HABITAT REQUIREMENTS OF AN INLAND POPULATION OF THE KEELED EARLESS LIZARD (*HOLBROOKIA PROPINQUA*), WITH COMMENTS ON MORPHOLOGY AND BEHAVIOR

THESIS

Presented to the Graduate Council of
Texas State University-San Marcos
in Partial Fulfillment
of the Requirements

for the Degree

Master of SCIENCE

by

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San Marcos, Texas
May 2010

Dedication -

To my wife Renee and my daughter Jenya,

I know I haven't always been there for you two while working on this project. I've tried my best. They say the best way to avoid your responsibilities is to have other responsibilities. I hope you'll understand.

ACKNOWLEDGMENTS

Many thanks to Dr. Thomas R. "Randy" Simpson, my committee chair, without whose invaluable help (and patience) I might still be stuck at step one. Thanks also to Dr. John Baccus and Dr. Francis Rose, my committee members, for their invaluable advice and assistance. Thanks to Dr. Floyd "Butch" Weckerly for his assistance with the statistical portions of this thesis, and to Dr. Clay Green for teaching me spatial ecology.

Thanks to Sheng Ma and Dana Spontak, my fellow graduate students who helped me with my field work. Thanks also to my wife Renee for her assistance in the field, the loan of her 4-wheel drive vehicle, and her patience and understanding while I completed this project.

Thanks to Dr. Travis J. LaDuc of the Texas Natural History Collections, for allowing me access to preserved specimens of my study species from many other populations.

Many thanks to Mike Stautzenberger and the owners of Diamond Half for allowing me access to my study area. Without you, none of this would be possible.

This manuscript was submitted on 19 March 2010.

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ABSTRACT

HABITAT REQUIREMENTS OF AN INLAND POPULATION OF THE KEELED EARLESS LIZARD (*HOLBROOKIA PROPINQUA*), WITH COMMENTS ON MORPHOLOGY AND BEHAVIOR

by

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May 2010

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I studied the habitat association, morphology, and behavior of the keeled earless lizard, *Holbrookia propinqua*, in Guadalupe County, Texas, near the type locality (Wilson County, Texas). Principal components analysis showed a positive association with kangaroo rat burrows, open sandy areas, and fine-quality, Arenosa-type sand and a negative association with stony soil, grassy or brushy habitat, heavy tree canopy, and leaf litter. An occupancy study showed an overall occupancy (Ψ) of 0.4038, with detectability (p) of 0.6570. The co-variate with highest influence on occupancy was the amount of sand, while grass, kangaroo rat burrows, and canopy were factors determining detectability. Adults of this population were similar to other mainland populations but significantly smaller and less massive than adults of coastal populations. Juveniles of this population and a coastal population showed no significant differences in size. Escape distance did not differ between males and females. Individuals preferred thorny vegetation as escape cover over kangaroo rat burrows by a factor of 3:2.

I. INTRODUCTION

The keeled earless lizard, *Holbrookia propinqua*, is a habitat specialist restricted to loose sandy soils of southern Texas and northeastern Mexico (Axtell 1998). This small, long-tailed, sand-burrowing earless lizard is a member of the family Phrynosomatidae, which also includes the horned (*Phrynosoma*) and spiny (*Sceloporus*) lizards (Conant and Collins 1998).

The keeled earless lizard inhabits mostly sandy areas of the South Texas Plain, and along the gulf coast from Cameron County as far north as Aransas County. It can also be found in adjacent areas of northern Tamaulipas, Mexico, southward along the Mexican Gulf Coast to northern Veracruz. The distribution also includes an inland stretch of Carrizo Sands Formation from Dimmit County northeastward to Guadalupe and Gonzales counties (Axtell 1998) (Fig. 1).

Axtell (1981) determined the type series for this species, caught by John H. Clark in 1851 (Baird et al. 1852), came from the Carrizo Sands Formation in Wilson County and narrowed down the specific locality to within a 15-km radius of 29°16'20"N-98°09'50"W. Judd (1973) characterized the population and habitat of this species on South Padre Island, and related his findings to mainland populations of the coastal counties of South Texas and barrier islands off the coast of Tamaulipas, Mexico (Axtell 1954, Selander et al. 1962).

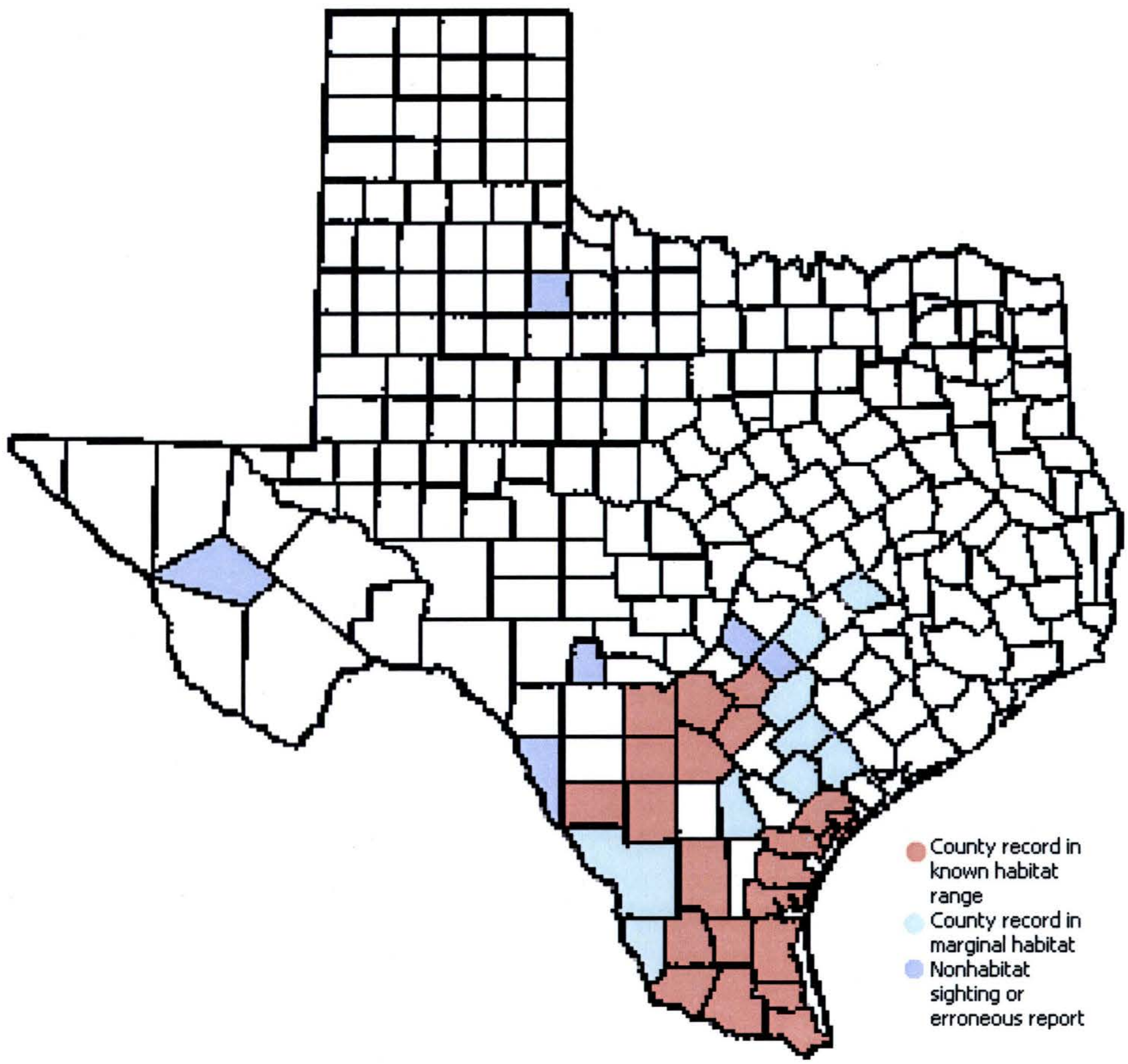

Fig. 1: Distribution by county of the keeled earless lizard in Texas. Modified from Interpretive Atlas of Texas Lizards (Axtell 1998).

Most studies of this species have been conducted on coastal (Judd 1973, Cooper and Clarke 1982, Selcer and Judd 1982, Dial 1986, Selcer 1986), South Texas (Cooper et al. 1983, Cooper 1984, 1985, 1986, 1988a, 1988b, 1998, 1999, 2000, 2003a, 2003b, 2003c, Adams and Cooper 1988), or Mexican populations (Smith and Berger 1950, Axtell and Wasserman 1953, Selander et al. 1962), or various combinations thereof (Judd 1974, 1975, 1976a, 1976b, Judd and Ross 1978, McKee and Martinez 1981, Ross and

Judd 1982, Nieuwendaal 1993). Axtell (1954, 1958) included only three specimens collected near the type locality in his studies. I found no published work characterizing the population found at or near the type locality, or elsewhere along the Carrizo Sands Formation. This population appears to differ behaviorally and morphologically from other populations (T. R. Simpson and F. L. Rose, pers. comm.). The mean adult size for these lizards appears smaller than coastal populations (Axtell 1954, Selander et al. 1962, Judd 1973, and T. R. Simpson and F. L. Rose, pers. comm.).

Judd (1973) described the preferred habitat for this lizard on South Padre Island as vegetation arranged in clumps within relatively large, open, sandy areas. The vegetational and geological habitat components along the Carrizo Sands differ from those found in either the coastal or South Texas areas (McBryde 1933, United States Department of Agriculture 2010). No studies have been conducted on habitat associations of keeled earless lizard populations on the Carrizo Sands.

Cooper (2003a) studied distances from escape cover and initial escape run distance in a coastal mainland population in Kenedy County. He found significant differences in initial distances from nearest cover but not in distances fled between males and females. Lizards often stopped short of potential escape cover or pass nearby potential escape cover for more distant and presumably safer cover types (Cooper 2003a). The Carrizo Sands have reduced areas of open spaces between vegetative clusters in comparison to parts of South Texas. No studies have investigated how the dispersion of vegetation on the Carrizo Sands Formation affects escape behavior in these lizards.

Keeled earless lizards in South Texas and related lizards frequently use the burrows of kangaroo rats (*Dipodomys* sp.) and other small burrowing mammals for escape cover (Axtell 1958, Vaughn 1961). Several sites in my study area contained burrows characteristic of coastal kangaroo rats (*Dipodomys compactus*); however, initial observations of lizard behavior suggested this population rarely uses burrows for escape cover.

My study had four main objectives:

(1) Characterize the physical and vegetational habitat components of the Carrizo Sands Formation near the type locality of the keeled earless lizard and relate these data to those reported for the South Padre Island and coastal mainland habitats.

(2) Perform an occupancy study to determine the local distribution of keeled earless lizards, and characterize habitats occupied by these lizards.

(3) Characterize and compare morphological characteristics of keeled earless lizards occupying the Carrizo Sands Formation with available morphological data for this species from South Padre Island and coastal mainland habitats.

