PATTERNS OF SPACE USE IN ZEBRA-TAILED LIZARDS (CALLISAURUS DRACONOIDES) IN JOSHUA TREE NATIONAL PARK, CALIFORNIA, USA

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Abstract.—Zebra-tailed Lizards (*Callisaurus draconoides*) dwell on sandy soils in a variety of arid habitats. They have large home ranges and do not aggressively defend core areas. In May and June of 2000, I studied the home ranges of Zebra-tailed Lizards in Joshua Tree National Park, California, USA, to determine whether individuals share space through overlapping home ranges. I tested the hypothesis that patterns of space use would vary by sex, age, desert, or study site. I could not calculate estimates of home-range area for 63% of the lizards observed due to their transient nature in the study sites. For those lizards resident in the sites, my findings support a correlation between home-range area and body size, with no variation by sex, age, desert, or study site. Male and female lizards exhibited similar proportions of home-range area overlap; however, males overlapped greater numbers of females than did females. Analyses did not reveal differences in the pattern of space use relating to age, desert, or by site; however, lizards occupying a narrow wash had significantly more home range overlap than those in broad washes, despite home-range area being similar across study sites. Males and females partitioned space differently, and it may be that when space is shared, it is partitioned temporally, with individuals using the space at different times.

Key Words.—habitat; home range; landscape; overlap; resident; topography; transient

INTRODUCTION

Home range is defined as the area of the habitat in which an individual carries out its routine activities (e.g., finding food, basking sites, shelter, and mates; Burt 1943; Rose 1982). By definition, it differs from a territory in that the home range is not necessarily defended against entry by conspecifics or other intruders (Schoener 1968). Average home-range area is a key character in describing the ecology of a species (Börger et al. 2008); yet, the home range for an individual in a population may vary around the average reported for the species (Perry and Garland 2002; Börger et al. 2008). These differences may relate to factors intrinsic to the individual, such as sex, age, reproductive status, and/or body condition (Turner et al. 1969; Rose 1982; Van Sluys 1997), conditions of the population, such as age structure, density, and/or presence of a dominance hierarchy (Rose 1982; Alberts 1993; Van Sluys 1997; Frost and Bergmann 2012), local environmental factors, such as recent rainfall, season, and/or temperature (Rose 1982; Alberts 1993; Van Sluys 1997; Frost and Bergmann 2012), and condition of sympatric species populations including food species (Scoular et al. 2011), competitors (Tinkle et al. 1962), predators (Tinkel et al. 1962), and pathogens (Bouma et al. 2007).

Many studies have documented that body size, which is frequently correlated with age, is an important factor associated with home-range area (e.g., Turner et al. 1969; Christian and Waldschmidt 1984; Perry and

Garland 2002). Larger animals with greater energetic needs may require larger home ranges in which to forage (McNab 1963; Schoener 1968). In species with sexual size dimorphism, this may result in larger home ranges for the larger sex (Turner et al. 1969). Furthermore, larger individuals may simply possess the ability to travel over a greater area, and larger individuals in species that maintain territories may be capable of defending a greater area than smaller conspecifics.

Additionally, wide-ranging foragers typically have larger home-range areas than sit-and-wait predators (Rose 1982; Van Sluys 1997). The sex and breeding condition of an animal can also have an effect on home range size. Breeding males may traverse greater areas in search of females (Rocha 1999), or, as found both for eutherian and marsupial mammals, pregnant females may have larger ranges than non-pregnant ones, perhaps in an effort to find sufficient nutritional resources (Bixler and Gittleman 2000; Fisher and Owens 2000). The reverse may be true in ectothermic animals; for example, pregnant *Niveoscincus microlepidotus* skinks were found to decrease their home-range areas (Melville and Swain 1999).

As extrinsic factors, aspects of the environment can also influence the home range size of an individual. Traeholt (1997) found that Water Monitor Lizards (*Varanus salvator*) exhibited different home range sizes in different habitats. Seasonal changes in habitat can result in a change in home range size (Van Marken and Wouter 1993) as a result of changing resource

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FIGURE 1. An adult male Zebra-tailed Lizard (*Callisaurus draconoides*) in Riverside County, California, USA. (Photographed by Marina M. Gerson).

availability (Eifler and Eifler 1998; Melville and Swain 1999). Home range fluctuates inversely with population size, at least in territorial lizards (White 1964; Tinkle 1967). The distribution of competitors (Sheldahl and Martins 2000) and mates (Jenssen and Nunez 1998) has also been shown to influence the space use of individuals. The social structure of the population also influences the spatial relationships of juvenile (Civantos 2000) and adult lizards (Griffiths 1999).

