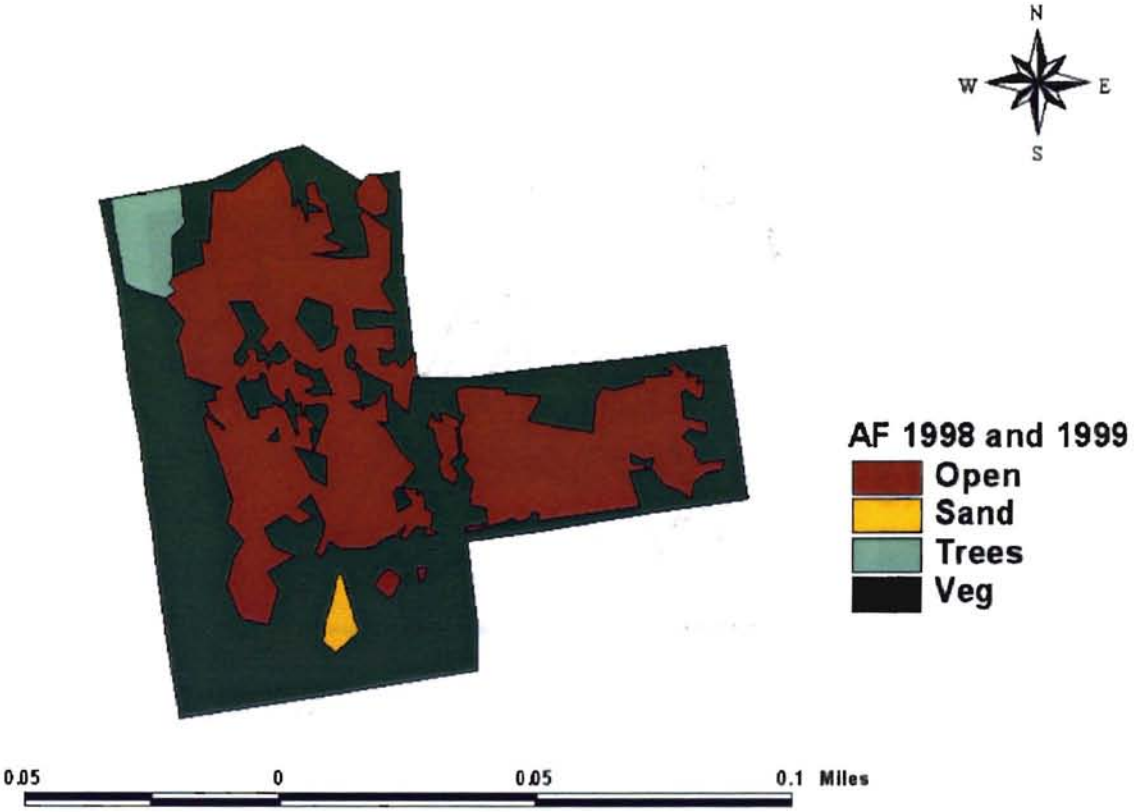

Figure 2

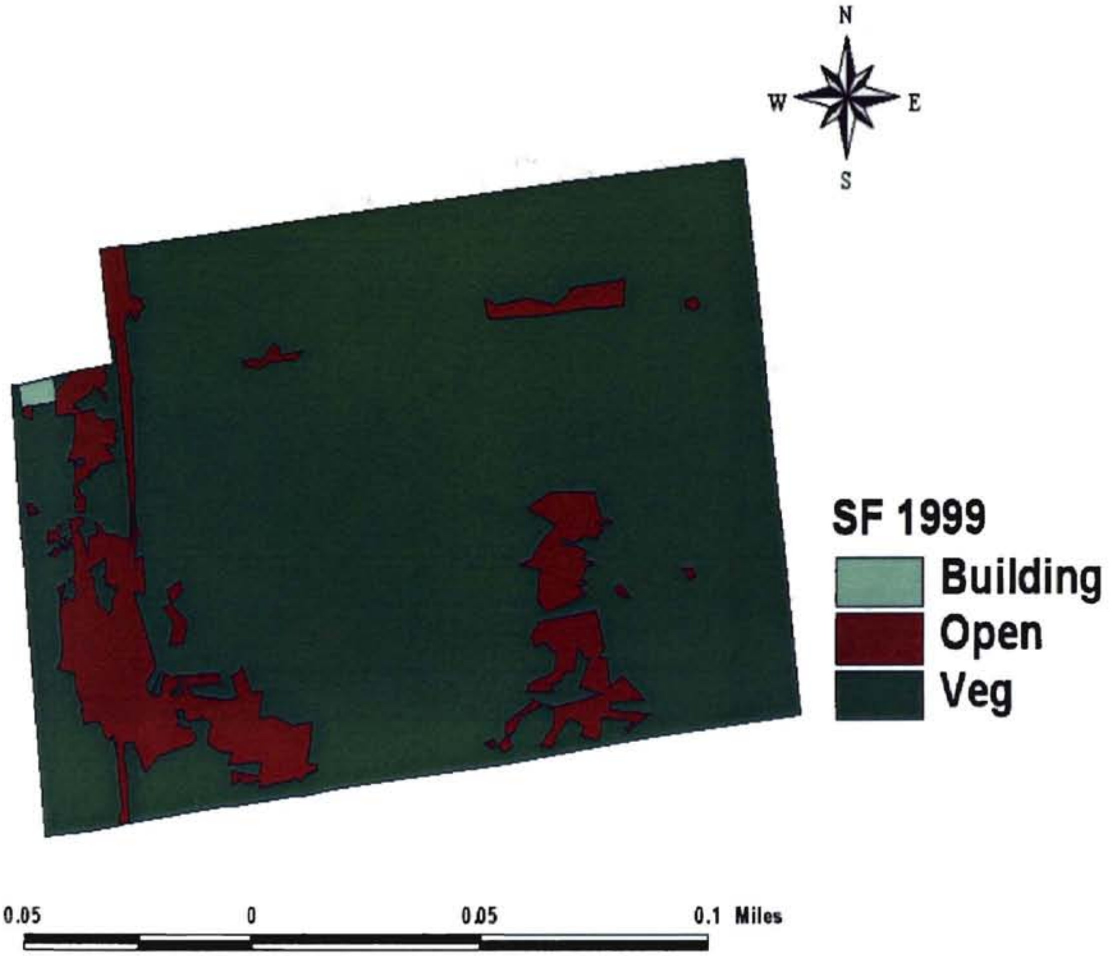

Figure 3

Chapter III

DAILY MOVEMENTS OF TEXAS HORNED LIZARDS IN NORTH-CENTRAL OKLAHOMA

DAILY MOVEMENTS OF TEXAS HORNED LIZARDS IN NORTH-CENTRAL OKLAHOMA

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ABSTRACT– Texas horned lizards, Phrynosoma cornutum, were tracked using fluorescent powder to determine exact daily movements. Daily linear movements and day home ranges among males, females, and juveniles, and between just males and females, were compared. Lizards that traveled the greatest linear distances also had the largest day ranges. In Oklahoma, adults emerge from hibernation in late April and early May and mate soon afterward. Males traveled significantly greater distances (and had significantly larger day ranges) than females in May but not after May. This difference in space use between sexes provides insight into selective pressures on this species and may be related to limited visibility of its patchy habitat. A possible mate searching polygyny model is applied to this species.

The Texas horned lizard, Phrynosoma cornutum, was once abundant in Oklahoma (Price, 1991; Carpenter et al., 1993) but has declined in abundance and distribution in the state over the past several decades; similar trends have occurred in Texas (Donaldson et al., 1994). Currently, the Texas horned lizard is a species of special concern in Oklahoma (ODWC, 1992) and threatened in Texas (Texas Parks and Wildlife Code, 1987).

Texas horned lizards are active from April to October (Potter and Glass, 1931; Munger, 1984a; Collins, 1993). They are considered diurnal (Stebbins, 1954; Whitford and Bryant, 1979; Munger, 1984a), although nocturnal activity has been reported (Williams, 1959). They tend to have bimodal activity patterns and are usually most active during mid-morning and late afternoon. Peak feeding activity of lizards coincides with peak feeding activity of ants (Whitford and Bryant, 1979; Munger, 1984a). Texas horned lizards seek shelter and remain inactive during the hottest parts of the day by climbing into a grass clump, burrowing beneath the soil, and resting in shaded areas (Whitford and Bryant, 1979; Sherbrooke, 1981). These lizards are reported to have restricted home ranges (Munger, 1984a) but most likely are not territorial (Whitford and Whitford, 1973; Stamps, 1977) because home ranges of individuals tend to overlap (Fair and Henke, 1999; Munger, 1984a) and territorial defense has