

*Habitat selection and coexistence in small mammals of the southern Andean foothills (Argentina)*

**Agustina Novillo, M. Fernanda Cuevas,  
Agustina A Ojeda, Ramiro J. A Ovejero,  
Mosca Torres, M. Eugenia & Ricardo A  
Ojeda**

**Mammal Research**

ISSN 2199-2401

Mamm Res

DOI 10.1007/s13364-017-0309-1



**Mammal Research**

 Springer

 Mammal Research Institute  
Polish Academy of Sciences  
Białowieża

 Springer

**Your article is protected by copyright and all rights are held exclusively by Mammal Research Institute, Polish Academy of Sciences, Bia#owie#a, Poland. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at [link.springer.com](http://link.springer.com)".**

# Habitat selection and coexistence in small mammals of the southern Andean foothills (Argentina)

Agustina Novillo<sup>1</sup> · M. Fernanda Cuevas<sup>1</sup> · Agustina A Ojeda<sup>1</sup> · Ramiro J. A Ovejero<sup>1</sup> · Mosca Torres<sup>1,2</sup> · M. Eugenia<sup>2</sup> · Ricardo A Ojeda<sup>1</sup>

Received: 19 September 2016 / Accepted: 20 March 2017

© Mammal Research Institute, Polish Academy of Sciences, Białowieża, Poland 2017

**Abstract** Habitat partitioning is considered one of the main mechanisms of coexistence among small mammals. This is especially evident in arid environments where resources are particularly scarce. Habitat characteristics such as vegetation heterogeneity and complexity are expected to increase species coexistence, increasing the number of microhabitats that can be occupied by species with different requirements. The Andean foothills can be considered as an ecotone between the Monte and Altoandina phytogeographic provinces as they harbor species from both. Consequently more species are thought to coexist in this area. The objectives of this study were to assess the macro- and microhabitat selection of the small mammal assemblage inhabiting the Andean foothills during wet and dry season and to determine how animals segregate environmental resources to ensure their coexistence. We found that habitat selection occurs at both scales in the Andean foothills. Two species, *Eligmodontia moreni* and *Phyllotis xanthophygius*, were capable of distinguishing among macrohabitat types, whereas all species showed habitat selection at the microhabitat scale. We registered selection during both seasons, with some overlap of resource selection

during the wet season and the greatest segregation of microhabitat resources during the dry season. Therefore, this work evidence that the assembly of small mammals is sensitive to habitat structure especially in dry seasons where resources are constraints due to arid conditions of Andean foothills.

**Keywords** Species coexistence · Small mammals · Habitat selection · Andean foothills

## Introduction

Habitat partitioning is considered an important mechanism for coexistence among small mammal species (Schoener 1974; Stevens and Tello 2009). Therefore, partitioning in some of the available resources (e.g., space, food, time) enhance coexistence of two species with similar ecological requirements (Shenbrot 1992; Chesson 2000).

The climatic conditions of arid environments such as strong seasonality, low productivity, and precipitation lead to seasonal, scarce, and patchy resources (Ojeda et al. 2000; and references therein). Seasonal changes in habitat structure (i.e., changes in available vegetation cover) promote variations in the use of resources by small mammals (Cramer and Willig 2002). Therefore, it leads to significant consequences on the population dynamics of species, especially in periods of scarcity (i.e., dry season) (Ostfeld and Keesing 2000). Hence, competition is expected to be strong and makes habitat partitioning more evident (Wiens 1977; De Boer and Prins 1990). Therefore, arid environments represent an excellent scenario to evaluate how ecologically similar species cope with resource partitioning.

Habitat complexity (i.e., vertical vegetation variation) and habitat heterogeneity (i.e., horizontal vegetation variation) are expected to increase species coexistence, as they increase the

---

Communicated by: Communicated by: Emerson M. Vieira

✉ Agustina Novillo  
anovillo@mendoza-conicet.gov.ar

<sup>1</sup> Consejo Nacional de Investigaciones Científicas y Técnicas (CCT Mendoza), Instituto Argentino de Zonas Áridas (IADIZA), Avenida Ruiz Leal s/n Parque General San Martín, CP 5500, CC 507 Mendoza, Argentina

<sup>2</sup> Consejo Nacional de Investigaciones Científicas y Técnicas (CCT Mendoza), Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA), Avenida Ruiz Leal s/n Parque General San Martín, CP 5500, CC 507 Mendoza, Argentina

number of microhabitats that may be occupied by species with different requirements (Rosenzweig and Winakur 1969; Price 1978; Cramer and Willig 2002; Corbalán and Ojeda 2004). Likewise, more available microhabitats offer more refuges from predators and provide more diversity of food resources (Simonetti 1989; Taraborelli et al. 2003; Corbalán and Ojeda 2004; Traba et al. 2010).

Co-occurrence processes depend on the spatial scale at which species assemblages are analyzed (Barrio and Hik 2013). Spatial scale may alter species assemblage's patterns perception and the order of importance of the explanatory variables (Morris 1987, Whittaker et al. 2001). Especially since spatial scale represents the way animals perceive their environment (Morrison et al. 2006). Abiotic constraints may shape species distribution at a coarse scale, which not necessarily implies that species coexist at smaller patches. Thus, analyzing different spatial scales (macro and microhabitat, in this study) is determinant to understand how small mammals use the resources and the environment to coexist.

