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Universidade de São Paulo
Instituto de Biociências
Programa de Pós-Graduação em Ecologia

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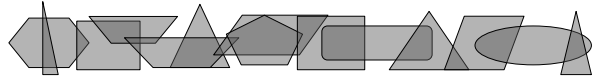
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CONTENTS

1. RESUMO

Territórios resultam de competição por interferência que leva ao uso exclusivo do espaço. A territorialidade então depende da variação espaço-temporal na disponibilidade de recursos e está, geralmente, associada ao sistema de acasalamento. A defesa de território deve ocorrer quando os benefícios superam os custos, e essa relação custo-benefício deve ser afetada por fatores ecológicos (disponibilidade de recursos e densidade populacional), assim como variações individuais (sexo e maturidade) e sazonais (época reprodutiva) que determinam *quais* e *quando* os recursos são importantes. Embora as estratégias territoriais dos indivíduos devam variar com as condições ambientais, potencialmente levando a diferentes sistemas territoriais/ de acasalamento em diferentes populações, estudos prévios sobre territorialidade geralmente avaliam somente uma população e/ou consideram condições ambientais relativamente homogêneas. Utilizando um banco de dados extenso de captura-marcação-recaptura em 9 populações de um roedor generalista (*Akodon montensis*), e usando a sobreposição da área de vida como proxy de não-territorialidade, pretendemos entender os determinantes ecológicos, individuais e sazonais das estratégias territoriais dos indivíduos, e avaliar se a variação nas estratégias individuais pode levar a uma transição entre sistemas territoriais/ de acasalamento. Como previsto, identificamos que a sobreposição das áreas de vida foi maior entre machos do que entre fêmeas e aumentou com a densidade populacional. Também aumentou de machos imaturos para machos maduros, mas diminuiu de fêmeas imaturas para fêmeas maduras, sugerindo que a diferença na territorialidade entre os sexos é definida após a maturidade sexual. O efeito negativo da disponibilidade de fêmeas na sobreposição da área de vida entre machos foi mais forte na época reprodutiva, como esperado. Mais importante, no entanto, o efeito da disponibilidade de fêmeas na sobreposição da área de vida foi fortemente dependente do sexo. À medida que a disponibilidade de fêmeas aumenta, a sobreposição da área de vida aumentou entre fêmeas, mas diminuiu entre machos, indicando que quando as fêmeas deixam de defender território (e ficam mais agregadas) devido ao aumento da competição entre elas, os machos passam a defender território. Nosso estudo ressalta que as estratégias territoriais são muito variáveis entre indivíduos, o que é consistente com a plasticidade ecológica e fisiológica em *Akodon montensis* reportada em outros trabalhos, e sugere que diferenças suficientes nas condições ambientais podem levar à transição entre sistemas territoriais/ de acasalamento.

Palavras-chave: Akodontini, área de vida, disponibilidade de recurso, estratégia individual, Mata Atlântica, sistema de acasalamento, sistema territorial, uso do espaço
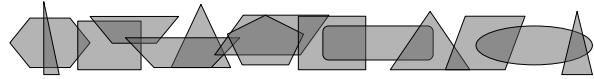
2. ABSTRACT
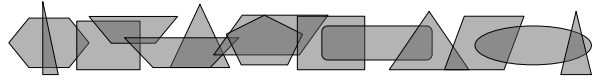
Territories result from interference competition that leads to exclusive use of space. Territoriality thus depends on the spatial and temporal variation in resource availability, and is usually associated with mating systems. Territorial defense should occur when benefits outweigh costs, and this balance should be determined by ecological factors (resource availability and population density), as well as individual (gender and sexual maturity) or seasonal (breeding season) variations that determine *which* and *when* resources are important. Although individual territorial strategies should vary with changing environmental conditions, possibly leading to multiple territorial/mating systems among populations, previous studies on territoriality focused mostly on single populations and/or on relatively homogeneous environmental conditions. Relying on an extensive capture-recapture dataset from 9 populations of a generalist rodent (*Akodon montensis*), and using home range overlap as a proxy of non-territoriality, we aim to understand the ecological, individual and seasonal determinants of individual territorial strategies, and investigate whether variation in individual strategies can lead to transitions between territorial/mating systems. We identified that home range overlap was larger between males than females and increased with population density, as expected. It also increased from immature to mature individuals among males, but the opposite was true among females, suggesting that differences in territoriality between genders is established after sexual maturity. The negative effect of female availability on home range overlap between males was stronger in the breeding season, as expected. More importantly, though, the effect of female availability on home range overlap was strongly gender dependent. As female availability increased, home range overlap increased between females but decreased between males, suggesting that when females become non-territorial (and thus more aggregated) because of increased competition with other females, males become territorial. Our study highlights territorial strategies are extremely variable among individuals, which is consistent with previously reported ecological and physiological plasticity in *Akodon montensis*, and suggests that sufficient changes in environmental conditions could lead to transitions between territorial/mating systems.

Key words: Akodontini, Atlantic forest, home range, individual strategy, mating system, resource availability, territorial system, use of space

3. INTRODUCTION

Home range is the area used by an individual during its daily activities such as foraging, search for mates or care of young (Burt 1943). If this area or part of it is defended, preventing conspecifics or individuals from other species to access valuable resources, it is named territory (Noble 1939). Territories, then, result from a kind of interference competition called territoriality that leads to an exclusive, non-overlapping, use of space (Ostfeld 1990, Maher & Lott 1995). Home ranges and territories depend on how individuals use space given the spatial and temporal variation in resource availability, and intra and interspecific interactions (Armitage 1988, Brashares & Arcese 2002, Verdolin 2009). Territoriality thus influences social and mating systems (Ostfeld 1985, Adler 2011) and is associated with population dynamics (Newton 1992, Lopez-Sepulcre & Kokko 2005, Matthiopoulos et al. 2015).

Whether or not individuals are territorial is a critical question in behavioral ecology. Focusing on this question, Brown (1964) proposed an economic model according to which individuals will defend a territory whenever the benefits provided by the defended area (e.g. food, mates, nest sites) overcome the costs involved in its defense (e.g. energetic cost, injury risk). According to the model, benefits and costs are strongly dependent on ecological factors that affect population dynamics, particularly resource availability that is tightly related to population density (Maher & Lott 2000). When resource availability is low, home ranges are expected to be large and, as individuals spend most of the time looking for resources and the cost involved in defending such a large area is high, they do not defend any part of the area (even so their home ranges may not overlap extensively because population density is low). In contrast, when resource availability is high, although home ranges are expected to be small as individuals have all the resource needed in a small area, the cost of defense should be high given the high population density, and again individuals do not defend any part of the area and their home ranges overlap extensively (McLoughlin et al. 2000). Therefore, because limiting resources and population density are usually correlated, benefits of territoriality should only overcome costs at intermediate levels of resource availability. Although this should result in an inverted-U shape relationship between territoriality and resources availability or population density (McLoughlin et al. 2000), home range overlap should increase as these variables increase. At low resource availability, even though defense of home range area is not expected to occur, home range overlap should not be observed given the low population density. Moreover, although home range area per se is not a measure of territoriality, it directly influences the defense costs and is important to understand home range overlap and territoriality.