not been documented (Stamps, 1983; Olsson and Madsen, 1998). Fair and Henke (1999) suggested that Texas horned lizards may have mobile weekly home ranges where individual lizards occupy only a part of their complete home range for several days and then move to a new section for several days, possibly to locate unharvested ant mounds. Conspecifics exhibit little overlap of these weekly ranges.

Information on daily space use of Texas horned lizards is very limited. In fact, daily movements of herpetofauna in general have mostly been ignored because cryptic characteristics and small size of many species make them difficult to track (Zug, 1993). Recently, however, techniques such as radio-telemetry (Fair and Henke, 1999; Fisher and Muth, 1995) and fluorescent powder (Blankenship et al., 1990; Butler and Graham, 1993; Keller, 1993; Lemen and Freeman, 1985; Stark and Fox, in press) have allowed researchers to track small and/or cryptic species.

A lizard's daily movements are generally for predator avoidance, feeding, thermoregulation, and mating. Knowledge of daily space use is important because it gives insight into a species' life history and selective pressures. Previously, researchers have gained information on daily movements of Texas horned lizards by adding linear distances between radiolocations for each day of radiotelemetry (Fair and Henke, 1999) and through observations (Whitford and Bryant, 1979), but these methods have disadvantages. It is likely that the distance covered by a lizard between two points is greater than a straight line between them, and presence of an observer may affect behavior of the animal (Blankenship et al., 1990; Munger, 1984a, b, c, 1986).

This paper presents a part of the findings of an investigation of the space and habitat use of Texas horned lizards in north-central Oklahoma. I used the fluorescent powder method to obtain space and habitat use data because it allowed me to track exact daily movements of lizards. Here I report the daily space use of Texas horned lizards and compare the daily linear movements and day ranges (total area within which all activity occurs during a day) of male, female, and juvenile horned lizards. Day ranges and daily linear movements were assessed because it was theoretically possible for a lizard to travel a greater linear distance than another lizard but to cover a smaller area if that individual remained in a small area and often crossed its own trail, while the other individual tended to travel to new areas.