Zebra-tailed Lizards (*Callisaurus draconoides*; Fig. 1) are a small (63–101 mm snout-to-vent length; Stebbins 2003), primarily insectivorous (Kay et al. 1970; Pianka and Parker 1972; Vitt and Ohmart 1977) phrynosomatid species native to the American Southwest (Stebbins 2003). They are found in a range of arid landscapes (Vitt and Ohmart 1977) and are associated with open habitats, often with loose, sandy soils (Pianka and Parker 1972; Germano and Hungerford 1981; Stebbins 2003). Tanner and Krogh (1975) found home ranges for adult males in creosote scrub habitat in Nevada, USA, to vary between 3,500–6,000 m².

While some authors have stated that Zebra-tailed Lizards are territorial (Clarke 1963; Eifler and Eifler 2010), no definitive field study has been published. Furthermore, this behavior could be variable among populations, across seasons and years, and between sexes and age classes. Agonistic encounters, including fighting, have been described for both sexes and a range

of age classes, but these were recorded in lizards held captive in relatively small enclosures ($< 21 \text{ m}^2$; Clarke 1963) when compared with the recorded home range size; thus, lizards may have been unable to employ non-agonistic strategies such as avoidance. Reported field observations in support of territoriality have been limited to display behaviors, and in one case the observation of two males in close proximity was described as a stand off without further detail (Tanner and Krogh 1975). To the contrary, Frost and Bergmann (2012) found random distribution patterns for both adult female and adult male Zebra-tailed Lizards in Tucson, Arizona, USA, suggesting a lack of territorial behavior for either sex.

Very large home ranges are indefensible (Carpenter 1958), and no authors have proposed that Zebra-tailed Lizards defend a smaller core territory. Thus, for the purpose of this study, I consider that Zebra-tailed Lizards may defend a limited personal space, such as described by Gates (1957), against intrusion but I will not consider them to be genuinely territorial (i.e., regularly defending a set area in the habitat against intrusion). Nonetheless, it is not necessarily the case that they share space in the habitat or overlap in their home ranges. In a desert environment with scarce resources, lizards might require large, unshared home ranges in which to meet their daily nutritional needs. Even without aggressive territoriality, avoidance may provide a mechanism for reducing overlap. Alternatively,

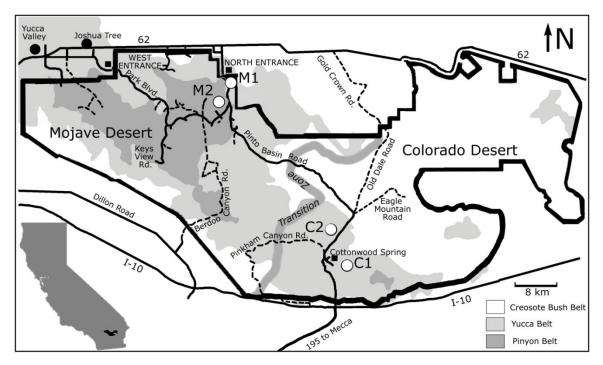


FIGURE 2. Joshua Tree National Park (Riverside and San Bernardino counties, California, USA) straddles higher elevation Mojave Desert characterized by yucca (*Yucca* sp.) and pinyon pines (*Pinus* sp.), and lower elevation Colorado Desert, characterized by creosote bush (*Larrea tridentata*) flats (modified from Miller and Stebbins 1973). The field sites Mojave-1 and Mojave-2 were located near the north entrance of the park, while Colorado-1 and Colorado-2 were located in the southern portion of the park.

individuals might share space in overlapping home ranges (e.g., Tevis 1944) or they might temporally partition the space. This study investigated the use of space by Zebra-tailed Lizards at four study sites in Joshua Tree National Park, California, USA, to determine whether lizards share home range space and whether there are patterns in space use that may vary by sex, age, desert, or study site.

MATERIALS AND METHODS

sites where Zebra-tailed Lizards were the most common lizards present in Joshua Tree National Park in Riverside and San Bernardino counties, California, USA (Fig. 2, Table 1). All four sites were located in dry, sandy washes with vegetation present. I located two sites in the higher elevation Mojave Desert (Mojave-1 and Mojave-2) and two in lower elevation Colorado Desert (Colorado-1 and Colorado-2). All four sites were located out of view of roads and popular tourist areas, to reduce disturbance of the sites by park visitors. I located Mojave-1 in a wide wash close to the North Entrance of the park. The three most common plants at the site were Creosote (Larrea tridentata), Jojoba (Simmondsia chinenesis), and yucca (Yucca spp.). I located Mojave-2 in a relatively narrow wash southwest of Mojave-1 with

Desert Willow (*Chilopsis linearis*), Catclaw Acacia (*Acacia greggii*), and Creosote the most common perennial plants. In the Colorado Desert, I located Colorado-1 in a narrow canyon approximately 2.9 km down the Lost Palms Trail near Cottonwood Spring in the south of the park where Desert Willow, desert thorn (*Lycium* spp.), and Catclaw Acacia dominated. I located Colorado-2 in the broad Smoke Tree Wash with the three most common plants being Smoke Tree (*Psorothamnus spinosus*), Desert Willow, and Catclaw Acacia.

