

Core area overlap in a neotropical lizard, *Liolaemus quilmes*: relationship with territoriality and reproductive strategy

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Investigating space use in animals and determining the amount of overlap with neighbours may help to understand whether territoriality is part of a social system, and can help in inferring possible reproductive strategies of males and females. Here we examine these issues in the lizard *Liolaemus quilmes* from northwestern Argentina based on space use of core areas. We studied a population comprising 119 “large” (LA) and 52 “small” (SA) adults over two consecutive years. We compared core areas of males and females during the reproductive and post-reproductive season, documenting the occurrence and amount of overlap among core areas. We found that the average size of core areas of both LA and SA individuals did not significantly differ from each other across two study years. However, LA male core areas were significantly larger than those of LA females, and LA male core areas were significantly larger than those of SA males. LA and SA male core areas were significantly larger during the reproductive than during the post-reproductive season, possibly indicating the need of males to gain access to females. SA females had significantly smaller core areas during the reproductive season than during the post-reproductive season, whereas LA female core areas were not different between seasons. The amount of core area overlap among males did not exceed 23%, supporting the idea of territory defence. Female core areas did not overlap. The core areas of LA males and females overlapped with up to two females and three males, respectively, suggesting a polygynandrous mating system.

Key words: core areas, Iguania, Liolaemidae, reproduction, Sauria, spatial distribution

INTRODUCTION

An animal's home range generally refers to the area used during its daily activities (Burt, 1943). Understanding how a home range is being used may reflect various aspects of its natural history, and the degree of overlap among neighbours helps to understand the social structure of a population (Ferner, 1974). When animals are territorial, they display aggressively to potential intruders and have exclusive or better access to specific resources in an area (Noble, 1939; Sheldahl & Martins, 2000). Within a home range, some parts are more frequently used than others, often overlapping less with territories of other individuals (Auffenberg, 1978; Samuel et al., 1985; Christian et al., 1986; Kerr & Bull, 2006; Manteuffel & Eiblmaier, 2008). In lizards, these core areas within home ranges may contain valuable limiting resources such as refuges (Osterwalder et al., 2004; Kerr & Bull, 2006), dependable food sources (Samuel et al., 1985, and references therein) or mating partners (Haenel et al., 2003). Core areas are equivalent to what Stamps (1977) has referred to as more specific sites defended within the home range, including basking sites, shelters or mating territory. Interactions between individuals may be more important inside these areas, influencing their spacing patterns (Börger et al., 2006). Core area overlap among males and females may also help to infer reproductive strategies (e.g. Abell, 1999 for *Sceloporus virgatus*; Halloy & Robles, 2002 for

Liolaemus quilmes). In this study, we investigate space use and core areas in the neotropical lizard *L. quilmes* from northwestern Argentina. We quantify the amount of overlap among males and females of two size categories in the reproductive and post-reproductive season.

MATERIALS AND METHODS

The *Liolaemus* genus (Liolaemidae) belongs to an iguanian group of lizards from South America (Frost et al., 2001), ranging from Peru and Bolivia in the north to Tierra del Fuego in southern Argentina (Cei, 1986; Etheridge & De Queiroz, 1988). Close to 210 species are known (Abdala et al., 2008). The species *L. quilmes* is found in northwestern Argentina between 1600 m and almost 3000 m in altitude, in arid to semi-arid regions of the phyto-geographic province of the Monte (Cei, 1993; Etheridge, 1993) and the Prepuna (Halloy et al., 1998; for phyto-geographic provinces, see Cabrera & Willink, 1980). It is a diurnal, oviparous and insectivorous species (Ramirez Pinilla, 1992; Halloy et al., 2006).