METHODS AND MATERIALS — I conducted the study in Payne County, Oklahoma, on two urban study sites (36 ° 06' 30" N and 97 ° 01' 30" W) that I named Antique Field (AF) and South Field (SF). Both sites had flat terrain and areas of dense grass, and herbaceous vegetation, and open areas of bare ground and sparse vegetation. AF was a 2-ha site dominated by the grasses little bluestem (Schizachyrium scoparium), silver bluestem (Bothriochloa saccharoides), and switchgrass (Panicum virgatum). The dominant forbs were Himalayan bush clover (Lespedeza cuneata), Illinois bundleflower (Desmanthus illinoensis), and western ragweed (Ambrosia psilostachya). Lizards were tracked there over two field seasons: 2 May - 6 August 1998, and 8 May - 25 July 1999. SF was a 4.4-ha site about 0.40 km southwest of AF. Dominant grasses at SF were little bluestem (Schizachyrium scoparium), Japanese brome (Bromus japonicus), and tall dropseed (Sporobolus asper). The dominant forbs were annual broomweed (Gutierrezia dracunculoides), Himalayan bush clover (Lespedeza cuneata), and western ragweed (Ambrosia psilostachya). Lizards were tracked at SF only during the second field season: 28 May - 25 July 1999.

To locate lizards, I used visual searches that consisted of 1–3 researchers walking parallel lines until the entire study area was searched. I located 24 horned lizards at AF in 1998 (4 females, 12 males, 8 juveniles) and 25 in 1999 (10 females, 6 males, 9 juveniles). At SF, I located 15 horned lizards (6 females, 7 males, 2 juveniles). After capture, a lizard was toe clipped for future identification, dipped in the flourescent powder, and released at the place of capture (Fig. 1; Stark and Fox, in press). The trail of powder was tracked that night with the aid of a portable ultraviolet lamp, and a marker flag was placed in the ground every 5 m along the trail of powder to determine daily linear movements of the lizards.

I set up a grid system on each study site using survey equipment so that the X-Y coordinates of all lizard locations could be determined. The ArcView animal movements extension (Hooge and Eichenlaub, 1997) was used to delineate day ranges using 100% minimum convex polygons.

Kruskal-Wallis tests were used to compare daily linear distances traveled and day ranges among males, females, and juveniles, and between just males and females. Significance (at the 0.05 overall level) was determined using the sequential Bonferroni procedure for two related tests (Rice, 1989): daily linear distances and day ranges. Statistical tests reported as significant reflect these Bonferroni corrections. Only lizards that were tracked to their sleeping spots (end of the day's trail where the lizard had taken cover for the night), or lizards not tracked to their sleeping spots but that moved $\geq$ 50 m for adults and $\geq$ 10 m for juveniles were used in analyses (92.4% of tracking instances used in the analyses were to sleeping spots). Averages were used for lizards tracked on more than one occasion. I conducted tests on data collected in May alone (except at SF in 1999 where tracking did not begin until late May) and on data collected after 31 May (post-May) for each site and also on pooled data from both sites and years. The SYSTAT program (Wilkinson, 1990) was used to conduct statistical analyses.

RESULTS — Daily Linear Distances Traveled — The average daily movement of all lizards at AF in 1998 was 32.8 m (range = 5–80 m). Females, males, and juveniles differed significantly in daily distances moved in May but not after May, with males traveling greater linear distances in both cases (Fig. 2). When only adults were compared, males moved greater daily distances than females in May and after May, but differences were not significant. The average daily distance moved at AF in 1999 was 43.0 m (range = 5–185 m). Females, males, and juveniles differed significantly in daily distances moved in May only, and males traveled the greatest distances (Fig. 2). Comparing just adults, males and females differed significantly only in May, with males moving greater distances. At SF in 1999, the average daily movement was 28.1 m (range = 10–40 m). There were no significant differences between females, males, and juveniles; but females, on average, traveled the greatest linear distances (Fig. 2). Data collected in May alone were not available for this site because tracking did not begin there until 28 May.

For data pooled between sites and years, average daily movements of all lizards was 35.7 m (range = 5–185 m). Females, males, and juveniles differed significantly in May and after May, with males traveling notably greater distances in May (Fig. 2). For just adults, males moved significantly further than females in May, but not after May when their average daily movements were very similar.

Day Ranges — The average day range at AF in 1998 was 153.4 m^2 (range =

5.3–677.0 m^2). There were no significant differences in the size of day ranges between females and males in May (juvenile data were not available for May) or among females, males, and juveniles after May; however, day ranges of males were always greater than those of females and juveniles (Fig. 3). At AF in 1999, the average day range was 310.9 m^2 (range = 1.0–3011.4 m^2). Males, females, and juveniles differed significantly in May only, and males covered greater areas (Fig. 3). When only adults were compared, males had significantly larger ranges than females in May but not after May. The average day range at SF in 1999 (where only post-May data were available) was 61.7 m^2 (range = 2.5–221.6 m^2). Females had larger day ranges than males or juveniles, although not significantly larger (Fig. 3).

When sites and years were pooled, the average day range of all lizards was 194.9 m^2 (range = 1.0–3011.4 m^2). Females, males, and juveniles differed significantly in May but not after May (Fig. 3). Males had larger day ranges than females and juveniles, and when only adults were compared, sexes differed significantly in May but not after May.

Inconsistencies between daily linear distances traveled and size of the day range were not observed. Lizards that traveled the greatest linear distances also had the largest day ranges ($r = 0.95$, $P < 0.0001$). Contrary to my expectations, distances traveled by adult lizards (standardized as $(X_i - \overline{X})/SD$, where X_i is distance traveled by an individual, and $\overline{X}$ and SD are the mean and standard deviation of the sex/site class to which that individual belongs) did not relate to time of day when the lizard was dipped and released at AF in 1998 (r = 0.04, $df = 33$, $P > 0.50$), AF in 1999 ($r = 0.05$, $df = 35$, $P > 0.50$), or SF in 1999 (r

= 0.09, *df* = 22, *P* > 0.50). Time of day that an individual was dipped was not different between sexes at AF in 1998 (Mann-Whitney U-test, *Z* = 116.00, *df* = 1, *P* > 0.50), AF in 1999 (Mann-Whitney U-test, *Z* = 130.00, *df* = 1, *P* > 0.50), or SF in 1999 (Mann-Whitney U-test, *Z* = 78.50, *df* = 1, *P* > 0.50).