(4) Study initial run distance behavior and preferred escape cover and compare these data with the behavior of this species from coastal mainland habitats.

My study was conducted under IACUC permit numbers 0808_0118_09 and 0911_0218_10 and scientific permit number SPR-0993-638.

II. MATERIALS AND METHODS

Study Area

The Carrizo Sands Formation (Fig. 2) is a strip of fine sand that runs nearly parallel to the gulf coast from South Texas to Louisiana and Arkansas. Most of this formation lies underground, but on its northwestern margin, it forms a 720-km long by 10 to 20-km wide surface band of deep, beach-like sand (McBryde 1933). This area

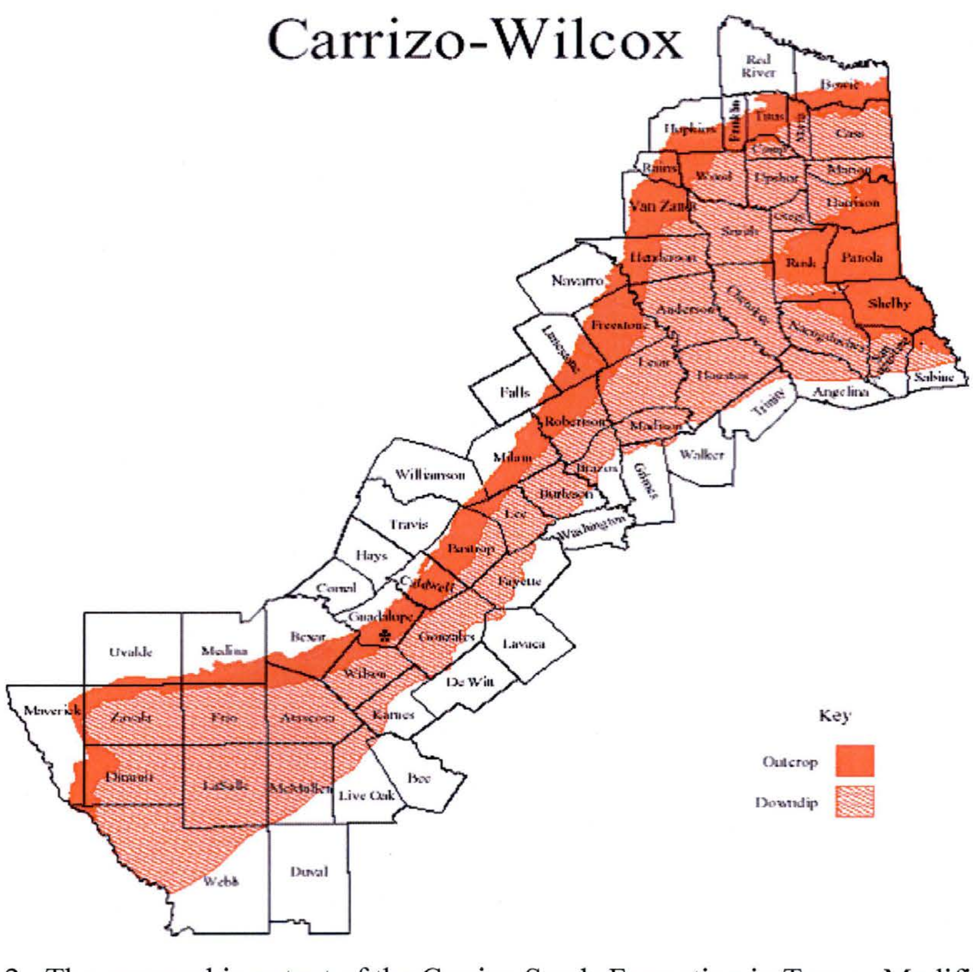

Fig. 2. The geographic extent of the Carrizo Sands Formation in Texas. Modified from Thorkildsen and Price (1991). My study site is indicated by the asterisk (*).

receives about 84 cm of rainfall annually. Mean July high temperatures are 35.6° C and January lows 5.6° C (Texas State Historical Association, 2010).

Diamond Half Ranch (Fig. 3) is approximately 2,800 ha in size and located in southern Guadalupe County, Texas, (29°25'44"N-97°57'02"W), approximately 27 km northeast of the type locality for the keeled earless lizard, and 15 km due south of Seguin, Texas. Except for a few outcrops of iron-bearing sandstone, most of the ranch lies within the Carrizo Sands Formation.

The plant community is generally open post oak (*Quercus stellata*) woodlands, alternating with a tallgrass savanna and patches of sand with sparse vegetation (McBryde 1933, USDA 2010). Nearby are improved pastures of coastal Bermudagrass (*Cynodon dactylon*). Changing land use practices have generated several areas of oak scrubland and oak woodland communities. The scrubland areas have a more closed-canopy, the notable addition of prickly ash (*Zanthoxylum hirsutum*) and bull nettle (*Cnidoscolus texanus*), and the replacement of little bluestem (*Schizachyrium scoparium*) and Indiangrass (*Sorghastrum nuttans*) with more shade-tolerant grasses. Woodland areas often lack grasses or other understory vegetation, and also include live oak (*Quercus virginiana*) and black hickory (*Carya texana*) at the canopy level.

Most of the ranch is used for recreation; however, there is also a cattle-grazing operation. Hunting for white-tailed deer (*Odocoileus virginianus*) and other game is allowed from October through February (Mike Stautzenberger, pers. comm.). Other hunting-related activities such as the maintenance of deer feeders and blinds continue year-round (Mike Stautzenberger, pers. comm.).

Fig. 3. Satellite view of Diamond Half Ranch in Guadalupe County, Texas, with approximate boundaries shown in red.

My study site on the Diamond Half Ranch is locally known as the Saddle, due to the proximity of two sandstone hills with a sandy gap between them. The soils (Fig. 4) are characterized by Patilo and Arenosa sandy soil (PaD) with inclusions of Arenosa fine sands (ArD) (USDA 2010). The Arenosa fine sands are typified by loose, sandy soil to a depth of at least 2.4 m (USDA 2010). The PaD soil type is similar, but has an underlying

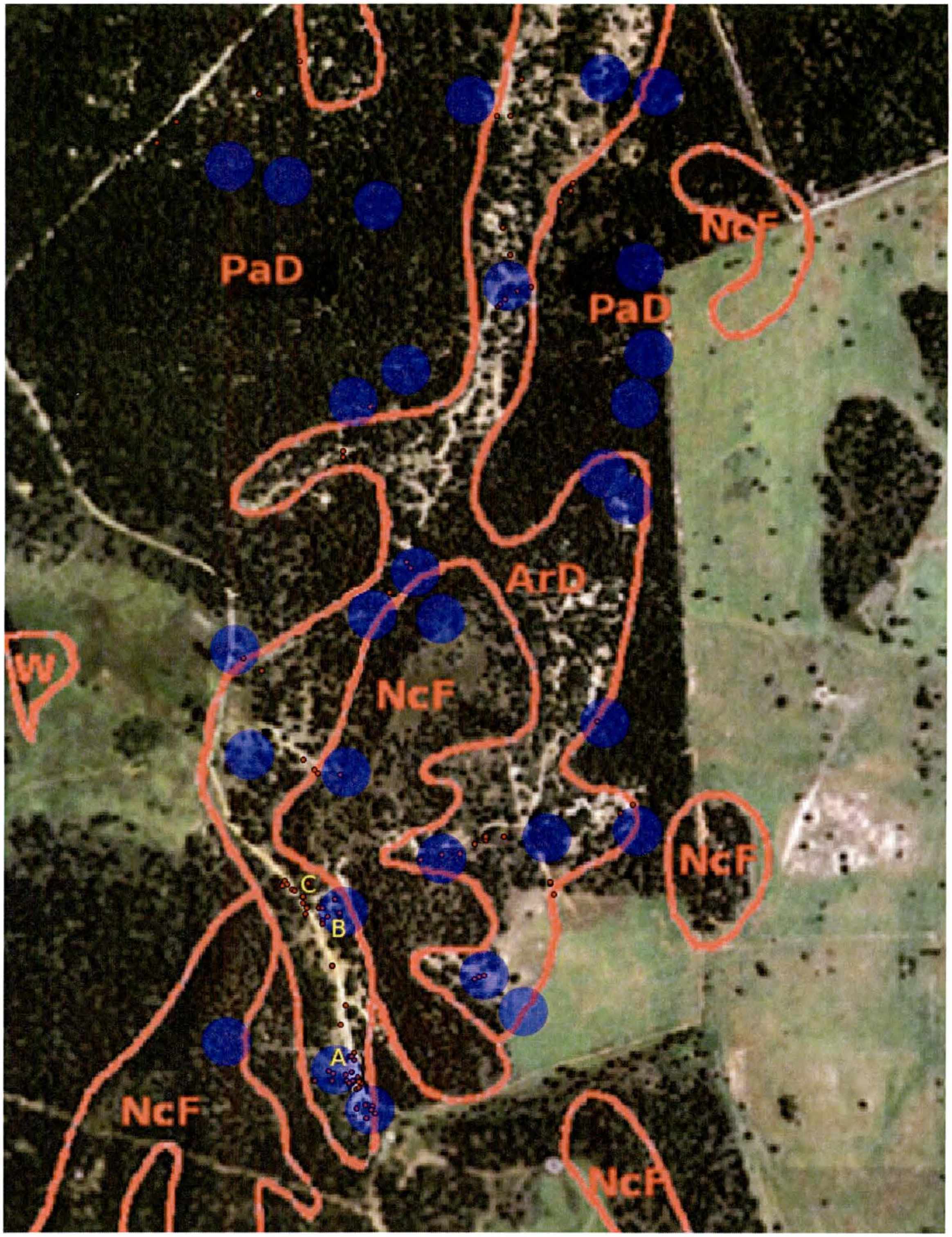

Fig. 4. Soil map of the Saddle and adjacent areas. Blue circles are randomly-generated 50-m point-plots. A, B, and C represent initial 50-m grids. Small red dots are locations of lizard sightings or captures. NcF, ArD, PaD, and W are Nebgen-Jedd formation sandstone hills, Arenosa fine sands, Patilo and Arenosa soils, and Water, respectively.

layer of loamy soil at about 1.8 m (USDA 2010). Also the aforementioned ridge of iron-bearing red sandstone hills, part of the Nebgen-Jedd Formation (NcF) (USDA 2010) extends through the area.

Methods

Vegetation and Habitat Components

Initially, I set up three 50 x 50-m grids in nearby locations in what I predicted to be good, mediocre, and poor habitats to study the vegetation and ground cover components of the habitat. I ran three 50-m line intercepts and canopy estimates on each grid using a Daubenmire frame and convex mirror densiometer per season for a year to document ground and canopy cover changes at each location over time. I took Daubenmire frame measurements and canopy cover estimates every 10 m along each line. I spaced the lines parallel to each other at 25-m intervals.