Our study took place during two austral springs and summers (September 2005 – March 2006, and October 2006 – March 2007). The study site was an area of 75 × 100 m divided into 5 × 5 m quadrants at Los Cardones, Tucumán province, Argentina (26°40'1.5"S, 65°49'5.1"W, datum: WGS84; elevation 2725 m). A total of 171 lizards were captured, measured, weighed and marked using a

Table 1. Average number of sightings ($X \pm 1$ standard deviation (SD), and ranges, for large (LA) and small (SA) adult male and female *Liolaemus quilmes*, by year. n : number of individuals per category.

		Males			Females		
		n	$X \pm SD$	Range	n	$X \pm SD$	Range
2005/2006	LA	31	30.2 \pm 11.4	13–51	33	23.5 \pm 12.1	9–67
	SA	13	21.3 \pm 11.0	10–43	18	18.4 \pm 10.4	9–47
2006/2007	LA	21	21.2 \pm 10.1	9–45	19	19.5 \pm 6.0	10–32
	SA	14	19.5 \pm 8.1	10–37	30	19.2 \pm 6.0	9–33

unique combination of coloured beads attached to the base of their tail (Fischer & Muth, 1989; Halloy & Robles, 2002). The lizards were released at the site of capture.

Two adult size categories were considered based on work by Ramirez Pinilla (1992). The “large” (LA) category included males and females with a snout–vent length above 5.5 cm and a weight above 5.0 g. The “small” (SA) category, encompassing individuals entering their first reproductive event, included lizards with a snout–vent length of 4.5–5.5 cm and a weight of 3.0–5.0 g. *Liolaemus quilmes* is reproductively active mainly in October and November (Ramirez Pinilla, 1992; Salica & Halloy, 2009).

We determined the locations of lizards using the visual encounter technique (Heyer et al., 1994; Robles & Halloy, 2008), walking systematically through the area searching for any exposed lizards two to three times a day. When a lizard was sighted, its coordinates were registered on a datasheet. To calculate the size of core areas, we considered only those individuals with a minimum of nine sightings, the smallest sample size at which numbers of sightings are not correlated with home range size (Rose, 1982; Halloy & Robles, 2002; Robles & Halloy, 2009). The overall average number of sightings for the core area per individual was 22 (see Table 1 for more details). Core areas were determined using the adaptive kernel method (Worton, 1989) based on CALHOME Version 1.0. The adaptive kernel method is a non-parametric method that

produces a distribution that estimates the probability of finding an animal at a particular location in its home range, and is more appropriate than the minimum convex polygon method because it quantifies the use of particular areas within a home range. Because home ranges tend to show considerable overlap in some lizards, we preferred to use core areas that potentially contain vital resources. We used the 60% option of the kernel method to consider close to two-thirds of the time a lizard spent in a given area (e.g. Frutos, 2009). To calculate the amount of overlap in core areas between two animals, we calculated the size of the overlapping areas among individuals (in m²) with Image Tool version 3.00 based on JPEG image files. To compare core areas, we used the non-parametric Wilcoxon–Mann–Whitney test (Siegel & Castellan, 1988) and SPSS 17.0 to calculate Spearman rank-order correlation coefficients between core areas, snout–vent length and weight.

RESULTS

Annual core areas

LA males and females did not significantly differ in their core areas between the two years ($Z=1.2$; $P=0.1$; $Z=0.2$; $P=0.4$, respectively, Table 2). However, LA male core areas were significantly larger than those of LA females for both years (on average six times larger, first year: $Z=5.9$, $P<0.001$; second year: $Z=5.2$, $P<0.001$; exam-

Table 2. Average ($X \pm 1$ standard deviation (SD) and minimum to maximum ranges of core areas (in m²) for large (LA) and small (SA) adult male and female *Liolaemus quilmes*, for each year of the study. n : number of individuals per category.