The Andean foothills or "piedemonte" is an ecotonal area between the Monte and the Altoandina phytogeographic provinces. Due to its transitional characteristics, this region is expected to harbor species that belong to both provinces. Biodiversity studies in scrublands of the Monte Desert found 10 co-occurring species of rodents (*Eligmodontia typus*, *E. moreni*, *Graomys griseoflavus*, *Thylamys pallidior*, *Calomys musculus*, *A. molinae*, *Akodon sp.*, *Abrothrix andinus*, *Salinomys delicatus*, and *Phyllotis xanthopygus*). Records of *P. xanthopygus* in the Monte are scarce and restricted to scrublands above 900 m a.s.l. (Gonnet and Ojeda 1998; Rodríguez and Ojeda 2011). Studies of habitat use by these species found that microhabitat variables such as vegetation structure and substrate composition are important for distribution and abundance patterns of these small mammals (Ojeda 1989; Simonetti 1989; Bos et al. 2002; Corbalán 2006). These studies highlight that high diversity was found in more heterogeneous habitats, and that almost all species avoided open areas. Several studies emphasize that open areas are very important components in structuring assemblages of small mammals (Rosenzweig 1973; Jaksic et al. 1981; Gonnet and Ojeda 1998), and that species density is positively correlated with vegetation density. There is also evidence that small mammals of the Monte desert use the habitat in a non-random fashion (Campos et al. 2001; Tabeni and Ojeda 2005; Corbalán 2006; Ojeda et al. 2011), and that species are capable of distinguishing among macrohabitats. However, selection at the microhabitat scale seems to be weaker than selection at macrohabitat (Corbalán and Ojeda 2004; Corbalán 2006; Tabeni et al. 2007; but see Traba et al. 2016).

Small mammal assemblages at the Altoandina province is composed by 15 species (Novillo and Ojeda 2014) (*P. xanthopygus*, *Loxodontomys micropus*, *Euneomys chinchilloides*, *E. mordax*, *A. spegazzinii*, *A. andinus*,

*A. longipilis*, *A. olivaceous*, *Chelemys macronyx*, *E. morgani*, *E. moreni*, *E. typus*, *G. griseoflavus*, *C. musculus*, and *A. molinae*). Among them, six species were registered only at low elevations among 1300 and 1800 m a.s.l. (Novillo and Ojeda 2014). Simonetti et al. (1985) analyzed the habitat use of two of these species of rodents (*P. xanthopygus* and *A. andinus*) in the high Andes of Chile and show that the two species select different habitat types, with *P. xanthopygus* selecting habitats with prevalence of rock outcrops, while *A. andinus* shows a preference for shrubby habitats.

Gonnet and Ojeda (1998) evaluated the habitat use of an assemblage of small mammals in the Andean foothills of Mendoza, Argentina. Their study showed that small mammal species were selective about habitat types (e.g., some showed stronger selection towards dense vegetated habitats), hence species composition and abundance differ between habitats. They also found that some species in the ecotone area occupy vegetation patches similar to those that occupy in the Monte desert.

The purpose of our study was to assess macro- and microhabitat selection by the small mammals that inhabit the Andean-Monte Desert ecotone and to determine how these small mammal species segregate environmental resources to ensure their coexistence. We hypothesize that vegetation complexity influences the composition and distribution of small mammal assemblages. Therefore, sites and seasons with higher availability of resources will support more species. We also assess microhabitat selection using models to predict how changes in resource availability affect each species preferences.

Based on natural history information about the species, we predict that at microhabitat scale *P. xanthopygus* will select areas with some prevalence of rocks and shrub cover (Gonnet and Ojeda 1998; Kramer et al. 1999) while *A. molinae* will be more abundant in grassland areas with high vegetation cover (Corbalán et al. 2006). We also predict that *C. musculus* will select more complex covered habitats and avoid open areas (Corbalán and Debandi 2009) while *E. moreni* will be associated with open areas (Lozada et al. 2000; Lanzone et al. 2012).

## Material and methods

### Study site

The arid Andean foothills extend as a narrow transitional belt between the Andes and the western plains of the Monte desert (Martinez Carretero and Mendez 1992; Méndez 2011). The area is a mosaic of shrubby-grassy habitats of varying structure and complexity that result from a combination of local and regional processes such as climate, vegetation, substrate,

and slope (Roig 1976). Due to its geographic position, the Andean foothill presents scarce precipitations (fewer than 100 mm per year in its northern region and 300 mm in its southern part). This region may be considered an elevated substrate of the Monte desert, named “Andean foothills District of the Monte Province” (Roig 1989). Climate in the Monte desert is semiarid and strongly seasonal, with hot humid summers (from November to April) and cold dry winters (from May to October) (Claver and Roig-Juñent 2001; Labraga and Villalba 2009).

