

Original Contribution

Space Use and Social Mating System of the Hantavirus Host, *Oligoryzomys longicaudatus*

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Abstract: The long-tailed mouse, *Oligoryzomys longicaudatus* (Cricetidae: Sigmodontinae), is the major host of Andes hantavirus, the etiological agent of hantavirus pulmonary syndrome in the south of Argentina and Chile. Studying the ecology of this species is necessary to understand how Andes hantavirus is maintained in nature. In this study, we examine the home range size and intra- and intersexual overlap degree of male and female *O. longicaudatus* in order to elucidate the mating system of this species. To our knowledge, this research provides the first documentation, obtained from a specific design, of spacing and mating systems in this species in Argentina. The study was conducted seasonally from April (autumn) 2012 to October (spring) 2013 in a shrubland habitat of Cholila, Andean region, Argentina. We studied spacing patterns using 59 and 51 home ranges established by adult males and females, respectively, in two 3.24 ha capture-marked and recapture grids. Significant differences between sexes in home range size and overlap degree were found. Male home ranges were always larger than those of females. We observed exclusive space use both among males and females (13.15 ± 18.67 , and $3.60 \pm 3.43\%$, respectively). Considering only those males that get access to receptive females (40%), average intersexual overlap value was about $30.82 \pm 19.73\%$. Sexual differences in home range sizes and the spatial avoidance between breeding males, that would reflect intrasexual competition for receptive females, allows us to propose a polygynous mating system for *O. longicaudatus*.

Keywords: Home range, Mating system, Hantavirus reservoir, Population density

INTRODUCTION

At the individual level, the way an organism uses space can influence its survival and reproductive success (Greenwood 1980; Madison 1980; Clutton-Brock 1989; Agrell et al. 1996). Space use decisions and the resulting spacing patterns exhibited by individuals have profound ecological

consequences, affecting individual fitness and population dynamics (Brown and Orians 1970; Waterman 2007). However, in general, zoonotic diseases researchers have often minimized the importance of those ecological aspects in the host–pathogen dynamics. According to Holsomback et al. (2013), a better understanding of the factors that maintain the virus in wild populations hinges upon a deeper knowledge of space use and social mating system of hosts species.

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Space use of individuals may be strongly influenced by sex, reproductive condition, availability of potential mates, and abundance and distribution of potential competitors (Batzli and Henttonen 1993; Bond and Wolff 1999; Priotto and Steinmann 1999; Priotto et al. 2002). Because of the relationship between spacing patterns and the different constraints on reproduction in males and females, such patterns are often used to infer the mating system of cryptic individuals within a given population (Trivers 1972; Ostfeld 1985, 1986, 1990; Gaulin and FitzGerald 1988; Blondel et al. 2009; Maher and Burger 2011). Thus, sex-specific differences in home range size and overlap degree, and the identification of the territorial sex during the breeding season, can improve understanding of mating systems (Shier and Randall 2004; Klemme et al. 2006; Steinmann et al. 2005, 2006a, b, 2009; Solomon and Keane 2007). In accordance with Emlen and Oring (1977), the mating systems of a species should represent the outcome of reproductive strategies of individuals. Whereas mating system is a characteristic of a population or a species, a mating strategy refers to all the tactics used by an individual to obtain fertilizations (Alonzo and Warner 2000; Solomon and Keane 2007; Waterman 2007; Taborsky et al. 2008).

Among mammals, due to the high costs associated with pregnancy and lactation, females typically provide greater parental investment than males, which results in sexual differences in space use (Clutton-Brock and Harvey 1978; Clutton-Brock 1989; Adler 2011). Since males are basically emancipated from having to provide parental care, promiscuity and polygyny specially have been considered the predominating mating systems in most mammal species (Emlen and Oring 1977; Ostfeld 1986; Clutton-Brock 1989). In both mating systems, males tend to have larger home range size compared to females and greater intersexual overlap, reflecting a mechanism to increase access to receptive females ensuring optimal mating (Gaulin and FitzGerald 1988; Steinmann et al. 2005; Bonatto et al. 2012; Waterman 2007; Wolff 2007). Several studies have inferred social mating system in voles and mice through patterns of space use. In species where males have larger home ranges than females and extensively overlap with both female and male home ranges, researchers proposed a promiscuous mating system (Bond and Wolff 1999; Wolff and Macdonald 2004; Steinmann et al. 2005; Blondel et al. 2009). In contrast, in species where males have larger home ranges than females but keep mutually exclusive home ranges that extensively overlap with more than one female home range, it was proposed a polygynous mating system, in which a

minority of males control or gain access to multiple females leaving other males without access to them (Ostfeld 1986; Shier and Randall 2004; Loughran 2007; Wolff and Sherman 2007; Bonatto et al. 2012, 2015).