I prepared each site for home range surveys by creating a coordinate grid system on the floor of the wash (Fig. 3). The dimensions and area of each site differed (Table 1) due to site topographies, as well as to accommodate the entire home ranges of approximately 12 lizards at each site. During the survey, if I observed a study lizard outside of the site perimeter, the study area and grid were expanded to include that part of the home range of the lizard. The grid was prepared using a 25 m measuring tape and a compass (Suunto, Vantaa, Finland) to keep gridlines straight. I wrote grid coordinates in permanent marker on biodegradable flagging ribbon that I then attached to stones of 3-4 cm in diameter found at the margins of the site. I placed grid markers 10 m apart. I began data collection 24 h after site preparation, to allow lizards to resume daily behavior following the

Site Name	Coordinates	Dimensions	Elevation	Dates of Study
Mojave-1	34°04.470'N, 116°01.753'W	61 m \times 230 m (14,000 m ²)	900 m	11–26 June 2000
Mojave-2	34°01.343'N, 116°01.335'W	83 m × 212 m (17,596 m ²)	1,050 m	10–26 June 2000
Colorado-1	33°43.931'N, 115°47.616'W	$26 \text{ m} \times 190 \text{ m} (4,940 \text{ m}^2)$	1,010 m	20 May to 4 June 2000
Colorado-2	33°48.123'N, 115°46.965'W	95 m \times 240 m (22,800 m ²)	915 m	25 May to 8 June 2000

TABLE 1. Location, dimensions, elevation, and dates of study of the four study sites for Zebra-tailed Lizard (*Callisaurus draconoides*) in Joshua Tree National Park, Riverside and San Bernardino counties, California, USA in May and June 2000.

disturbance. During daily surveys, I took care to confirm that rock markers had not been moved, and if a marker was out of place, I re-measured its proper location and replaced it before I recorded any data.

Data collection.—Between 25 May and 26 June 2000, I sampled for 15–17 consecutive days at each site (Table 1). I sampled two sites in the same time frame, and I arbitrarily alternated morning and afternoon sampling

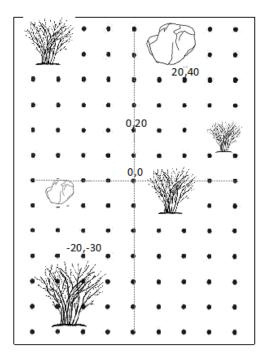


FIGURE 3. A 10-m coordinate grid of non-obtrusive stone markers was created amidst the shrubs and boulders on the floor of each study site. The dashed line indicates the primary axes of the coordinate system, and four representative coordinates are shown.

between the two sites being studied. I captured using a noose each Zebra-tailed Lizard encountered in a study area during the first 3 d of working in the site and I recorded the following measurements: weight, snout-tovent length (SVL), tail length, and head width. I noted the sex of each individual and any identifying characteristics, such as a regenerated tail, scar, or missing digits. I recorded the time of the initial sighting and air temperature in the shade. Prior to release at the site of initial observation, I assigned each lizard a unique color code, which I marked on the dorsum using felttipped markers. It was thus possible to visually identify individuals, negating the need to disturb the animals with successive recaptures.

I recorded the initial coordinate grid location $(\pm 0.10 \text{ m})$ of each lizard, measured from the nearest flagging marker. No sooner than the day following the initial capture and marking of each lizard, I began to record additional sightings. Moving slowly, so as not to cause lizards to flee prior to observation, I recorded the position of each lizard in the study area. Following the initial pass through the study area, I left the site undisturbed for at least 2 h before I made another pass to collect lizard locations.

If I observed an unmarked lizard after the initial capture period, I noosed and processed it as I did original individuals (if believed to be a new individual) and then I made additional observations of its locations. Occasionally, one of the study lizards would shed its skin, and thus also shed its dorsal identification marking. If an unmarked lizard appeared with shed skin clinging to the limbs or tail, I captured this unmarked animal and marked it with a new code. If its measurements matched those of a missing animal and the original lizard did not appear through the rest of the study period, then I considered them to be the same and I grouped their sightings.