In order to verify my assessment of the relative habitat quality, I canvassed these grids a total of 10 times over the summer and fall of 2008, counting all lizards seen or caught within or near each. Care was taken to spend approximately equal amount of time on each grid. I continued to note when a lizard was seen or caught on or near a grid throughout the rest of my study.

I calculated the mean vegetation, ground cover components, and maximum mean summer canopy for each grid for each season. I then compared the grids to one another, noting how many lizards were found on each during the course of the study.

Because my study dealt with both habitat components and occupancy, I collected vegetation and occupancy data concurrently for the next portion of my study. I defined minimum and maximum UTM eastings in the statistical program R Version 2.9.0 (R

Development Core Team 2009) and used the randomization function to generate 30 random points in the study area within this range. I generated the northings in a similar manner, and paired each easting with a northing to get my random coordinates. I used 50-m radius plots based on these points. I visited each plot three times to determine presence or absence of the lizards, remaining at each site until lizards were observed up to a maximum of 10 min for each visit. I recorded Daubenmire frame estimates of percent ground cover of herbaceous plants, low-lying brush, open sand or soil, leaf litter, and rocks for each point. I used a convex mirror densiometer to assess percent canopy cover of tree and taller understory vegetation. I also recorded the presence or absence of kangaroo rat (K-rat) burrows within 50 m of the point. In addition, I recorded the soil type for each location. In such cases where a lizard was sighted in habitat within the 50-m radius that clearly differed from the habitat at the point, I also gathered similar data at the point of capture of the lizard. I performed principal components analysis (PCA) on the habitat parameter data from the point-plot survey to assess which vegetational and habitat components were important in defining habitat appropriate for the keeled earless lizards (Pearson 1901, Aitchison 1983), substituting the point-of-capture data where warranted.

Occupancy

I performed an occupancy study on the habitat dataset corrected for lizard point-of-capture and the presence or absence data. I followed Zylstra and Steidl (2009) in my occupancy methodology. I analyzed the data using program PRESENCE (MacKenzie et al. 2002, Hines 2006, MacKenzie et al. 2006). I began by estimating overall occupancy and detectability among all sites by generating occupancy models with constant occupancy and either constant or survey-dependent detectability. I changed the effective sample size to 30 to force PRESENCE to default to AICc rankings for low sample sizes (Phidot.org 2010).

I modeled occupancy (Ψ) and detectability (p) in program PRESENCE 3.0 to determine which habitat components affected occupancy. Model building progressed in three steps. I first examined factors that might affect occupancy while maintaining a constant general model for detectability. Any Akaike score within 2 units of the best model was included among the top models in accordance with PRESENCE documentation (Donovan and Hines 2007). After determining which covariates were present in these top models, I next used these covariates to build a constant general model for occupancy while examining models for detectability.

Finally, I used covariates present in the best models for both occupancy and detectability to generate several candidate models for occupancy and detectability together. Top models were the lowest AICc ranked model and those within 2 AICc units of the best model. I made sure that the most general of these top models fit the data by performing chi-square goodness-of-fit. Finally, I averaged the site-specific occupancy and detectability for each of my top models (Zylstra and Steidl 2009).

I had more covariates than could be easily examined in PRESENCE 3.0. Therefore, I followed the example of Zylstra and Steidl (2009) in separating covariates into broad categories for each step but the last.

Morphology and Physical Characteristics

To document the mean morphological characters of individuals in my study site population, I captured lizards by hand, noose, and/or butterfly net (Judd 1973). The net proved to be the most successful method. I recorded standard measurements including snout-vent lengths (SVL), total length, weight, cloacal temperature, age class, and sex for each lizard captured. Standard lengths were measured with a ruler and/or calipers (Mitutoyo Corp., Aurora, IL). Weights were measured with a 20-g Pesola scale (Pesola AG, Baar, Switzerland) and a Ziploc® bag to hold the lizards. Cloacal temperature was taken using a Schultheis thermometer (Miller & Weber, Inc., Queens, NY). I also noted the UTM location of each individual seen or caught with a Garmin eTrex Legend HCx (Garmin International Inc., Olathe, KS).

I used an analysis of variance (ANOVA) to test for differences in snout-vent lengths for adults from my population and four other populations (Selander et al. 1962, Judd 1973) as well as preserved specimens in the Texas Natural History Collection at the University of Texas using the statistical program R Version 2.9.0 (R Development Core Team 2009). When differences were detected between populations, I used Tukey's multiple comparison procedure to determine which populations differed. I also compared unregenerated tail lengths between males and females of my population with a Student's *t*-test, and between juveniles and adult males and females of my population and other populations with ANOVA. I have also included means, ranges, and standard errors for snout-vent lengths, tail lengths, mass, and temperatures in tabular form.

To obtain an accurate estimate of cloacal temperature, I analyzed data only from lizards unchased or chased < 1 m when the air temperature exceeded 30°C and/or sand surface temperature exceeded 45° C. This was to ensure lizards had reached their eccretic body temperature prior to capture and to eliminate measurements of lizards that may have built up excess heat in the course of capture.

I defined age classes according to Judd (1973). Any lizard showing breeding coloration as described by Judd (1973) was considered an adult, regardless of snout-vent length. I found Judd's sex determination method unreliable for individuals < 30 mm SVL because I was unable to positively distinguish the enlarged postanal scales Judd reported for hatchling males (1973). I therefore combined all hatchlings and smaller subadults into a combined category of "juveniles". Enlarged postanal scales were easily identified in males > 30 mm. Any lizard > 30 mm SVL but not showing breeding coloration was considered a subadult. There was some overlap between adults and subadults in snout-vent length and mass because some individuals showed mating behavior and breeding coloration earlier than others.

Gender for uncaptured lizards was determined by the presence of sharply-defined lateral bars on males and indistinct or absent lateral bars on females, as well as relative body:tail length ratios. Gender for captured lizards was determined by the presence or absence of hemipenal bulges.

Escape Behavior

I measured the distance of each lizard's initial escape run, and noted the potential escape cover (if any) toward which it ran to document behaviors associated with initial run distance and seeking preferred escape cover. I also noted the final escape cover of lizards chased but not caught to determine the frequency of use for various types of escape cover. I performed a single-factor ANOVA between males and females of my population and males and females of the South Texas population to determine any differences in mean escape run distances (Cooper 2003a).

III. RESULTS

Vegetation and Habitat Components

Table 1 shows the mean Daubenmire frame scores in percentages, the maximum percent tree canopy in the heat of summer, and the number of lizards seen in the initial three grids. More lizards were found in grid A, which had more sand than grids B or C, and much less canopy than grid C. There are no other clear differences between grids A

Table 1. Seasonal mean percent for ground cover components, maximum summer canopy, and number of lizards observed in three grids at the Diamond Half Ranch in Guadalupe County, Texas in 2008.

		Parameter					
Grid	Season	Sand	Litter	Rock	Grass	Forb	Brush
A	Fall	28 8	5 4	0 0	45 4	15 3	0 0
	Winter	53 2	31 5	0 0	11 5	2 2	0 0
	Spring	34 0	25 0	0 0	24 4	9 9	2 1
	Summer	39 3	18 3	0 0	12 6	6 4	5 6
	Maximum Summer Canopy			6.389			
	No. Lizards Seen			35			
B	Fall	24 0	8 9	0 0	38 6	11 3	8 3
	Winter	31 8	48 8	1 0	10 8	1 3	0 8
	Spring	31 0	23 1	1 1	26 9	9 2	6 3
	Summer	25 4	30 3	0 3	23 1	7 5	2 2
	Maximum Summer Canopy			7.944			
	No. Lizards Seen			9			
C	Fall	25 3	20 4	6 1	28 1	5 8	0 8
	Winter	26 0	59 2	0 3	4 0	2 2	0 0
	Spring	25 8	32 8	2 4	21 7	15 8	0 0
	Summer	23 1	35 7	5 0	13 2	10 8	0 0
	Maximum Summer Canopy			27.89			
	No. Lizards Seen			15			

and B, despite the obvious differences in the numbers of lizards seen at each grid.

Table 2 lists the variable loadings on the components. Sand, kangaroo rat presence, canopy, litter, and soil type (ArD) had high loadings on Component 1. Grass, rock, and soil type (NcF) had high loadings on Component 2. Brush heavily loaded on Component 3 and grass less so. Also in Table 2 is the proportion of variance represented by each component and the cumulative variation in the data set explained by each component. The first two principal components only explain about 56% of the variation in the data set. I have therefore included the third component in the analysis.

Table 2. Variable loadings of habitat data corrected for point-of-capture scores and proportion of variance represented by each component.
* Denotes a significant loading.

	Comp.1	Comp.2	Comp.3	Comp.4	Comp.5
Grass	-0.085	*0.344	*0.395	-0.551	0.511
Forb	0.212	0.072	0.076	0.698	0.647
Brush	-0.003	0.129	*-0.816	-0.187	0.320
Litter	*-0.452	0.019	-0.276	0.240	-0.142
Sand	*0.477	-0.131	0.116	0.083	-0.272
Rock	0.008	*-0.603	-0.046	-0.167	0.144
Canopy	*-0.417	0.18	0.105	0.212	-0.019
Kangaroo rat	*0.456	0.117	-0.063	0.033	-0.010
Soil type: ArD	*0.363	0.249	-0.256	-0.154	-0.057
Soil type: NcF	-0.036	*-0.609	-0.014	-0.108	0.314
Standard Deviation	1.83375	1.50151	1.08078	1.03765	0.83781
Proportion of Variance	0.33626	0.22545	0.11681	0.10767	0.07019
Cumulative Proportion	0.33626	0.56172	0.67852	0.78619	0.85639

There were strong positive correlations with open areas of Arenosa fine sands, and with the presence of kangaroo rat burrows (Fig. 5a). There were strong negative correlations with tree canopy and leaf litter, grass, and brushy habitat (Fig. 5b), and weaker negative correlations with rock and Nebgen-Jedd Formation (NcF) sandstone hills (Fig. 5a).