		Males			Females		
		n	$X \pm SD$	Range	n	$X \pm SD$	Range
2005/2006	LA	31	86.1 \pm 41.2	15.8–193.3	33	12.1 \pm 7.1	4.0–36.1
	SA	13	56.3 \pm 33.9	19.4–115.8	18	14.0 \pm 7.4	1.0–32.6
2006/2007	LA	21	74.5 \pm 35.4	11.5–146.1	19	13.7 \pm 9.8	3.3–35.7
	SA	14	46.1 \pm 31.6	7.7–110.2	30	15.0 \pm 8.4	4.4–29.7

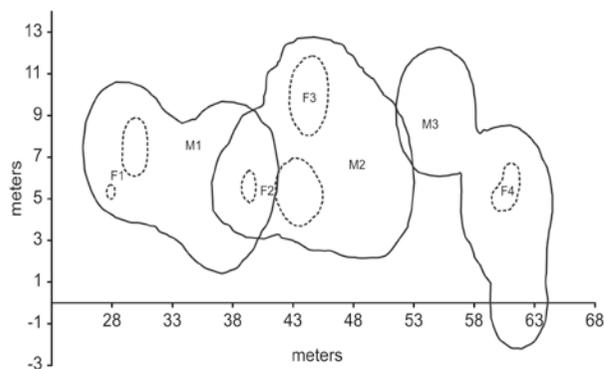


Fig. 1. Examples of core areas for three large adult males (M, full lines) and 4 large adult females (F, dashed lines) during the reproductive season of the first year. Female 1 (F1) and female 2 (F2) have two core areas each. Only a portion of the study site is shown (core area for M3 extended outside the site).

ples are shown in Fig. 1). SA males and females also did not significantly differ in their core areas between the two years ($Z=0.7$, $P=0.2$; $Z=0.2$, $P=0.4$, respectively, Table 2). However, as for LA males, SA male core areas were significantly larger than those of SA females (on average 3.6 times larger; first year: $Z=4.9$, $P<0.001$; second year: $Z=3.4$, $P<0.001$). Core areas of LA males were significantly larger than those of SA males in both study years (on average 1.6 times larger; $Z=2.2$, $P<0.01$; $Z=2.4$, $P<0.01$, respectively, Table 2), whereas core areas of LA females were not significantly different from those of SA females ($Z=0.3$, $P=0.4$; $Z=0.4$, $P=0.3$, respectively).

Core areas during the reproductive and post-reproductive seasons

Because the size of core areas during the reproductive and post-reproductive seasons did not differ between years ($P>0.05$ in all cases), data were pooled. LA male core areas were significantly larger during the reproductive than during the post-reproductive season ($Z=2.0$, $P<0.02$, $n=26$, Fig. 2), whereas LA female core areas did not differ between the reproductive and post-reproductive seasons

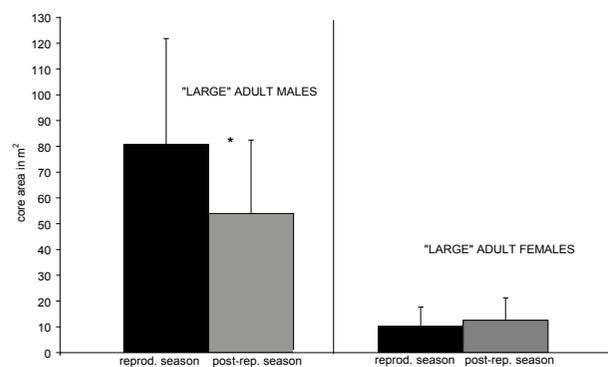


Fig. 2. Averages ± 1 standard deviation of reproductive (dark bars) and post-reproductive (grey bars) core areas (in m^2) for large adult male and female *Liolaemus quilmes*. *: $P<0.05$

($Z=1.2$, $P=0.11$, $n=36$, Fig. 2). For SA males, there was no significant difference between core areas in the reproductive and post-reproductive seasons ($Z=0.6$, $P=0.3$, $n=12$, Fig. 3). SA females, however, had core areas that were significantly larger during the post-reproductive season ($Z=2.3$, $P<0.01$, $n=14$, Fig. 3).