DISCUSSION — My results for the overall average daily movements of Texas horned lizards are similar to previous studies. Fair and Henke (1999) reported an average movement of 36.5 m/day (range = 0.0–246.7 m), and Whitford and Bryant (1979) reported an average of 46.8 m/day (range = 9–91 m).

In north-central Oklahoma, Texas horned lizards mate soon after they emerge from hibernation in late April and May, and, in this study, male lizards tended to move greater distances than females during this time, but not later. Females invest much more in initial parental investment than do males by producing relatively few but large, nutrient-rich immobile gametes, while males produce many tiny, mobile sperm. Males could potentially fertilize more eggs than are produced by a single female, so a male can increase its reproductive success by locating and copulating with many females during the breeding season (Trivers,1972; Stamps, 1983). One strategy to locate more females would be to increase home-range size (Stamps, 1983) or daily movements during the mating season. For males of non-territorial species, as is suspected for Texas horned lizards (Whitford and Whitford, 1973; Munger, 1984a; Fair and Henke, 1999), this strategy may work especially well because an increase in movements and home-range size beyond what is required for food acquisition and survival does not result in increased costs of defending a larger territory from other males (Stamps, 1983). Although a male's probability of parenthood is less when it does not defend a territory from other males for the breeding rights of the females within the home range (Stamps, 1983), the adequate defense of a territory requires a habitat in which visibility is good. Habitat in this study was a patchwork of bare ground and dense vegetation that would not provide good visibility for horned lizards. For example, an intruding male in a patch of bare ground mostly surrounded by vegetation may go unnoticed by the resident male if he is in another patch of bare ground on the opposite side of the vegetation. Such reduced visibility may be the norm for horned lizards in their typical habitat (Lynn, 1965) and may be responsible for the general lack of territorial assertion displays (Lynn, 1965).

The genus Phrynosoma is a monophyletic clade within the family Phrynosomatidae (Reeder and Weins, 1996). Most members of Phrynosomatidae are territorial (Martins, 1995), including the sister taxon of Phrynosoma, the so-called sand lizards (Uma, Callisaurus, Cophosaurus, and Holbrookia) (Gennaro, 1972; Stamps, 1983; Olsson and Madsen, 1998). Evidently, territoriality was present in the common ancestor of the sand lizards and the Phrynosoma clade but was lost as species of Phrynosoma appeared. Perhaps this loss of territoriality (and associated behavioral displays) occurred as a result of reduced visibility in the habitat of early horned lizards (or the way in which these lizards used their habitat), just as in the extant taxa of the genus today.

Compromised visibility (Lynn, 1965) also may play an important role in shaping possible strategies of sexes to increase reproductive success. If female horned lizards, as suggested for males, also mate with several partners during the mating season, and if multiple copulations with different males result in multiple paternity, as is common in reptiles (Smith, 1984; Olsson and Madsen, 1998; Schwartz et al., 1989; Barry et al., 1992; Olsson et al., 1994), both females and males could benefit. Both sexes could increase genetic diversity of their offspring, and females also could benefit by increasing chances that she has mated with a fertile male (but see Olsson and Shine, 1997). Additionally, if there is sperm competition (Parker, 1970) in the female's reproductive tract, females can select genetically superior males (Madsen et al., 1992; Birkhead and Moller, 1993; Olsson and Shine, 1997), in a way analogous to traditional female mate choice, which most likely is lacking due to the visibility constraints of the habitat. A male that travels considerable distances early in the season to locate and copulate with many females would benefit because he is increasing the chances that he will sire at least some of the offspring of each female he inseminates, thereby increasing his overall reproductive success. If sperm competition occurs, a male that mates with only one female runs the risk of siring none or very few offspring if that female also mates with a male with superior sperm (Madsen et al., 1992; Olsson et al., 1994). Thus, by moving about more to locate and copulate with numerous females early in the season when they are receptive (and if females mate with more than one male), both sexes could benefit by increasing genetic variability of their offspring. Moreover, a male could increase his reproductive success by siring at least a portion of the clutch of several females.

The mating system of Texas horned lizards suspected here is similar to a recently described mating strategy called "mate searching polygyny" (King and

Duvall, 1990). In this strategy, intrasexual selection works on traits of males that affect their ability to locate widely-dispersed females that are receptive in unison for a brief period of time, and males do not defend resources important to females. Differences in movements or activity during the breeding season between males and females has been reported for other reptiles (Morreale et al., 1984; Shine, 1987; Shine and Lambeck, 1990; Brown and Brooks, 1993; Thompson et al., 1999), and it is likely that males in other species also are under strong selection to cover considerable distances to locate many females early in the mating season to increase their reproductive fitness.

Juvenile horned lizards moved less than adults. Horned lizards are cryptic lizards and rely on camouflage and their sharp occipital spines to avoid predation. Occipital spines of juveniles, however, offer much less protection than the spines of adults (Pianka and Parker, 1975) because they are shorter and less sharp. When a juvenile remains motionless, however, it is very difficult to distinguish from the surrounding substrate (R. C. Stark, pers. observation), and, therefore, juveniles may benefit by restricting their movements. Juveniles also need only move to search for food and thermoregulate, whereas adults move to thermoregulate and search for food, nest sites, and mates.