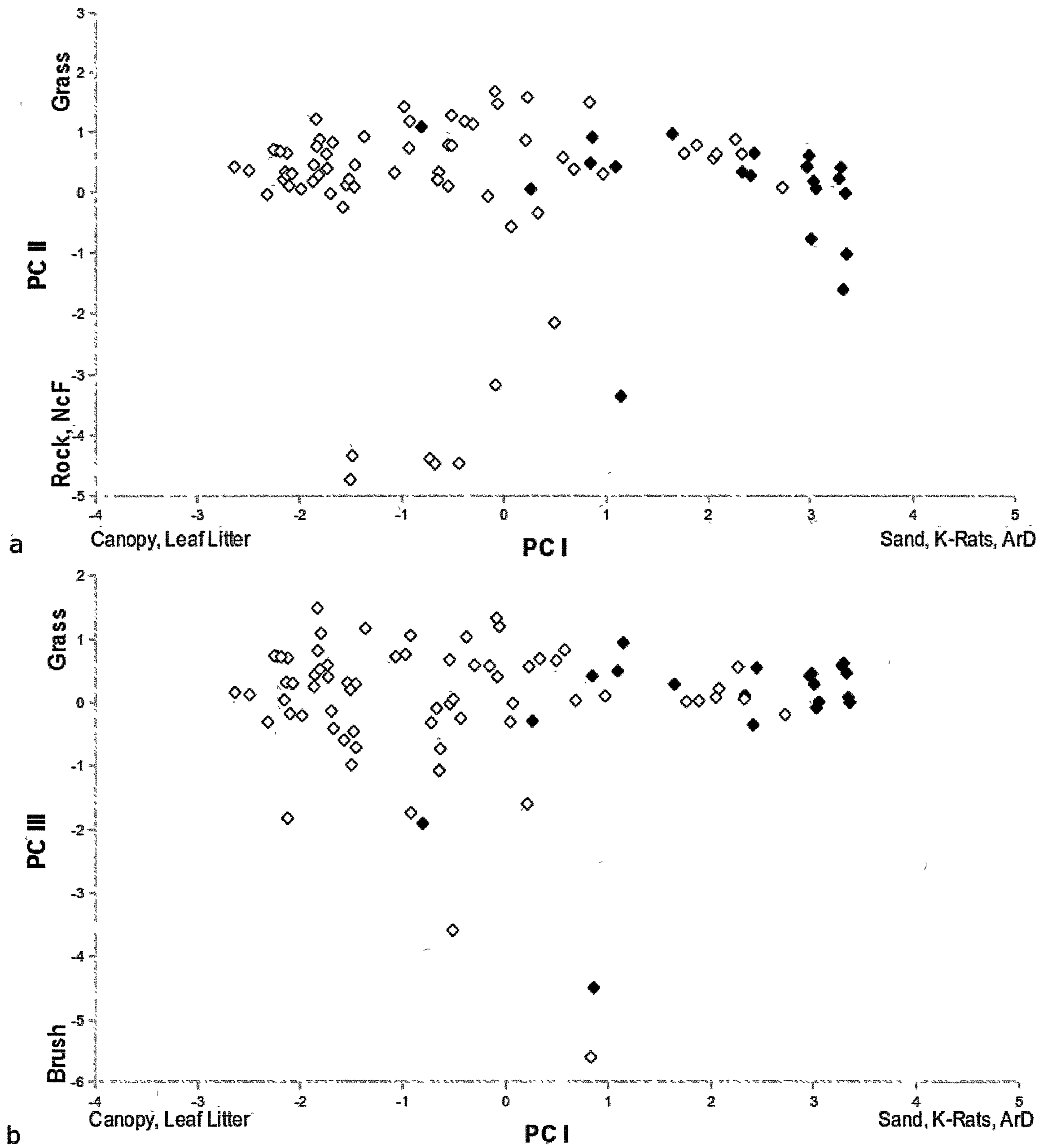

Fig. 5. Principal components analysis of habitat components based on the presence or absence of *Holbrookia propinqua*, corrected for point-of-capture locations. The comparison of principal components I and II is shown in (a), I and III in (b). Black and white diamonds represent surveys where lizards were detected and not detected, respectively.

The correlation of lizard observations with Arenosa fine sands is further illustrated in figure 4. Of the 117 total observations, 114 (97%) were found on or within 10 m of Arenosa fine sands.

Occupancy

The naïve occupancy estimate was 0.400. Table 3 shows the AICc of the two simple overall models generated. The constant detectability model had a significantly lower AICc score, meaning there was no significant change in overall detectability over the course of the study. The overall proportion of sites occupied (Ψ) in the simple model was 0.4377 (SE = 0.1017). The overall detectability (p) was 0.558531 (SE = 0.098693).

Table 3. Comparison of simple models for overall occupancy and detectability.

Model	AICc	ΔAICc	K	-2*LogLike
1 group, Constant P	91.18	0.00	2	86.74
1 group, Survey-specific P	96.14	4.96	4	86.54

There are several assumptions involved in modeling occupancy (MacKenzie et al. 2006). These include: sites are assumed to have constant occupancy, factors affecting occupancy and detectability are adequately modeled by covariates, and detection at each site is independent of detection at other sites.

Table 4 shows the AICc of the occupancy models generated with a fixed, general detectability p(Grass,Forb,Brush,Litter,Sand,Canopy,K-Rat). From the physical group, sand was the only variable present in the top model. Vegetation group, litter, grass, and

Table 4. Results of models examining factors determining occupancy, using general model for detectability p(Grass,Forb,Brush,Litter,Sand,Canopy,K-Rat).

Models	K	-2*LL	AICc	ΔAICc	Model Weight
Physical Group					
Ψ(Sand)	10	41 10	72 68	0 00	0 6761
Ψ(Sand+PaD)	11	40 00	76 67	3 99	0 0920
Ψ(Sand+ArD)	11	40 06	76 73	4 05	0 0892
Ψ(Sand+K-Rat)	11	40 82	77 49	4 81	0 0610
Ψ(Sand+Rock)	11	41 03	77 70	5 02	0 0549
Ψ(Sand+Rock+PaD)	12	39 81	82 16	9 48	0 0059
Ψ(Sand+K-Rat+PaD)	12	39 92	82 27	9 59	0 0056
Ψ(Sand+K-Rat+ArD)	12	40 02	82 37	9 69	0 0053
Ψ(Sand+Rock+ArD)	12	40 06	82 41	9 73	0 0052
Ψ(Sand+Rock+K-Rat)	12	40 76	83 11	10 43	0 0037
Ψ( )	9	60 93	87 93	15 25	0 0003
Ψ(Sand+Rock+K-Rat+PaD)	13	39 76	88 51	15 83	0 0002
Ψ(Sand+Rock+K-Rat+ArD)	13	40 01	88 76	16 08	0 0002
Ψ(Rock)	10	59 80	91 38	18 70	0 0001
Ψ(K-Rat)	10	60 64	92 22	19 54	0 0000
Ψ(ArD)	10	60 85	92 43	19 75	0 0000
Ψ(PaD)	10	60 92	92 50	19 82	0 0000
Ψ(Rock+PaD)	11	59 80	96 47	23 79	0 0000
Ψ(Rock+K-Rat)	11	60 64	97 31	24 63	0 0000
Ψ(K-Rat+PaD)	11	60 64	97 31	24 63	0 0000
Ψ(K-Rat+ArD)	11	60 64	97 31	24 63	0 0000
Ψ(Rock+ArD)	11	60 85	97 52	24 84	0.0000
Ψ(Rock+K-Rat+ArD)	12	60 64	102 99	30 31	0 0000
Ψ(Rock+K-Rat+PaD)	12	60 64	102 99	30 31	0 0000
Vegetation group					
Ψ(Grass+Litter)	11	41 22	77 89	0 00	0 3092
Ψ(Grass+Canopy)	11	41 65	78 32	0 43	0 2494
Ψ(Grass)	10	46 75	78 33	0 44	0 2481
Ψ(Forb+Litter)	11	46 13	82 80	4 91	0 0265
Ψ(Grass+Forb)	11	46 56	83 23	5 34	0 0214
Ψ(Grass+Litter+Canopy)	12	40 98	83 33	5 44	0 0204
Ψ(Grass+Forb+Litter)	12	40 99	83 34	5 45	0 0203
Ψ(Litter+Canopy)	11	46 71	83 38	5 49	0 0199
Ψ(Grass+Brush)	11	46 75	83 42	5 53	0 0195
Ψ(Grass+Brush+Litter)	12	41 14	83 49	5 60	0 0188
Ψ(Grass+Forb+Canopy)	12	41 65	84 00	6 11	0 0146
Ψ(Grass+Brush+Canopy)	12	41 65	84 00	6 11	0 0146
Ψ(Litter)	10	54 83	86 41	8 52	0 0044
Ψ(Forb+Litter+Canopy)	12	45 57	87 92	10 03	0 0021
Ψ( )	9	60 93	87 93	10 04	0 0020
Ψ(Forb+Brush+Litter)	12	46 11	88 46	10 57	0 0016
Ψ(Grass+Forb+Brush)	12	46 56	88 91	11 02	0 0013
Ψ(Brush+Litter+Canopy)	12	46 68	89 03	11 14	0 0012
Ψ(Grass+Forb+Litter+Canopy)	13	40 85	89 60	11 71	0 0009

Table 4-Continued.

Models	K	-2*LL	AICc	ΔAICc	Model Weight
Ψ(Grass+Brush+Litter+Canopy)	13	40 91	89 66	11 77	0 0009
Ψ(Grass+Forb+Brush+Litter)	13	40 93	89 68	11 79	0 0009
Ψ(Canopy)	10	58 22	89 80	11 91	0 0008
Ψ(Grass+Forb+Brush+Canopy)	13	41 65	90 40	12 51	0 0006
Ψ(Brush+Litter)	11	54 83	91 50	13 61	0 0003
Ψ(Forb)	10	60 89	92 47	14 58	0 0002
Ψ(Brush)	10	60 93	92 51	14 62	0 0002
Ψ(Forb+Brush+Litter+Canopy)	13	45 56	94 31	16 42	0 0001
Ψ(Forb+Canopy)	11	57 97	94 64	16 75	0 0001
Ψ(Brush+Canopy)	11	58 22	94 89	17 00	0 0001
Ψ(Grass+Forb+Brush+Litter+Canopy)	14	40 79	96 79	18 90	0 0000
Ψ(Forb+Brush)	11	60 89	97 56	19 67	0 0000
Ψ(Forb+Brush+Canopy)	12	57 97	100 32	22 43	0 0000

canopy were each present in at least one of the top models; however, these models were all more than 2 AICc units from the top model in the physical category and can be eliminated.

The sole top model for occupancy using the general model for detectability was Ψ(Sand). As a consequence, I used Ψ(Sand) alone as the general occupancy model for the analysis of factors affecting detectability. The results of this analysis are presented in Table 5. Only the K-Rat term from the physical group was present in the model with the lowest AICc score. No other models ranked within 2 AICc units of the best model.

Finally, I used all top factors for detectability and occupancy to generate candidate models for detectability and occupancy together. The most general of these models fit the data reasonably well ($\chi^2 = 6.4940$, P = 0.3477). The best models from this stage are ranked in Table 6. Mean occupancy (Ψ) for all models was 0.4038 (SE = 0.0583), and detectability (p) was 0.6570 (SE = 0.1048).

Table 5. Results of models examining factors determining detectability, using general model for occupancy p(Sand).