The operational sex ratio (OSR), defined as the average ratio of sexually active males to fertilizable females at any given time, provides an empirical measure of the degree of monopolizability of mates (Trivers 1972; Emlen and Oring 1977). A greater degree of imbalance in the OSR leads to a greater expected variance in reproductive success among members of the limited sex, affecting directly the degree of polygyny (Trivers 1972; Clutton-Brock and Parker 1992; Mitani et al. 1996; Aloise King 2013). Many studies at the population level have revealed the impact of population density and OSR on spacing and mating behaviours of vole and mice (Ochiai and Susaki 2002; Steinmann et al. 2006a, b; Stradiotto et al. 2009; Sommaro et al. 2010; Steinmann and Priotto 2011; Bonatto et al. 2015; Ávila et al. 2016). For example, in some promiscuous and polygynous vole species, male home range size and overlap degree are negatively correlated with population density (Ostfeld et al. 1985; Ostfeld 1986; Nelson 1995a, b; Bond and Wolff 1999; Moorhouse and Macdonald 2008; Ávila et al. 2016) and receptive female availability (Steinmann et al. 2006a; Steinmann and Priotto 2011), while females maintain the size and exclusivity of its home ranges regardless of population density (Saitoh 1981; Ostfeld 1985; Erlinge et al. 1990; Sommaro et al. 2010; Ávila et al. 2016).

Oligoryzomys longicaudatus (Cricetidae: Sigmodontinae) is a small rodent species (adult average mass, 33 ± 8 g) commonly known as long-tailed pygmy rice rat or “colilargo”. This species is the major host of Andes hantavirus, the etiological agent of the human illness hantavirus pulmonary syndrome (HPS) in the south of Argentina and Chile (Enría and Levis 2004; Levis et al. 1998; Padula et al. 2004). In some *Oligoryzomys* species, behavioural interactions and space use patterns are factors that strongly affect viral transmission since both are closely related to their reproductive strategies, social organization, and population dynamics (Suárez et al. 2003; Mills et al. 2007; Polop et al. 2010, 2016). Young et al. (1998) proposed that the Andes virus (ANDV) is maintained in rodent populations by direct contact between individuals through fighting and/or social grooming. Padula et al. (2004) proposed that transmission mainly occurs among adult males, indirectly by saliva and urine, or directly through wounds. However, despite its epidemiological importance, the patterns of space use and reproductive

strategies of *O. longicaudatus* remain unclear. Most previous studies on *O. longicaudatus* have focused mainly on epidemiological issues and were not designed to determine patterns of space use and reproductive strategies. However, some prior studies of *O. longicaudatus* revealed a great variation in home range size throughout the year in the same habitat, and between different habitats and different population densities (Contreras 1972; Murúa et al. 1986; González et al. 2000; Piudo 2011; Monteverde 2013). For example, in forest habitats with similar population abundance values, home range sizes of 215.2 m² (\pm 117.8) (Murúa et al. 1986) and 2071.4 m² (\pm 986.0) have been reported (González et al., 2000). This variation could be a consequence of differences in the methodological approach in relation to the spatial and temporal scales or different trapping designs employed (Murúa et al. 1986; Kelt et al. 1994; González et al. 2000).

Spacing and mating behaviours researches on *O. longicaudatus* become relevant due to the fact that a better knowledge of these topics may help to understand the hantavirus dynamic. To our knowledge, this research provides the first documentation, obtained from a specific design, of spacing and mating systems in this species in Argentina. Since species mating system reflect sex-specific mating strategies, we attempt to elucidate *O. longicaudatus*' mating system by examining its home range size and intra- and intersexual overlap degree. In addition, we analysed the influence of population density on space use of males and females.

MATERIALS AND METHODS

The Study Species

Oligoryzomys longicaudatus is primarily found in forest and shrublands in Chile and southwestern Argentina (Palma et al. 2005; Polop et al. 2010). In Argentina, this species inhabits multiple habitat types including disturbed habitats (cultivated field borders and peridomestic settings), as well as pasture, shrublands, and Andean Patagonian forest (Piudo et al. 2005, 2011; Porcasi et al. 2005; Carbajo and Pardiñas 2007; Polop et al. 2014a). Several studies suggest a marked flexibility in habitat use by this species, which is characterized by opportunistic behaviour and high mobility (Murúa and González 1986; Murúa et al. 1986). With regard to its diet, *O. longicaudatus* has been described as granivorous by Murúa and González (1981), Pearson (1983) and Meserve et al. (1988), as omnivorous by Mu-

