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Social spacing of the montane lizard *Tropidurus montanus*

Running title: Montane lizard space use

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Abstract

The form individuals use the space can be a key to understand species' sociobiology. We studied the social spacing of the lizard *Tropidurus montanus*. Males were found to have larger home ranges than females. The males' body size was not associated with home range area and the number of females associated to a male's home range was small when compared to other Iguanian lizards, thus forming small harems. The larger home range areas and overlaps found during the final period of the reproductive season might occur as a consequence of reduced social interactions at the end of the reproductive season. We provide evidence that the tropidurid *T. montanus* may be establishing short-term exclusive-use areas.

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INTRODUCTION

Animals generally use a restricted portion of the physical space available to them to perform the activities necessary for survival and reproduction during their lives. This space used by individuals is termed the home range (Brown & Orians, 1970). Intraspecific interactions should predict how individuals are distributed in space, and therefore information on home ranges should provide insights into the ecology and conservation of a species (Kamler et al., 2003). In addition, the arrangement of individual home ranges in a given population are a key aspect in the understanding of a species' sociobiology (Hinze et al., 2013; Kaneko et al., 2014). For example, the occurrence of mutual avoidance is evidenced in cases where neighbouring individuals have few home range overlaps (Osterwalder et al., 2004; Kerr & Bull, 2006; Wegge & Mosand, 2015). The way animals use the space across time might also depend on whether species are territorial or not. Territoriality requires fidelity to the space used, thus territorial species are expected to use a relatively unchangeable

location throughout time as found for gibbons (*Hylobates*), for example (Bartlett et al., 2015). Moreover, the arrangement of home ranges of males and females can also shed light on a species mating system. Thus, intersexual home range overlap can be indicative of whether males monopolise females resulting in the formation of harems, thereby revealing a polygynous mating system, or if they live in pairs, as expected for a monogamous system (Langergraber et al., 2013; Hibbitts et al., 2012). Hence, information about the home ranges of species is of importance to unveil aspects of social organisation in populations, especially in species that are difficult to observe.

Squamates have been long neglected for studies of sociability as it is assumed that species from this group of vertebrates present few social behaviours apart from dominance hierarchies and territorial behaviours (Stamps, 1977). However, studies on individual's spacing patterns have revealed complex social behaviours for squamates in relation to group formation and mating pair fidelity (Osterwader et al., 2004, Qi et al., 2012). Nonetheless, there is still a need for studies on squamata social behaviour (Chapple, 2003). In lizards, home range size is expected to differ by sex due to the different social behaviour of males and females. Thus, in territorial species it is common that males will have larger home ranges when compared to females (Baird et al., 2001; Ribeiro et al., 2009). These differences are frequently related to selective pressures for males to increase area use as a means to monopolise females, thereby increasing their reproductive success (Lappin & Husak, 2005). Therefore, in these cases, home range sizes can be related to male body size since larger males are able to dominate smaller ones, thus gaining access to a larger area with a greater number of females (Perry & Garland, 2002).

It has been shown that lizards change their social behaviour according to a population's breeding status. For example, the collared lizard *Crotaphytus collaris* exhibits low frequency of displays and patrolling at the onset of reproductive season, and territory

sizes are also smaller during this period (Baird et al., 2001). Hence, the pattern of space use by individuals should change seasonally, according to reproduction, as observed by *Liolaemus quilmes* (Robles & Halloy, 2010). In this sense, one could expect for lizards that home range sizes will change in response to seasonal differences in behaviour. However, even considering temporal variation in home range size, individuals may use a relatively fixed space indicating that they are philopatric over time (e.g. Bull & Freake, 1999). For neotropical lizards, home range sizes and their spatial arrangement are expected to increase during the reproductive period or during periods of decreased resource availability (e.g. Van Sluys, 1997).

The lizard *Tropidurus montanus* is an endemic species from rocky outcrop areas of the Espinhaço Mountain Range, south-eastern Brazil (Rodrigues, 1987). This species strictly uses rocky substrate during its daily activities (Filogonio et al., 2010) and as with most of the iguanian lizards, it can be characterised as a sit-and-wait forager species, feeding mainly on ants and termites (Kiefer, 1998). Reproduction of the species lasts from the middle of the dry season to the end of the rainy season (Van sluys et al., 2002).