This study was conducted during the wet and dry seasons, from September 2007 to June 2008. We selected two different study sites between 900 and 1400 m a.s.l. One of the study sites was a priori defined as “grassland” (−33.9670 S, −69.9887 W; 1300 m a.s.l.), with low vegetation cover and mainly dominated by *Stipa spp.* The second site was named a priori “shrubland” (−32.9712 S, −68.9650 W; 1000 m a.s.l.). It shows more vegetation complexity with several species of bushes such as *Larrea divaricata*, *Zuccagnia punctata*, and *Condalia microphylla* among others.

**Sampling design** We established two trapping grids per study site. Each grid consisted of  $5 \times 10$  trapping stations with 50 Sherman live traps on the ground (each spaced by 10 m), covering a total area of 3600 m<sup>2</sup>. All traps were baited with a mixture of rolled oats and peanut butter. Small mammals were sampled monthly from October 2006 through March 2007 (wet season) and April through June 2007 (dry season). Monthly trapping sessions consisted of three consecutive trap-nights per grid. The total trapping effort was 5400 trap-nights. All animals were weighed, sexed, examined for reproductive status, and identified to species before being marked and released to their capture site.

Each study site was considered as macrohabitat and we would refer to it as macroscale. To quantify microhabitat characteristics, we estimated mean percent vegetation cover in  $2 \times 2$  m quadrants surrounding every trap of the grid, based on independent assessments by two observers. We visually estimated the percent cover of each species and also the percentage of bare soil, litter, and rocks. We estimated the vegetation composition (habitat complexity) at the two habitat types measuring the percentage of vegetation cover at nine different height levels every 25 cm. Additionally, we characterized the vegetation life forms estimating the percentage of herb, grass, shrub, and sub-shrub (shrub less than 1 m tall) covers.

### Statistical analysis

The habitat was characterized using principal component analysis (PCA) with vegetation data obtained from all trap stations. The following variables were used for the analysis: percentage of vegetation cover; life forms; and the percentage

of bare soil, litter, and rocks. This allowed us to examine which variables best explained the differences in structure among the two habitats found in the study area. PCA was performed using Infostat software.

To detect patterns of habitat use at macroscale, we used Chi-squared goodness of fit test with Yates correction to determine whether there was a significant difference between the observed frequency of small mammal presence in each habitat and the expected frequency of its use. When significant differences were found, we applied Bonferroni confidence intervals Broomhall et al. (2004); Liu et al. 2005). This analysis allowed us to determine which type of habitat was selected or not selected (i.e., the use was proportional or not to what was available). If the expected proportion lay outside the interval, we concluded that the expected and actual use were significantly different and thus allowed us to determine preference by the species (if the proportion of usage was greater than expected) or avoidance (if the proportion of usage was lower than expected) (Neu et al. 1974; Lopez-Cortes et al. 2007). Microhabitat selection of small mammal's assemblages was analyzed using resource selection functions (RSF) considering capture success as the response variable (Manly et al. 2002). Manly (1974) described resource selection indices calculated as (% use)/(% availability) of each type. The set of these ratios for all habitat types is termed the “resource selection function” (Manly et al. 1993). Each ratio estimates the relative probability that a type would be selected, compared to the probabilities of selection for the other types; however, when the comparison is between used and unused samples, the logistic model can be used to estimate the probability of use, described by Manly et al. (2002) as the “resource selection probability function” (RSPF): (relative) probability of animal use of a given area during a given time, based on the environmental conditions that influence or account for selection. We used these mathematical (functions) approaches that uses linear combination of weighted values of predictor variables (environmental, on this design), where responses by small mammals (during wet and dry season) were true 0s (absence) and 1s (presence), so standard logistic (equation) regression was used, on binomial response (used = 1 and unused = 0). The SD of the estimates for each parameter was our estimate of the SE for each coefficient, and the central 90% of the distribution for each coefficient was used as the 90% CI (Manly 2007).

An assumption for this type of model is that the probability of use of plot  $i$  was given by the equation

$$E[\pi_i] = \frac{\exp(\beta_0 + \beta_1 B_{i1} + \beta_2 C_{i2} + \beta_p x_{ip})}{1 + \exp(\beta_0 + \beta_1 B_{i1} + \beta_2 C_{i2} + \beta_p x_{ip})}$$

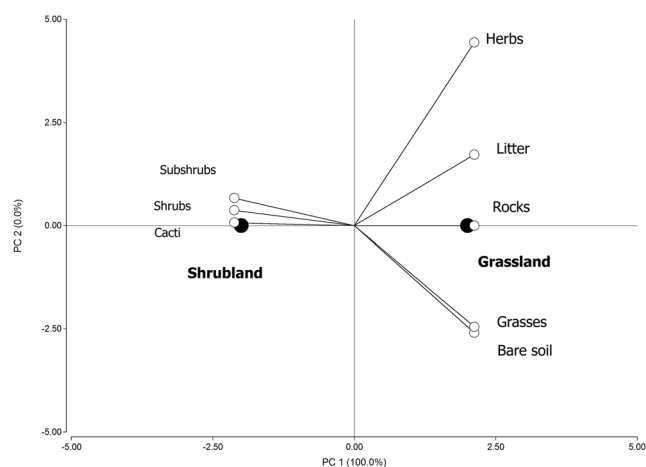
where  $\beta_0$  to  $\beta_p$  are constants to be estimated from the available data, and  $X_1$  to  $X_p$  are the variables that the probability of a success is to be related to. It is also usually assumed that the

number of successes observed in  $n$  trials follows a binomial distribution with mean  $n\pi$  and variance  $n\pi(1 - \pi)$ , which implies that the outcome for each trial is independent of the outcome of any of the other trials.