ñoz-Pedrerros et al. (1990), and as frugivorous by Polop et al. (2014b). According to Sbriller and Sepúlveda (2007) and Polop et al. (2014b), this species feeds primarily on fruits of *Rosa* spp. in forests and shrublands. Population abundance is low in summer (December–February) and peaks in autumn–winter (April–June) (Murúa et al. 1986; Polop et al., 2010). The lifespan of *O. longicaudatus* individuals is approximately 12 months, and is dependent on environmental conditions and the behavioural interactions (Pearson 1983; Murúa et al. 1986; Meserve et al. 1995; Palma et al. 2005; Sage et al. 2007). The reproductive period of *O. longicaudatus* has been described as strongly seasonal (Murúa et al. 1986; González-Ittig et al. 2015). Females reach sexual maturity at 30 days (Pearson 1983), and juveniles (1 month old) are promptly incorporated into the breeding population (González-Ittig et al. 2015). The average proportion of pregnant females increases from spring to summer and decreases in the fall (Pearson 1983; Polop et al. 2016). *O. longicaudatus* has a gestation length of 23 days (Murúa et al. 1986), the average number of embryos registered between spring and summer is about 5.66 (\pm 1.9) (Polop et al. 2016), each female can produce between 3 and 4 litters in her lifetime (4.7 pups per litter), and they exhibit postpartum oestrous (Pearson 1983; Sage et al. 2007).

Study Area

The study was conducted seasonally from April (autumn) 2012 to October (spring) 2013 in Cholila (42°31S; 71°27W), Andean region, Chubut Province. This Province is one of the Argentine regions where ANDV has been associated with HPS disease (Levis et al. 1998; Enría and Pinheiro 2000; Padula et al. 2000). The study area is a steppe-rainforest transition zone. The topography is primarily mountainous with most features formed by glacial processes (Cabrera and Willink, 1980). The dominant climate is temperate with most rainfall occurring between April and September (600 mm) (Cabrera and Willink 1980; León et al. 1998). There is an abrupt precipitation gradient from west to east due to the rain shadow effect of the Andes, which results in a strongly defined vegetation structure and floristic composition (Cabrera and Willink 1980). Phytogeographically, this region corresponds to “Dominio Subantártico, Distrito del bosque Caducifolio” characterized by different arboreal (*Austrocedrus chilensis*, *Nothofagus antartica*, *N. pumilio*, *Maytenus boaria*, *Schinus montanus*, etc.), and native (*Berberis buxifolia*, *B. serrate-*

dentata, *Fragaria chilensis*, *Ribes cucullatum*, *Schinus molle*, *Passiflora ligularis*, etc.) and exotic shrubby species such as *Rosa* spp. (Dimitri 1977, 1981).

This study was conducted in a shrubland habitat in which *Rosa* spp. prevails and where high population abundances of *O. longicaudatus* occurred (Polop et al. 2010, 2014a; Andreo et al. 2012). The study site is bounded at southwest by the Rivadavia Lake, at east and west by two streams that flow into this lake, and at north by a mountain in which slope begins a wooded area. Due to these physical barriers that surrounded the study area, our sampling area functioned as a seminatural enclosure.

Study Design

We captured *O. longicaudatus* on two grids of 10×10 traps, with an interstation distance of 20 m. Thus, each grid covered an area of 3.24 ha. The grids were separated by a distance of 150 m. Two live traps ($8 \times 9 \times 23$ cm) similar to a Sherman trap (Alejandro Möller manufacturer, Argentina) were placed at each station and baited with rolled oats, bovine fat, and vanilla scent. To reduce the probability of death, cotton bedding was placed inside the traps. Throughout the study, we conducted a total of 8 trapping sessions of ten consecutive nights in every season, except winter of 2012 due to the fact that a severe snowfall prevented the capture of animals. During trapping sessions, traps were checked each morning. In order to identify captured animals, individuals were foot-tagged with numbered metal rings. Trapped animals were weighted, and body and tail length were registered. Sex, reproductive state (for males, scrotal or abdominal testicles; for females, perforate or imperforate vagina, nipples visible or not, and evidence of pregnancy), trap location, and wounds and scars were also recorded. *O. longicaudatus* population density was calculated for each trapping session as the number of unique individuals captured per hectare. Handling of rodents followed standardized safety guidelines recommended by the Centers for Disease Control and Prevention (Mills et al. 1995).