Lizards from the genus *Tropidurus* have historically been termed as (or even presumed to be) territorial. However, there is still a lack of empirical evidence confirming territoriality in *Tropidurus* species: since to be considered territorial individuals have to be able to use exclusive areas and to maintain their territory area across time (e.g. Sheldahal and Martins 2000). In addition, taxonomic issues have confused even more the understanding of territoriality in this genus. In this study, we: *i*) evaluated if males and females had exclusive areas; *ii*) evaluated the persistence of individuals in the studied population across a two year period; *iii*) evaluated sex and seasonal differences in the home range sizes; and *iv*) evaluated the extent of intrasexual and intersexual home range overlap between wet and dry seasons.

METHODS

Study site

Fieldwork was conducted in rocky outcrop habitat at 1100 m above sea level at Serra do Cipó National Park (19º20´S and 43º40´W), in the southern portion of Espinhaço Mountain Range, Minas Gerais State, Brazil. At Serra do Cipó altitudes vary from 870 to 1400 m (above sea level), and above 1000 m the habitat is dominated by typical rocky outcrop vegetation forming open "Campos Rupestres" physiognomy (rocky meadows) (Giulietti et al., 1987) with the predominance of shrubs and herbs (Giulietti et al., 1987). Climate in the region is highly seasonal with monthly average temperature varying between 17ºC and 23.5ºC and monthly rainfall averaging between 11.9 mm and 281.1 mm. Rains occur between October and April and the dry season lasts from May to September.

Procedures

We sampled lizards from July to September in the years 2011 and 2013. This period corresponds to the middle dry period, when *T. montanus* starts its reproductive season. We also sampled individuals during the rainy season from December 2013 to January 2014 at the end of reproductive season for this species (Van Sluys et al., 2002). In the study site, we delimited a 2 ha grid partitioned into 10m x 10m quadrats by attaching flags on the vegetation and by painting coordinate points on rocks. The spatial data on *T. montanus* were obtained by intensively sampling the grid area (31 days from July to September 2011, 17 days through July to September 2013 and 25 days in December 2013 to January 2014). Lizards found within the grid were captured by noose and permanently marked using coloured beds strung with surgical nylon monofilament at the base of each lizard's tail (Galdino et al., 2014). Captured lizards had their body size measured (snout-vent-length) to the nearest 1mm. The sex of individuals was assigned based on the presence of dark colouration of the ventral face of the thigh and anal flap (marks present only in adult males).

Spatial data of individuals *T. montanus* were obtained by censusing the grid during the main activity period of the species (1000-1500h) (following Filogonio et al., 2010). During each census, we recorded a lizard's position in relation to the grid limits (used as a cartesian axis reference). As a means to decrease temporal dependency in the spatial data, we took care to not perform the same sample route within the grid during the same sample week. In addition, for a given individual we only registered more than one point on the same day of observations if locations were separated by a minimum interval of two hours.

Spatial organisation of *T. montanus* was evaluated by estimating the area and location of their home ranges by the minimum convex polygon (MCP) analysis. For each individual, we removed 5 percent of the points farthest from the centroid of the cloud of locations before estimating home ranges (HR) (Bath et al., 2006; Calenge, 2006). This procedure excludes extreme location points, generally associated with an individual's occasional sallies. Home range areas and mapping were obtained by using adehabitatHR package (Calenge, 2006) in R (R Core Team Development, 2015). As it is known that HR areas increases with the number of locations (Stone & Baird, 2002), we plotted HR size against number of individual sightings (Ln transformed) to evaluate the minimum number of locations necessary to estimate unbiased areas (e.g. Sheldahl & Martins, 2000; Halloy & Robles, 2002). Home range overlaps were estimated by calculating the overlaps of the polygons using the R package rgeos (Bivand & Rundel, 2013). Spatial analyses were performed by using the "HunteR" script (https://github.com/NeoLiBE/NeoLiBE/), an implementation of routines of the aforementioned packages from Passos et al. (2015).