Models	K	-2*LL	AICc	ΔAICc	Model Weight
Vegetation group					
p(Grass)	4	50 63	60 23	0 00	0 2824
p(Grass+Canopy)	5	48 96	61 46	1 23	0 1527
p(Grass+Forb)	5	49 94	62 44	2 21	0 0935
p(Grass+Litter)	5	50 53	63 03	2 80	0 0696
p(Grass+Brush)	5	50 58	63 08	2 85	0 0679
p(Grass+Litter+Canopy)	6	47 79	63 44	3 21	0 0567
p(Grass+Forb+Canopy)	6	48 66	64 31	4 08	0 0367
p( )	3	57 56	64 48	4 25	0 0337
p(Grass+Brush+Canopy)	6	48 90	64 55	4 32	0 0326
p(Canopy)	4	55 85	65 45	5 22	0 0208
p(Grass+Forb+Brush)	6	49 88	65 53	5 30	0 0200
p(Grass+Forb+Litter)	6	49 93	65 58	5 35	0 0195
p(Grass+Forb+Litter+Canopy)	7	46 76	65 85	5 62	0 0170
p(Grass+Brush+Litter)	6	50 47	66 12	5 89	0 0149
p(Grass+Brush+Litter+Canopy)	7	47 73	66 82	6 59	0 0105
p(Litter)	4	57 46	67 06	6 83	0 0093
p(Forb)	4	57 50	67 10	6 87	0 0091
p(Brush)	4	57 51	67 11	6 88	0 0091
p(Litter+Canopy)	5	54 65	67 15	6 92	0 0089
p(Grass+Forb+Brush+Canopy)	7	48 60	67 69	7 46	0 0068
p(Brush+Canopy)	5	55 79	68 29	8 06	0 0050
p(Forb+Canopy)	5	55 83	68 33	8 10	0 0049
p(Grass+Forb+Brush+Litter)	7	49 88	68 97	8 74	0 0036
p(Grass+Forb+Brush+Litter+Canopy)	8	46 76	69 62	9 39	0 0026
p(Forb+Litter)	5	57 33	69 83	9 60	0 0023
p(Brush+Litter)	5	57 41	69 91	9 68	0 0022
p(Forb+Brush)	5	57 45	69 95	9 72	0 0022
p(Brush+Litter+Canopy)	6	54 59	70 24	10 01	0 0019
p(Forb+Litter+Canopy)	6	54 63	70 28	10 05	0 0019
p(Forb+Brush+Canopy)	6	55 77	71 42	11 19	0 0010
p(Forb+Brush+Litter)	6	57 28	72 93	12 70	0 0005
p(Forb+Brush+Litter+Canopy)	7	54 57	73 66	13 43	0 0003
Physical Group					
p(Sand,K-Rat)	5	49 35	61 85	0 00	0 4482
p(K-Rat)	4	52 86	62 46	0 61	0 3304
p( )	3	57 56	64 48	2 63	0 1203
p(Sand)	4	55 23	64 83	2 98	0 1010

Table 6. Candidate models for occupancy (Ψ) and detectability(p).

Models	K	-2*LL	AICc	ΔAICc	Model Weight	mean Ψ	mean P
Ψ(Sand),p(Grass+K-Rat)	5	47 31	59 81	0 00	0 4447	0 4033	0 6494
Ψ(Sand),p(Grass)	4	50 63	60 23	0 42	0 3604	0 4011	0 7076
Ψ(Sand),p(Grass+Canopy)	5	48 96	61 46	1 65	0 1949	0 4071	0 6139

Morphology and Physical Characteristics

Snout-Vent Length

Mean snout-vent lengths of lizards from my study site as well as other examined populations are presented in Table 7. These data give a general picture of size variation of lizards from various populations; however, caution should be taken when viewing these data, as specimens were collected at different times throughout the year, and not all months of the year are represented in all age classes of the samples from the Texas Museum of Natural History. Additionally, snout-vent lengths were only taken by Selander et al. (1962) during July.

Snout-vent length comparisons of adult males and females were made within the same season in order to analyze population differences accurately. I followed Judd (1973) in using only measurements from summer months (May-August) for this comparison. Populations analyzed in this manner were South Padre Island (Judd 1973), Tamaulipas (Selander et al. 1962), Mustang Island, Rockport/Fulton, and Carrizo Sands – Guadalupe County (Table 8).

Table 8: Snout-Vent Lengths of selected age groups and populations of keeled earless lizards. Measurements in millimeters.
*Denotes an estimated standard error.

Population and Authority	Adult Males				Adult Females				Overall Adults			
	N	Range	$\bar{x}$	SE	N	Range	$\bar{x}$	SE	N	Range	$\bar{x}$	SE
South Padre Island (Judd 1973)	170	48-60	54.1	0.23	162	43-55	49.6	0.21	332	43-60	51.9	0.19*
Tamaulipas (Selander et al. 1962)	33	49-62	56	0.5	14	47-53	50.9	0.5	47	47-62	54.5	0.56*
S. Texas Sand Sheet (TNHC)	10	41.5-53.6	46.7	1.29	12	40.3-51.9	45.8	0.93	22	40.3-53.6	46.2	0.24
Rockport/Fulton (TNHC)	31	40.9-53.1	47.5	0.63	25	40-51.9	45.1	0.68	56	40-53.1	46.4	0.48
North Padre Island (TNHC)	15	41.4-51.3	47.8	0.92	10	40.1-51.2	47.0	0.98	25	40.1-51.3	47.5	0.67
Mustang Island (TNHC)	36	40.3-57.0	48.7	0.88	17	41.1-51.8	46.7	0.85	53	40.7-57.0	48.1	0.67
Carrizo Sands – Guadalupe Co.	28	40-52	48.0	0.63	30	43-53	47.3	0.42	58	40-53	47.6	0.37

	Subadult Males				Subadult Females				Juveniles			
	N	Range	$\bar{x}$	SE	N	Range	$\bar{x}$	SE	N	Range	$\bar{x}$	SE
South Padre Island (Judd 1973)	-	-	-	-	-	-	-	-	52	23-27	24.5	1.28*
Rockport/Fulton (TNHC)	9	32.3-38.7	36.4	0.68	12	30.2-38.7	34.9	0.80	-	-	-	-
Mustang Island (TNHC)	12	30.5-38.9	36.4	0.90	11	30.0-39.8	35.2	0.98	-	-	-	-
Carrizo Sands - Somerset(TNHC)	12	32.4-39.8	36.2	0.77	6	31.7-37.7	33.9	0.94	12	25.7-29.2	27.1	0.31
Carrizo Sands – Guadalupe Co.	14	30-50	36.3	1.41	5	35-44	41.0	1.58	24	22-30	25.1	0.46

Table 8. Snout-Vent Lengths of adult keeled earless lizards for five populations, May-August. Measurements in millimeters. South Padre Island data are from Judd (1973), Tamaulipas data are from Selander et al. (1962), and Mustang Island and Rockport data are from specimens in the Texas Natural History Collection.

Population	Adult Males				Adult Females			
	N	Range	x	SE	N	Range	x	SE
South Padre Island	170	48-60	54.1	0.23	162	43-55	49.6	0.21
Tamaulipas	33	49-62	56.0	0.50	14	47-53	50.9	0.50
Rockport	8	48.1-52.2	50.0	0.53	8	44.9-51.8	47.6	0.78
Mustang Island	11	52.2-57.0	54.8	0.47	6	47.8-51.7	49.5	0.68
Guadalupe Co.	15	48-52	50.1	0.63	27	44-52	47.4	0.45

The analyses of variance showed differences among the populations ($F_{(4/235)}$ = 19.474, $P < 0.001$ for males and $F_{(4/212)} = 6.5391$, $P < 0.001$ for females). The results of Tukey's multiple comparison test showed a clear difference between males (Table 9) of the mainland populations (Rockport and Carrizo Sands – Guadalupe County) and the island populations (Mustang Island, South Padre Island, and Tamaulipas). Males from the Carrizo Sands of Guadalupe County grow to a similar size as those in the Rockport population ($t_{(21)} = -0.103$, $P = 1.00$; Fig. 6).

Lizards from the adjacent Mustang Island population are larger than the Rockport and Guadalupe populations, and similar in size to both the South Padre Island and Tamaulipas populations, which show a significant difference from each other, based on this comparison.

Table 9. Tukey's MCP of adult male keeled earless lizard snout-vent lengths for five populations, May-August. South Padre Island data are from Judd (1973), Tamaulipas data are from Selander et al. (1962), and Mustang Island and Rockport data are from specimens in the Texas Natural History Collection.

Populations	difference	95% CI	*p*-value
Mustang Island-Guadalupe Co.	4.72	1.65 - 7.78	< 0.001
Rockport-Guadalupe Co.	-0.10	-3.17 - 2.96	0.9999834
South Padre Island-Guadalupe Co.	4.01	1.93 - 6.09	< 0.001
Tamaulipas-Guadalupe Co.	6.36	3.96 - 8.77	< 0.001
Rockport-Mustang Island	-4.82	-8.11 - -1.53	< 0.001
South Padre Island-Mustang Island	-0.71	-3.11 - 1.70	0.9278732
Tamaulipas-Mustang Island	1.65	-1.04 - 4.34	0.4437373
South Padre Island-Rockport	4.11	1.71 - 6.51	< 0.001
Tamaulipas-Rockport	6.47	3.78 - 9.15	< 0.001
Tamaulipas-South Padre Island	2.36	0.89 - 3.82	< 0.001

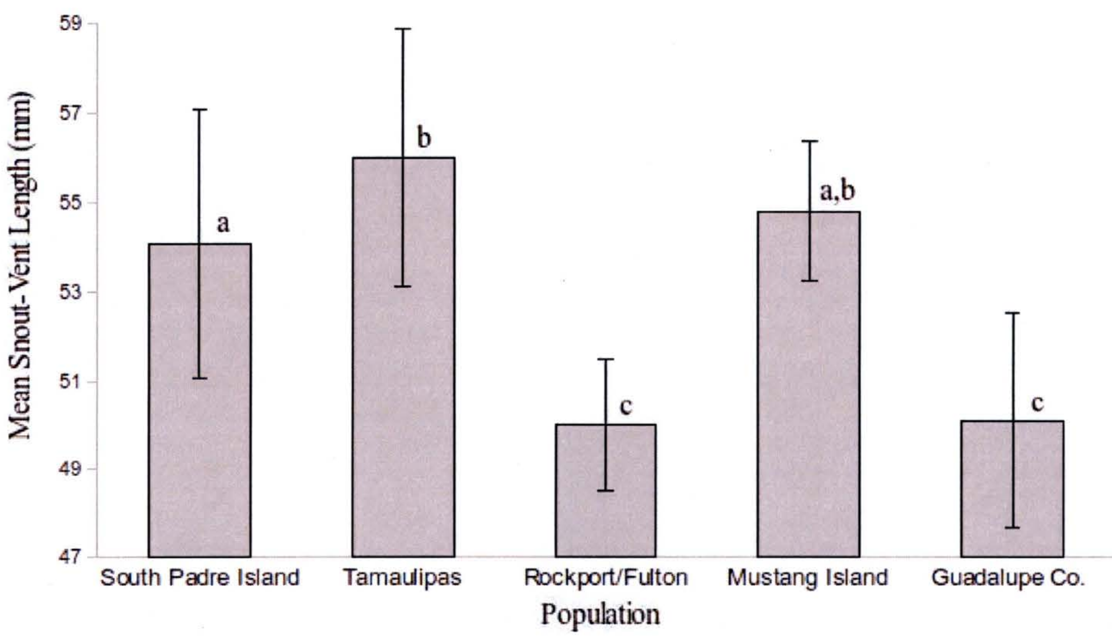

Fig. 6. Mean snout-vent lengths (± SD) for males of 5 examined populations of specimens captured May-August. Populations with same letter (a, b, c) have no difference ($P > 0.05$).