A complement way of representing the probability of occurrence (PO) of an event of interest is through the use of odds, expressed as a quotient between the number of events and the number of “no events” [ $PO = (p\{A\} = h/n)/(1 - p)$ ]. We calculate the odds of use for each small mammal species from our RSPF model; an assumption for this type of analysis is that the probability of use of plot  $i$  is given by the equation  $(\exp(\text{estimates}/100) - 1) * 100$ , where “estimates” are the coefficient values (the output data model) of each model built for each species. Modeling counts of use is acceptable, but it is often preferable to make inference to the relative frequency distribution of animal use within the study area during the study period. We predicted intensity of use by small mammals as a function of covariates in the standard logistic regression (on binomial response) RSPF based on 1000 bootstrap replicates treating the individual animal as the experimental unit. The predicted relative probabilities of use calculated from this function represent the median predicted value for each level of the covariate. All this analyses of “relative probabilities of use” indicated that in the case of the odds ratios for mean values, for every 1-unit increase in mean values between the scaled predicted values, there was an expected increase or decrease in small mammal habitat use.

## Results

A total of 303 individuals were captured along the entire study excluding recaptures. Individuals belonged to six different species (*E. moreni*, *C. musculus*, *A. molinae*, *P. xanthopygus*, *G. griseoflavus*, *T. pallidior*). We registered 208 individuals in the grassland environment and 95 in the shrubland one. Both sites share almost all species with exception of *G. griseoflavus* that was only registered in shrubland habitat. PCA analysis showed that grassland is characterized by presence of herbs, grasses, rocks, and litter. Meanwhile, shrubland presents shrubs, sub-shrubs, and cacti (Fig. 1). *G. griseoflavus* and *T. pallidior* were excluded from the analysis due to their low abundances ( $n = 2$  and  $n = 6$ ). At macrohabitat scale, only the observed frequency of *E. moreni* and *P. xanthopygus* were significantly different from expected frequency of the two habitat types ( $\chi^2 = 35.93$ ,  $df = 1$ ,  $p < 0.001$ ,  $n = 190$  and  $\chi^2 = 8.60$ ,  $df = 1$ ,  $p < 0.01$ ,  $n = 10$ ; respectively), while the rest of the species did not show significant differences between macrohabitats (*A. molinae*:  $\chi^2 = 3.12$ ,  $df = 1$ ,  $p = 0.07$ ,  $n = 40$ ; *C. musculus*:  $\chi^2 = 0.59$ ,  $df = 1$ ,  $p = 0.44$ ,  $n = 51$ ). Bonferroni confidence intervals showed that grassland was positively selected by *E. moreni* and shrubland was used more than expected by chance by *P. xanthopygus* (Table 1).



**Fig. 1** Biplot of habitat and vegetation variables resulting from a principal component analysis (PCA) in the Andean foothills

At microhabitat scale, each species used different microhabitat characteristics (Table 2). During wet season, *A. molinae* and *P. xanthopygus* selected sites with 0.25 m vegetation cover and presence of rocks. Meanwhile, *C. musculus* selected microhabitats with higher proportion of litter and *E. moreni* selected sites with abundance of herbs (Table 2). The odds ratio for mean 0.25% vegetation cover indicated that for every 1-unit increase in mean 0.25% vegetation cover (between 0 and 1%), there was an expected 6.5% increase in *A. molinae* use. Also, an increase in mean percentage of rock presence incurs an expected 7% increase in *A. molinae* use (Fig. 2a). For every unit increase in letter percentage cover, there was an expected 7% increase in *C. musculus* habitat use (Fig. 2b). *E. moreni* probability of selection tends to increase 9% with an increase of herb cover. The odds ratios for *P. xanthopygus* are evidence that the probability of selection tends to increase in order of 9 and 8% for every unit of increase in mean percentage of 0.25 m vegetation cover and presence of rocks (Fig. 2d).

During dry season, only two species evidenced microhabitat selection. *A. molinae* selected sites with high 0.25% cover and avoided sites with herbs, rocks, shrubs, and sub-shrubs. On the other hand, *E. moreni* avoided sites with 0.25% cover and presence of cacti (Table 2). Odds ratios indicate that the probability of selection of *A. molinae* was expected to decrease by 18, 14, and 21% for every 1-unit of increase in mean percentage of herbs, shrubs, and sub-shrub cover, respectively (Fig. 2a).

Increases in the amount of 0.25% cover and presence of cacti determine an expected decrease of 5 and 26% of *E. moreni* probability of selection (Fig. 2c).