The effects of ecological factors, as resource availability and population density, on home range overlap, however, should depend on both individual characteristics (Gordon 1997, Sergio et al. 2009) that determine *which* resources are important, and seasonal variations (Fortier & Tamarin 1998, Endries & Adler 2005, Sanecki et al. 2006) that determine *when* resources are important. Gender is a crucial individual characteristic influencing resource needs. For example, among mammals, in which parental care is provided mainly by females (Ostfeld 1992), use of space by females is commonly determined by the availability of food resources and nest sites, especially during lactation, whereas the use of space of males should be determined by female availability, especially during the breeding season (Ostfeld 1990). Therefore, gender, sexual maturity and seasonality, particularly the breeding season, are also expected to be important in defining resource needs, and should, thus, influence home range overlap.
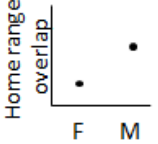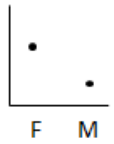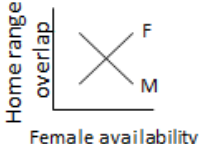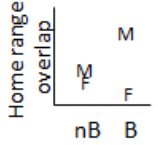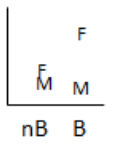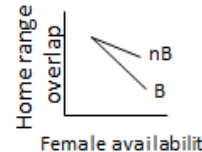
Due to the differences between genders, territoriality and mating system are closely linked (Emlen & Oring 1977), with variation in individual territorial strategies resulting in different mating systems. In mammals, polygynous mating systems are expected as gender differences are pronounced, and are, indeed, the most common systems (Clutton-Brock 1989). Females have commonly smaller home ranges than males, such that male home ranges overlap the home ranges of several females, and each male mates with several females. Usually only one gender adopts the territorial strategy (Ostfeld 1990). When most females are territorial to defend offspring or limiting food or nest resources (Ostfeld 1990, Wolff 1993), they are dispersed instead of aggregated, and home ranges of males are too large to be defended against other males. In contrast, when most females are not territorial and are thus more aggregated, males are territorial, defending exclusive access to mature females (Ostfeld 1990).

The economic model has originally been proposed to explain the evolution of territoriality among bird species, and has ever since been used to identify the territorial and mating systems of different species (Innes et al. 2009, Gerber et al. 2010, Hilgartner et al. 2012). However, as the model predicts that individual strategies should vary with changing environmental conditions (Maher & Lott 2000, Savini et al. 2009, Oldfield et al. 2015), multiple territorial/mating systems may be found among populations within the same species (Moorhouse & Macdonald 2008, Rousseu et al. 2014). Nonetheless, previous studies on mammals focused mostly on a single population (e.g. Luque-Larena et al. 2004, Asher et al. 2008, Innes et al. 2009, Hilgartner et al. 2012), limiting the ability to encompass environmental and ecological variation and different individual strategies, and thus to detect transitions

between territorial/mating systems (but see Eberle & Kappeler 2004). In this group, the transition from a polygynous mating system with territorial females to one with territorial males is expected to occur when resource availability increases and females, previously defending a territory, begin to tolerate home range overlap due to increasing defense costs. As their limiting resource (females) becomes more abundant, males then should avoid home range overlap, becoming territorial (Table 1).

Small rodents are a good model for studying determinants of territoriality as their spatial distribution can be analyzed through capture-mark-recapture techniques, and their short life span, small home ranges, and high population densities compared to other mammals allow access to representative data in a relative short period of time and space (e.g. Feliciano et al. 2002, Martins 2011). Relying on an intensive capture-recapture dataset from 9 distinct populations of a widespread and abundant generalist rodent (*Akodon montensis*), we here aim to contribute to the understanding of the determinants of individual territorial strategies, and to investigate whether variation in individual strategies lead to the transition between distinct territorial/mating systems (Table 1). We focus on home range overlap between individuals of the same gender as a measure of non-territoriality, but we also considered home range area to facilitate interpretation of the results. As determinants of individual territorial strategies, we considered not only ecological factors (population density and female availability), but also seasonal variation (breeding or non-breeding season) and individual characteristics (gender and sexual maturity). Based on the economic model and the particularities of the reproduction and parental care in mammals, we expect that ecological factors should interact with gender and breeding season in different ways to define home range overlap, possibly leading to transitions between territorial/mating systems. These different predictions are summarized in Table 1.

TABLE 1: Predicted effects and interactions between ecological factors and gender or breeding season determining home range overlap (between individuals of the same gender), considering each of the 2 most common territorial/mating systems in small rodents: polygyny with territorial females and polygyny with territorial males.

	Territorial female	Territorial male	Explanations
Gender F = female M = male			Home range overlap is smaller between individuals of the territorial gender than between individuals of the non-territorial gender.
Population density			A positive effect of population density on home range overlap is expected because costs involved in the defense against neighbors increase as population density rises. As both genders should respond equally to population density, this factor is not expected to influence mating systems, i.e. no transition between systems is expected as population density increases.
Gender*female availability			If females are the limiting resource for males, female availability is predicted to decrease home range overlap between males. Changes in female availability could lead to the transition between the 2 systems: where females are territorial (low home hange overlap) their availability is low, and males are non-territorial (high home range overlap); as female density increases, they may become non-territorial (high home range overlap) and more aggregated, enabling males to became territorial (low home hange overlap).
Gender * breeding season nB = nonbreeding B = breeding			If resources are important for females mainly when offspring is present and for males reproductive females are the main limiting resource, the differences in territoriality between genders should increase in the breeding season, with home range overlap decreasing between individuals of the territorial gender and increasing between individuals of the non-territorial gender.
Breeding season * Female availability			As females are a resource to males, we depict the predicted influence of female availability for males only. The negative effect of female availability on home range overlap between males is expected to occur mainly in the breeding season, where males are searching for females.

4. MATERIALS AND METHODS
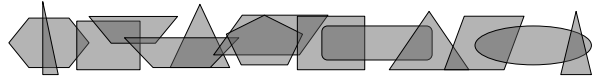
4.1. Study species

The Montane grass mouse, *Akodon montensis*, is a Neotropical small rodent (Cricetidae: Sigmodontinae) that occurs from northeast Argentina and east Paraguay to central Brazil. It is a habitat generalist species occupying both forest and open area habitats (Umetsu & Pardini 2007), being present in different biomes, such as the Pampa (dominated by open fields), the savanna-like Cerrado and the Atlantic Forest (Paglia et al. 2012), and in broad altitudinal range. Mean weight, body and tail length are 29.8 g, 104.3 mm and 83.9 mm, respectively (Rossi 2011), with no evidences of sexual dimorphism (Jordão et al. 2010). This species is terrestrial and insectivorous-omnivorous (Paglia et al. 2012). Although *Akodon montensis* is generally abundant, it is more common in early successional stages (Pinotti et al. 2015) and at the edges between forest and open areas (Naxara 2008), with reported densities ranging from 1.8 to 17.5 individuals/ ha in different places (Rossi 2011). Given its niche breadth in terms of habitat requirements, *Akodon montensis* is positively affected by forest fragmentation (Püttker et al. 2013).