Females of the Carrizo Sands – Guadalupe County population had a mean SVL similar to the Rockport population ($t_{(33)}$ = 0.16, P = 1.00; Table 10). Mustang Island and Tamaulipas populations were similar ($t_{(18)}$ = 1.46, P = 0.773), and the South Padre Island ($t_{(168)}$ = 2.03, P = 0.190) and Mustang Island ($t_{(12)}$ = -1.92, P = 0.637) populations were also similar in length to the Rockport population (Fig. 7).

Table 10. Tukey's MCP of adult female keeled earless lizard snout-vent lengths for five populations, May-August. South Padre Island data are from Judd (1973), Tamaulipas data are from Selander et al. (1962), and Mustang Island and Rockport data are from specimens in the Texas Natural History Collection.

Population	difference	95% CI	*p*-value
Mustang Island-Guadalupe Co.	2.08	-1.11 - 5.26	0.3808887
Rockport-Guadalupe Co.	0.16	-2.69 - 3.00	0.9998851
South Padre Island-Guadalupe Co.	2.18	0.72 - 3.65	< 0.001
Tamaulipas-Guadalupe Co.	3.53	1.21 - 5.86	< 0.001
Rockport-Mustang Island	-1.92	-5.73 - 1.89	0.6374661
South Padre Island-Mustang Island	0.11	-2.83 - 3.04	0.9999753
Tamaulipas-Mustang Island	1.46	-1.99 - 4.90	0.7729536
South Padre Island-Rockport	2.03	-0.53 - 4.59	0.1899449
Tamaulipas-Rockport	3.38	0.25 - 6.51	0.0273639
Tamaulipas-South Padre Island	1.35	-0.62 - 3.31	0.3296204

There was no difference between snout-vent lengths of juveniles from South Padre Island and juveniles from Guadalupe County ($t_{(77)}$ = -0.365, P = 0.7161). Within the Guadalupe County population, there was no difference in snout-vent length between adult males and females ($t_{(56)}$ = 0.8866, P = 0.3791 and subadult males and females ($t_{(17)}$ = -1.8362, P = 0.08388).

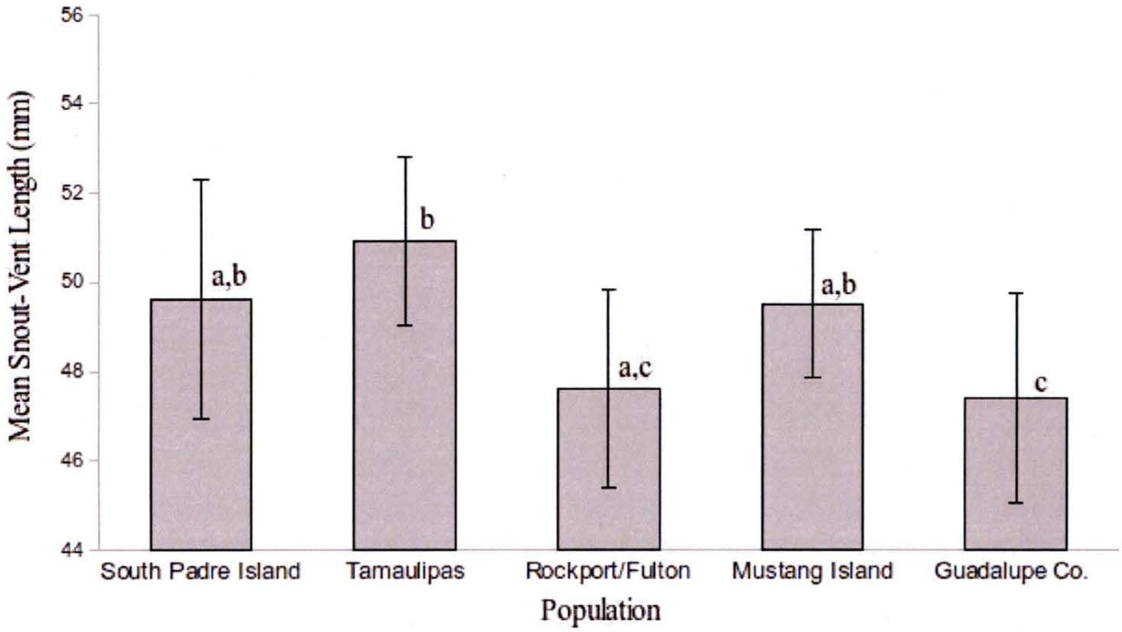

Fig. 7. Mean snout-vent lengths (± SD) for females of 5 examined populations of specimens captured May-August. Populations with same letter (a, b, c) have no difference ($P > 0.05$).

Tail Length

Only lizards with non-regenerated tails were used for this part of the study. Table 11 shows mean tail lengths of males, females, and juveniles of three studies.

There were significant differences in tail length among adult males of the five examined populations ($F_{(4/86)} = 6.6578$, $P < 0.001$). Males from Guadalupe County had similar tail lengths only to the mainland population at Rockport ($t_{(28)} = 6.24$, $P = 0.824$; Table 12). Males of all other populations had similar tail lengths (Fig. 8).

Table 11: Unbroken tail lengths of adult males, adult females, and juveniles among selected populations of keeled earless lizards. Measurements in millimeters. An estimated standard error is indicated by *. South Padre Island data are from Judd (1973), Tamaulipas data are from Selander et al. (1962), and Mustang Island, Rockport, and Carrizo Sands - Somerset data are from specimens in the Texas Natural History Collection.

Population	N	Range	Mean	SE
Adult Males				
South Padre Island	17	?-89	78.0	1.40*
Tamaulipas	33	69-85	77.0	0.70
Rockport/Fulton	5	63.8-70.6	66.9	1.28
Mustang Island	11	68.3-79.6	75.4	0.96
Guadalupe County	25	47-72	60.5	1.34
Adult Females				
South Padre Island	17	?-74	64.4	0.88*
Tamaulipas	14	57-68	62.2	0.90
Mustang Island	5	55.3-63.3	59.5	1.44
Guadalupe County	27	41-58	52.1	0.83
Juveniles				
South Padre Island	51	24-35	31.6	0.30*
Carrizo Sands–Somerset	8	29-35.4	33.0	0.79
Guadalupe County	23	23-35	29.0	0.73

Table 12. Tukey's MCP of adult male keeled earless lizard unbroken tail lengths for five populations. South Padre Island data are from Judd (1973), Tamaulipas data are from Selander et al. (1962), and Mustang Island and Rockport data are from specimens in the Texas Natural History Collection.

Population	difference	95% CI	*p*-value
Mustang Island-Guadalupe Co.	14.71	2.64 - 26.79	0.0089358
Rockport-Guadalupe Co.	6.24	-10.11 - 22.59	0.8244458
South Padre Island-Guadalupe Co.	17.05	6.56 - 27.54	< 0.001
Tamaulipas-Guadalupe Co.	12.23	3.39 - 21.08	0.0020437
Rockport-Mustang Island	-8.47	-26.47 - 9.52	0.6844071
South Padre Island-Mustang Island	2.33	-10.58 - 15.24	0.9867998
Tamaulipas-Mustang Island	-2.48	-14.10 - 9.13	0.9754395
South Padre Island-Rockport	10.81	-6.17 - 27.78	0.3951620
Tamaulipas-Rockport	5.99	-10.02 - 22.00	0.8346425
Tamaulipas-South Padre Island	-4.82	-14.78 - 5.15	0.6627185

There were significant differences in tail length among adult females ($F_{(3/59)}$ = 44.011, $P < 0.001$; Table 13). Tukey's MCP for females indicated a significant difference between the Guadalupe County population and the Mustang Island ($t_{(30)}$ = 7.32, $P = 0.001$), the South Padre Island ($_{t(42)}$ = 12.48, $P < 0.001$), and the Tamaulipas ($t_{(39)}$ = 10.18, $P < 0.001$) populations (Table 13). The Rockport population was excluded from this part of the test due to small sample size ($N = 3$). There was also a significant difference in tail length between adult female lizards from Mustang Island and South Padre Island ($t_{(20)}$ = 5.16, $P = 0.049$; Table 13, Fig. 9).

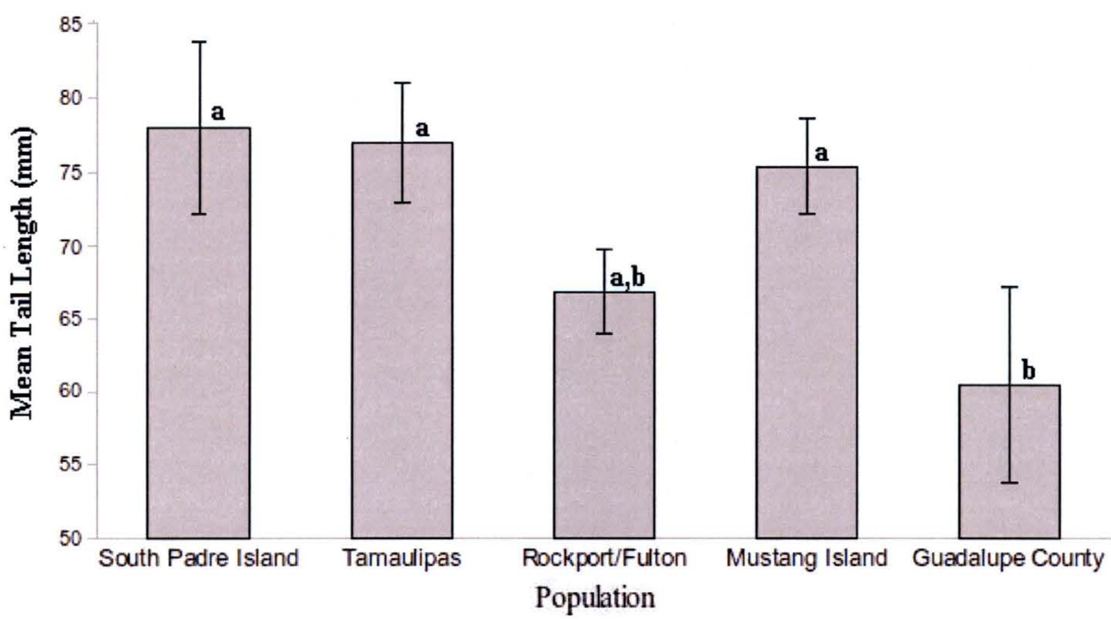

Figure 8. Mean unbroken tail lengths (± SD) for adult male specimens captured May-August. Populations with same letter (a, b) have no difference ($P > 0.05$).

Table 13. Tukey's MCP of adult female keeled earless lizard unbroken tail lengths for four populations. South Padre Island data are from Judd (1973), Tamaulipas data are from Selander et al. (1962), and Mustang Island and Rockport data are from specimens in the Texas Natural History Collection.