We also used the Half Weight Index (HWI) (Whitehead, 2008) as a measurement of temporal association between pairs of individuals. The index is defined as:

$$HWI = x/(x+Y_{ab}+((Y_a+Y_b)/2)$$

where: x= number of sampling days when both individual "a" and individual "b" were observed, Ya= number of sampling days when just individual "a" was observed, Yb= number of sampling days when just individual "b" was observed, Yab= number of sampling days when both, individual "a" and individual "b" was observed but not in association. The HWI varies between 0 (no association) to 1 (maximum association). Therefore, we only considered spatial home ranges overlaps for individuals with HWI > 0.5 as a form to exclude spatial overlaps that did not reflect temporal associations among lizards. For HWI calculations we used the program SOCPROG (Whitehead, 2009).

We evaluated data normality using Shapiro-Wilk test. The effect of sex and reproductive period on HR areas was evaluated by a two-way ANOVA. The association among male HR sizes (log10 transformed values) and body size was evaluated by the Pearson's correlation test. We used the G-test to evaluate differences in the proportion of males with overlapped home ranges. In addition, we used Mann-Whitney U-test to evaluate differences for number of intrasexual home ranges overlaps, and to evaluate the number of intersexual home ranges overlaps and HWI values between reproductive seasons (one test per dependent variable). For all tests the significance level was set at 0.05, and the descriptive statistics throughout the text are mean ± one standard deviation.

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RESULTS

We sampled 146 individual *T. montanus*, 53 males and 70 females, for whom we obtained a total of 877 spatial points. For each of the sampled seasons, home ranges estimated using at least seven points were less variable than those with fewer locations (Figure 1), thus we only considered individuals that had seven or more sightings. During 2011 we marked 34 lizards, 17 of both sex with a mean of 7.16±4.70 spatial locations per individual. For this period 19 individuals had more than seven visual recaptures. In the beginning of the reproductive season of 2013 we marked 39 *T. montanus* with a mean of 6.85 ± 3.34 spatial points per lizard and were able to estimate the home ranges of 22 lizards for this period. We sampled 50 individuals during the end of reproductive season of 2013, with a mean of 5.5 ± 4.8 spatial points, resulting in the estimated home ranges for 17 lizards.

We found that home range of males and females were both smaller at the start of reproductive season of 2013 (526.40±564.43m²; 142.83±131.39m², respectively) compared to the end of reproductive period of 2013 (males = 988.56±861.02 m²; females = 307.43±333.28 m²) (Figure 1) (p = 0.02). However, male home ranges were larger than those of females during both the beginning and the end of reproduction in 2013 (Figure 2) (p = 0.006), but with no significant result for the interaction term (p = 0.40). Home range size was not associated with male body size in both sampled periods of 2013 (p > 0.05). The proportion of males that had their home range overlapped by at least one other male was greater at the end of reproductive season (0.90) than for the start of the reproductive season (0.44); however, no difference was found for the proportion of males with overlapped home ranges between seasons (G test, p > 0.05). The mean number of intrasexual home range overlaps at the start of the reproductive period for males was 0.78 ± 1.09 (Figure 2) and at the end of reproduction was 3.56 ± 1.59 (Figure 2), this difference being significant between seasons (Mann-Whitney U-test, p = 0.04). The mean number of female overlapping home ranges with males was

1.56±1.13 at the beginning of reproduction in 2013 and 1.44 ± 1.23 in the end of the reproductive period (Figure 2) with no difference found between sampling periods (Mann-Whitney U-test, p>0.05). Concerning the time associations of pairs of individuals overlapping their home ranges, the mean HWI for male-male associations from the beginning of reproduction was 0.4 ± 0.18 (n = 4) while that of male-female pairs was 0.29 ± 0.25. We found at the end of reproductive season four pairs (male-female), which despite having overlapped home ranges were not time-associated (i.e. HWI = 0). At the beginning of the reproductive season in 2013, HWI male-male time associations were 0.39±0.05, whereas that of male-female pairs was 0.49±0.15. Values of HWI for male-female time association differed between periods with values at the start of the reproductive season in 2013 being significantly higher than those from at the end of reproduction in the same year (Mann-Whitney U-test: W = 49.5; p = 0.03).