4.2. Study area

The study was conducted in a region of the Atlantic Plateau of São Paulo, Brazil, originally covered by Atlantic Forest, where elevation ranges between 800 and 1,000 m and annual rainfall between 1,222 and 1,810 mm, and where mean minimum and maximum temperatures are 17.3°C and 28.4 °C for the warm-wet season (October-March), and 12.1 °C and 24.9 °C for the cool-dry season (April-September). In this region, we chose 3 different areas (~10,000 ha each) with different percentage of remaining native forest, located in the municipalities of Cotia (continuously-forested area), Piedade-Tapiraí (50% native forest cover) and Ibiúna (30% native forest cover) (Figure 1; Püttker et al. 2013). In each area, we chose 3 study sites in remnants of secondary forest at least 1.5 km apart from each other (Figure 1), resulting in 3 study sites in a continuously-forested area and 6 in forest fragments similar in size (min = 13.9 ha; max = 19.7 ha), but surrounded by different amounts of remaining forest (see Püttker et al. 2013, for more details). As *Akodon montensis* is positively affected by forest fragmentation and edge effect, the 9 sites should encompass a wide variation in ecological aspects and in *Akodon montensis* population density.
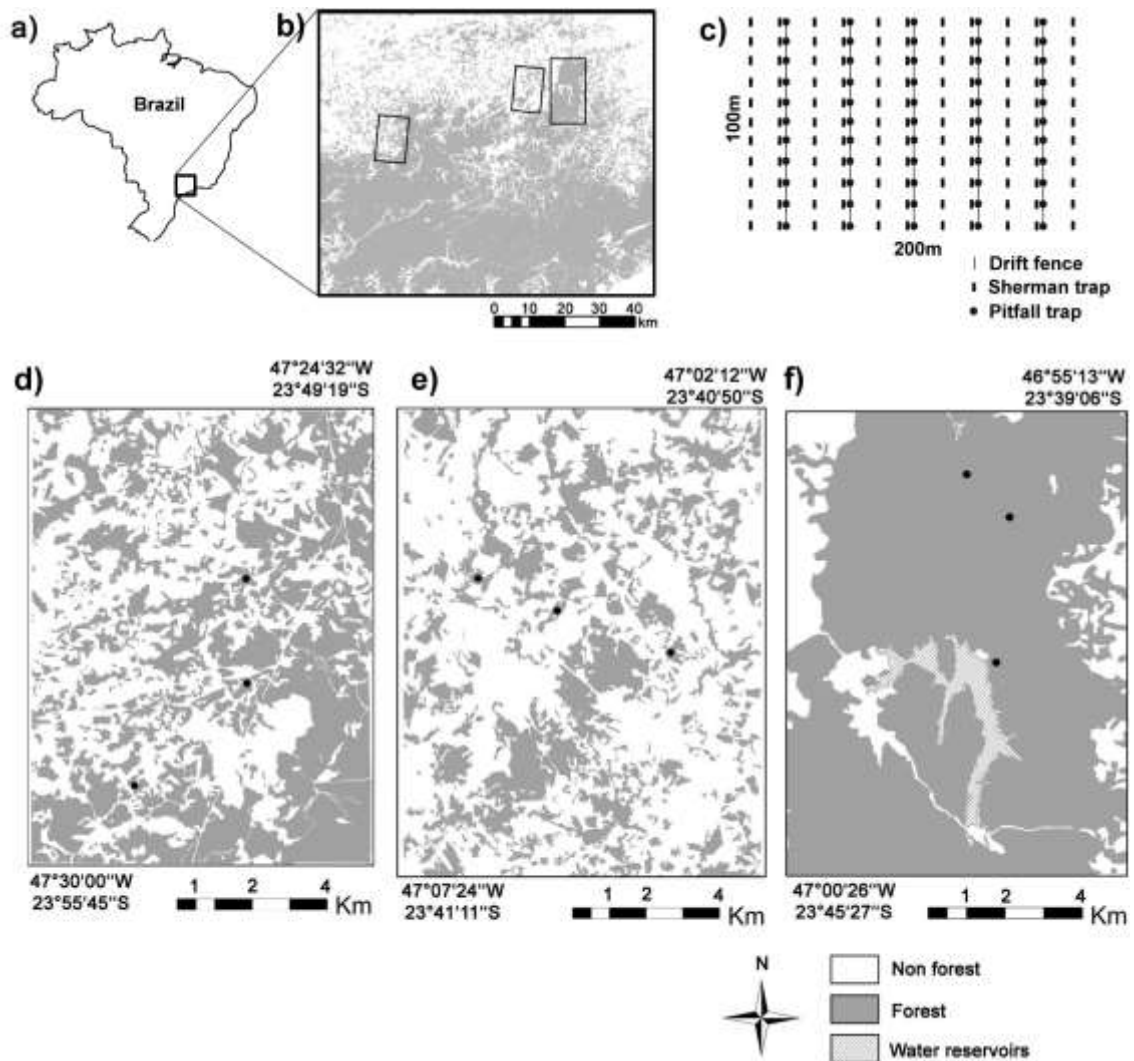
FIGURE 1: Location of the 3 study areas and 9 study sites in the Atlantic Plateau of São Paulo. a) Location of the Atlantic Plateau of São Paulo in the map of Brazil. b) Location of the 3 study areas (rectangles) in the Atlantic Plateau of São Paulo. c) Trapping grids used to capture *Akodon montensis*. d)-f) From the left to the right, in the same order as the rectangles in figure 1b, the areas Piedade-Tapiraí (50% native forest cover), Ibiúna (30% native forest cover) and Cotia (continuously-forested area), and the location of the 9 study sites within them (black dots).

4.3. Data collection

A trapping grid was installed at each of the 9 sites (Figure 1c). Each grid covered 2 ha and consisted of 11 100-m long parallel lines that were 20 m apart from each other, with trapping stations located every 10 m containing 1 Sherman trap (37.5 x 10.0 x 12.0 cm or 23.0 x 7.5 x 8.5 cm; H. B. Sherman Traps, Inc., Tallahassee, Florida) placed on the ground. Additionally, pitfall traps (60-l buckets, 53.0 cm in depth and 40.0 cm in diameter) connected by a 50-cm-high plastic fence were placed at each trap station in 5 alternated lines (Figure 1c).

8

Drift fences were lowered on the ground between capture sessions to allow movement of small mammals. In total, each grid consisted of 121 Sherman traps and 55 pitfall traps.

Five-day capture sessions were conducted monthly; in 3 of the 9 grids (continuously-forested area), 24 capture sessions were carried out between February/2008 and January/2010, while in the remaining 6 grids (located in fragmented areas) 5 capture sessions were carried out between February and June/2008. Trapping effort was 2640 trap nights per session, adding up to 84,480 trap nights in total. Each captured individual was sexed, marked with individual ear tags (small animal tags OLT; A. Hartenstein GmbH, Würzburg/Versbach, Germany) for latter recognition and had its reproductive status determined at first capture in each session (for more details, see *4.5.2. Individual characteristics*). All capture, handling, and tagging protocols followed the guidelines of the American Society of Mammologists (Sikes & Gannon 2011).