## Discussion

Resource availability is not constant along the environment and time, especially in the Monte desert which

**Table 1** Simultaneous confidence intervals using the Bonferroni approach for rodents habitat use at the habitat-level during the period of study

Season	Category	Expected proportion of use	Observed proportion of use	95% confidence interval
<i>Eligmodontia moreni</i>	<b>Grassland</b>	0.56	0.78	0.713–0.847 <sup>a</sup>
	<i>Shrubland</i>	0.44	0.22	0.153–0.287 <sup>a</sup>
<i>Phyllotys xanthopygus</i>	<i>Grassland</i>	0.56	0.10	(–)0.112–0.312 <sup>a</sup>
	<b>Shrubland</b>	0.44	0.90	0.687–1.112 <sup>a</sup>

The habitat in bold is that preferred by the species

<sup>a</sup> The expected proportions of use that fell outside the confidence interval

presents strong climatic seasonality with most of the rainfall occurring during summer and a complex mosaic of different habitats (Albanese and Ojeda 2012). Hence, sites and seasons with fewer resources are supposed to yield higher competition among species.

Our results show that two of the four species considered in this study evidenced selection at macrohabitat level. *E. moreni* and *P. xanthopygus* segregate the habitat at this spatial scale. Possibly, there is selection of structural components of the environment as the habitat complexity, which determines that *E. moreni* selected habitats with low vegetation (i.e., grassland), while *P. xanthopygus* preferred high vegetation complexity (i.e., shrubland). *C. musculus* and *A. molinae* did not evidence any preference at this spatial scale. Our prediction that species would select environments with high vegetation complexity was not confirmed at macrohabitat scale. There was only one species (*P. xanthopygus*) that selected complex environments.

However, at microhabitat level, the four species showed selection. The occurrence in open areas by *E. moreni* supports previous studies of the genus *Eligmodontia* preferring open habitats with more patched vegetation (Ojeda 1989; Corbalán and Ojeda 2004; Corbalán et al. 2006; Ojeda et al. 2011) and supported our prediction. Most of the studies of *E. moreni* natural history recognized it as an open-area specialist. However, Rodriguez et al. (2012) considered that this species is habitat generalist with a wide habitat niche breath, although the greatest abundance was observed in open habitats as sand dunes. Also, this species is considered as omnivorous due to the high variability of its diet, including leaves, seeds, and insects, particularly in the dry season (Lanzone et al. 2012). Important advantages of *E. moreni* are several morphological characteristics which enables it to display bipedal and erratic saltatorial locomotion (e.g., longer hind legs; Taraborelli et al. 2003), allowing the individuals to exploit uncovered habitats due to its efficiency and velocity to escape from predators (Kotler 1984). Therefore, it seems that diet plasticity, preferences for open habitat, and

ecomorphological characteristics provide an advantage that allows *E. moreni* to coexist with other species (*C. musculus* and *A. molinae*) at microhabitat scale.

Shrubland preference by *P. xanthopygus* was partially consistent with that observed by Gonnet and Ojeda (1998) and Kramer et al. (1999) in other study areas. Those authors observed that *P. xanthopygus* selected areas with high proportion of rocks. Even more, Simonetti et al. (1985) and Monjeau et al. (1997) considered that rock outcrops are an important habitat characteristic for this species along its geographical range. In our study site, the presence of rocks was patched and scarce, so it is probably that the dense shrub cover could be used as the main choice of shelter, while rock outcrops could be preferred as a second option at a microhabitat scale. Species of the Andean foothills selected different microhabitat characteristics than in the lowland Monte Desert (Corbalán et al. 2006). Complex vegetation structure was avoided by *A. molinae* and *P. xanthopygus* on the Andean foothills. During wet season, both species selected sites with abundant 0.25 m vegetation cover and presence of rocks. Previous studies indicate dietary differences between *A. molinae* and *P. xanthopygus*. The diet of *A. molinae* includes high proportions of insects (Giannoni et al. 2005), whereas the diet of *P. xanthopygus* is primarily composed of herbs, grasses, and shrubs (Lopez-Cortes et al. 2007). Therefore, both species evidenced no spatial segregation in microhabitat, since each species relies on different diet resources which allow both of them to coexist.

*C. musculus* and *E. moreni* evidence differentiation of resource utilization. The first one selected sites with high percentage of litter, whereas the latter preferred sites with abundant herbs. Likewise, both species attest different preferences over diet items. *C. musculus* is a predominantly granivore species, while *E. moreni* is omnivorous with a strong tendency towards the insectivory particularly in the dry season (Giannoni et al. 2005; Lanzone et al. 2012). Therefore, both species evidence habitat and diet segregation.