This work was part of a study on the space and habitat use of Texas horned lizards in Oklahoma. Financial support was provided by the Wildlife Diversity Program of the Oklahoma Department of Wildlife Conservation, the

Department of Zoology at Oklahoma State University, and the Oklahoma Cooperative Fish and Wildlife Research Unit (Okla. State Univ., Okla. Dep. Wildl. Conserv., U.S.G.S. Biol. Resour. Div., and Wildl. Manag. Inst., cooperating). I thank ARC Communities and Lambert Construction for allowing us to conduct the study on their properties. I also thank John Dyer, Matt Sivils, and Joe Hackler for their valuable help in the field.

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FIGURE LEGENDS

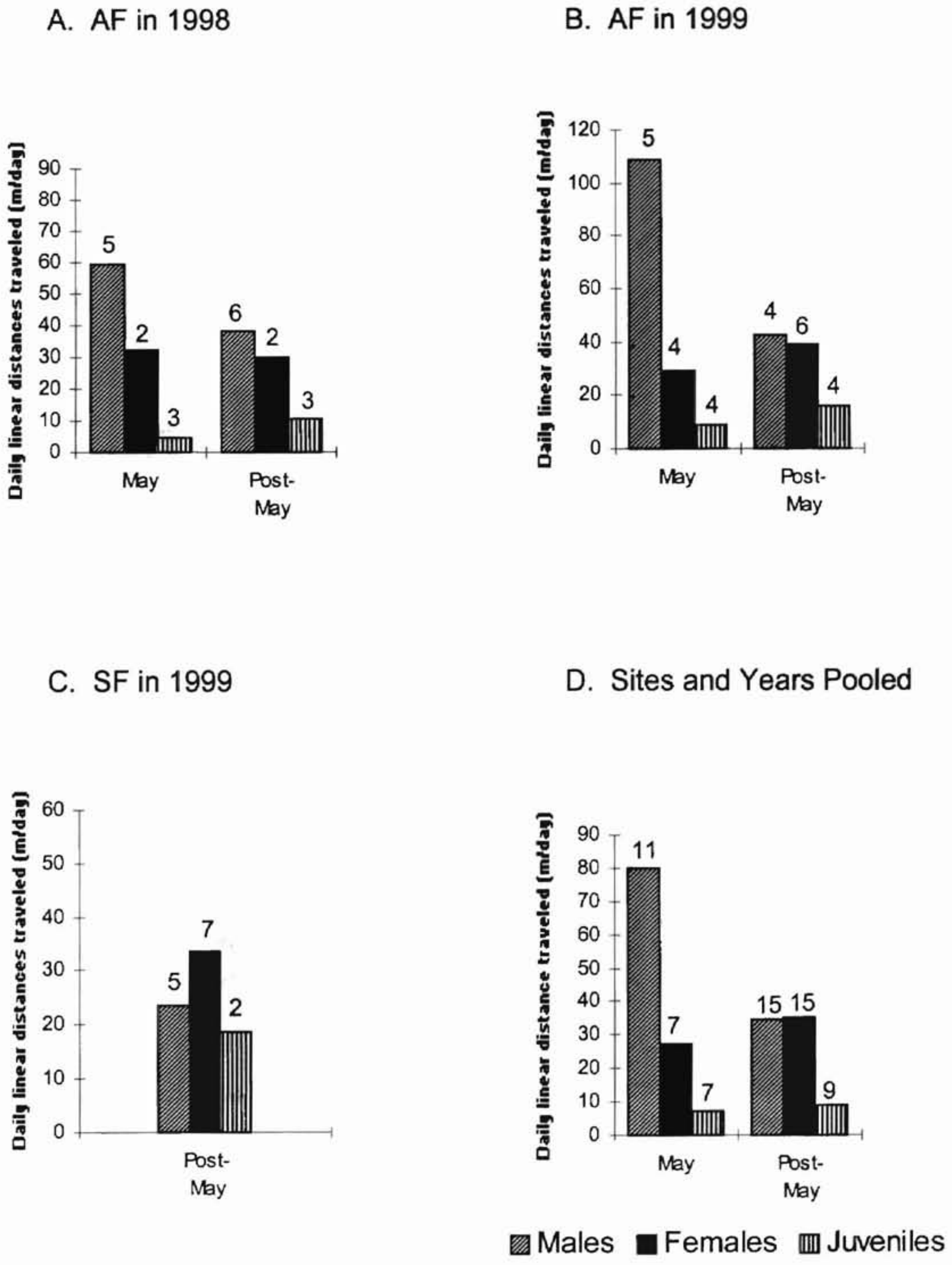
Fig.1.— A Texas horned lizard that has been recently dipped in fluorescent powder and released at the place of capture marked by a flag.

Fig. 2.— Mean daily linear distances traveled by males, females, and juveniles (N = numbers above bars) during May and after May at AF in 1998 and 1999, after May at SF in 1999, and during May and after May when sites and years were pooled.

Fig. 3.— Mean area covered daily by males, females, and juveniles (N = numbers above bars) during May and after May at AF in 1998 and 1999, after May at SF in 1999, and during May and after May when sites and years were pooled. Juvenile data were not available for May at AF in 1998. At SF in 1999, there were fewer males for day ranges than daily linear distances traveled because the flags of one male were lost before the coordinates were determined.