4.4. Home range area and overlap

We used the minimum convex polygon (MCP) to estimate the home range area of the 142 individuals that were captured at least 3 times in different traps (see *Data analysis* for a description of how we controlled for differences in the number of captures among individuals). In 2 of the 9 study sites, population density was very low and no individual was captured at least 3 times in different traps. To estimate home range overlap, we considered 2 variables as the data was zero-inflated (see *Data analysis* for more details): (1) a binary variable quantifying whether or not the home range area of each individual overlapped with that of at least another individual of the same gender (probability of home range overlap); and (2) a continuous variable quantifying the area of the home range of each individual that overlapped with the home range of 1 or more individuals of same gender (area of home range overlap). Home range overlap was calculated considering only those individuals captured within the same capture sessions (Figure 2). Both home range area and overlap were calculated using R environment (R.2.15.1; R Development Core Team 2012) and *gpclib* package.
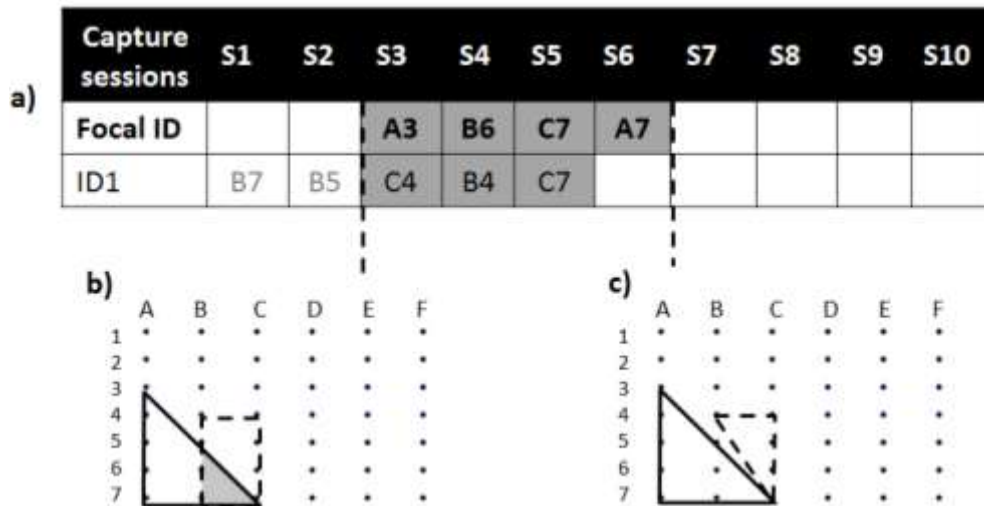
Figure 2: Schematic explanation on how we calculated home range overlap for every focal individual. a) Captures used to calculate home range overlap of a particular focal individual are in gray. In this case, we only considered the captures of individual ID 1 because only this individual had temporal and spatial overlap with the focal individual. However, we considered only those captures of this individual obtained within capture sessions that the focal individual was also captured. b) If we had considered all captures of both individuals, we would assume that their home range overlapped, but we cannot be sure of this given that ID 1 was captured within the home range of the focal individual only prior to the first capture of the focal individual. c) Considering only the captures of ID 1 that occurred when the focal individual was also captured, we estimated a more conservative measure of home range overlap, not considering the apparent overlap caused by a possible turnover of individuals using a particular area.

4.5. Determinants of home range area and overlap

4.5.1. Ecological factors

We used the minimum number known alive (MNKA; Krebs 1999) per grid and capture session as an estimate of population density as in our dataset MNKA is strongly correlated to estimates of population density that takes into account imperfect detection (Banks-Leite et al. 2014). We quantified sex ratio among mature individuals (MNKA of mature female/ MNKA of mature male) per grid and session to estimate female availability. We then calculated, for each individual, the mean MNKA and the mean female availability among all sessions between the first and the last session the individual was captured. The mean population density and mean female availability calculated for the 142 individuals varied from 4 to 50 individuals/ha and from 0 to 6 mature female/mature male, respectively (Figure 3).
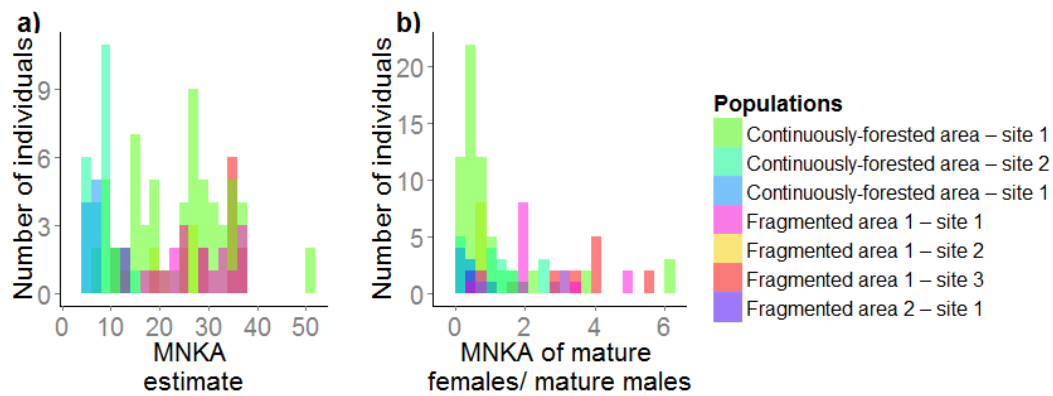
FIGURE 3: Histogram of the distribution of the explanatory variables (a) population density (MNKA) and (b) female availability (MNKA of mature female/ MNKA mature males) among the 142 individuals of *Akodon montensis*. For each individual, the value of each variable represents the mean among all capture sessions the individual was assumed to be present in the grid (i.e. all capture sessions between the first and the last capture sessions the individual was trapped).

4.5.2. Individual characteristics

Females were considered sexually mature from the capture when they presented any of the following characteristics that indicate that first estrus had already occurred: visible teats, open vagina, vagina with post-copulatory plug or palpable pregnancy. Males were considered sexually mature from the capture when they presented scrotal testicles. Because sexual maturity could change during the study, individuals were classified as either sexually mature or immature whether they were mature or immature during most of the period between the first and last captures. In total, 92 males (34 immature; 58 mature) and 50 females (18 immature; 32 mature) were included in the analyses.

4.5.3. Seasonal variation

Histological and anatomical analyses of *Akodon montesis* testicles have shown males have a higher spermatogenesis and reproductive activities between October and February (warm-wet season; Couto & Talamoni 2005). Accordingly, during the same period, there was a higher proportion of pregnant or lactating female in our study sites (unpublished data). Individuals were classified as either in the breeding season or not in the breeding season based on whether most of the period between the first and last captures occurred during the breeding season (October to February) or out of the breeding season (March to September), respectively.

No collinearity was identified among the different determinants of home range overlap (*Variance Inflation Factor* < 2; Table 2).

TABLE 2: Variance inflation factor (VIF) for each categorical and continuous explanatory variables in relation to all other variables together. For categorical variables, "0" and "1" values were attributed to each category according to the order included in the model selection analyses.

	VIF
Gender	1.037
Sexual maturity	1.065
Breeding season	1.181
Female availability	1.342
Population density	1.461

4.6. Data analysis

We used a model selection approach to compare a set of candidate models to investigate the importance and interactions of ecological factors, individual characteristics and seasonal variation in determining home range area and home range overlap. As sampling design was hierarchical (individuals within grids within study areas), we used generalized linear mixed models (GLMM) with both study area and grid included as nested random factor in all candidate models.

