

## THE TERRITORIAL BEHAVIOR OF THE WESTERN FENCE LIZARD, *SCELOPORUS OCCIDENTALIS*

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**ABSTRACT:** In this study, we investigated the territorial behavior of *Sceloporus occidentalis* by focusing on three questions: do individuals of *S. occidentalis* (1) exhibit site-fidelity, (2) defend the site with aggressive behavior, and (3) maintain exclusive use of the defended area? Spatial distributions and aggressive behavior were studied in two natural populations. We also used a small arena to observe aggressive behavior in paired interactions. Repeatability analysis revealed that individuals of *S. occidentalis* maintain home ranges of similar areas and in similar locations across years. While lizards use pushup displays to delimit territories that are approximately 61% of total home range area, overt aggression (e.g., chases, bites) was infrequent. Furthermore, lizards maintained exclusive use of only a small proportion of their defended areas. We discuss our results in the context of what it means to be "territorial".

**Key words:** Home range; Territory; *Sceloporus*; Aggression; Behavior; Lizard; Pushup Display; Communication

CONSIDERABLE effort has been devoted to providing a universal definition for territoriality (Hinde, 1956; Kaufmann, 1983; Maher and Lott, 1995; Mathis et al., 1995; Tinbergen, 1957). However, differences in spatial distributions and defense strategies make it difficult to find similarities in territorial behavior across species. Noble (1939) defined a territory as any defended space. Other definitions include requirements involving, for example, the amount of space defended, the way the space is defended, and whether defense provides exclusive use (see Maher and Lott, 1995, for a recent review). However, problems arise when researchers develop operational definitions with one system and then try to apply these definitions to other groups of animals. In the current study, we examine space use and aggressive behavior of the western fence lizard, *Sceloporus occidentalis*, in an effort to describe the extent of territorial behavior that is characteristic of this species.

In a broad sense, territorial behavior is a relationship between aggressive behavior and the consistent use of a particular area, and most definitions involve elaboration of these aspects. For example, Stamps (1977) described two types of areas that might be defended: (1) all or a large part of the

home range or (2) specific sites within the home range (e.g., basking sites). Aggressive behavior also may manifest itself in many forms, including everything from violent aggression to advertisements such as visual displays and scent marking (Martins, 1994). Some researchers (Brown and Orrians, 1970; Ferner, 1974; Smith, 1985) have focused on the idea that the territory holder must use a space exclusively. Others have concentrated on determining what resources are being defended, such as mates (Ruby, 1978) or food (Simon, 1975). Maher and Lott (1995) broaden the definition of territoriality to include group defense strategies.

Nevertheless, most definitions of territoriality become less clear in the light of detailed empirical studies. As an example, Maher and Lott (1995) defined a territory as "a fixed space from which an individual, or group of mutually tolerant individuals, actively excludes competitors for a specific resource or resources." However Simon and Middendorf (1976) demonstrated that individuals of *S. jarrovi* may share space simply by being active at different times of the day. Are these animals actively excluding competitors? Similarly, Stamps and Krishnan (1994a,b, 1995, 1998) found a number of problems with the assumptions underlying definitions of territoriality. For one, persistence can be more important

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than the ability to win fights in determining which animal is able to maintain residence in a particular location (Stamps and Krishnan, 1995). Further, both winners and losers avoid locations where fights took place (Stamps and Krishnan, 1995).

On the other hand, there do seem to be a few critical similarities found across all territorial animals. First, territories remain in one place. An animal that travels over a vast range during a year, but defends only the small area within its immediate vicinity, does not exhibit site-fidelity, and would not be considered territorial. Second, territorial animals exhibit defense of a space. Animals that inhabit an area without ever showing aggression towards a competitor may not be territorial. Finally, some degree of exclusive use or priority of use of an area is important. Animals that are aggressive but are never able to retain exclusive use or priority of access to some area may not be territorial. These three components are found in virtually all definitions of territorial behavior (e.g., Brown and Orians, 1970; Mathis et al., 1995).