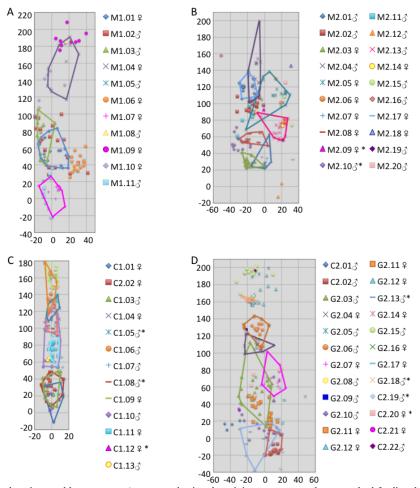


FIGURE 4. Observation locations and home ranges (constructed using the minimum convex polygon method for lizards with sufficient data points) of Zebra-tailed Lizard (*Callisaurus draconoides*) in four study sites: (A) Mojave-1, (B) Mojave-2, (C) Colorado-1, and (D) Colorado-2; an asterisk (*) denotes a juvenile lizard.

Home range calculations.---I calculated lizard home ranges daily, by the minimum convex polygon method, using the program Antelope (unpubl.; Bradbury and Vehrencamp, Cornell University, Ithaca, New York, USA). Thus, I was able to follow the suggestion by Rose (1982) that the number of data points collected should be sufficient such that additional sightings no longer contribute to an increase in home-range area. The minimum convex polygon method, which is commonly used in lizard studies, was appropriate for my calculations because lizards appeared to have fairly regularly shaped home ranges (e.g., Rose 1982; Brown et al. 1995; Van Sluys 1997; Rocha 1999), partly constrained by the shapes of the washes they inhabit. One drawback that has been noted for the convex polygon method is that the constructed home ranges may include unsuitable habitat (Traeholt 1997): however, the study sites were relatively uncomplicated and little area considered unsuitable for lizard occupation existed.

Statistical analyses.—After log-transforming the home-range areas to meet normality assumptions (Sokal and Rohlf 1995), I used STATISTICA (StatSoft, Inc., Tulsa, Oklahoma, USA) to perform statistical analyses, using $\alpha = 0.05$ in all tests. I regressed home range on body size (SVL) and after finding a significant relationship, I tested for the effect of sex while holding SVL constant (one-way ANCOVA). I also tested for differences in home-range area between deserts (oneway ANCOVA) and sites (one-way ANCOVA) while controlling for body size. To calculate area of home range overlaps, I used ArcView GIS 3.2 software (ESRI, Redlands, California, USA) to create home range maps using minimum convex polygons and to measure the overlapping areas. Then, I tested for effects of sex on percentage overlap of each sex with males and with females using a Student's *t*-test. Additionally, I tested for the effects of desert and site on home range overlap using a two-way ANOVA. Finally, I compared the proportions of resident and transient lizards between

Study Site	Lizard ID	Sex	SVL (mm)	No. of Sightings	Home-range area (m ²)
Mojave-1	M1.01 M1.03	+0 03 03 +0	73 74	23 15	1,137.28 830.55
	M1.04	ð	85	11	2,258.53
	M1.07	Ŷ	72	17	850.51
Mojave-2	M2.01	3	72	21	959.36
	M2.03	Ŷ	65	21	249.21
	M2.04	ð	79	20	866.88
	M2.05	, Ŷ	70	20	1,600.06
	M2.07	50 0+ 50 0+ 0+ 0+ 50 05	69	17	486.43
	M2.08	ģ	68	21	362.84
	M2.13	3	77	19	662.21
Colorado-1	C1.01	Q	70	18	609.71
colorado 1	C1.01	+	65	10	667.46
	C1.02	*	92.5	19	686.51
	C1.05	3*	50	18	245.95
	C1.06	ð	85	19	422.64
	C1.08	3*	52	14	321.79
	C1.09	Ŷ	66.5	18	469.04
	C1.10	ð	90	18	1,059.42
	C1.11	0+0+% % % % 0+% 0+	77	17	295.01
Colorado-2	C2.02	ð	19	19	418.29
	C2.03	8	22	22	2,374.38
	C2.04	<pre>%</pre> %%	20	20	472.54
	C2.06	3	19	19	621.61
	C2.07	Ŷ	17	17	904.40
	C2.13	3*	14	14	1,412.86
	C2.18	3*	15	15	46.92

TABLE 2. Summary of home range data for Zebra-tailed Lizard (*Callisaurus draconoides*), including sex, snout-to-vent length (SVL), and the number of sightings used to generate a home-range area using the convex polygon method; an asterisk (*) indicates a juvenile lizard.

males and females through Chi-squared frequency analysis using Yates correction for 2×2 contingency tables.