Population	difference	95% CI	*p*-value
Mustang Island-Guadalupe Co.	7.32	2.39 - 12.25	0.0012782
South Padre Island-Guadalupe Co.	12.48	9.34 - 15.61	< 0.001
Tamaulipas-Guadalupe Co.	10.18	6.84 - 13.51	< 0.001
South Padre Island-Mustang Island	5.16	0.01 - 10.31	0.0493724
Tamaulipas-Mustang Island	2.86	-2.41 - 8.13	0.4837544
Tamaulipas-South Padre Island	-2.30	-5.95 - 1.35	0.3514652

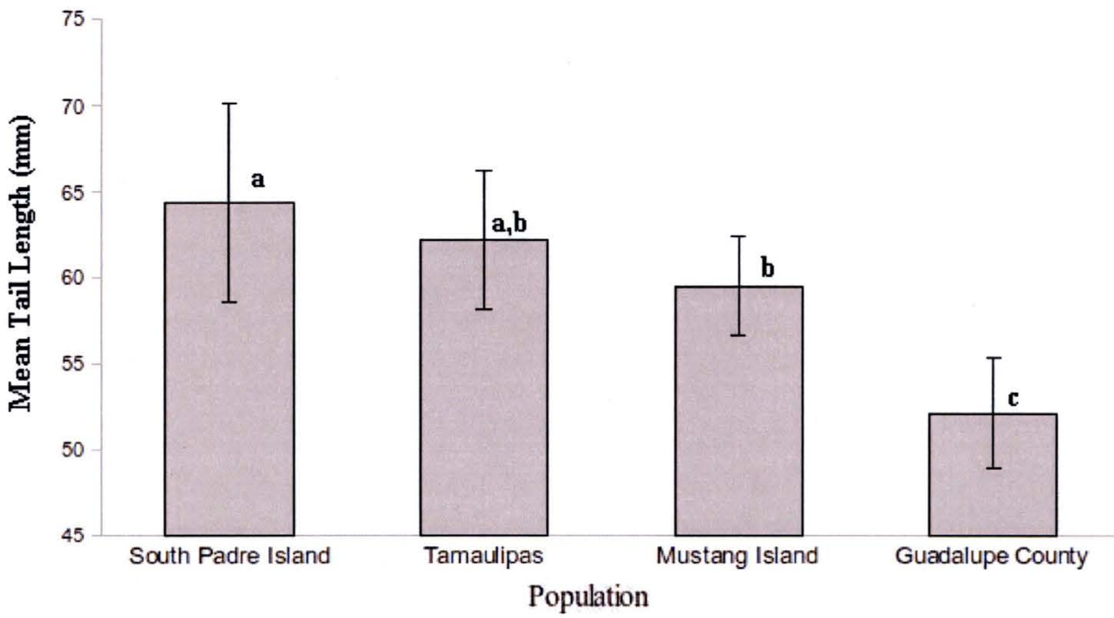

Figure 9. Mean unbroken tail lengths (± SD) for adult female specimens captured May-August. Populations with same letter (a, b, c) have no difference ($P > 0.05$).

There were significant differences in tail lengths for juveniles ($F_{(2/79)} = 9.3056$, $P < 0.001$) among the Carrizo Sands – Somerset, Carrizo Sands – Guadalupe County, and South Padre Island populations. There were significant differences between the Guadalupe County population and the Somerset ($t_{(29)} = 4.91$, $P = 0.003$) and South Padre Island ($t_{(72)} = 3.40$, $P < 0.001$) populations, and no significant difference between the Somerset and South Padre Island populations ($t_{(57)} = -1.51$, $P = 0.501$), even though one is further inland than the Guadalupe County population and the other is an island population (Table 14 and Fig. 10). The significance of this finding is unclear.

Table 14. Tukey's MCP of juvenile keeled earless lizard unbroken tail lengths for three populations. South Padre Island data are from Judd (1973) and Carrizo Sands – Somerset data are from specimens in the Texas Natural History Collection.

Population	difference	95% CI	*p*-value
Somerset-Guadalupe Co.	4.91	1.46 -8.36	0.0030462
South Padre Island-Guadalupe Co.	3.40	1.29 -5.51	0.0007049
South Padre Island-Somerset	-1.51	-4.71 -1.69	0.5006591

There was a significant difference in tail lengths between males and females for the Guadalupe County population ($t_{(50)} = 5.3604$, $P < 0.001$). This agrees with the general observation for this species that males have significantly longer tails than females.

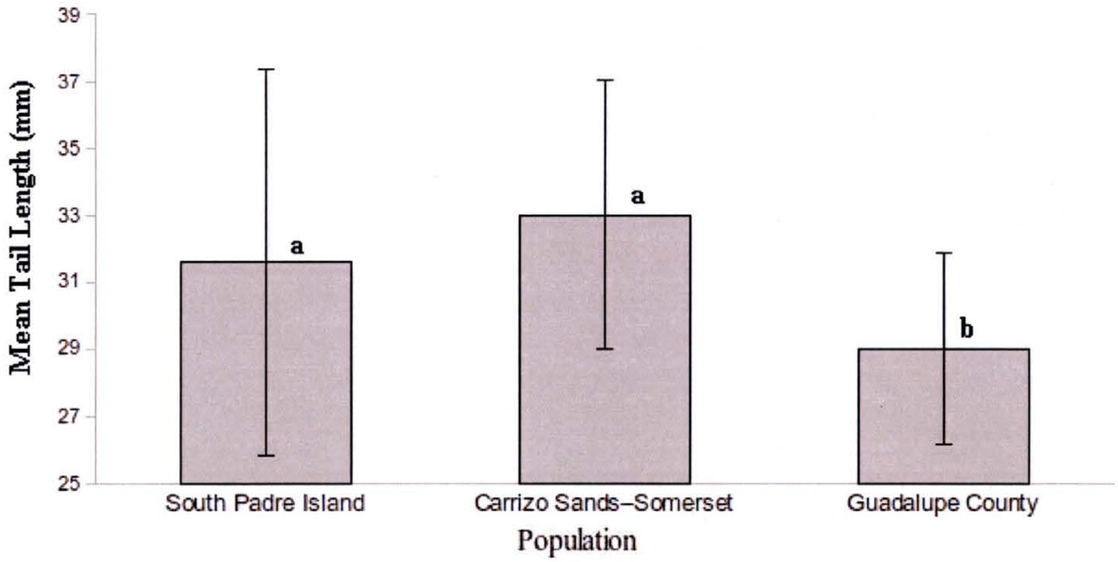

Figure 10. Mean unbroken tail lengths (± SD) for juvenile specimens. Populations with same letter (a, b) have no difference ($P > 0.05$).

Temperature

I observed the earliest movements by lizards at 0925 h. The lowest body temperature at emergence was 27.0° C. Lizards ceased escape behavior at a body temperature of about 42.5° C. The hottest surface temperature under which lizards were active was 56.0° C.

Table 15 shows the mean cloacal temperatures of lizards chased < 1m on days and times when the air temperature exceeded 30° C and/or surface temperatures exceeded 45° C. Cloacal temperatures for adult males and females were approximately 38° C. There was no difference ($t_{(14)} = -0.1032$, $p = 0.9193$) between the sexes.

Table 15. Cloacal Temperatures of keeled earless lizards of the Guadalupe County population. Measurements in °C.

	N	Range	Mean	SE
Adult Males	7	35.6-40.2	38.11	0.246
Adult Females	9	36.8-40.5	38.19	0.231
Total Adults	16	35.6-40.5	38.16	0.347

Body Mass

Table 16 shows the mean body mass for male and female adults, overall adults, juvenile, and male and female subadult keeled earless lizards and compares these measurements to equivalent findings for the South Padre Island population (Judd 1973).

Table 16. Body masses of adult males, adult females, subadult males, subadult females, and juveniles of the Guadalupe County and South Padre Island populations of the keeled earless lizard. Measurements in grams. An estimated standard error is indicated by *. South Padre island data are from Judd (1973).

Population	N	Range	Mean	SE
Adult Males				
South Padre Island	20	?-6.9	5.12	0.23*
Guadalupe County	27	2.5-4.4	3.76	0.11
Adult Females				
South Padre Island	20	?-6.1	4.26	0.08*
Guadalupe County	31	2.7-5.7	3.88	0.15
Overall Adults				
South Padre Island	40	?-6.9	4.69	0.15*
Guadalupe County	58	2.5-5.7	3.82	0.09
Juveniles				
South Padre Island	48	0.44-0.78	0.63	0.03*
Guadalupe County	24	0.5-1.2	0.65	0.04
Subadults – Guadalupe County				
Males	14	1.0-3.0	1.79	0.16
Females	5	1.4-3.5	2.64	0.36

There were significant differences between body mass of adult males ($t_{(46)}$ = -7.2253, $P < 0.001$) and adult females ($t_{(48)}$ = -2.0261, $P = 0.04833$) from the Guadalupe County population and the South Padre Island population (Judd 1973), but not in juveniles ($t_{(70)}$ = 0.141, $P = 0.8883$). However, there was no difference in body mass between adult males and adult females of the Guadalupe County population ($t_{(56)}$ = -0.6227, $P = 0.536$).

Judd (1973) divided his tail length and body mass results into more age classes than I did for the Guadalupe County population. Neither Judd (1973) nor Selander et al. (1962) gave a combined sample size of overall adults or juveniles for snout-vent length, tail length, or body mass. However, inclusion of standard errors in their data allowed me to use program R to generate an estimated standard error for each combined sample, thus allowing me to perform statistical tests.

Escape Behavior

Table 17 shows recorded run distances of earless lizards, separated as total adults, males, total females, non-gravid females, gravid females, subadults, and juveniles. Also shown are the published results of Cooper's study on run distances (Cooper 2003a). Run distances > 10 m were omitted from these data.

Table 17. Mean initial escape run distances of adult males and adult females, subadults, and juveniles of the Guadalupe County and South Texas populations of the keeled earless lizard. Measurements in cm. South Texas data are from Cooper (2003a).

	N	Mean Run Lengths (cm)	SE	Extremes
Guadalupe County				
Total Adults	49	219.1	27.7	0-600
Adult Males	22	213.2	44.2	0-500
Adult Females	27	223.9	35.9	0-600
Non-gravid Females	15	245.0	48.9	10-600
Gravid Females	12	197.5	54.0	0-600
Subadults	17	86.2	31.5	0-500
Juveniles	22	59.3	17.4	0-300
South Texas				
Total Adults	98	142.0	13.0	8-762
Adult Males	47	155.0	21.0	8-762
Adult Females	50	132.0	17.0	15-610

There was a significant difference in the mean run distance between adult male and female lizards of the Guadalupe County population and the South Texas population (Cooper 2003a)($F_{(3/151)} = 9.1797$, $P < 0.001$). However, there was no difference in the mean run distance between males and females within each population ($t_{(47)} = 99.33$, $P = 0.490$ for the Guadalupe County population, $t_{(95)} = 21.16$, $P = 0.980$ for the South Texas population; (Table 18). There was no difference in run distances of gravid and non-gravid females ($t_{(25)} = -0.651$, $P = 0.521$).