**Table 2** Resource selection functions and odds ratios for small mammals of the Andean foothills

	Coefficient	Intercept	0.25 m	1 m	Rocks	Litter	Shrubs	Sub-shrubs	Herbs	Grass	Cacti
<i>Akodon molinae</i>											
Wet season	Estimate	-8.023	6.345	-2.730	6.532	-1.524	1.719	3.621	1.915	3.13	18.894
	SE	2.55	3.25	2.72	3.90	8.04	2.58	2.72	4.46	2.10	24.49
Alpha = 0.1	90% CI	NA	1.00	-7.20	0.10	-14.75	-2.52	-0.86	-5.43	-0.65	-21.40
			11.68	1.74	12.95	11.70	5.96	8.10	9.26	6.25	59.19
Dry season	Odds ratio		6.56	-2.69	6.75	-1.5	1.73	3.69	1.93	2.83	20.79
	Estimate	-1.82	14.95	0.66	-3.83	3.70	-14.98	-23.73	-20.26	-7.33	21.51
Alpha = 0.1	90% CI	1.71	6.06	4.27	3.87	6.10	6.89	8.19	9.67	4.94	26.77
			4.98	-6.37	4.98	-6.33	-26.32	-37.21	-36.17	-15.47	-22.53
	Odds ratio		24.93	7.70	2.54	13.75	-3.63	-10.25	-4.35	0.81	65.55
			16.13	0.67	-3.76	3.78	-13.91	-21.12	-18.34	-7.07	24.00
<i>Calomys musculus</i>											
Wet season	Estimate	-3.75	2.19	1.95	2.96	6.77	-2.08	-1.54	-4.19	2.67	23.41
	SE	1.06	2.21	2.53	2.28	3.35	2.43	2.73	5.05	1.95	19.64
Alpha = 0.1	90% CI		-1.43	-2.20	-0.80	1.25	-6.09	-6.04	-12.50	-0.54	-8.89
			5.83	6.12	6.73	12.30	1.92	2.95	4.12	5.89	55.72
Dry season	Odds ratio		2.22	1.98	3.0	7.01	-2.06	-1.53	-4.10	2.71	26.38
	Estimate	-2.50	0.55	2.06	1.56	0.98	0.67	0.78	-0.34	1.22	-10.82
Alpha = 0.1	90% CI	1.48	2.677	2.48	2.51	5.01	2.08	1.94	3.15	2.44	19.83
			-3.85	-2.02	-2.56	-7.26	-2.74	-2.41	-5.52	-2.78	-43.44
	Odds ratio		4.95	6.15	5.69	9.23	4.10	3.98	4.83	5.24	21.80
			0.55	2.08	1.57	0.98	0.68	0.79	-0.34	1.23	-10.25
<i>Eligmodontia moreni</i>											
Wet season	Estimate	-0.913	-1.44	-0.82	-0.41	2.08	2.96	2.76	8.38	3.53	3.09
	SE	0.61	2.24	1.91	1.65	2.87	2.37	2.35	4.11	2.40	18.52
0.1	90% CI		-5.14	-3.97	-3.13	-2.64	-0.94	-1.10	1.60	-0.41	-27.38
			2.25	2.33	2.30	6.80	6.64	6.64	15.15	7.48	33.56
Dry season	Odds ratio		-1.43	-0.82	-0.41	2.10	3.00	2.80	8.74	3.60	3.14
	Estimate	4.26	-5.57	0.65	-3.43	-0.06	2.59	-0.89	3.36	-1.54	-30.66
Alpha = 0.1	90% CI	1.59	2.89	2.60	2.63	5.44	2.31	2.11	3.44	2.57	17.57
			-10.33	-3.63	-7.77	-9.02	-1.20	-4.35	-2.29	-5.77	-59.57
	Odds ratio		-0.82	4.94	0.89	8.89	6.40	2.57	9.01	2.69	-1.75
			-5.42	0.66	3.38	-0.06	2.63	-0.88	3.41	-1.53	-26.40
<i>Phyllotys xanthopygus</i>											
Wet season	Estimate	-7.53	8.69	0.03	7.79	-0.47	-2.50	-1.16	-13.11	-2.70	31.74
	SE	2.39	4.32	2.91	3.41	5.69	3.95	3.71	9.57	3.76	22.23
Alpha = 0.1	90% CI		1.57	-4.76	2.17	-9.85	-9.00	-7.27	-28.85	-8.90	-4.83
			15.80	4.82	13.42	8.89	4.00	4.94	2.62	3.49	68.32
Dry season	Odds ratio		9.07	0.03	8.11	-0.47	-2.47	-1.15	-12.29	-2.66	37.36
	Estimate	-6.49	6.23	3.05	3.03	3.36	-2.67	-0.20	-13.31	0.53	23.88
Alpha = 0.1	90% CI	2.99	5.13	4.47	5.46	9.20	5.09	3.35	13.05	4.37	27.71
			-2.20	-4.29	-5.94	-11.76	-11.05	-5.72	-34.77	-6.65	-21.69
	Odds ratio		14.67	10.40	12.02	18.50	5.69	5.31	8.14	7.72	69.46
			6.43	3.10	3.09	3.43	-2.64	-0.20	-12.47	0.54	26.97