RESULTS

I made 752 sightings of 66 lizards and I determined that there were 11 adult and four juvenile males and 12 adult females resident on the four study sites. I considered additional lizards to be possible transients in the site and determined that there were 24 adult and five juvenile males and 14 adult and three juvenile females that were transients. There was no difference in the proportion of transients that were male versus female, both when juveniles were included ($X^2 = 0.147$, df = 1, P = 0.701) and excluded ($X^2 = 0.822$, df = 1, P = 0.365) in the analysis.

I was able to construct home ranges for 23 adult and four juvenile Zebra-tailed Lizards. I mapped four home ranges in Mojave-1, seven in Mojave-2, nine in Colorado-1, and seven in Colorado-2 (Fig. 4, Table 2).

TABLE 3. Average home-range areas (and standard deviation) for Zebra-tailed Lizards (*Callisaurus draconoides*) at sites in the Mojave and Colorado deserts of Joshua Tree National Park, Riverside and San Bernardino counties, California, USA in May and June 2000.

Sex	Mojave-1	Mojave-2	Colorado-1	Colorado-2
М	1544.53 m^2	764.54 m^2	547.26 m ²	974.81 m ²
	(± 202.8)	(± 152.1)	(± 331.2)	(± 928.2)
F	993.95 m ²	731.58 m ²	510.30 m ²	658.77 m ²
	(± 1009.7)	(± 624.5)	(± 166.0)	(± 305.4)

For resident lizards, the average home range size (mean \pm SD) for all lizards combined was 788.6 m² \pm 568.95 (n = 27; range, $46.9-2,374.4 \text{ m}^2$). The overall average for adult lizards was 837.6 $m^2 \pm 560.40$ (n = 23; range, 249.2–2,374.4 m²) and for juveniles was 506.9 m² \pm 615.01 (n = 4; range, 46.9-1,412.9 m²). The average home-range area for adult females was 675.4 $m^2 \pm$ 393.04 (n = 12; range, 249.2–1,600.1 m^2) and for adult males was 1014.6 $m^2 \pm 674.49$ (n = 11; range, 418.3– 2,374.4 m²). Snout-to-vent length (SVL) of lizards (adult and juvenile combined) showed a significant relationship to home range size ($F_{1.25} = 4.142$, P = 0.002, $r^2 = 0.638$). Holding body size constant, home-range area did not differ significantly by sex ($F_{1.26} = 0.918$, P =0.343). No significant differences were found in homerange area between those lizards in the Mojave and Colorado deserts ($F_{1,26} = 0.264$, df = 26, P = 0.617) nor between any of the sites ($F_{3,26} = 0.481$, df = 26, P = 0.691).

The average overlap of home ranges of male Zebratailed Lizards with other males was 1.78 (range 0-3) and with females was 1.90 (0-2); females with males was 1.65 (0-3) and with other females was 0.55 (0-2). Male and female home ranges showed similar mean overlap of area with conspecifics; both males and females shared approximately 44.6% (range 0-100%) of their home range ($F_{1,26} = 0.001$, df = 26, P = 0.973). Female lizard home ranges overlapped with significantly fewer home ranges of other females than males overlapped with females (t = 4.07, df = 26, P = 0.001); however, both males and females overlapped with equivalent numbers of males (Table 3). There were significant effects of desert ($F_{1,26} = 7.42$, P = 0.012) and site ($F_{3,26} = 20.27$, P= 0.001) on the percentage of home range overlap, due to the significantly greater overlap observed in the Colorado-1 study site (Fig. 5).

DISCUSSION

This study adds to the general knowledge of the ecology of Zebra-tailed Lizards across the range of the species, by providing baseline information on home range and space use at Joshua Tree National Park, a

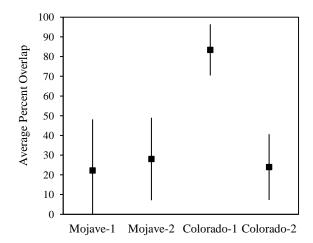


FIGURE 5. Average percentage overlap of home ranges for all Zebratailed Lizards (*Callisaurus draconoides*) at four study sites in Joshua Tree National Park in Riverside and San Bernardino counties, California, USA. Error bars are one standard deviation.

locality for which these specific data have not been reported previously (Table 4). Nonetheless, the small number of sites sampled, the small proportion of individual lizards for which home-range areas could be calculated, and the limited duration of data collection in a single year are shortcomings of this work. Because I spent only 15-17 d in each site, my study was unable to address the possibility that home-range areas and locations may change seasonally (Van Sluys 1997; Griffiths 1999) or from year to year. Furthermore, visual detection rates of this lizard, even by trained observers, can be less than perfect (Miller and Stebbins 1973), and the presence of an observer could affect the behavior of the animals leading to skewed results. More reliable conclusions can be drawn using more recently developed radio-tracking technologies, including light-weight radio collars (e.g., Germano and Rathbun, In press), and further research efforts are encouraged.