In this study, we explore these three components of territorial behavior in the western fence lizard, *Sceloporus occidentalis*, an animal traditionally considered to be territorial (Davis and Ford, 1983; Fitch, 1940). Lizards in the genus *Sceloporus* have been studied extensively in relation to spatial distributions and territoriality (see Martins, 1994, for review). *Sceloporus* is well known for its use of visual displays such as the pushup display when defending territories (Carpenter, 1967; Martins, 1993). *Sceloporus occidentalis* can also discriminate the chemical cues produced by different individuals (Duvall, 1979), and it is likely that they use chemical signals in territorial behavior (Alberts, 1993a).

As shown in Martins (1994), the common ancestor of all species of *Sceloporus* was most likely territorial, aggressively defending the majority of its home range. Some components of territorial behavior appear to have been lost within groups of *Sceloporus* over time. For example, lizards in the *variabilis* group appear to have lost most overt aggression. Similarly, animals in the *torquatus* group aggregate during the

non-breeding season rather than maintain exclusive use of a site (Martins, 1994). *Sceloporus occidentalis* is within a clade that seems to have retained the ancestral character of territorial behavior (Martins, 1994).

In this study, we mapped home range and territorial areas for two populations of *S. occidentalis*, and conducted a series of behavioral tests to examine aggressive behavior. Previous observations suggest that individuals of *S. occidentalis* defend territories (Davis and Ford, 1983; Fitch, 1940), but the behavior has not been described in detail. Our goal was to determine to what degree this species exhibits the following three components of territorial behavior: site-fidelity, aggressive defense of the site, and successful defense (e.g., exclusive access) of that area.

#### MATERIALS AND METHODS

##### *Study Organism and Site*

*Sceloporus occidentalis* is a small (<75 mm SVL) diurnal lizard found throughout most of the western United States. We conducted this study during the summer months (mostly June and July) in western Oregon on the saddle dam at Blue River Reservoir (1996 and 1997) and on Pigeon Butte in the William L. Finley Wildlife Refuge (1997 and 1998). In this region, this time period corresponds primarily to the mating season for *S. occidentalis* and slightly afterwards. The site at Blue River varied between 0.3 ha and 0.6 ha (as the reservoir emptied) and consisted primarily of rounded rocks interspersed with patches of gravel. The study site at Pigeon Butte was a 0.9 ha section of exposed rock from an abandoned rock quarry, surrounded by oak woodland and grasslands. Both field sites were partitioned into 5 m × 5 m quadrats using small flags marked with coordinates so that locations of lizards could be determined to within 0.25 m. Animals were captured and permanently marked with colored beads strung on surgical wire through the base of the tail (Fischer and Muth, 1989). The marked population at Blue River consisted of 17 males and nine females in 1996, and 11 males and eight

range area. In contrast, the Fourier method will not incorporate the unused space between two divided areas, and is likely to give the most accurate estimate of true home range size (Anderson, 1982). All of our spatial analyses were performed using Antelope v. 2.0.1 (Huber and Bradbury, 1996).

Home ranges were estimated using all points at which an animal was observed within a field season. Push-up displays are believed to function in territorial defense (Carpenter, 1967). Thus, territories were estimated using only coordinates where an individual was observed giving a pushup display. Most observations of pushup displays occurred during focal animal samples, which were mainly conducted with males. Thus, the territory sizes for females are often based on few observations. We conducted multiple regression analyses to determine the relative importance of the number of observations, individual, sex, and population differences in explaining variation in home range and territory sizes. Observer identity was excluded after preliminary regression analyses showed that differences in the data collected by different observers were quite small and not statistically significant. Area estimations were natural-log transformed to reduce heteroscedasticity in the error terms of regression analyses and to normalize area distributions when calculating repeatabilities (see below).