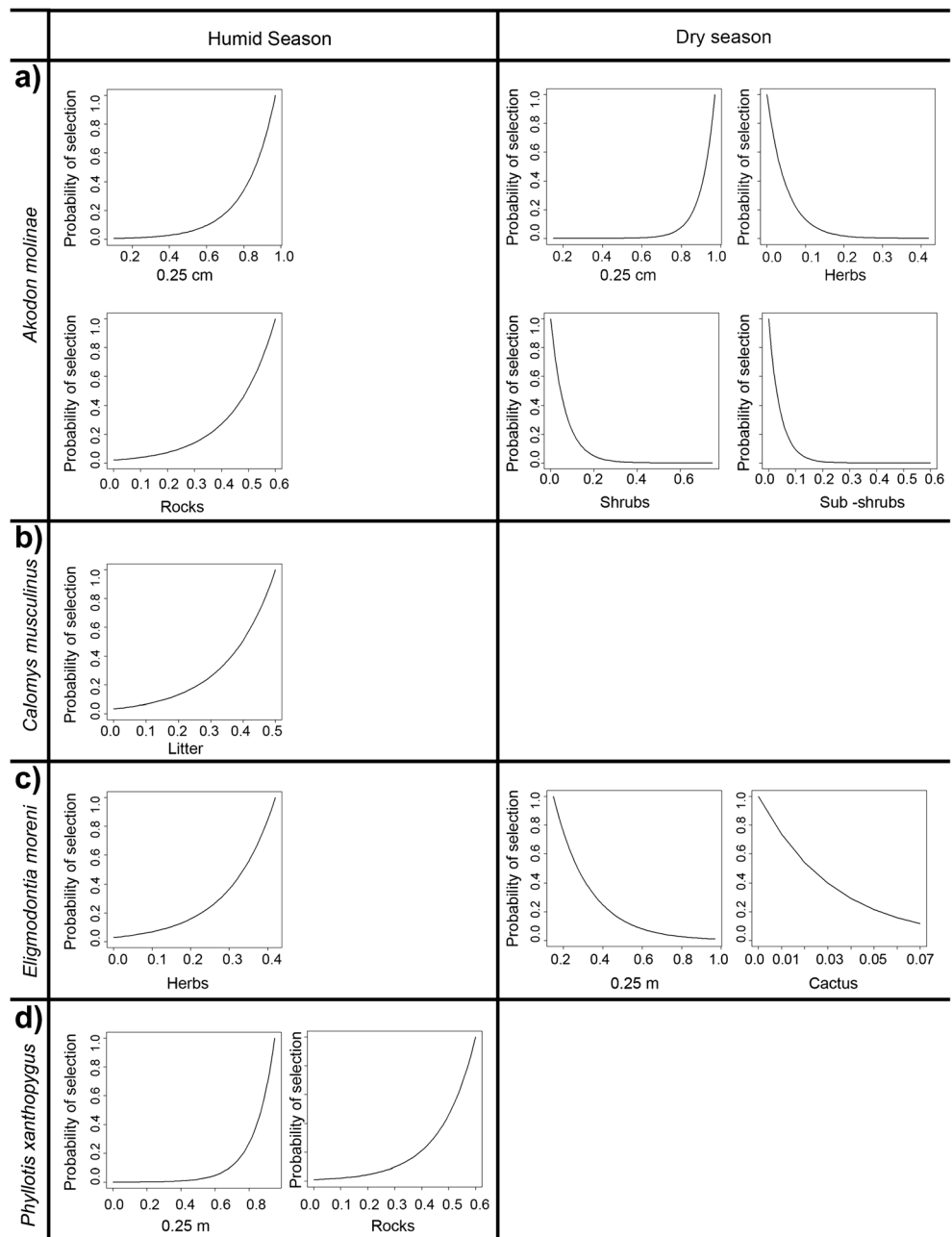
Model-averaged parameter estimates, 90% confidence intervals (CI), and odds ratios for predictor variables at microhabitat scale, for each rodent species. If 90% confidence interval (CI) does not cover 0.0, then the estimate is statistically significant at an alpha level of 0.1 (in italics)

During dry season, only *A. molinae* and *E. moreni* evidenced resource selection without overlap in their preferences at microhabitat scale. *A. molinae* avoided sites with herbs, shrubs, and sub-shrubs, whereas it selected sites with 0.25 m cover. On the other hand, *E. moreni* avoided sites with high proportion of 0.25 m vegetation cover and cactus. These two rodent species evidence a differential use of microhabitat characteristics that probably enhance their coexistence during scarcity of resources (dry season) in the Andean foothills.

Previous reports of *A. molinae* in the central Monte stated that this species evidences a strong preference for habitats with dense vegetation and high plant cover (Ojeda 1989; Corbalán and Ojeda 2004; Tabeni et al. 2007; Ojeda et al. 2011). Likewise, it was the first species to disappear from the population on sites that were burned, and it remained at low abundance levels during vegetation recovery (Ojeda 1989). *A. molinae* showed a contrasting habitat selection pattern in the Andean foothills, avoiding high vegetation cover sites and evidencing a strong negative association with shrubs and sub-shrub cover.



**Fig. 2** Marginal plots showing probability of selection for habitat predictors of each rodent species, during wet and dry season. **a** *Akodon molinae*. **b** *Calomys musculus*. **c** *Eligmodontia moreni*. **d** *Phyllotis xanthopygus*. In each plot, all other variables were held constant at their respective median



Our study evidenced habitat selection for all four species at a microhabitat scale; this is a plausible explanation why there was no signal of segregation at macroscale between most of the species. These results were also found for medium-sized mammalian herbivores, which coexist at landscape scale by partitioning their ecological niches at microscale level (Barrio and Hik 2013).