Similar to Tanner and Krogh (1975) in Nevada, the average home-range area for adult male Zebra-tailed Lizards was greater than that for females; this appears to be due to sexual size dimorphism (Turner et al. 1969; Pianka and Parker 1972; Rocha 1999). Thus, as is common across lizard groups (Turner et al. 1969; Perry and Garland 2002), body size appears to be a good predictor of home-range area for Zebra-tailed Lizards. Compared to the lizards at the study site of Tanner and Krogh (1975), adult male Zebra-tailed Lizards in Joshua Tree National Park lizards had smaller home ranges: 418.29–2,374.38 m² observed in this study compared to $3,500-6,000 \text{ m}^2$ in Nevada. Thus, variation potentially exists in resource needs for this species across its range. Contrary to expectation, there were no differences in lizard home-range area between the sites in the Mojave Desert compared to those in the Colorado Desert, nor between the four sites in general. With the most distant sites (i.e., Mojave-1 and Colorado-1) being located only 43.8 km apart, perhaps all four sites were situated close enough geographically to provide equivalent habitat.

Similar to the findings of other researchers (Tevis 1944; Tanner and Krogh 1975; Frost and Bergmann 2012), I found that all age and sex classes of Zebra-tailed Lizards overlapped in home range with conspecifics; adults shared 44.6% of their home ranges. Zebra-tailed Lizards showed their highest rates of home range overlap between, rather than within, the sexes. Females only shared space with 0.55 other females on average, but with 1.65 males. The low rate of overlap between females may have been due to their relatively smaller size, and associated smaller home-range areas compared to males. Male Zebra-tailed Lizards sampled in this study overlapped home ranges with 1.90 females on average. It should be to the benefit of a male lizard to overlap with as many females as possible to increase his mating opportunities, even if this results in an overlap with other males (Smith 1985; Van Sluys 1997). My results differ in that males overlapped with similar numbers of males as they did females. However, examination of 399 observation coordinates of males produced only 20 records of two males ≤ 10 m apart; thus, male lizards were only in close proximity for 5% of sightings. While female Zebra-tailed Lizard appeared to segregate spatially, males may have segregated temporally such that individuals rarely encountered one another despite using the same space (Schoener 1974). In addition to longer-term studies, removal experiments would provide valuable information on the social structure of both home-range area and overlap in this species.

The statistical difference in overlap between deserts and sites was driven by the high level of overlap (83.4%; range, 65.9–100%) observed at the Colorado-1 study site; the other study sites had average levels of overlap < 30%. The Colorado-1 site was unique in that it was located in a narrow wash bordered by steep canyon walls. Zebra-tailed Lizards appeared not to climb out of the wash, restricting their activity along the dry streambed (Gerson 2004). The other three sites were located in wide washes. Thus the amount of overlap in home ranges might partially be governed simply by the topography of the habitat. While Natsumeda (2007) noted topography as a factor influencing home range size in fish, it has not been explored in lizards and would benefit from further investigation.

Of the 73 lizards encountered, 27 were observed a sufficient number of times to permit calculation of home-range areas. Some individuals were observed only at the beginning of the study period, and others did not appear at a study site until the finals day(s) of data collection. Three of the lizards that disappeared after the initial marking period were observed a few days later

Study	Locality	Sample Size	Home Range Area	Notes
Tevis (1944)	Baja California, Mexico	-	-	Site fidelity noted; axis of home range reported to be 15.24 m with home range overlap between individuals; agonistic encounters observed between lizards.
Smith (1946)	Not Given	-	-	Reported possible agonistic signaling (head bobs and display of the throat fan) between conspecifics.
Gates (1957)	Wickenburg, Arizona	-	-	Noted site fidelity of individuals and agonistic behavior between males.
Clarke (1963)	Lake Texoma and Norman, Oklahoma	-	-	A primarily ethological study conducted in indoor and outdoor enclosures $< 21 \text{ m}^2$ in size; reported agonistic or territorial behavior between males.
Pianka and Parker (1972)	Phoenix, Arizona	19	-	Distance between original capture site and recapture site ranged from 0–120.0 m for lizards sampled in pitfall traps.
Tanner & Krogh (1975)	Mercury, Nevada	> 50	3,500– 6,000 m ²	Used mark and recapture methods and multi-year data; home range area reported for males only; females' home ranges were noted to overlap those of males.
Vitt and Ohmart (1977)	Lower Colorado River, Arizona	-	-	Males and females used same basking sites as juveniles but appear later in the day.
Frost and Bergmann (2012)	Tucson, Arizona	229	-	Used nearest neighbor methods to describe spatial distributions of individuals, concluding that males and females were distributed randomly.