We measured site-fidelity by estimating home range size and location for each animal in each year for which it was observed, giving us 1–2 areas for each animal in the study. We then estimated the repeatability of home range size using the within- and among-animal variance components from a one-way ANOVA (for details, see Lessells and Boag, 1987; Lynch and Walsh, 1998). Repeatabilities range from 0.0–1.0 (Lynch and Walsh, 1998). We also estimated the correlation between home range areas across consecutive years using only those lizards observed in consecutive years. In order to estimate the consistency of home range location, we used the harmonic mean center-of-activity (COA). We estimated separate Pearson

product-moment correlations first between X-coordinates across years, and second between Y-coordinates across years. The direction of X and Y-axes were chosen arbitrarily on each site, so these analyses were conducted separately for the two populations.

Finally, we overlaid the home range and territory maps for all individuals of the same sex at each population to calculate the degree of overlap. The amount of non-exclusive area was estimated as the ratio of area shared with at least one other animal to the total area used by that animal. Multiple regression analysis was used to determine whether territories exhibited less overlap than did home ranges, including sex, population, and individual in the model as well.

## RESULTS

### *Home Range and Territory Sizes*

Home range size depended on the number of observations per lizard regardless of the method that we used to estimate area. Areas estimated with eight or fewer sightings were far more variable than were areas estimated with over eight points, even when natural-log transformed (Fig. 1). Hereafter, we present results only for animals observed over eight times during the study. We explain the majority of our results in terms of the Fourier 95%-use (F95) technique, but we offer minimum convex polygon (MCP) and ellipse 95%-use (E95) results for comparison.

Home range sizes ranged between 0.2 and 2675 m<sup>2</sup> depending on the method used to estimate the area, the sex, and the population of the animal. The average home range size was approximately 118.6 m<sup>2</sup> (SE = 10.82; Table 1). At Blue River, male and female lizards held similar home range areas while at Pigeon Butte, female home ranges were about two-thirds the size of male home ranges. In multiple regression analyses, this difference led to a significant sex by population interaction effect (F95 and E95,  $P < 0.05$ ; MCP,  $P > 0.05$ ) and population effect (F95 and MCP,  $P < 0.01$ ; E95,  $P > 0.05$ ). The effect of sex was not statistically significant ( $P > 0.05$ ).

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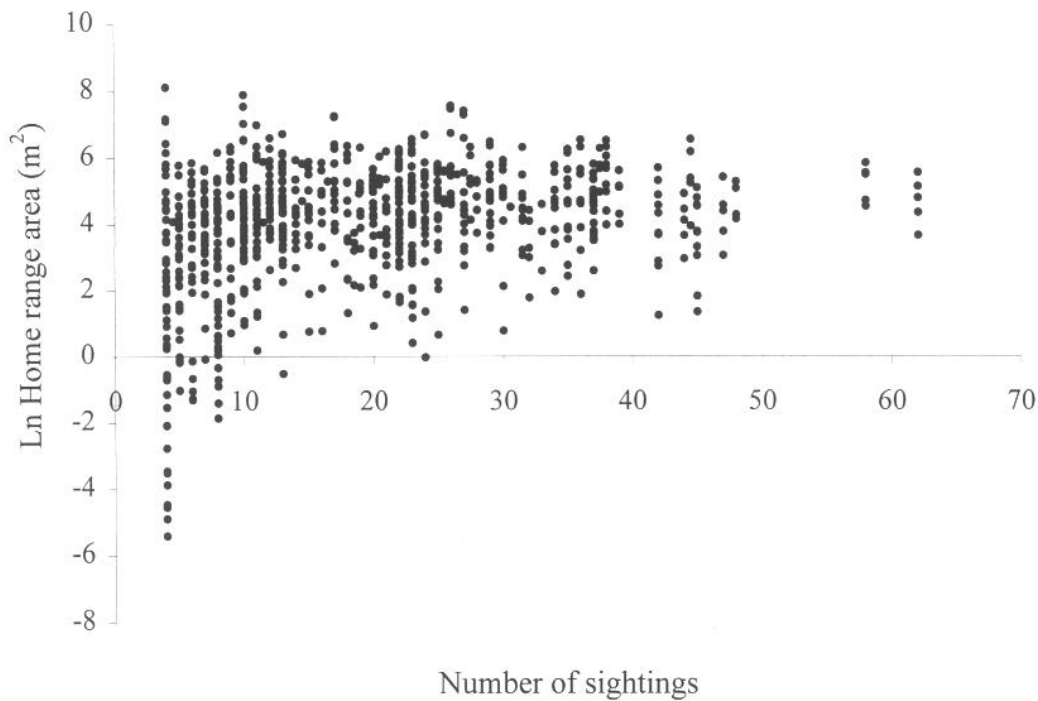