Figure 1

Figure 2


A. AF in 1998

B. AF in 1999

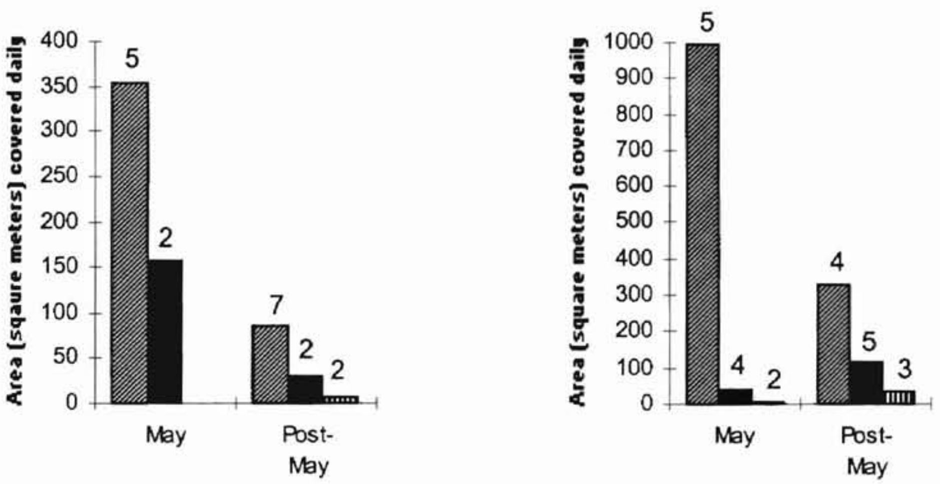
C. SF in 1999

D. Sites and Years Pooled

Figure 3

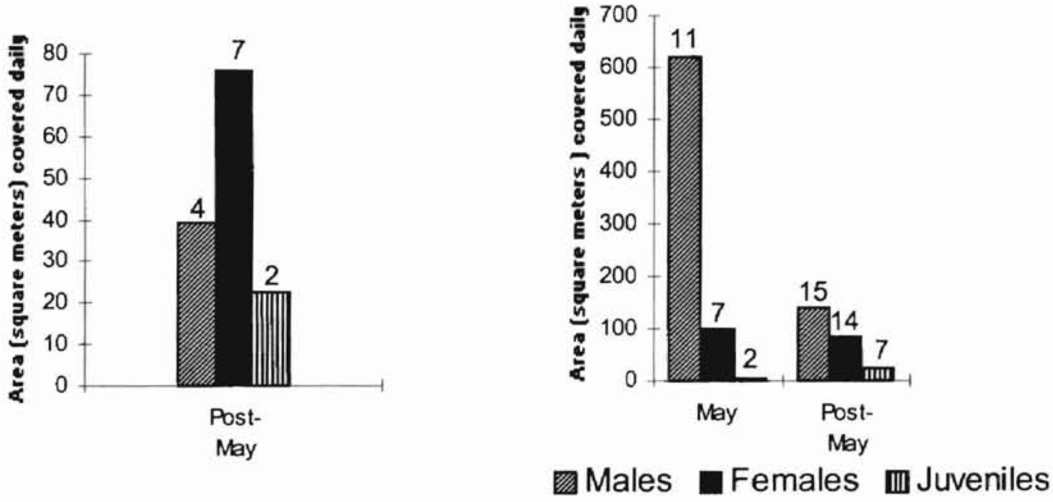
A. AF in 1998

B. AF in 1999



C. SF in 1999

D. Sites and Years Pooled



Chapter IV

VARIATION IN BODY SIZE AND SEXUAL SIZE DIMORPHISM BETWEEN TWO WIDELY SEPARATED POPULATIONS OF THE TEXAS HORNED LIZARD

Variation in Body Size and Sexual Size Dimorphism Between Two Widely Separated Populations of the Texas Horned Lizard

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Texas horned lizards (Phrynosoma cornutum) range from the northern states of Mexico through the southeastern corner of Arizona, the southern one-half, central and northeastern portions of New Mexico, and throughout most of Texas and Oklahoma to central Kansas (Price, 1990). Because the species is currently listed as threatened in Texas (Texas Parks and Wildlife Code, 1987), and as a species of concern in Oklahoma (ODWC, 1992), future studies may be needed for conservation purposes.

Studies on the basic biology of this species are limited, especially from Oklahoma populations. Here, I report results of a comparative study on body size and sexual size dimorphism (SSD) between a population in north-central Oklahoma and south Texas (Figure 1). Studies of this kind are important because there are numerous factors that may affect the distribution of adult body sizes in any population (Stamps, 1993), and studies of this type can provide insight into factors affecting individual populations.

I collected data on snout-vent length (SVL) from two urban study sites in north-central Oklahoma (36° 06' N and 97° 01' W) that I named Antique Field (AF) and South Field (SF). SF was located about 0.40 km southwest of AF. Lizards were located using visual searches, and SVL was measured to the nearest 0.1 mm using vernier calipers. All lizards were toe clipped for future identification and released at the place of capture. Lizards were sampled from AF during summers 1998 and 1999 and from SF during summer 1999. Data for the Texas population were collected by personnel at the Chaparral Wildlife Management Area (WMA) in southern Texas (28° 20' N and 99° 30' W) in 1991-1997 and generously made available by Chip Ruthven of the Texas Parks and Wildlife Department.

I tested for differences in adult body size and differences in SSD between the north-central Oklahoma (N = 48; 23F:25M) and Texas (N= 930; 555F:375M) populations using 2-way ANOVA on ranked data. In this ANOVA, a significant interaction between population and sex would indicate that size differences between sexes varied between the two populations (differential SSD) and also would require separate testing of all possible population x sex combinations (Oklahoma female vs. Texas female, Oklahoma male vs. Texas male, Oklahoma male vs. Oklahoma female, Texas male vs. Texas female). I considered 40-mm SVL the minimal adult length in the Oklahoma population because that is the minimum size that I could distinguish between the sexes. Although other authors have suggested a larger minimum adult size for Texas horned lizards such as 64 mm (Ballinger, 1974; Pianka and Parker, 1975) and 75 mm (Henke and Montemayor, 1997), those suggested adult sizes were for lizards in Texas, and lizards in the north-central Oklahoma population may mature at smaller sizes. For example, I observed a male and female mating with SVL of 53.8 and 56.0 mm, respectively, and a female with SVL of 67.5 mm excavating a nest. Also, only one lizard from the Oklahoma sample was larger than 75 mm (78.2 mm), and the overall mean adult SVL for Oklahoma was 56.6 mm.