Regarding individual persistence in the sampled population: no marked lizard from July - September 2011 was recaptured in July - September 2013 or in December 2013 - January 2014. However, 21% (n = 62) individuals from July - September 2013 were observed in December 2013 - January 2014. Unfortunately, due to our method to estimate *T. montanus* home ranges, we were only able to estimate the fidelity of space use for two individuals among those lizards that persisted in the area. One individual presented a home range overlap of 68% from July - September 2013 to December 2013 - January 2014.

DISCUSSION

For *T. montanus,* the size of home ranges differed between the sexes and also between the reproductive period. Males and females used smaller areas during the initial period of reproduction, increasing their use of space (i.e. larger home ranges) at the end of the reproductive period. In addition, the proportion of males that had their home range

overlapped by other individuals did not different between periods, however, the number of neighbouring lizards overlapping their home ranges with a given male was greater at the end of reproduction in comparison with the beginning of the reproductive season. Body size of males was unrelated to home range size. In addition, the majority of individuals did not persist in the studied population, thus we observed a high turnover of individuals across the total sampling period from 2011 to 2013.

We showed that males of *T. montanus* had larger home ranges than females. A similar pattern was observed for other *Tropidurus* species from the torquatus group (e.g. *T. itambere*, Van Sluys et al., 1997; *T. torquatus,* Ribeiro et al., 2009; *T. hispidus,* Melo et al., in prep). In general, selective pressures for males to monopolise a larger number of females, thereby increasing their reproductive success by enlarging their home ranges, explains the sexual dissimilarities in the size of home ranges (Aragón et al., 2001; Haenel et al., 2003a). Therefore, a territorial and polygynous mating system with males forming harems of exclusive use would be expected in this case. Nevertheless, concerning the mating system of *T. montanus*, one might consider that the mean number of females associated to a male's home range was small if compared to a typical polygynous lizard species. For example, in *Crotaphytus collaris* the mean number of females overlapping their ranges with males was 5.4 (Lappin & Husak, 2005), while a mean of 3.7 was found for *Sceloporus undulatus* (Haenel et al., 2003a). Therefore, our data suggest that male *T. montanus* form small harems, thus reducing the pressure for them to enlarge their home ranges to increase reproductive success due to the consequent increase in the number of females in their home range. The sex ratio of the studied population is 1:1, with females being settled spatially apart from each other. Thus, we suggest that males *T. montanus* would have great energetic expenditures to maintain larger harems, thus favouring the maintenance of small harems by males.

Despite the increase of home range size of males at the end of the reproductive period, we observed no proportional change in the number of females that overlapped their home ranges with males. This result is unexpected if males increase their reproductive success by copulating with as large number of females as possible (e.g. Haenel et al., 2003b). In this sense, although December and January correspond to the end of reproductive season of the species, females might be apt to reproduce in these months as they can still be found with mature gonads (Van Sluys et al., 2002). On the other hand, December and January are the last month before the non-reproductive season of *T. montanus* starts (Van Sluys et al., 2002). Hence it would be expected that males might decrease their performance of behaviours related to reproduction during December/January with a consequent reduction in social activities. The aforementioned prediction is supported by the larger values of time associations (HWI) among males and females at the beginning of reproduction compared to the end of the reproductive period. Therefore, social interactions between individuals of both sexes have more chance to occur during the first months of the reproductive season. Hence, we suggest that the larger home range size of males during December/January might be related to a release in social activities of males (*i.e.* maintenance of exclusive areas of use for courtship and mating) imposed by the ending of the reproductive period. This release in social activities of males was supported by the increase in the number of home range overlap per male at the ending of reproduction, which in turn might reflect reduced intra-individual avoidance. Therefore, the increase in home range overlaps in December/January might be viewed as a consequence of reduced social interactions during a period in which individuals of both sexes are reducing their reproductive activity.

We expected that home range size would be related to the body size of males, however, no relationship was found. Such a relationship would be expected in cases where intrasexual competition for mates favoured larger males who are expected to use larger areas

and thereby gain access to a greater number of females when compared to smaller males (Haenel et al., 2003a). Indeed, male body size can be related to their fitness due to attracting a greater number of females (e.g. Robles & Halloy, 2009) and thus impacting on the number of offspring an individual can sire (Salvador et al., 2008). However, our results point to males having small harems, which reduces the pressure for them to have large home ranges.