FIG. 1.—Relationship between ln-home range area (estimated using Fourier-95% method) and number of sightings for each individual lizard. All results presented in this study apply only to animals observed at least nine times.

The average territory size (grouping sex and population) was about two-thirds of the average home range size (Tables 1, 2), but this difference was not significant in multiple regression tests ( $P > 0.5$ ). Male territories were consistently larger than female territories, and again Blue River animals had larger territories than Pigeon Butte animals. Nevertheless, multiple regression analyses did not find these differences to be statistically significant.

#### Site-fidelity

Repeatabilities of home range size from a one-way ANOVA were relatively high, varying from 0.53 (E95) to 0.59 (F95) to 0.62 (MCP), all of which were significantly different from zero ( $P < 0.05$ ). Of the 163 lizards that we observed during this study, 33 were observed over eight times in each of two consecutive years. Correlation coefficients considering only these 33 animals were only slightly lower than the repeatability estimates, ranging from 0.37

(MCP) to 0.38 (E95) and 0.46 (F95, Fig. 2). Again, all were significantly different from zero ( $P < 0.05$ ).

Fence lizards also tended to remain in the same location across years (Table 3). Most correlation coefficients between X-coordinates or between Y-coordinates for 2 yr equaled or exceeded 0.90. All correlations, except that for males at Blue River, were positively correlated and significantly different from zero ( $P < 0.05$ ). Blue River males had less site-fidelity, with a correlation between X coordinates of 0.45, and between Y coordinates of  $-0.45$  ( $P > 0.05$ ).

#### Aggressive Defense

In 69.5 h of focal animal samples on the two sites, we observed a total of 644 push-up displays performed by 64 adult males. An average frequency of 5.9 displays/h (SE = 0.64) at Pigeon Butte, and 12.2 displays/h (SE = 0.57) at Blue River was observed. The vast majority of these were "Broad-

TABLE 1.—Mean home range areas ( $m^2$ ) and one standard error (in parentheses) for *S. occidentalis* at the two study sites. Home ranges were estimated using Fourier-95% (F95), minimum convex polygon (MCP), and ellipse-95% (E95) techniques.

	No. of animals	F95	MCP	E95
Pigeon Butte				
Males	69	142.5 (17.63)	299.9 (42.55)	348.4 (52.15)
Females	33	47.6 (9.08)	159.2 (46.51)	171.4 (50.47)
Total	102	111.8 (13.02)	253.9 (32.96)	291.1 (39.60)
Blue River				
Males	23	137.4 (21.41)	289.8 (43.48)	219.9 (30.79)
Females	7	156.3 (23.27)	331.3 (41.11)	251.8 (50.85)
Total	30	141.8 (17.18)	299.5 (34.52)	227.3 (26.12)
Grand total				
Males	92	141.2 (14.21)	297.4 (33.53)	316.3 (40.19)
Females	40	66.6 (10.68)	189.3 (40.24)	185.4 (42.64)
Total	132	118.6 (10.82)	264.4 (26.61)	276.6 (31.21)

cast" displays (cf. Martins, 1994), performed without a conspecific in the immediate vicinity.