To estimate home range configuration of each animal, all captures and recaptures were plotted on graph paper for each trapping session following the Boundary Strip methods (Stickel 1954). To calculate home range size (m^2), occasional outings or exploratory movements were excluded (Bondrup-Nielsen, 1985) and the minimum convex polygon method was selected (Jenrich and Turner, 1969). We choose this method for its mathematical simplicity,

because it is easy to implement graphically and it is a useful method for comparison with previous studies. The number of captures for each estimated home range varied from 4 to 8, and this number did not have effect on home range estimations (Juan 2015). In each trapping session, the intra- and intersexual home range overlaps were estimated for each individual by the method suggested by Batzli and Henttonen (1993). This method assumes that when the home range overlap is significantly lower ($\leq 10\%$) than it would be expected by random placement, individuals are avoiding one another, and this is considered as an evidence of territorial behaviour (Wolff et al. 1983; Wolff 1993; Steinmann et al. 2009; Bonatto et al. 2012). Assuming that intersexual overlap values higher than 10% reflect mating (Clutton-Brock 1989; Bonatto et al. 2012, 2015), we considered reproductively males (RMs) as those that overlapped their home ranges $> 10\%$ with female home ranges during a trapping session, and non-reproductive males (NRMs) as those that overlapped $\leq 10\%$ and males that established home range without intersexual overlap. In this study, the OSR was calculated for each trapping session as: $OSR = \text{number of males that overlapped their home ranges more than } 10\% \text{ over female home ranges} / \text{number of breeding females that established home ranges}$. The animals were treated in humane manner according to the current Argentinean Laws (National Law 14346).

Data Analysis

We used a generalized linear model (GLM) approach to examine the relationships between each response variable (home range size and home range overlap) and predictor variables. For home range size analysis, the predictor variables were sex (fixed factor with two levels) and trapping session (fixed factor with four levels). For home range overlap analysis, the predictor variables were overlap type (fixed factor with three levels: male/male; female/female; male/female) and trapping session. Akaike information criterion was used as a measure of the fit of a model (the smaller the AIC, the better the fit). In all cases, normality assumption was tested by Shapiro–Wilk’s test, and variance homogeneity was tested by Levene’s test (Crawley 2002). We had to apply log transformation to the data in order to solve problems with heterogeneity of variances (Underwood 1997). Statistical analyses were carried out using R version 3.0.3 library (nlme) (R Development Core Team 2010, www.r-project.org).

Table 1. Average Home Range Sizes (HRZ), Standard Deviation (SD), and Sample Size (*n*) of Male and Female and Population Density of *Oligoryzomys longicaudatus* by Trapping Session.

Trapping session	Density (Ind/ha)	Home range	Males			Females		
			HRZ	(DS)	<i>n</i>	HRZ	(DS)	<i>n</i>
April 2012	24.7	General	1875.0	1502.5	12	1005.6	389.1	9
		Overlapping	3050.0	1796.6	3			
		Non-overlapping	1483.3	1149.1	9			
October 2012	18.0	General	5406.2	2504.0	4	2015.0	780.5	5
		Overlapping	5406.3	2504.0	4			
		Non-overlapping						
February 2013	5.7	General	2600.0		1	1200.0	1000.0	2
		Overlapping						
		Non-overlapping	2600.0		1			
April 2013	16.8	General	4350.0		1	1000.0		1
		Overlapping						
		Non-overlapping	4350.0		1			
August 2013	59.9	General	1090.6	705.9	8	721.4	526.3	7
		Overlapping	1683.3	501.8	3			
		Non-overlapping	868.8	544.7	4			
October 2013	75.5	General	880.0	532.0	34	844.0	774.6	23
		Overlapping	802.5	356.0	15			
		Non-overlapping	883.6	545.4	19			

Males home range size were discriminate in: general (all the home ranges established independently of intersexual overlapping); overlapping (with intersexual overlap); and non-overlapping (without intersexual overlap).

RESULTS

From April 2012 (autumn) to October 2013 (spring), 1072 individuals of *O. longicaudatus* were captured with a total effort of 26,517 trap nights. During the study, population density fluctuated between 5.71 and 75.46 ind/ha. Two maximum density peaks were observed: one in the fall of 2012 (24.69 ind/ha) and the other in spring 2013 (75.46 ind/ha). The lowest density occurred during the summer 2013 (5.71 ind/ha).

Due to the fact that all captured females showed evidence of being reproductively active throughout the year, the OSR was estimated for all trapping sessions in which intersexual overlap was recorded, including those corresponding to autumn and winter. The OSR values were always biased towards females: 0.5 in autumn (April–May 2012), 0.8 and 0.48 in spring (October 2012 and 2013, respectively), and 0.6 in winter (August 2013).