Overlapping core areas between males and females

During the breeding seasons, the core areas of on average 43% of LA males had an average of 7% overlap with the core areas of up to two females, and the core areas of 44% of LA females had an average of 70% overlap with the core areas of up to three males (Table 3; in Fig. 1, the four female core areas were entirely within male core areas). During the post-reproductive seasons, the core areas of on average 54% of LA males had an average of 14% overlap with core areas of up to two females (Table 3). An average of 50% of females had 56% of their core areas overlapped with those of up to three males. For SA individuals, the core areas of on average 56% of males had an average of 12% overlap with the core areas of up to three females, whereas an average of 35% of females had 52% of their core areas overlapped with those of up to two males (Table 3).

Overlapping core areas between size categories

The core areas of in average 63% of LA males had an average of 20% overlap with core areas of up to four LA males (Table 4). Only 4% of LA females had core areas that overlapped among each other, based on a single pair of females whose core areas overlapped by about 61%. LA and SA males had core areas that overlapped with up to three males of the other size category. Fewer LA males (33%) had core areas overlapping with an SA male than did LA females have core areas overlapping with an SA female (56%, Table 4).

DISCUSSION

Core areas of *L. quilmes* did not significantly vary between the two study years. However, core areas of males were significantly larger than core areas of females,

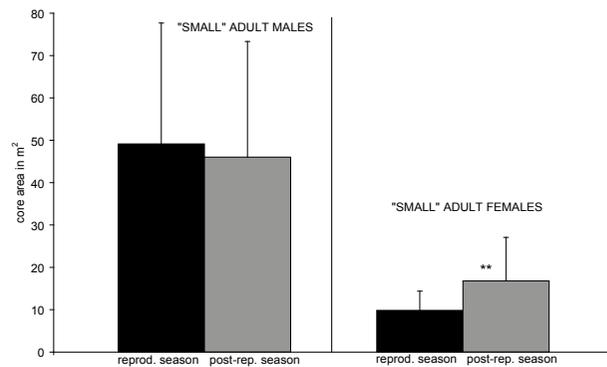


Fig. 3. Averages ± 1 standard deviation of reproductive (dark bars) and post-reproductive (grey bars) core areas (in m^2) for small adult male and female *Liolaemus quilmes*. **: $P<0.01$.

Table 3. Minimum to maximum number (range) of large adult male and female *Liolaemus quilmes* encountered in core areas of the opposite sex for reproductive (RS) and post-reproductive seasons (PRS), and for small adults of each sex for two years of study (2Y). The percentage of individuals that overlapped with the opposite sex and the mean percentage of their core area overlapping with them is given. *n*: number of individuals per category. See methods for details.

	Season	<i>n</i>	Range	% individuals	% area
Large adult males	RS	42	0–2 F	42.9	6.6
Large adult females	RS	34	0–3 M	44.1	69.6
Large adult males	PRS	26	0–2 F	53.8	13.9
Large adult females	PRS	36	0–3 M	50.0	55.9
Small adult males	2Y	27	0–3 F	55.6	12.2
Small adult females	2Y	48	0–2 M	35.4	52.3

which is also reflected in their home ranges (Halloy & Robles, 2002; Robles & Halloy, 2009). That male home ranges tend to be larger than those of females has been observed in many other species of lizards (e.g. Turner et al., 1969; Ruby, 1978; Rose, 1982; Schoener & Schoener, 1982; Smith, 1985; Abell, 1999; Perry & Garland, 2002; Haenel et al., 2003; Wone & Beauchamp, 2003; Germano, 2007).