Since Werner (1977), *Tropidurus* lizards had been considered as territorial (e.g. Wiederhecker et al., 2003; Kohlsdorf et al., 2006; Ribeiro et al. 2009). Notwithstanding, for a species to be considered as territorial, individuals should possess a fixed area, which in turn is actively defended against intruders by behavioural acts, thus securing exclusive use of that space (Brown & Orians, 1970). However, *T. montanus* showed low persistence in the population with a huge turnover of individuals within a two-year period and a considerable loss of individuals within six months. A pattern that differs for other iguanian, for example, the lizard *Uta stansburiana* presents a marked inter-annual fidelity in its use of space (Scoular et al., 2011), and *Phtynocephalus vlangalii* shows high site fidelity between seasons (Qi et al., 2012). Alternatively, the high turnover of individuals we observed might be accounted for by mortality. Nonetheless, we intensively sampled the study area through both periods and did not observe any predatory events on *T. montanus*. In addition, no dead individuals were found during the sampling periods. These considerations are critical for samples in 2013 in which 79% of the individuals that were observed from July to September were not found in the grid in December 2013. Hence, we suggest that mortality is probably playing a minor role in the low lizard persistence found. Thus, it seems that males of *T. montanus* used a fixed area during a short time period. The used areas by *T. montanus* seemed to have some degree of exclusive use by individual, at least at the beginning of reproduction since during this time there were few home range overlaps. Hence, our results

provide evidence that dispersion might be playing a role in the social spacing of *T. montanus* with residents establishing short-term exclusive-use areas.

Finally, home range overlaps are important in the studies of social behaviour. Our results point to the importance of the measurement of time associations to ensure that spatial overlap is corroborated by the occurrence of individuals at the same time in space. For example, we had two cases of females that were spatially overlapped with males that were not time associated. Thus, to provide a time (or even better, behavioural) association metric would be of importance to produce unbiased home range overlap estimates.