Some measures of the pushup display were not obtained when animals were partially hidden from view, but complete data were available for 509 of the 644 displays observed. *Sceloporus occidentalis* was observed using up to 18 up-and-down motions in a single pushup display, with an average of 7.4 (SE = 0.15) head-bobs per display. Sixty nine percent (350) involved extension of the front two legs. Approximately 16% (82) involved extension of all four legs, and the remaining 15% (77) had no obvious motion of the legs (true "head-bobs"). About 14% (72) of the displays in-

cluded the use of at least one display-specific body posture. The most common body posture was the tail raise (T), lateral flattening (L), or gular extension (G) alone (16, 13, 13, displays, respectively). The combination of all four body postures was the next most common (nine displays). Gular extension was often paired with other body postures (G + arched back (A): seven displays, G + T: three, G + L: two, G + L + A: three), and the T + L (six displays) combination was also relatively common.

Multiple regression analyses of the total number of head-bobs showed no significant effects of observer or population [ $X = 6.86$  (SE = 0.217) headbobs/display at

TABLE 2.—Mean territory areas ( $m^2$ ) and one standard error (in parentheses) for *S. occidentalis* at the two study sites. Territories were estimated using Fourier-95% (F95), minimum convex polygon (MCP), and ellipse-95% (E95) techniques.

	No. of animals	F95	MCP	E95
Pigeon Butte				
Males	29	77.4 (18.77)	95.1 (23.68)	257.0 (60.22)
Females	12	19.2 (9.63)	17.1 (8.62)	60.8 (24.66)
Total	41	61.4 (14.39)	72.3 (17.75)	203.1 (46.13)
Blue River				
Males	10	121.9 (33.35)	169.8 (34.7)	169.4 (24.07)
Females	2	35.8 (18.80)	30.7 (18.9)	165.0 (79.96)
Total	12	107.6 (29.28)	146.6 (32.72)	168.7 (22.02)
Grand total				
Males	39	88.8 (16.45)	114.2 (20.21)	234.6 (45.40)
Females	14	21.7 (8.54)	19.0 (7.72)	76.84 (24.95)
Total	53	72.0 (13.11)	89.1 (16.04)	195.13 (35.77)

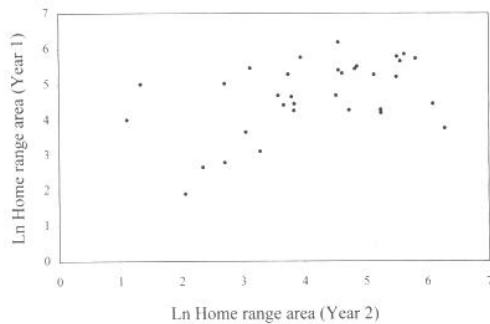


FIG. 2.—The relationship between home range size (estimated using Fourier-95% method) calculated for all animals measured in two successive years ( $r = 0.46$ ,  $P < 0.05$ ,  $df = 31$ ).

Blue River; 7.44 (SE = 0.302) head-bobs/display at Pigeon Butte;  $P > 0.05$ ], but they did show marked differences among individual lizards ( $P < 0.05$ ). The number of head-bobs was best explained by a model including individual identity ( $F = 3.761$ ,  $P < 0.001$ ), the number of legs extended (0, 2, or 4 treated as a categorical variable,  $F = 3.557$ ,  $P < 0.03$ ), and a dichotomous variable coding for whether or not body postures were used ( $F = 22.0$ ,  $P < 0.001$ ). The relationship among measures of display structure was positive, such that displays with a high number of head-bobs tended to include extension of all four legs and the use of body postures (Table 4).

Aggressive behavior other than pushup displays was rarely observed in the field. For example, only three aggressive chases were observed during 110 h of field observation in 1997 (all involved one male chasing another). Aggressive behavior was also uncommon in the arena trials. In a total of 63 arena trials, only one incidence of physical aggression was observed when a sub-adult male bit an adult male. Pushup displays were observed in about two-thirds (40) of the trials. Open-mouth gaping, an indicator of aggressive behavior (Carpenter, 1967), was observed in four trials (five individuals). Submissive flattening (a posture in which the lizard flattens its head and body against the substrate; Hunsaker, 1960) was observed in seven trials (11 individuals). Display body postures (thought to be an aggressive signal in *Sceloporus*

TABLE 3.—Pearson product-moment correlation coefficients describing the relationship between the centers of activity of individual lizards across two years.