LA male core areas were significantly larger than those of SA males, whereas no difference was found in females. Haenel et al. (2003) found that body size was positively correlated with home range areas in male *S. undulatus*, whereas in *L. quilmes* male body size was not correlated with home range areas (Robles & Halloy, 2009), nor was it correlated with core areas (snout–vent length, $r_s = -0.02$, $P = 0.90$, $n = 52$; weight, $r_s = 0.03$, $P = 0.80$, $n = 52$). During the reproductive seasons, core areas of LA males were significantly larger than during the corresponding post-reproductive seasons (SA males showed a similar trend; Figs 2 and 3). This may reflect males extending their core areas and home ranges during the reproductive season to gain access to more females (Haenel et al., 2003; Robles & Halloy, 2009).

Table 4. Minimum to maximum number (range) of large (LA) and small (SA) adult male and female *Liolaemus quilmes* encountered in core areas of the same sex in two study years. The percentage of same sex individuals that overlapped in their core areas and the mean percentage of their core area overlapping with them is given. *n*: number of individuals per category. See methods for more details.

	<i>n</i>	Range	% individuals	% area
Large adult males	52	0–4 (LA)	63.5	20.0
Large adult females	52	0–1 (LA)	3.8	61.5
Large adult males	52	0–3 (SA)	32.7	12.3
Small adult males	27	0–3 (LA)	55.6	22.9

The pattern observed in males was reversed in SA females, which had a significantly larger core area during the post-reproductive season. Smaller females may need to recover from oviposition during the post-reproductive season as well as invest in growth, leading to the use of a larger area in order to satisfy dietary needs. Robles & Halloy (2009) reported a similar tendency for larger adult females with respect to home ranges. Except for SA females, the core areas of about 50% of the study individuals overlapped with those of at least two other individuals of the opposite sex (Table 3). However, whereas male core areas overlapped between 7% and 14% with a female core area, female core areas overlapped between 52% and 70% with a male core area. This difference may be due to different core area sizes (Fig. 1, Table 2).

Close to two-thirds of LA male core areas overlapped with those of up to four other LA males, whereas only one-third of core areas overlapped with up to three SA males (Table 4). On the other hand, the core areas of about 56% of SA males overlapped with core areas of up to three LA males. Nevertheless, the amount of core area overlap never exceeded 23% (examples in Fig. 1). Manteuffel & Eiblmaier (2008) consider an overlap of less than 25% of core areas as an indicator of territoriality. The low overlap seen among male *L. quilmes*, together with agonistic displays observed in the field (pers. obs.) and in captivity (Halloy, 1996), support the idea of territory defence in this species (other examples in lizard species in Stamps, 1977; Sheldahl & Martins, 2000; Kerr & Bull, 2006).

That more SA males covered more LA male core areas than the reverse may indicate that the former consider areas occupied by the latter as being of high quality with respect to distribution and availability of food resources (M'Closkey et al., 1987; Stamps, 1988). In addition, once in the core area of an LA male, SA males might be better able to assess their chances of overcoming a resident LA male (Ruby & Dunham, 1987) or of gaining access to an unguarded female (Zamudio & Sinervo, 2003). They might also adopt subordinate behaviour, which would allow them to remain in the territory of an LA male (Baird et al., 2003).

LA females did not overlap with each other except for one pair in two years of observation (Table 4). This may be due, in part, to the fact that their core areas and home

ranges are small and widely spaced (Halloy & Robles, 2002; Robles & Halloy, 2009; see also Haenel et al., 2003, for female *S. undulatus*). LA males tended to overlap with up to two LA females, whereas females tended to overlap with up to three males (Fig. 1, Table 3). This would indicate a polygynandrous mating system comprising groups of two to three males and two to three females (Andersson, 1994; Abell, 1999; Baird et al., 2003), allowing females to mate with several males (e.g. Abell, 1997; Laloï et al., 2004; Calsbeek et al., 2007; Salvador et al., 2008). The pattern is reversed when looking at SA individuals, suggesting a more opportunistic reproductive strategy in smaller, younger males as opposed to LA males that may be exhibiting mate-guarding and polygyny (e.g. Zamudio & Sinervo, 2003; Laloï et al., 2004; Kerr & Bull, 2006; Robles & Halloy, 2009).

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