TABLE 4. Summary of previous studies relating to Zebra-tailed Lizard (Callisaurus draconoides) home range or social aspects of space use.

more than 100 m away from the study site and then never sighted again. Other individuals exhibited site fidelity, even from year to year (Gerson 2004). These observations suggest that while some Zebra-tailed Lizards are resident to a particular site, there may be other individuals that could be considered transients, moving through the area to a new location. Because both male and female transients occurred in relatively high proportions, it may be that both sexes disperse in this species. A multi-year study, tracking individuals over time, would elucidate whether a difference in dispersal or other movement patterns exists for males and females. Future studies should make use of current technology (e.g., radio transmitters) to examine the patterns of dispersal in Zebra-tailed Lizards, including the distance, timing, and causes of these movements in both sexes.

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LITERATURE CITED

- Alberts, A.C. 1993. Relationship of space use to population density in an herbivorous lizard. Herpetologica 49:469–479.
- Bixler, A., and J.L. Gittleman. 2000. Variation in home range and use of habitat in the Striped Skunk (*Mephitis mephitis*). Journal of the Zoological Society of London 251:525–533.
- Börger, L., B.D. Dalziel, and J.M. Fryxell. 2008. Are there general mechanisms of animal home range behaviour? a review and prospects for future research. Ecology Letters 11:637–650.
- Bouma, M.J., C.J. Smallridge, C.M. Bull, and J. Komdeur. 2007. Susceptibility to infection by a haemogregarine parasite and the impact of infection in the Australian Sleepy Lizard *Tiliqua rugosa*. Parasitology Research 100:949–954.

- Brown, R.M., D.H. Gist, and D.H. Taylor. 1995. Home range ecology of an introduced population of the European Wall Lizard *Podarcis muralis* (Lacertilia: Lacertidae) in Cincinnati, Ohio. American Midland Naturalist 133:344–359.
- Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346–352.
- Carpenter, C.R. 1958. Territoriality: a review of concepts and problems. Pp. 224–250 *In* Behavior and Evolution. Roe, A., and G.G. Simpson (Eds.). Yale University Press, New Haven, Connecticut, USA.
- Christian, K.A., and S. Waldschmidt. 1984. The relationship between lizard home range and body size: a re-analysis of the data. Herpetologica 40:68–75.
- Civantos, E. 2000. Home range ecology, aggressive behaviour, and survival in juvenile lizard, *Psammodromus algirus*. Canadian Journal of Zoology 78:1681–1685.
- Clarke, R.F. 1963. An ethological study of the iguanid lizard genera *Callisaurus*, *Cophosaurus*, and *Holbrookia*. Ph.D. Dissertation, University of Oklahoma, Norman, Oklahoma, USA. 136 p.
- Eifler, D.A., and M.A. Eifler. 1998. Foraging behavior and spacing patterns of the lizard *Cnemidophorus uniparens*. Journal of Herpetology 32:24–33.
- Eifler, D.A., and M.A. Eifler. 2010. Characteristics and use of the tail in signaling by the Zebra–tailed Lizard (*Callisaurus draconoides*). Southwestern Naturalist 55:104–109.
- Fisher, D.O., and I.P. Owens. 2000. Female home range size and the evolution of social organization in the macropod marsupials. Journal of Animal Ecology 69:1083–1098.
- Frost, C.L., and P.J. Bergmann. 2012. Spatial distribution and habitat utilization of the Zebra-tailed Lizard (*Callisaurus draconoides*). Journal of Herpetology 46:203–208.
- Gates, G.O. 1957. A study of the herpetofauna in the vicinity of Wickenburg, Maricopa County, Arizona. Transactions of the Kansas Academy of Sciences 60:403–418.
- Germano, D.J., and C.R. Hungerford. 1981. Reptile population changes with manipulation of Sonoran desert shrub. Great Basin Naturalist 41:129–138.
- Germano, D.J., and G.B. Rathbun. In press. Home range and habitat use by the Blunt-nosed Leopard Lizards in the southern San Joaquin Desert of California. Journal of Herpetology.
- Gerson, M.M. 2004. Aspects of the ecology of a desert lizard, *Callisaurus draconoides* (Blainville 1835), in Joshua Tree National Park with an emphasis on home range and diet. Ph.D. Dissertation, University of Texas at Arlington, Arlington, Texas, USA. 151 p.