As GLMM do not yet have a clear solution to deal with zero-inflated data, we considered as response variables 2 separated measures of home range overlap (probability of home range overlap and area of home range overlap), besides home range area. Neither of the 2 continuous response variables (home range area and area of home range overlap) was normally distributed. Instead, best error distribution was gamma, and the log link-function was the best linearizing function, in both cases (Appendix 1). Probability of home range overlap was modeled as a binomial variable with a logit link-function.

MCP estimates usually depend on the number of captures (Stickel 1954, Kie et al. 2010, Püttker et al. 2012), as observed in our dataset (Figure 4). To take the variable number of captures among individuals into account, either the number of captures or the number of capture sessions per individual was included as a co-variable in all candidate models for each of the 3 response variables (Appendix 2).

Home range area can also influence home range overlap (either the probability of home range overlap or the area of home range overlap). To account for this effect, home range area was included as a co-variable in the models for the response variable probability of home range overlap, and the logarithm of the home range area was included as an offset (i.e.

co-variable with coefficient fixed at 1) in the models for the response variable area of overlap (as the link function in this case was *log*). By including log (home range area) as an offset, the response variable is divided by the home range area (McCullagh & Nelder 1989, Venables & Ripley 2002, Crawley 2007) and can be interpreted as a percentage of home range overlap. As very few females had their home ranges overlapping with the home ranges of other females, only males were included in the models for the response variable area (or percentage) of home range overlap.

This basic model structure (i.e. study area and grid as random factors + number of captures or of capture sessions as co-variate + home range area as co-variate or offset when needed) was used in all candidate models. For each response variable, candidate models varied in which explanatory variables were included as fixed factors. The set of candidate models included: (1) an intercept-only model for reference (that does not include any fixed factors); (2) simple models containing each of the ecological, individual and seasonal factors alone as fixed factors; and (3) models containing all possible combinations between ecological, individual and seasonal factors as fixed factors, but including only the pairwise interactions we predict to be important (Table 1) plus the pairwise interactions between sexual maturity and either gender or female availability as they were biologically plausible. Given that females were not included in the models for the response variable percentage of home range overlap, all models with the variable gender were excluded in this case. Models were selected based on AICc (Burnham & Anderson 2002) and considered equally plausible whenever ΔAICc < 2. Analyses were carried out in R environment (R.2.15.1; R Development Core Team 2012) with *lmer4* and *MuMin* packages.
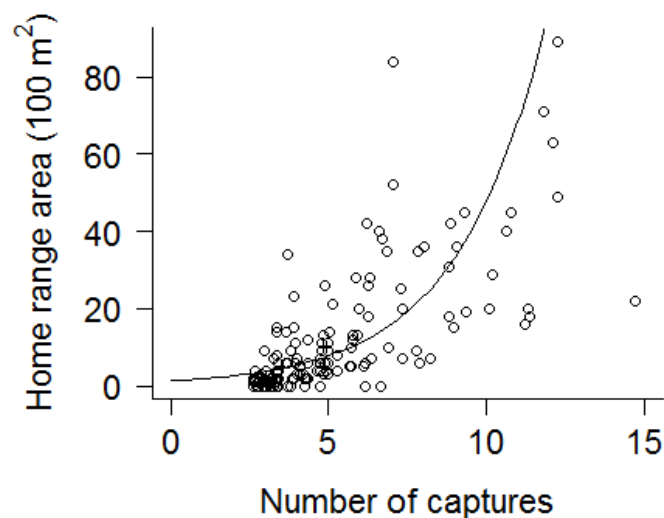
FIGURE 4: Home range area estimated by MPC as a function of the number of captures for 142 individuals of *Akodon montensis*.
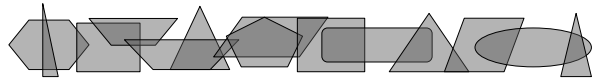
Considering the raw dataset for 142 *Akodon montensis* individuals (not controlling for the variation in the number of captures among individuals), mean home range area was greater for males than females, and greater for mature than immature individuals in both genders (Figure 5a). Mean percentage of home range area overlapping with the home range of individuals of the same gender was also greater between males than between females (Figure 5b), and comparatively fewer females than males overlapped their home ranges with the home range of individuals of the same gender (10 of 43 females compared to 42 of 82 males). However, mean percentage of home range overlap was greater in mature than immature individuals for males, but lower in mature than immature individuals for females (Figure 5b). Variation in both home range area and percentage of home range overlap was greater between males than females (Figure 5).
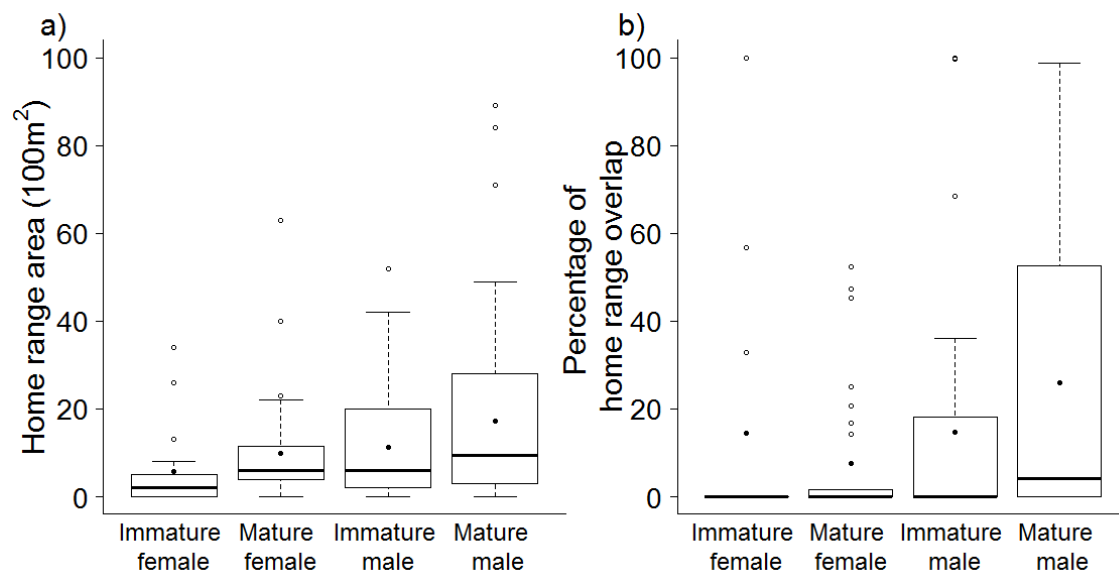
FIGURE 5: a) Home range area and b) percentage of home range overlap for immature and mature females and males of *Akodon montensis*. Thicker lines represent the median, values between second and third quartile (25% < x < 75%) are inside the box, dashed lines indicate lower and upper values inside 1.5 of the interquartile interval, filled dots represent mean and empty dots are outliers.

5.1. Home range area

Three models were selected to explain the variation in home range area among individuals of *Akodon montensis* (Table 3). The first-ranked model was the one containing only female availability (besides the co-variate number of captures), followed by the reference model (only the covariate number of captures), and by the model including female availability and gender. Selected models indicate that males have bigger home range areas than females, and that in both genders home range area is bigger when female availability is lower. However, as the reference model was also selected, the effects of both gender and female availability are not strong.