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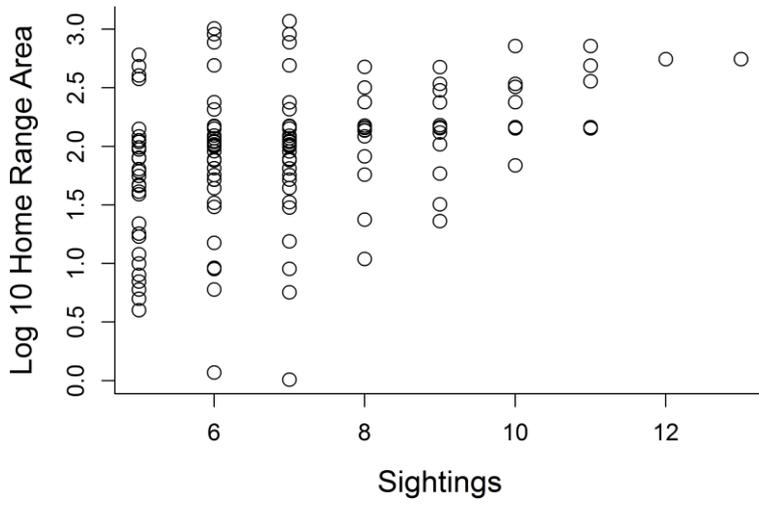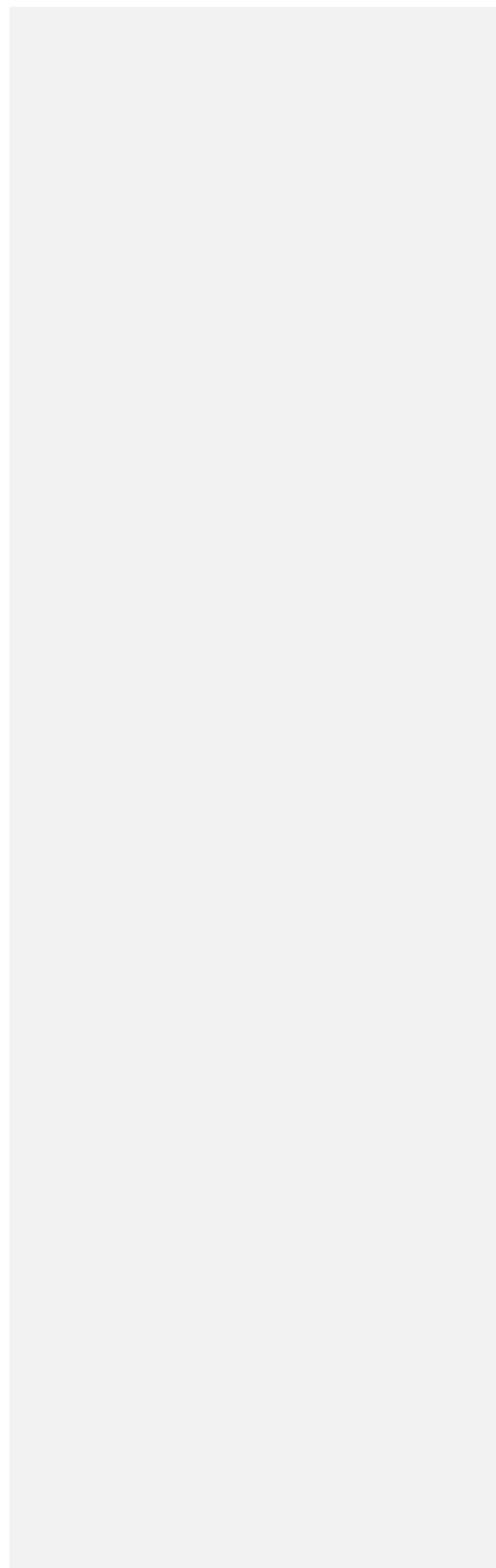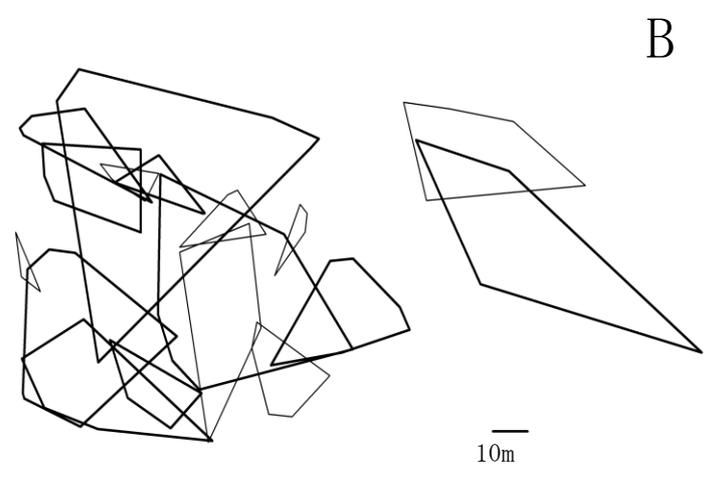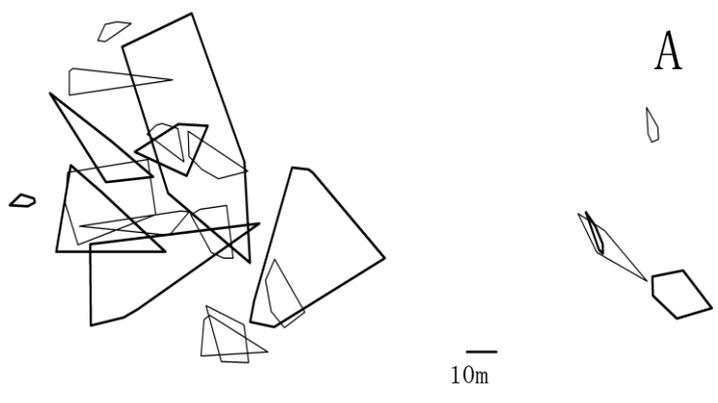
Fig1

Fig2

A

10m

B

10m

Figure captions:

Figure 1: Relationship between home range area (ln transformed) and number of sightings for individual *Tropidurus montanus* at Serra do Cipo, southeast Brazil.

Figure 2: Spatial distribution of the home ranges of *Tropidurus montanus.* A) Map of the home ranges at the beginning of reproductive season. B) Map of the home ranges at the end