	No. of animals	X-axis	Y-axis
Home range location			
Pigeon Butte			
Males	12	0.93**	0.96**
Females	7	0.99**	0.98**
Blue River			
Males	9	0.45	-0.45
Females	5	0.99**	0.90*

\*  $P < 0.05$ , \*\*  $P < 0.0001$ .

*graciosus*: Martins, 1993) both in pushup displays and other contexts, were used in 32% of the trials.

#### Exclusive Use

Estimates of overlapping home range and territory areas include only those marked animals observed over eight times, so they are likely to be underestimates of true overlap values. Male western fence lizards tend to have at least one other male overlapping their home range, and the total area overlapped averaged 28–67% (Fig. 3, Table 5). Female fence lizards maintained a higher proportion of exclusive area than males (F95 and E95,  $P < 0.01$ ; MCP,  $P > 0.05$ ). Nevertheless, there was usually one other female within the home range, and an average of 5–24% overlap, depending on the method used to estimate home range area.

Territories exhibited less overlapping area for male lizards, with about 14–52% shared area (Table 5). Male fence lizards tend to have at least one conspecific male

TABLE 4.—Mean number (and one standard error) of up-and-down motions per display produced in combination with display-specific body postures and different numbers of legs used to produce the up-and-down motion (4: all four legs together, 2: the front two legs alone, and 0: a true "head-bob").

Number of legs	With body postures	Without body postures	Total
4	10.5 (0.84)	7.7 (0.40)	9.1 (0.82)
2	8.7 (0.47)	6.9 (0.19)	7.2 (0.17)
0	7.0 (0.17)	6.4 (0.46)	6.3 (0.43)
Total	8.8 (0.41)	6.8 (0.16)	7.0 (0.18)

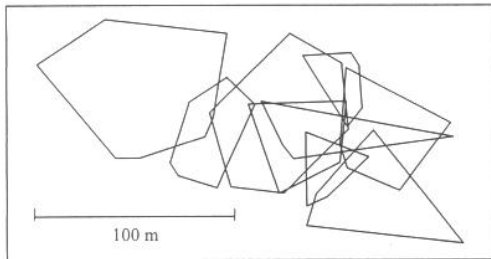


FIG. 3.—An illustration of the degree of overlap (30%) between male home ranges at Pigeon Butte calculated using the minimum convex polygon method. Calculations done using other methods lead to even larger estimates of overlap (about 50%; Table 5).

overlapping their territories. Home range overlap was slightly greater than territory overlap, but this difference was only statistically significant in multiple regression analyses utilizing the MCP method of area estimation ( $P < 0.05$ ).

#### DISCUSSION

In this study, *S. occidentalis* demonstrated considerable fidelity to a fixed area, both in terms of the location held and the amount of area occupied. They also produced pushup displays (thought to serve a function in territorial maintenance and defense) frequently. Thus, we are tempted to conclude that individuals of *S. occidentalis* are indeed territorial. Nevertheless, the

animals in our study only rarely exhibited overt aggression of any sort, whether in natural social interactions or in an experimental enclosure. Furthermore, home ranges of *S. occidentalis* overlap extensively, with each individual maintaining exclusive use of only about half of its "territory". From this perspective, it is less clear that *S. occidentalis* is territorial.

There are many possible explanations for why *S. occidentalis* might still be considered territorial despite the lack of overt aggression observed in this study. Stamps and Krishnan (1994a,b) determined that the highest levels of aggression between conspecifics occur when territories are first established. The results of our study show that individuals of *S. occidentalis* remain in the same territories across years. Thus, it seems that territory establishment occurs only once, early in life. As most individuals in the population are mature adults, we are unlikely to see much of the aggression expected during that initial territory establishment.