5.2. Probability of home range overlap

Three similar models were selected to explain the variation in the probability of home range overlap among individuals of *Akodon montensis*, all containing female availability, gender, the interaction between gender and female availability, and population density (Table 4). The first-ranked model contained additionally sexual maturity and its interaction with gender, and the third-ranked model contained also sexual maturity. Selected models indicate that the probability of home range overlap is higher between males than females, female availability positively affects the probability of home range overlap between females but negatively affects the probability of home range overlap between males, and population density increases the probability of home range overlap in both genders. When sexual maturity is included, the models indicate that the probability of home range overlap is higher in mature compared to immature individuals among males, but is lower for mature compared to immature individuals among females (first-ranked model), or that the probability of home range overlap is higher in mature compared to immature individuals for both genders (third-ranked model).

5.3. Percentage of home range overlap

Five models were selected to explain the variation in the percentage of home range overlap among males of *Akodon montensis*, all of them including population density (Table 5). Selected models included female availability and breeding season besides population density (first-ranked model), these same variables plus the interaction between female availability and breeding season (second-ranked-model), only population density (third-ranked model), breeding season besides population density (fourth-ranked model) and female availability

besides population density (fifth-ranked model). Selected models indicate that the percentage of home range overlap between males increased with population density and in the breeding season, whereas it decreases with female availability. The second-ranked model indicates that this negative effect of female availability on the percentage of home range overlap between males is stronger in the breeding season than in the non-breeding season.

TABLE 3: Results of GLMM model selection for the home range area of *Akodon montensis* as a function of ecological, individual and seasonal factors. All models with Wi > 0.03 are shown. Selected models are in bold (AICc < 2). K: number of parameters. AICc: AICc value. Δ: difference in AICc value to the first-ranked model. Wi: Akaike weights.

Models	K	AICc	Δ	Wi	Estimated coefficients (standard error)				
					FA	BS	SM	G	PD
FA	**6**	**2183.61**	**0.000**	**0.1343**	**-0.160 (0.060)**				
Reference model	**5**	**2184.85**	**1.239**	**0.0723**					
FA + G	**7**	**2185.47**	**1.865**	**0.0529**	**-0.154 (0.062)**			**0.139 (0.181)**	
FA + BS	7	2185.77	2.157	0.0457	-0.157 (0.061)	0.061 (0.200)			
FA + SM	7	2185.77	2.159	0.0456	-0.162 (0.060)		-0.053 (0.179)		
FA + PD	7	2185.79	2.182	0.0451	-0.152 (0.068)				-0.002 (0.009)
PD	6	2185.92	2.313	0.0423					-0.011 (0.008)
G	6	2186.35	2.737	0.0342				0.196 (0.189)	

All models include study area and grid as random factors, the number of captures as a co-variate, and one or more of the following explanatory variables as fixed factors: FA = female availability; BS = breeding season; SM = sexual maturity; G = gender; PD = population density. For categorical variables, coefficients refer to males, breeding season and mature individuals, respectively.

TABLE 4: Results of GLMM model selection for the probability of home range overlap between individuals of *Akodon montensis* of the same gender as a function of ecological, individual and seasonal factors. All models with Wi > 0.03 and the reference model are shown. Selected models (AICc < 2) are in bold. K: number of parameters. AICc: AICc value. Δ: difference in AICc value to the first-ranked model. Wi: Akaike weights.

	K	AICc	Δ	Wi	Estimated coefficients (Standard error)								
					FA	BS	SM	G	PD	FA:SM	FA:G	SM:G	PD:G
FA*G + SM*G + PD	**11**	**126.2**	**0.00**	**0.1242**	**0.38 (0.31)**		**-0.69 (1.02)**	**1.84 (1.19)**	**0.11 (0.03)**		**-1.23 (0.45)**	**2.10 (1.25)**	
FA*G + PD	**9**	**126.5**	**0.25**	**0.1095**	**0.32 (0.30)**			**3.02 (0.99)**	**0.10 (0.03)**		**-1.14 (0.42)**		
FA*G + SM + PD	**10**	**126.6**	**0.43**	**0.1002**	**0.25 (0.32)**		**0.83 (0.57)**	**2.98 (1.02)**	**0.11 (0.03)**		**-1.08 (0.44)**		
FA*G + SM*G + PD + BS	12	128.6	2.38	0.0377	0.39 (0.32)	-0.19 (0.74)	-0.71 (1.03)	1.82 (1.20)	0.11 (0.03)		-1.24 (0.45)	2.16 (1.27)	
FA*G +SM*G + FA*SM + PD	12	128.6	2.41	0.0372	0.33 (0.41)		-0.85 (1.31)	1.82 (1.19)	0.11 (0.03)	0.08 (0.41)	-1.23 (0.45)	2.17 (1.30)	
FA*G + SM*G + PD*G	12	128.6	2.42	0.0370	0.39 (0.32)		-0.70 (1.01)	1.58 (1.91)	0.10 (0.06)		-1.26 (0.49)	2.13 (1.26)	0.01 (0.07)
FA*G + BS+ PD	10	128.7	2.53	0.0350	0.32 (0.30)	0.20 (0.69)		3.03 (0.99)	0.10 (0.03)		-1.14 (0.42)		
FA* G + PD*G	10	128.8	2.58	0.0341	0.30 (0.32)			3.27 (1.69)	0.10 (0.06)		-1.11 (0.46)		-0.01 (0.06)
FA*G + PD*G + SM	11	129.0	2.81	0.0304	0.23 (0.34)		0.82 (0.57)	3.19 (1.75)	0.11 (0.06)		-1.05 (0.49)		-0.01 (0.07)
FA*G + FA*SM + PD	11	129.0	2.81	0.0304	0.30 (0.48)		0.91 (0.82)	3.00 (1.03)	0.11 (0.03)	-0.06 (0.43)	-1.10 (0.45)		
FA*G + PD + SM +BS	11	129.0	2.83	0.0301	0.25 (0.32)	-0.01 (0.72)	0.83 (0.58)	2.98 (1.02)	0.11 (0.03)		-1.08 (0.44)		
Reference model	5	137.0	11.40	0.0003									

All models include study area and grid as random factors, the number of capture sessions and home range area as co-variates, and 1 or more of the following explanatory variables as fixed factors: FA = female availability; BS = breeding season; SM = sexual maturity; G = gender; PD = population density. ":" means the interaction between the 2 variables. For categorical variables, coefficients shown refer to males, breeding season and mature individuals, respectively.