During this study, 110 home ranges of adult *O. longicaudatus* were estimated (59 males, 51 females). Males had a minimum home range size of 200 m² in October 2012

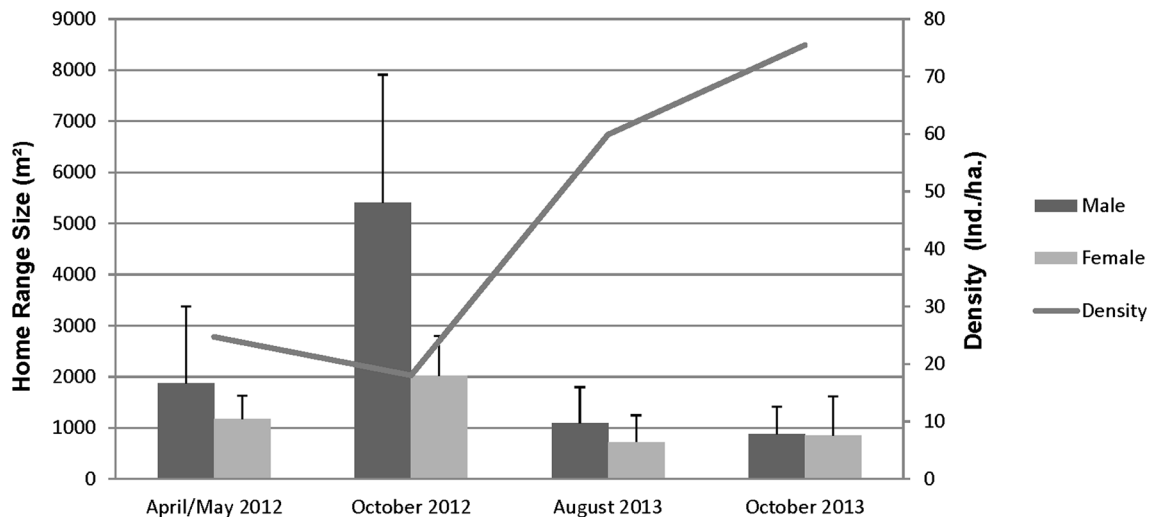
and a maximum home range size of 9050 m² in October 2013, whereas female's minimum and maximum home range size values were 200 m² in February 2013 and 3450 m² in October 2013, respectively (Table 1). In most seasons, home range size of males that overlapped the home ranges of females was higher than those that not register intersexual overlap (Table 1). Only on October 2013 (spring), home range size of males that overlapped and non-overlapped with those of females reached very similar size values (Table 1). Besides, 44.5% of males without intersexual overlap showed wounds in their bodies, while only 28% of males with intersexual overlap exhibited bodily injuries.

GLM analysis based on Δ AIC revealed that sex and trapping session were the most important factors affecting *O. longicaudatus* home range size (Table 2). The best model included the interaction effect between sex and trapping session, and this was the only model with substantial support. Coefficients for the best model are shown in Table 3. Although average home range size of males was always larger than those of females, the biggest difference was

Table 2. Model Selection Based on AIC Comparison of General Linear Model (GLM) Describing Home Range Size of *Oligoryzomys longicaudatus* in a Shrublands Habitat in the Valley of Lake Rivadavia (Province of Chubut, Argentina).

Response variable	Model	AIC	Δ AIC
Home range size	Sex \times trapping session	1746.95	0
	Sex + trapping session	1764.40	17.45
	Trapping sesión	1769.32	22.37
	Sex	1805.29	58.34
	Null	1805.85	58.90

The best model is indicating in boldface type. Models are ordered by Δ AIC

**Fig. 1.** Home range size (mean + SD) and population density (Ind./ha.) of *Oligoryzomys longicaudatus* in relation to sex and trapping session, from spring 2012 to winter 2013, in a shrubland habitat in the valley of the Rivadavia Lake, in Chubut-Argentina Province.**Table 3.** Coefficients (β) for the Best Linear Model of Space Use of *Oligoryzomys longicaudatus*, Which Included Interaction Between Sex and Trapping Session, in a Shrublands Habitat in the Valley of Lake Rivadavia (Province of Chubut, Argentina).