Levels of aggression may also be low because overt aggression is energetically costly, particularly for ectotherms (Burghardt, 1988). Several authors (e.g., Martins, 1994) have noted that aggression lies on a continuum from passive avoidance to threat to violent battles, all of which may be sufficient to maintain territories. Al-

TABLE 5.—Extent of minimum home range and territory overlap ( $m^2$ ) given as the percent of a resident's area that is shared by other animals. Standard errors are given in parentheses. Data were only available for two females at Blue River, and these are not included here. Fourier-95%-use (F95), minimum convex polygon (MCP), and ellipse 95%-use (E95) techniques are used.

	No. of animals	F95	MCP	E95
Home range				
Pigeon Butte				
Males	29	55.8 (5.96)	27.5 (6.54)	48.1 (7.85)
Females	8	23.7 (8.04)	15.4 (8.80)	4.8 (3.27)
Blue River				
Males	10	62.5 (9.45)	55.6 (13.04)	66.8 (9.13)
Territory				
Pigeon Butte				
Males	29	41.5 (6.27)	13.9 (5.63)	48.8 (8.13)
Females	8	23.6 (9.72)	0.0 (0.00)	11.4 (8.14)
Blue River				
Males	10	51.6 (9.98)	39.0 (11.72)	50.0 (10.30)



though many territorial lizard species will aggressively attack conspecifics when placed into paired encounters (McMann, 1993; Molina-Borja et al., 1998; Tokarz, 1985), this overt aggression may not be necessary in *S. occidentalis*.

The finding that individuals of *S. occidentalis* maintain exclusive use of only about half of the area that they defend is more problematic. Territorial animals are thought to maintain exclusive use of most of their home range most of the time (Maher and Lott, 1995; Schoener, 1968; Stamps, 1977). Nevertheless, the degree of home range overlap shown in our study is not unusual for *Sceloporus*. For example, studies of *S. virgatus* found measures of home range overlap quite similar to our own (about 30% for females and 75% for males: Abell, 1999; Rose, 1982; Smith, 1985). The more surprising result is that overlap between territories of *S. occidentalis* is also quite high (15–52%). Thus, animals are not successful at maintaining exclusive access even to the area that they are actively defending.

A probabilistic approach to exclusive use (e.g., Mathis et al. 1995) may solve the problem. Most overlap seems to occur on the outer edges of an individual's home range and territory (but see Simon and Middendorf, 1976, who suggested that lizards can share the same space by maintaining exclusive use at different times of the day). Further, Smith (1985) showed that lizards closer to the center of their own territories were more likely to win in aggressive encounters. Thus, perhaps instead of focusing on exclusive use, we should consider a territory to be any area within which individuals have a high probability of resisting intrusion by competitors. Note that this area is not necessarily the same area in which fights have been won (Stamps and Krishnan, 1995).

Another possibility is that *S. occidentalis* may really not be "territorial". Attempts to determine what resources territorial lizards might be defending have been mixed. Males may defend mates (M'Closkey et al., 1987; Rand, 1965) or not (Deslippe and M'Closkey, 1991). Relationships between food abundance and territory size may be

present (Simon, 1975), or there may be no evidence of a correlation (Rose, 1976). Nesting sites (Rand and Rand, 1976), basking sites (Stamps, 1977), and predator refuges (Stamps, 1983) may also be important resources to defend. In our own study, despite the superficial similarity between the two study sites in terms of availability of food, population density, and other ecological factors, we found considerable sex and population differences in the amount of space defended (Tables 1, 2).

Phylogenetic analysis (Martins, 1994) shows that territorial behavior is a primitive condition for the genus *Sceloporus*, and that any explicit function underlying territorial behavior may have disappeared long ago. This idea is supported by the apparent loss of most overt aggression in *S. occidentalis* and by the high levels of conspecific home range overlap. Over time, animals expending high amounts of energy defending a site without gaining fitness advantages could undergo selection toward forms of aggression that are less energetically costly. Thus, individuals of *S. occidentalis* may limit their present use of overt aggression because of the high energetic costs involved, but they remain superficially territorial because their ancestors were territorial.

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