Table 18. Tukey's MCP of initial escape run distances between males and females of the Guadalupe County and South Texas populations of the keeled earless lizard. South Texas data are from Cooper (2003a).

Population	difference	95% CI	*p*-value
South Texas males vs. females	21.16	-119.60 - 161.92	0.9797234
Guadalupe County males vs. females	99.33	-82.72 - 281.39	0.4904545
Females – Guadalupe Co. vs. South Texas	185.29	25.29 - 345.30	0.0160978
Males – Guadalupe Co. vs. South Texas	263.47	98.07 - 428.87	0.0003351

Table 19 shows escape cover types for uncaught individuals and for individuals for whom a definite escape cover destination could be determined. Relative abundance of each type of escape cover was not included in this table, however, grass clumps, bull nettle, prickly ash, and kangaroo rat (*Dipodomys compactus*) burrows were ubiquitous in the habitat. Other types of cover were relatively rare in the habitat, but were more common in non-habitat areas.

Table 19. Escape cover types used by individuals of different age groups of the Guadalupe County population of the keeled earless lizard.

Primary Escape Cover	Adults	Subadults	Juveniles
Grass Clump	3	0	2
Kangaroo Rat Burrow	7	4	3
Bull Nettle	2	2	2
Prickly Ash	8	2	1
Bumelia	3	0	0
Pencil Cactus	1	0	0
Brush/Forb (Misc)	5	0	0
Leaf Litter	1	0	0

Among all individuals, prickly or thorny vegetation was used 21 times, as opposed to kangaroo rat burrows, which were only used as escape cover 14 times. Individuals occasionally passed nearby kangaroo rat burrows for more distant thorny vegetation, but the reverse was never observed.

IV. DISCUSSION

Vegetation and Habitat Components

The difference in the number of keeled earless lizards caught at each grid can be best explained by the spatial distribution of sand and vegetation: Grid A consists of clumps of vegetation separated by relatively large areas of open sand, while the ground cover of grid B is more evenly distributed. This pattern agrees with Judd's study (1973), where lizard density was dependent more on the spatial distribution of vegetation clumps and less on the actual percent ground cover. However, without assessing the relative spatial distribution of ground cover between my study site and South Padre Island, it is difficult to make any conclusion about how closely the spatial distributions of sand and vegetative clumps of the two sites resemble each other.

Principal components analysis indicated keeled earless lizards positively associated with open areas of the Arenosa fine sands component of the Carrizo Sands Formation. There was also a high association with the presence of kangaroo rat burrows. In contrast, keeled earless lizards negatively associated with stony soils such as the sandstone hills, exceptionally grassy or brushy environments, and areas with heavy overstory canopy and associated leaf litter.

Keeled earless lizards occupied Arenosa fine sands almost exclusively over Arenosa and Patilo soils, even though sand quality appeared to be the same. An in-depth examination of sand structure and composition might explain why keeled earless lizards selected this substrate.

The sand depth of the Arenosa fine sands (2.4 m) is similar to the gulf coast barrier islands (essentially bottomless) and the South Texas sand sheet (up to 2.3 m) (USDA 2010) where the species is abundant. Most localities with fewer voucher specimens (Axtell 1998) were from lesser sand depth and/or sand quality (USDA 2010).

Keeled earless lizards on South Padre Island were more numerous in pioneer communities, such as those found along the margins of washouts (Judd 1973). My results agreed, as there was a high incidence of lizard captures in proximity to disturbed sites such as unpaved driving trails through the Arenosa fine sands. I posit that in pre-settlement times, keeled earless lizards on the Carrizo Sands Formation were most abundant in areas of Arenosa sand where the post oak savanna community has been disturbed, such as after wildfire, similar to the Texas horned lizard (*Phrynosoma cornutum*) (Fair and Henke 1997).

Occupancy

The co-variate with greatest influence on occupancy was the percent of bare sand in the ground cover. The amount of grass was the common factor in all three models predicting detection probability. The presence or absence of kangaroo rat burrows and the amount of canopy cover also figured into two of the detectability models.

Occupancy modeling is still in its infancy (MacKenzie et al. 2006). Although it has been used on tortoises (Gu and Swihart 2004, Zylstra and Steidl 2009), this is the first published attempt to use this method for lizard occupancy. While relatively few studies have been published to date, the field and associated software appear to be evolving at a rapid rate, and it will be interesting to watch it evolve.

Morphology and Physical Characteristics

Snout-Vent Length

As expected, males of the Guadalupe County population were significantly smaller in snout-vent length than adults of the South Padre Island (Judd 1973), Tamaulipas Barrier Island (Selander et al. 1962), or Mustang Island populations. Males were similar to mainland populations at Rockport/Fulton. Females of the Guadalupe County population were similar in size to the Rockport/Fulton/Live Oak Peninsula and South Padre Island populations but markedly smaller than the Mustang Island and Tamaulipas populations.

Males of the South Padre Island (Judd 1973) and Tamaulipas Barrier Island (Selander et al. 1962) populations have significantly larger snout-vent lengths than females. In contrast, the Guadalupe County population showed no significant difference in snout-vent lengths between males and females. Similarly, Axtell (1954) suggested keeled earless lizards as a species have little difference in snout-vent lengths between males and females. There was no significant difference between juveniles of the South Padre Island population and my population, indicating similar sizes at hatching. This is further backed up by the similarities in minimum observed juvenile size.

Tail Length

Tail lengths of keeled earless lizards from Guadalupe County were significantly shorter at all age classes than tail lengths of coastal populations, which corresponded with smaller snout-vent lengths. Male tail lengths were longer than females, but all individuals had tails significantly shorter in relation to snout-vent length than individuals from other populations (Selander et al. 1962, Judd 1973,). The mean tail length for females of the Guadalupe County population was nearly the same length as the body. The original, unregenerated tails of some females were actually shorter than the snout-vent length. This is atypical for the species (Axtell 1958).

Temperature

Thermal ecology did not differ substantially between the Guadalupe County population and other populations (Clarke 1965, Judd 1973,1975). The lowest body temperature at emergence in the Guadalupe County population was 27.0° C. Keeled earless lizards on South Padre Island emerged at a similar mean ground temperature (and presumably body temperature) of 27.6° C, however, the lowest ground temperature recorded at emergence was 26.1° C (Judd 1975). The earliest activity observed in Guadalupe County was at 0925 h; however, Judd (1975), observed lizards emerging as early as 0644 h. The difference in onset of activity may be due to the tree canopy on the Carrizo Sands Formation preventing the heating of the sand until later in the morning when the sun was more directly overhead.

Panting behavior began at a mean body temperature of 42.6° C for 12 adults (Judd 1973). The highest body temperature observed for a chased lizard in my study reached 42.5° C, at which point the lizard became sluggish enough to catch by hand. Judd (1973, 1975) reported mean body temperatures (T_b) of 37.5° C and 38° C, and Clarke (1965) reported a mean T_b = 37.5° C, with a range of 31° C-40.4° C, for 45 individuals in a laboratory setting. The Guadalupe County population had a similar mean (T_b = 38.2° C). The surface temperature (T_{sn}) for lizards during activity periods frequently exceeded 50°

C and occasionally 60° C on South Padre Island (Judd 1973, 1975). The hottest T_{sn} I observed at which lizards were still active was 56.0° C, on 27 June 2008.

Body Mass

Adult male and female body mass of the Guadalupe County population differed significantly from South Padre Island (Judd 1973), corresponding with the reduced snout-vent length. However, juveniles had essentially the same body mass, regardless of population. There was also no significant difference in body mass between males and females of the Guadalupe County population.

Escape Behavior

Run distance did not differ significantly between males and females within populations, however, they did among populations. Cooper (2003a) did not mention individuals running excessive distances; however, 6 adult males, 3 adult females, and 2 subadult females in my study ran distances of 10 m or more. In all such cases, the individual encountered an unpaved trail or road and ran straight along it for a great distance before seeking cover.

Individuals also preferred thorny vegetation as escape cover over kangaroo rat burrows by a factor of 3:2. Individuals occasionally passed up nearer kangaroo rat burrows for more distant thorny cover; the reverse was not observed.

The most surprising finding came when I performed the *t*-test between run distances of gravid and non-gravid females. I expected to find that gravid females would run significantly shorter distances than non-gravid females, due to increased weight and the metabolic requirements of gestation. Instead, it may be that these requirements are not significant enough to keep gravid females from running long distances, or there may be some instinctive drive to use more energy in this situation, in order to protect the developing eggs.

Strangely, I found no previous studies on the keeled earless lizards that mentioned escape cover, beyond the fact that they use kangaroo rat burrows as escape cover (Axtell 1958). I confirmed the Guadalupe County population of keeled earless lizards also used burrows as escape cover; however, thorny vegetation was preferred as escape cover by a ratio of 3:2.

The closely-related species *Holbrookia maculata* has been observed using burrows of pocket gophers (*Thomomys* and *Geomys*) in Colorado, but apparently preferred burrows of pocket mice (*Chaetodipus*) (Vaughn 1961).

Other Observations

The earliest juveniles in this study were observed was 27 June 2009. Judd (1973), first observed juveniles on 26 June 1970 and 23 June 1971. In 2008, I did not find hatchlings on 23 June or 27 June; instead, hatching occurred between 27 June and 26 July.

I found no evidence to confirm or refute that any individuals in my study were >1 year of age. Judd (1973) did not find differences that would allow age determination by size: one must have an individual's history from a mark-recapture study in order to ascertain age >1 year with any reliability.

Future Studies and Refinements

I had significant problems dealing with random point-plots on edge habitat. The landscape was so varied that many patches were quite small. The problem was the collage of post-oak woodlands, post-oak shrublands, post-oak savannah, or open sandy areas all occurred within a 50 m radius. Future studies in this area should have more plots with smaller radii.

I discovered the Guadalupe-San Marcos River drainage constituted a major disruption in the Carrizo Sands band. However, Axtell (1998) reported two county records for keeled earless lizards northeast of the Colorado River, another major barrier to migration by sand-associated lizards. Both records (16 km north of Bastrop, near Camp Swift, and northeast of Caldwell, Burleson County), moreover, are found on deposits of Arenosa fine sand, and may therefore provide good habitat for these lizards.

A Note on Conservation:

Most of the land management practices in place have benefits for the keeled earless lizard. The occasional vehicular traffic, mowing/haymaking, or grazing can create areas of open sand necessary for this lizard's survival.

Encroachment of the exotic coastal Bermudagrass into keeled earless lizard habitat is the biggest threat to the Guadalupe County population. At my study site, the prime habitat for this lizard adjoined large fields planted with Bermudagrass to the east (Fig. 4). Areas of Arenosa fine sands planted with coastal Bermudagrass are devoid of lizards, as grass ground cover approaches 100% in those areas. To insure the lizard population's survival, care should be taken to limit the spread of this grass.

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