Response variable	Factors	β (ES)	<i>t</i> value	<i>P</i> value
Home range size	Intercept	7.172 (0.213)	33.605	< 2e-16
	Females	- 0.189 (0.296)	- 0.637	0.525
	October 2012	1.311 (0.427)	3.071	0.003
	August 2013	- 0.487 (0.337)	- 1.445	0.152
	October 2013	- 0.566 (0.249)	- 2.272	0.025
	Females \times October 2012	- 0.773 (0.577)	- 1.338	0.184
	Females \times August 2013	- 0.179 (0.4837)	- 0.369	0.713
	Females \times October 2013	- 0.026 (0.358)	- 0.073	0.942

Standard errors (in parentheses) and the significance of the coefficients are also shown; $P < 0.05$ shown in boldface type. The effect of each term in the model is tested. *P* values tested the null hypothesis that $\beta = 0$. The terms with $P < 0.05$ have some discernable effect.

Table 4. Model Selection Based on AIC Comparison of General Linear Model (GLM) Describing Home Range Overlap (HRO) Type (Male/Male; Female/Female; Male/Female) of *Oligoryzomys longicaudatus* in a Shrublands Habitat in the Valley of Lake Rivadavia (Province of Chubut, Argentina).

Response variable	Model	AIC	Δ AIC
HRO	HRO type \times trapping session	833.10	0
	HRO type + trapping session	841.91	8.81
	Trapping session	849.21	16.11
	HRO type	871.63	38.63
	Null	875.67	42.57

The best model is indicating in boldface type. Models are ordered by Δ AIC.

Table 5. Coefficients (β) for the Best Model of Linear Model Analysis of Space use of *Oligoryzomys longicaudatus*, Which Included Home Range Overlap (HRO) Type and Trapping Session, in a Shrublands Habitat in the Valley of Lake Rivadavia (Province of Chubut, Argentina).

Response variable	Factors	(ES) β	<i>t</i> value	<i>P</i> value
(HRO)	Intercept	1.37 (0.314)	4.36	3.42 e-0.5
	HRO male/male	- 0.386 (0.574)	- 0.673	0.503
	HRO male/female	0.538 (0.453)	1.187	0.238
	Density (24.69 Ind/ha)	0.438 (0.612)	0.715	0.477
	Density (75.46 Ind/ha)	- 0.418 (0.41)	- 1.021	0.310
	HRO male/male:density (24.69 Ind/ha)	2.372 (0.975)	2.432	0.017
	HRO male/female:density (24.69 Ind/ha)	0.928 (0.871)	1.066	0.289
	HRO male/male:density (75.46 Ind/ha)	- 0.252 (0.716)	- 0.352	0.726
	HRO male/female:density (75.46 Ind/ha)	- 0.284 (0.583)	- 0.487	0.627

Standard errors (in parentheses) and the significance of the coefficients are also shown; $P < 0.05$ shown in boldface type. The effect of each term in the model is tested. *P* values tested the null hypothesis that $\beta = 0$. The terms with $P < 0.05$ have some discernable effect.

recorded in October 2012 (lower density value), when male home ranges were almost three times as large as females (Table 1). Contrarily, the minor differences between males and females home range size were observed when *O. longicaudatus* population density reached the highest value (Fig. 1). Males home range size showed statistically significant differences between spring 2012 (lowest population density) and spring 2013 (highest population density) (Table 3).

The mean male/male overlap percentage was $13.15 \pm 18.67\%$, while mean female/female overlap was $3.60 \pm 3.43\%$. The average intersexual male/female overlap was $10.16 \pm 17.33\%$. This value was calculated considering the totality of male home ranges, including those that did not overlap with any female. However, when we considered only those males that shared their home ranges with fe-

males, average intersexual overlap increased to $30.82 \pm 19.73\%$. GLM analysis based on Δ AIC revealed that overlap type (excluding those of males that did not overlap with females home range) and trapping session were the most important factors affecting home range overlap in *O. longicaudatus* (Table 4). The best model included the interaction effect between overlap type and trapping session, and this was the only model with substantial support (Table 5). Because female/female intra-sexual overlaps were always lower than 10%, we considered that females maintained exclusive home range (territories) throughout the trapping sessions. With regard to intra-sexual overlap values between males, although in most trapping sessions these were lower than 15%, in spring 2012 males almost quintupled its intrasexual overlap degree (Fig. 2).