TABLE 5: Results of GLMM model selection for the percentage of home range overlap between males of *Akodon montensis* as a function of ecological, individual and seasonal factors. All models with Wi > 0.03 are shown. Selected models (AICc < 2) are in bold. K: number of parameters. AICc: AICc value. Δ: difference in AICc value to the first-ranked model. Wi: Akaike weights.

|	K	AICc	Δ	Wi	Estimated coefficients (Standard error)				
					FA	BS	PD	SM	FA:BS
FA + BS + PD	**8**	**642.94**	**0.00**	**0.2000**	**-0.421 (0.150)**	**0.773 (0.306)**	**0.063 (0.014)**		
FA*BS + PD	**9**	**643.04**	**0.10**	**0.1896**	**-0.497 (0.144)**	**-0.132 (0.482)**	**0.061 (0.013)**		**1.162 (0.576)**
PD	**6**	**644.27**	**1.34**	**0.1024**			**0.035 (0.014)**		
BS + PD	**7**	**644.34**	**1.40**	**0.0990**		**0.632 (0.332)**	**0.048 (0.014)**		
FA + PD	**7**	**644.43**	**1.49**	**0.0948**	**-0.354 (0.174)**		**0.046 (0.015)**		
Reference model	5	645.40	2.46	0.0584					
FA + BS + PD + SM	9	646.20	3.26	0.0391	-0.421 (0.150)	0.771 (0.311)	0.063 (0.014)	0.007 (0.294)	
FA*BS + PD + SM	10	646.46	3.52	0.0342	-0.503 (0.144)	-0.129 (0.483)	0.060 (0.013)	-0.080 (0.277)	1.180 (0.577)

All models include study area and grid as random factors, the number of capture as a co-variate, home range area as an offset and 1 or more of the following explanatory variables as fixed factors: FA = female availability; BS = breeding season; SM = sexual maturity; PD = population density. ":" means the interaction between the 2 variables. For categorical variables, coefficients shown refer to breeding season and mature individuals, respectively.

6. DISCUSSION
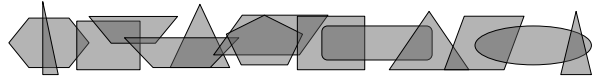
As expected by the economic model and the particularities of the reproduction and parental care in mammals (Table 1), all the studied explanatory variables affected at least one aspect of the use of space in *Akodon montesis*. Gender and female availability affected home range area and both measures of home range overlap, population density influenced both measures of home range overlap, sexual maturity influenced probability of home range overlap and breeding season influenced percentage of home range overlap. In particular, the distinct, opposite effects of female availability on home range overlap between males compared to females indicates that territorial strategies vary strongly among individuals, possibly leading to a shift in territorial/mating systems.

In the following paragraphs, we first argue that the observed interaction of gender and female availability indicates multiple territorial strategies adopted by individuals living in different conditions, which can lead to shifts in the territorial/mating system among populations. We then contextualize this finding in terms of what is known about ecological and physiological plasticity in *Akodon montensis* as well as about territorial and mating strategies within species of the same tribe and in small rodents in general. We follow by discussing the implications of the observed effects of factors other than female availability and gender on territorial strategies, and end up by discussing how distinct methodological approaches relates to the one used in the present study, pointing out research gaps for understanding territoriality.

By analyzing ecological, individual and seasonal factors together in 9 different populations, our study highlights that territorial strategies are extremely variable among individuals, and sufficient changes in environmental conditions could lead to the transition between different territorial/mating systems in distinct populations, as expected by the economic model (Maher & Lott 2000, Adler 2011, Oldfield et al. 2015). In particular, we observed that females with smaller home range areas and higher probability of overlapping their home ranges with those of other females were those living close to other females (i.e. higher female availability). This result suggests that when the number of females is higher, costs of defending a territory from neighboring females are elevated and overcome benefits, and females decrease their home range areas and tolerate increased overlap with other females, becoming more aggregated (i.e. less territorial). In contrast, we observed that males with smaller home range area but lower probability of overlapping home ranges with other males were those living in conditions with high female availability, as expected if females are the limited resources to males (Ostfeld 1990, McLoughlin et al. 2000). For males, then,

increased female availability reduces the area needed to find mates, lowering the costs of defending home range area, and making the benefits of excluding other males overcome costs (i.e. males became territorial). Thus, increased resource availability to females, leading to the increase in the number of females in an area, may trigger a shift from a polygynous mating system with territorial females to a polygynous mating system with territorial males.

Although phylogenetic constrains may reduce behavior plasticity, for example reducing the expression range of hormones linked to aggressiveness (Oldfield et al. 2015), this does not seem to be the case for *Akodon montensis* as we observed a wide range of individual strategies among the 9 studied populations. *Akodon montensis* is a habitat generalist species occupying a wide variety of habitats (Umetsu & Pardini 2007), persisting where forest loss is intense (Pardini et al. 2010, Püttker et al. 2013, 2015) and occupying biomes other than the Atlantic Forest (Paglia et al. 2012). In accordance to these ecological characteristics associated with an ample niche breadth, it has been recently shown that individuals of *Akodon montensis* present a higher physiological plasticity in water balance compared to individuals of co-occurring rodent species that are forest specialists (Castellar et al. 2015). Thus, although behavioral studies on *Akodon montensis* are lacking, the reported ecological and physiological plasticity is in agreement with our findings showing ample variation in individual territorial strategies, and suggests that populations of this species across its wide geographical and environmental range may present distinct territorial/mating systems. Recently, studies on mammals and birds have also shown variation in individual territorial strategies consistent with the economic model (Brashares & Arcese 2002, Sale & Arnould 2009), indicating that these strategies, besides influencing reproductive success, may indeed affect population mating systems (Banks et al. 2007, Rousseu et al. 2014, Sorato et al. 2015).

The strong variation in individual territorial strategies within *Akodon montensis* populations observed here contrasts, however, with the idea that polygynous mating system with territorial females is the characteristic mating system for all species of the Akodontini tribe (Gentile et al. 1997). Indeed, lineages living in constant environment for very long periods of time may present restricted behavioural and/ or physiological responses that limit territorial strategies and lead to less flexible mating systems. For example, in small-clawed otters and night monkeys, the constant low female availability may have led to monogamy, and then, to selection of parental care in males, leading to obligatory monogamy (Lukas & Clutton-Brock 2013). However, considering the evidence in favor to multiple territorial strategies in *Akodon montensis* we present here, and the variety of environments occupied by Akodontini species, it is reasobable to assume that their territorial/mating systems are variable rather than

obligatory or restricted. The conclusion that all Akodontini species present polygynous mating system with territorial females may be related to the limited number of studies conducted with these species, all of which focused on a single population (e.g. Heinemann et al. 1995, Magnusson et al. 1995, Gentile et al. 1997).

Results of studies on small rodents from other tribes and families do indeed suggest that territorial strategies and systems are flexible (e.g. Erlinge et al. 1990, Moorhouse & Macdonald 2008, Innes et al. 2009). Although these studies usually do not include measures of female availability, they commonly found that females decrease home range area and increase home range overlap in response to increased population density, and this has been interpreted as female response to variation in resource availability/ competition with other females (upper limit of territoriality; Erlinge et al. 1990, Fortier & Tamarin 1998). Similarly, the decrease in male home range area and overlap in response to population density has been interpreted as a response to female availability (Moorhouse & Macdonald 2008). Population density has indeed been indicated as the main factor determining mating systems in echimyid rodents, as a consequence to varying individual territorial strategies (Adler 2011). Moreover, several studies have found similar effects of population density but have not called attention to the implications of such results for the potential transition between territorial/mating systems among populations (e.g. Innes et al. 2009, Ruda et al. 2010). As in our study we included both female availability and population density, our results indeed suggest that the observed effects of population density in the literature may be better understood as responses to the variation in female availability.