I also attempted to estimate the maximal (asymptotic) size attained by both sexes of both populations and compare them. However, because of the large difference in sample size between the two data sets, the larger sample by chance may contain more large lizards, thus biasing the estimate of maximal possible size. Therefore, I conducted a randomization test (separately for each sex) that consisted of randomly selecting the same number of lizards from the Texas sample as in the Oklahoma sample (male, n = 25; female, n = 23) 10,000 times; calculating a mean for the five largest males and five largest females from the random samples; and comparing these means intrasexually to the invariant means for the five largest male and female lizards from Oklahoma. I chose to use the five largest lizards to represent the largest size class for individuals in the Oklahoma sample because the amount of inter-individual variance in size among the largest five males and females as determined by the coefficient of variation was less than the 5% level used in the "largest individual method" of Stamps and Andrews (1992) to estimate asymptotic size in another phrynosomatid lizard, Sceloporus merriami. (The program for the randomization test was created by Randy Tanner using Fox Pro.) Because data from the Texas population were collected over a 7-year period and data from Oklahoma were collected over just 2 years, 2-way ANOVA and a randomization test also were performed using data from Texas that were collected over a 2-year period only (1996-1997). ANOVAs were conducted using SYSTAT (Wilkinson, 1990).

There were no statistical differences between the entire Texas data set or the data set limited to a 2-year period, so the statistics reported here derive from tests using the entire Texas data set. Sexual size dimorphism varied between the Oklahoma and Texas populations (interaction of population x sex, $F = 7.6$, $df = 1, 974$, $p < 0.01$); therefore, LSD post-hoc tests were used to examine populations and sexes separately. Both sexes in the Texas population were significantly larger than their counterparts in the Oklahoma population ($p < 0.001$), and significant SSD was found only in the Texas population ($p < 0.001$), where females were larger than males (Figure 2).

Results of the randomization test were significant ($p < 0.001$); means of the five largest Texas lizards from the 10,000 random subsamples were larger than the Oklahoma means 100% of the time for both males and females. Thus, I conclude that the asymptotic size for both males and females is larger for the Texas population than for the Oklahoma population.

The geographic differences in body size cannot be determined from this study but could result from either a faster growth rate or better survivorship in Texas lizards compared with Oklahoma. Most evidence indicates that the latter possibility is more likely: Texas lizards are larger because they enjoy better survivorship than Oklahoma lizards and are thus able to live longer and grow larger on average. The two populations differed greatly in that the Oklahoma population was fragmented and located in an urban environment, whereas the Texas population occurred on a relatively undisturbed wildlife management area.

AF was bordered on the north by State Highway 51, on the east by a local street and buildings, on the south by a large trailer park, and on the west by a church and storage facility. SF was bordered on the north and east by the trailer park. Possible factors for increased mortality at the Oklahoma sites relative to the Texas site include high risk of death by automobiles when lizards attempt to cross or bask on the state highway and local neighborhood streets, increased predation by domestic and feral cats, and collection for pets by nearby residents. On numerous occasions, I witnessed stray cats on sites and heard several stories about pet horned lizards from local children.

The fact that Oklahoma lizards begin to reproduce at a much smaller size than those from Texas also lends support to the hypothesis of higher mortality at the Oklahoma sites. Organisms often adapt fecundity to survivorship, and Tinkle (1972) showed that to maximize individual fitness, phrynosomatid lizards in a population with heavy predation reproduced earlier than conspecifics in a population with lighter predation. Furthermore, lizards that reproduced earlier in life tended to remain smaller all their life compared with those that reproduced later (Tinkle, 1972).

Sexual size dimorphism where females are larger than the males in the Texas WMA population is not likely due to intersexual differences in growth rates. Henke and Montemayor (1997) marked and recaptured Texas horned lizards on the Chaparral WMA from 1991-1993 and found no difference in the growth rates between adult males and females. Rather, the difference may be a result of possible intersexual variation in survivorship. As noted above, if a population is characterized by greater survivorship, members of that population will be able to grow larger simply because they live longer. The same logic can be applied to the two sexes within a population. Male Texas horned lizards move greater distances than females early in the season, possibly searching for mates (Chapter 3). Other than their sharp dorsal spines, Texas horned lizards rely on their cryptic coloration to avoid predators (Pianka and Parker, 1975), and increased movement may result in greater exposure to predators and higher mortality in males. Consequently, females live longer and thus grow larger than males on average. Interestingly, the largest five lizards from the Oklahoma population were all females, and, although not significant, the females in the Oklahoma population tended to be larger than the males (Figure 2). But I maintain that males and females in the Oklahoma population suffer such high mortality that SSD never develops to a significant degree. If they were to live as long as the lizards from Texas, appreciable SSD would appear because females would outlive males, just as in Texas.