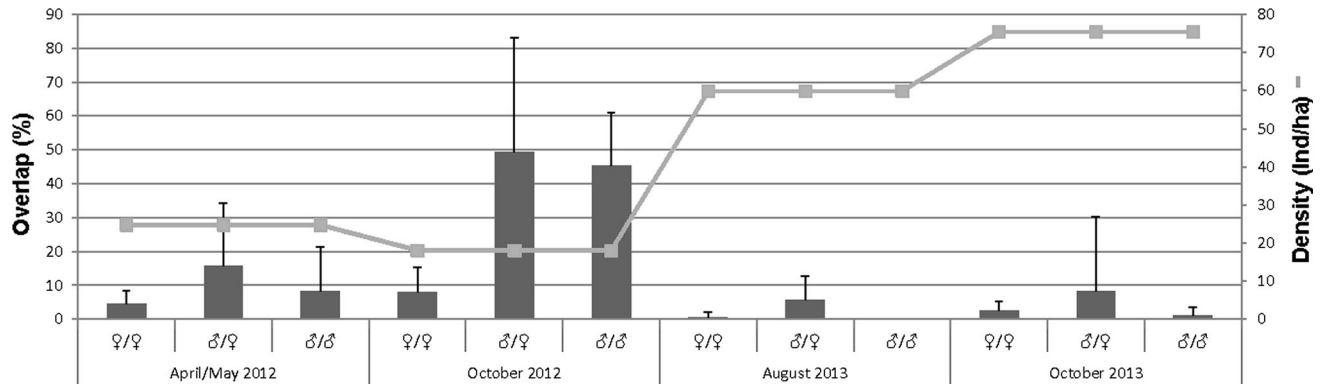


Fig. 2. Home range overlap (mean + SD) and population density (Ind/ha) of *Oligoryzomys longicaudatus* in relation to overlap type and trapping session, from spring 2012 to winter 2013, in a shrubland habitat in the valley of the Rivadavia Lake, in Chubut-Argentina Province.

DISCUSSION

Even though Pearson (1983), Murúa et al. (1986) and Muñoz-Pedrerros (2000) proposed that the reproductive period of *O. longicaudatus* is strongly seasonal, in this study we found evidence to suggest that females are reproductively active throughout the year. These findings are consistent with those made by Argel (2005) who found that this species remains reproductively active during the year. Because of this, in our study, the analyses of home ranges size and overlap degree were not discriminated into reproductive and non-reproductive periods.

Our data revealed evidence of differences in space use between male and female *O. longicaudatus*. The measured attributes of space use for males and females, obtained by recapture data in a shrubland habitat, would suggest that *O. longicaudatus* has a polygynous rather than a promiscuous mating system. Polygyny is a mating system in which a minority of males control or gain access to multiple females leaving other males without access to them (McEachern et al. 2009). A polygynous population is predicted to have sexual dimorphism in space use, with males having larger home ranges, which overlap with more than one female, and spatial exclusiveness in relation to other males (Gaulin and Fitzgerald 1986, 1988). The greater the home range sizes of males, the greater the proportion of females that they monopolize (Emlen and Oring 1977). In our study, even though males always had larger home ranges than females, males that monopolized females had even larger home ranges than those males whose home ranges did not overlap with any female. This suggests that *O. longicaudatus* males involved in reproduction would employ a strategy of home range placement as mechanism

evolved to increase the number of receptive females to ensure optimal mating (Cudworth and Koprowski 2010). According to Emlen and Oring (1977) and Dobson (1983, 1984), female defence polygyny usually occurs in conjunction with male resource defence and both mating strategies are characterized by breeding males being territorial during the breeding season, whereas conversely the absence of territoriality is considered as non-defence polygyny. In this study, male territoriality was assumed based on the limited overlapping degree between male home ranges, since an overlap degree significantly lower than the expected by random placement would indicate that individuals are avoiding one another (Batzli and Henttonen 1993; Priotto and Steinmann 1999; Bonatto et al. 2012). Male's territoriality, considered by several authors as a typical feature of polygynous voles and mice, would reflect competition between males to monopolize receptive females (Gaulin and FitzGerald 1988; Clutton-Brock 1989; Heske and Ostfeld 1990; Waterman 2007). Thus, the low values of overlap between males allowed us to reject a promiscuous strategy. Besides, the average OSR (0.6) observed in this study would indicate that in the population 40% of adult males have no access to females (assuming that the population sex ratio is 1:1). In our study, 44.32% of adult males show evidences of wounds, nearly double the number of adult females with evidence of bodily injuries. Besides, we found that males which shared or not their space with receptive females differed in bodily injuries percentage value, being greater in those who did not show intersexual overlap. In the polygynous species *Akodon azarae*, Bonatto et al. (2013) found that males that monopolized females tripled the time invested in aggressive exhibitions towards potentially intruder males to their

home ranges. According with Clutton-Brock and Parker (1992), Kvarnemo and Ahnesjö (1996) and Mitani et al. (1996), this would reflect strong pre-mating competition among males, and that *O. longicaudatus* males maintained mutually exclusive home ranges based on agonistic interactions. However, in a study conducted in *Oryzomys palustris*, the primary host for the hantavirus genotype Bayou, Holsomback et al. (2013) found that seropositive males distributional patterns are based on female receptivity and habitat preferences rather than just male aggression. This, even when McIntyre et al. (2009) described *O. palustris* seropositive males as socially dominant individuals. Holsomback et al. (2013) proposed this socio-ecological explanation of host distributional patterns as an alternative explanation to elucidate the links between hantaviral maintenance and circulation in natural host populations.