- Griffiths, A.D. 1999. Demography and home range of the Frillneck Lizard, *Chlamydosaurus kingii* (Agamidae), in northern Australia. Copeia 1999:1089–1096.
- Jenssen, T.A., and S.C. Nunez. 1998. Spatial and breeding relationships of the lizard *Anolis carolinensis*: evidence of intrasexual selection. Behaviour 135:981–1003.
- Kay, F.R., B.W. Miller, and C.L. Miller. 1970. Food habits and reproduction of *Callisaurus draconoides* in Death Valley, California. Herpetologica 26:431–436.
- McNab, B.K. 1963. Bioenergetics and the determination of home range size. American Naturalist 894:133–140.
- Melville, J., and R. Swain. 1999. Home-range characteristics of an alpine lizard, *Niveoscincus microlepidotus* (Scincidae), on Mt Wellington, southern Tasmania. Wildlife Research 26:263–270.
- Miller, A.H., and R.C. Stebbins. 1973. The Lives of Desert Animals in Joshua Tree National Monument. University of California Press, Berkeley, California, USA.
- Natsumeda, T. 2007. Estimates of home-range size of the adult Japanese Fluvial Sculpin, *Cottus pollux* (Pisces: Cottidae) in relation to bottom topography and sampling intervals. Journal of Ethology 25:87–93.
- Perry, G., and T. Garland, Jr. 2002. Lizard home ranges revisited: effects of sex, body size, diet, habitat, and phylogeny. Ecology 83:1870–1885.
- Pianka, E.R., and W.S. Parker. 1972. Ecology of the iguanid lizard *Callisaurus draconoides*. Copeia 1972:493–508.
- Rocha, C.F.D. 1999. Home range of the tropidurid lizard *Liolaemus lutzae*: sexual and body size differences. Revista Brasileira de Biologia 59:125–130.
- Rose, B. 1982. Lizard home ranges: methodology and functions. Journal of Herpetology 16:253–269.
- Schoener, T.W. 1968. Sizes of feeding territories among birds. Ecology 49:123–141.
- Schoener, T.W. 1974. The compression hypothesis and temporal resource partitioning. Proceedings of the National Academy of Sciences 71:4169–4172.
- Scoular, K.M., W.C. Caffry, J.L. Tillman, E.S. Finan, S.K. Schwartz, B. Sivervo, and P.A. Zani. 2011. Multiyear home-range ecology of Common Sideblotched Lizards in Eastern Oregon with additional analysis of geographic variation in home-range size. Herpetological Monographs 25:52-75.
- Sheldahl, L.A., and E.P. Martins. 2000. The territorial behavior of the Western Fence Lizard, *Sceloporus* occidentalis. Herpetologica 56:469–479.
- Smith, D.D. 1985. Home range and territory in the Striped Plateau Lizard (*Sceloporus virgatus*). Animal Behaviour 33:417–427.

- Smith, H.M. 1946. Handbook of Lizards. Cornell
- Sokal, R.R., and F.J. Rohlf. 1995. Principles of Biometry. W.H. Freeman and Co., New York, New York, USA.
- Stebbins, R.C. 2003. A Field Guide to the Western Reptiles and Amphibians. Houghton Mifflin Company, Boston, Massachusetts, USA.
- Tanner, W.W., and J.E. Krogh. 1975. Ecology of the Zebra-tailed Lizard *Callisaurus draconoides* at the Nevada test site. Herpetologica 31:302–316.
- Tevis, L., Jr. 1944. Herpetological notes from Lower California. Copeia 1944:6–18.
- Tinkle, D.W. 1967. The life and demography of the Side-blotched Lizard Uta stansburiana. Miscellaneous Publications of the Museum of Zoology, University of Michigan No. 132.
- Tinkle, D.W., D. McGregor, and S. Dana. 1962. Home range ecology of *Uta stansburiana* Stejnegeri. Ecology 43:223–229.

University Press, Ithaca, New York, USA.

- Traeholt, C. 1997. Ranging behaviour of the Water Monitor Lizard Varanus salvator. Malayan Nature Journal 50:317–329.
- Turner, F.B., R.I. Jennrich, and J.D. Weintraub. 1969. Home ranges and body size of lizards. Ecology 50:1076–1081.
- Van Marken, L., and D. Wouter. 1993. Optimal foraging of a herbivorous lizard, the Green Iguana in a seasonal environment. Oecologia 95:246–256.
- Van Sluys, M. 1997. Home range of the saxicolous lizard *Tropidurus itambere* (Tropiduridae) in southeastern Brazil. Copeia 1997:623–628.
- Vitt, L.J., and R.D. Ohmart. 1977. Ecology and reproduction of lower Colorado river lizards: 1. *Callisaurus draconoides* (Iguanidae). Herpetologica 33:214–222.
- White, J.E. 1964. An index of the range of activity. American Midland Naturalist 71:369–373.



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