Besides female availability and gender, other factors were also important in determining at least one aspect of the use of space in *Akodon montensis*. Population density increased home range overlap as predicted (Table 1), suggesting that as population density increases, individuals of both genders tolerate some home range overlap as the cost-benefit of territorial strategies decreases. However, the increase in home range overlap with population density was much larger for males than females, exemplified by the fact that most females did not overlap their home range with other females impeding the analysis of the percentage of home range overlap for females. Although a model including the interaction between gender and breeding season was not among the selected models as we initially expected, our results do suggest that home range overlap between males (but not between females) was larger in the breeding season. This is because breeding season influenced the percentage of home range overlap (which was possible to be analyzed only for males) but not the probability of home range overlap (males and females included). Thus, while differences in territorial

strategies between genders increased in the breeding season as expected, this seems to be mainly caused by males overlapping more with other males to access a larger number of mates (Bergallo & Magnusson 2004) rather than to females becoming territorial to guarantee exclusive access to food and nest sites during lactation (Ostfeld 1990, Wolff 1993). Indeed, our findings suggest that females of *Akodon montensis* do not defend territories exclusively when offspring is present. Finally, our results indicate that sexual maturity is also important for determining home range overlap interacting with gender, suggesting that the difference in territoriality between genders is established after sexual maturity, as mature females had smaller probability of home range overlap than immature females while the opposite occurred for males.

Observation of the use of space in natural, complex systems is one possible approach to the study of territoriality and mating systems, which, as other approaches, has advantages and limitations. The combination of different approaches is thus important to foster the understanding of territorial strategies and the implications to territorial and mating systems (Börger et al. 2008). The development of mechanistic models can indicate what rules of animal behavior may generate the spatial patterns observed in field studies (Giuggioli et al. 2011), indicating possible mechanisms responsible by these patterns. For example, the periodic scent marking of an area may generate non-overlapping areas, and agonistic interactions, which would involve high defense costs, are avoided (Potts & Lewis 2014). In turn, experimental studies can test proposed mechanisms, but are usually restrictive in terms of spatial and temporal scales and complexity of the system. These experiments have revealed, for example, that beavers recognize gender in scent marks, but that females do not respond to other females´ scent as expected for monogamous females (Cross et al. 2014). Finally, only field studies can investigate if the patterns of variation in space use among individuals expected by proposed mechanisms are indeed observed in nature. These 3 approaches are thus complementary but are rarely conducted together. Future studies on *Akodon montensis* should focus on experimentally testing if aggressiveness or scent marking is indeed more prominent among females than males at intermediate levels of resource availability to females, and if reducing resource availability to females or increasing female density lead instead to territorial behavior being more common in males than females. Observational studies, on the other hand, should include different populations, encompassing a larger variation in environmental conditions than we have done here, and should directly measure resource availability to females.

7. CONCLUSIONS
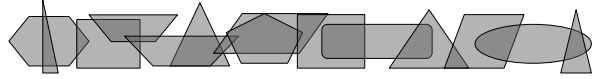
The observed strong gender-dependent effect of female availability on territorial strategies in *Akodon montensis* is in accordance with the economic model and the particularities of mammal reproduction and parental care, and indicates a strong variation in territorial strategies among individuals. Together with the previously reported ecological and physiological plasticity in *Akodon montensis*, this finding suggests that transitions from the polygynous system in which females are territorial to that in which males are territorial should be observed in populations inhabiting different environments. Although not as important as female availability and gender, other ecological, individual and seasonal factors influenced some aspects of the use of space of *Akodon montensis*. Finally, future studies should include larger variation in environmental condition and directly measure resource availability to females, and experimentally test aggressiveness and scent marking in both genders with varying resource availability.

8. REFERENCES
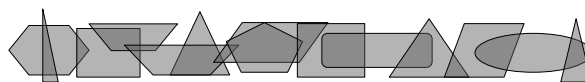
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9. APPENDICES
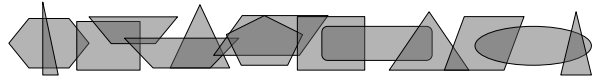
Appendix 1 - Detailed explanation on the choice of the probability distribution for continuous response variables (home range area and area of home range overlap)

Home range area and area of home range overlap are continuous variables, zero-inflated and left-skewed distributed. Considering these characteristics and the exponential family, for which it is possible to create a generalized linear mixed model (GLMM), the most adequate distributions and link-functions should be normal (log-link), gamma (inverse-link) and gamma (log-link). The last two probability distributions do not accept zero, and either a minimum value should be added to all values or zero values should be excluded to make the analysis possible. We used a model selection approach to determine which of these probability distributions best fit our data (Table S1) for each continuous response variable. For home range area, a small value of 0.25 was added to all values and for area of home range overlap, only values greater than zero were considered (given that we also analyzed separately the probability of overlap; see main text).

TABLE S1: Results of GLMM model selection for continuous response variables (home range area and home range overlap) to determine the best probability distribution. Selected models in bold. K: number of parameters. AICc: AICc value. Δ: difference in AICc value to the first-ranked model. Wi: Akaike weights.

	Models	K	AICc	Δ	Wi
Home range area	Gamma (log)	4	2238.36	0.0	0.500
	Gamma (inverse)	4	2238.36	0.0	0.500
	Normal (identity)	4	2502.50	264.1	< 0.001
	Normal (log)	4	2560.96	322.6	< 0.001
Home range overlap	Gamma (log)	4	916.27	0.0	1.000
	Gamma (inverse)	4	936.27	20.0	< 0.001
	Normal (log)	4	1068.46	152.2	< 0.001
	Normal (identity)	4	1072.64	156.4	< 0.001

Appendix 2 - Model selection to determine whether number of captures or number of capture session best explained variation in home range area, probability of home range overlap and percentage of home range overlap

To define whether the number of captures or the number of capture sessions was best associated with each of the response variables, we compared GLMM models containing as fixed factors each of these variables, choosing the variable present in the first-ranked model (Table S2).

TABLE S2: Results of GLMM model selection for home range area, probability of home range overlap and percentage of home range overlap in individuals of *Akodon montensis* as a function of the number of captures or the number of capture sessions. Selected models in bold. K: number of parameters. AICc: AICc value. Δ: difference in AICc value to the first-ranked model. Wi: Akaike weights, Coefficient 1: coefficient for the first variable in the model, Coefficient 2: coefficient for the second variable in the model when the model has 2 variables. In parentheses: standards errors for the coefficients.

	Models	K	AICc	Δ	Wi	Coefficient 1	Coefficient 2
Home range area	**Number of captures**	**5**	**2140.60**	**0.0**	**1.000**	**0.3320 (0.0370)**	
	Number of capture sessions	5	2173.30	32.7	< 0.001	0.3050 (0.0440)	
	Reference model	4	2196.80	56.2	< 0.001		
Probability of overlap	**Home range area + number of capture sessions**	**5**	**131.50**	**0.0**	**0.749**	**0.0009 (0.0002)**	**0.217 (0.134)**
	Home range area + number of captures	5	133.69	2.2	0.251	0.0008 (0.0003)	0.115 (0.132)
	Reference model	3	155.05	34.5	< 0.001		
Percentage of overlap	**Number of captures**	**5**	**632.81**	**0.0**	**0.492**	**0.1130 (0.0460)**	
	Reference model	**4**	**633.89**	**1.1**	**0.286**		
	Number of capture sessions	**5**	**634.40**	**1.6**	**0.222**	**0.1050 (0.0620)**	