To further test the theories of 1) higher mortality in the urban Oklahoma population and 2) that the observed SSD in Texas was due to higher male mortality rather than differences in growth rates, I limited the Texas data to the same range in size as the Oklahoma data and conducted 2-way ANOVA using population and sex as the factors. Because there was no interaction between population and sex ($F = 0.652$, $df = 1, 263$, $p > 0.10$), there was no longer variation in SSD between populations, and tests of the main effects were valid. There was no significant difference between sexes ($F = 2.7$, $p > 0.10$), but overall the lizards from the Texas population were significantly larger ($F = 55.62$, $p < 0.001$). These results support the idea of higher mortality in the urban Oklahoma sites and intersexual variation in mortality. The Texas lizards were still significantly larger, indicating that when the range of sizes was equal there were relatively more lizards of larger size in the Texas population, probably as a result of lizards living longer there. Loss of variation in SSD between populations and loss of SSD in Texas support the idea that growth rates of sexes are equal and that the significant difference between sexes in the overall Texas population is probably due to females living longer than the mate-searching males, and therefore growing larger.

In conclusion, I note that there are limitations to this comparative study and I have not offered all possibilities for the observed differences. For example, one limitation is that I observed the Oklahoma population for 2 years only, and samples collected from a population at different times could yield smaller or larger adults depending on the age structure of the population (Stamps, 1993). However, limiting the Texas data to a 2-year period and performing the same tests yielded the same results. Other possible explanations for the difference in size between the Texas and Oklahoma populations include a longer activity season in south Texas, difference in growth rates, and possibly a difference in prey abundance and availability. Also, it is interesting that there is a significant positive relationship between female body size and clutch size in Texas horned lizards, and it has been estimated that females produce one egg for about every 3 mm of body length (Ballinger, 1974). Therefore, it is likely advantageous for females to delay reproductive maturity when possible so that larger growth and clutch sizes will result. Delayed reproductive maturity and relatively larger sizes may be common in Texas horned lizard populations that experience relatively low mortality, and lizards in the urban Oklahoma population may be "making the best out of a bad situation" (Fox and McCoy, 1999: 327) by reproducing earlier in case they do not survive long.

Acknowledgements. — This work was part of a larger study on the space and habitat use of Texas horned lizards in Oklahoma. Financial support was provided by the Wildlife Diversity Program of the Oklahoma Department of Wildlife Conservation, the Department of Zoology at Oklahoma State University, and the Oklahoma Cooperative Fish and Wildlife Research Unit (Okla. State Univ., Okla. Dep. Wildl. Conserv., U.S.G.S. Biol. Resour. Div., and Wildl. Manag. Inst., cooperating). I thank ARC Communities and Lambert Construction for allowing us to conduct the study on their properties. I also thank John Dyer, Matt Sivils, and Joe Hackler for their valuable help in the field in Oklahoma, Randy Tanner for writing the program for the randomization tests, the personnel of the Chaparral Wildlife Management Area for collecting the data on the Texas lizards, and Chip Ruthven of the Texas Parks and Wildlife Department for sharing the Texas data for use in the study.

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Figure Legends

Figure 1. Map showing the locations of the north-central Oklahoma and the south Texas populations.

Figure 2. Mean snout-vent lengths (SVL) of male and female Texas horned lizards from the north-central Oklahoma and south Texas populations.

Figure 1

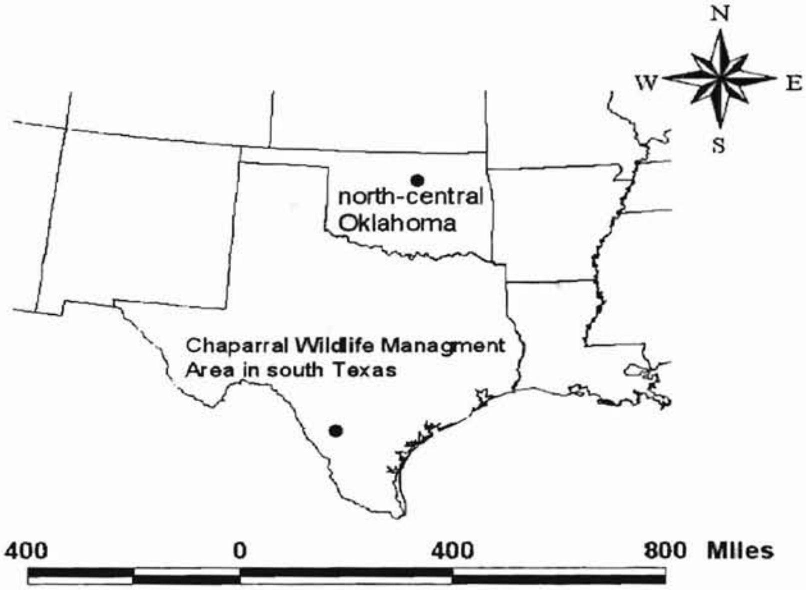
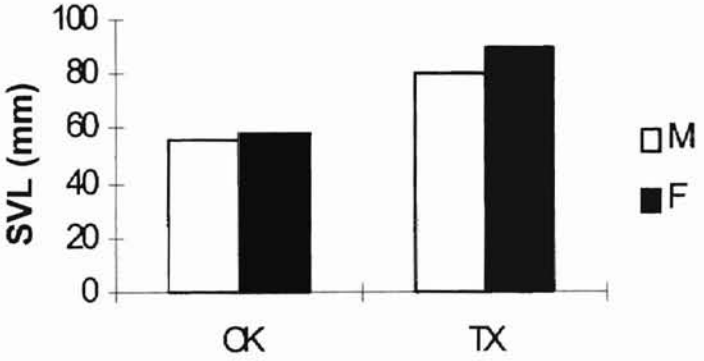

N
W
E
S
north-central
Oklahoma
Chaparral Wildlife Managment
Area in south Texas
400
0
400
800 Miles

Figure 2



VITA

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Master of Science

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