Even though the characteristics of space use and the OSR values obtained in this study are consistent with polygynous mating system features, a high intrasexual overlap degree was recorded between males (> 45%), in spring 2012. During this trapping session, population density value was low, and the OSR and sex ratio (number of adult males/number of adult females) values were equal. This may indicate that all males in the population could participate in reproduction, and so intrasexual competition among males for receptive females should be minimal. Thus, *O. longicaudatus* may present some flexibility in its mating system varying towards a less strict polygyny. Nevertheless, this exception does not invalidate our proposed mating system for *O. longicaudatus*. Although Emlen and Oring (1977) described three main mating systems, they also proposed a high degree of flexibility, both between and within populations. Breeding systems of species are the outcome of reproductive strategies of individuals rather than evolved characteristics of species (Clutton-Brock, 1989). In male voles and mice, those strategies are dependent on a number of factors including abundance as well as spatial and temporal distribution of receptive females, which in turn depends on variation in resource distribution, predation pressures, and male intrasexual competition (Nelson 1995a, b; Agrell et al. 1996; Schradin and Pillay 2006; Wolff 2007; Ávila et al. 2016). According to Bryja et al. (2008), Stradiotto et al. (2009) and Bonatto et al. (2015), mating systems can be varied in relation to total density population, resources, and receptive female's availability. Thus, several species that have been identified as polygynous under certain circumstances were considered

as promiscuous in others situations (Waterman 1998, 2007; Bond and Wolff 1999; Loughran 2007; Bonatto et al. 2015). According to this, *O. longicaudatus* males would adopt the most advantageous strategies in relation to specific ecological and social conditions.

Research on hantavirus host species in the southern hemisphere has found that adult individuals are more frequently infected than juveniles and males more frequently than females (Mills et al. 1997; Torres-Perez et al. 2004; Polop et al. 2010), suggesting that hantaviruses are maintained in reservoir populations by horizontal virus transmission primarily among male mice. In *O. longicaudatus*, Padula et al. (2004) found that the transmission of the virus between conspecific individuals is mainly mediated by saliva. Association of wounds or scars with the presence of hantavirus antibody has been used to suggest intraspecific agonistic encounters as a mechanism of hantavirus transmission within host populations (Mills et al. 1999). Therefore, the control and prevention of rodent-borne diseases largely depends upon understanding the biology and ecology of the host (Mills and Childs 1998). Given the role of *O. longicaudatus* in public health, it is of great interest to identify spacing and mating strategies, especially when they may involve aggressive interactions among adult individuals. Although some authors emphasize the point that genetic analyses would be the primary way to establish the mating system of the species (Klemme et al. 2006; Bryja et al. 2008; McEachern et al. 2009), observational studies of space use have also been useful in elucidating mating strategies and systems (Madison 1980; Wolff et al. 1994; Agrell et al. 1996; Blondel et al. 2009; Steinmann et al. 2005, 2009; Adler 2011; Bonatto et al. 2012). The approach taken in this study allowed us to argue that space use in this species is consistent with patterns characteristic of polygynous rodents.

CONCLUSION

We have argued that space use in *O. longicaudatus* is consistent with patterns characteristic of polygynous rodents. Our results demonstrate that *O. longicaudatus* males had larger home ranges than females and high intersexual home range overlap but spatial exclusiveness in relation to other males. The female-biased OSR in wild populations of *O. longicaudatus* likely indicates that a minority of males control or gain access to multiple females leaving other males without access to them; in our study population only

40% of adult males could have access to receptive females. This evidence, and the fact that 44.32% of breeding males show evidences of wounds, suggests a strong pre-mating competition among males. These behavioural characteristics are widespread in polygynous mating system. The next step in our research will be a comparison between *live-trapping* and *radiotelemetry* data, in order to delve the relationship between spacing patterns and mating strategies of *O. longicaudatus* males and females. Besides, taking into account the results obtained by Holsomback et al. (2013), in forthcoming studies on *O. longicaudatus* it would be important to consider the patterns of microhabitat selection in both males and females.

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