Our results at macro- and microhabitat seem to be opposed; there was few selection at macroscale while strong selection was registered at microscale. Microscale selection may evidence how sensitive the small mammal

assemblages of the Andean foothills are to environmental or vegetation changes.

**Acknowledgements** We are grateful to Ryan Nielson, Nataila Schroeder, Veronica Chillo, and Daniela Rodriguez for their help in the field and with the statistical analysis. This study is partially funded by PIP's CONICET 6179 and 5944 and Agencia—SECYT PICT 11768 and PICT 25778.

## References

- Albanese MS, Ojeda RA (2012) Habitat use by a Neotropical desert marsupial (*Thylamys pallidior*): a multi-scale approach. *Mamm Biol* 77:237–243
- Barrio IC, Hik DS (2013) Good neighbours? Determinants of aggregation and segregation among Alpine herbivores. *Ecoscience* 20:276–282
- Bos DG, Carthew SM, Lorimer MF (2002) Habitat selection by the small dasyurid *Ningau yvonneae* (Marsupialia: Dasyuridae) in South Australia. *Austral Ecol* 27:103–109
- Broomhall LS, Mills MGL, du Toit JT (2004) Home range and habitat use by cheetahs (*Acinonyx jubatus*) in the Kruger National Park. *J Zool* 261:119–128. doi:10.1017/S0952836903004059
- Campos CM, Giannoni SM, Borghi CE (2001) Changes in Monte Desert plant communities induced by a subterranean mammal. *J Arid Environ* 47:339–345
- Chesson P (2000) Mechanisms of maintenance of species diversity. *Annu Rev Ecol Syst* 31:343–366
- Claver S, Roig-Juñent SA (2001) El desierto del Monte: La Reserva de Biosfera de Ñacuñán. IADIZA - MAB - UNESCO. Mendoza
- Corbalán V (2006) Microhabitat selection by murid rodents in the Monte desert of Argentina. *J Arid Environ* 65:102–110
- Corbalán V, Debandi G (2009) Evaluating microhabitat selection by *Calomys musculus* (Rodentia: Cricetidae) in western Argentina using luminous powders. *Mastozool neotrop* 16:205–210
- Corbalán VM, Ojeda RA (2004) Spatial and temporal organisation of small mammal communities in the Monte Desert, Argentina. *Mammalia* 68:5–14
- Corbalán VM, Tabeni S, Ojeda RA (2006) Assessment of habitat quality for small mammal species of the Monte Desert, Argentina. *Mamm Biol* 71:227–237
- Cramer MJ, Willig MR (2002) Habitat heterogeneity, habitat associations, and rodent species diversity in a sand shinnery oak landscape. *J Mammal* 83:743–753
- De Boer WF, Prins HHT (1990) Large herbivores that strive mightily but eat and drink as friends. *Oecologia* 82:264–274
- Giannoni SM, Borghi CE, Dacar M, Campos CM (2005) Main food categories in diets of sigmodontine rodents in the Monte (Argentina). *Mastozool Neotrop* 12:181–187
- Gonnet JM, Ojeda RA (1998) Habitat use by small mammals in arid Andean foothills of Monte desert of Mendoza, Argentina. *J Arid Environ* 38:349–357
- Jaksic FM, Yáñez JL, Fuentes ER (1981) Assessing a small mammal community in Central Chile. *J Mammal* 62:391–396
- Kotler BP (1984) Risk of predation and the structure of desert rodent communities. *Ecology* 65:689–701
- Kramer KM, Monjeau JA, Birney EC, Sikes RS (1999) *Phyllotis xanthopygus*. *Mamm Species* 617:1–7. doi:10.2307/3504375
- Labraga JC, Villalba R (2009) Climate in the Monte Desert: past trends, present conditions, and future projections. *J. Arid Environ* 73:154–163
- Lanzone C, Chillo MV, Rodríguez MD, Dacar MA, Campos CM (2012) Dry season diet composition of *Eligmodontia moreni* (Rodentia, Cricetidae, Sigmodontinae) in a hyper-arid region of the Monte desert (Mendoza, Argentina). *Multequina* 21:25–30
- Liu X, Toxopeus AG, Skidmore AK, Shao X, Dang G et al (2005) Giant panda habitat selection in Foping nature reserve, China. *J Wildl Manag* 69:1623–1632
- Lopez-Cortes F, Cortes A, Miranda E, Rau JR (2007) Dietas de *Abrothrix andinus*, *Phyllotis xanthopygus* (Rodentia) y *Lepus europaeus* (Lagomorpha) en un ambiente altoandino de Chile. *Rev Chil Hist Nat* 80:3–12
- Lozada M, Guthmann N, Baccala N (2000) Microhabitat selection of five sigmodontine rodents in a forest-steppe transition zone in northwestern Patagonia. *Stud Neotrop Fauna Environ* 35:85–90
- Manly B (1974) A model for certain types of selection experiments. *Biometrics* 30:281–294
- Manly BFJ (2007) Randomization, bootstrap and monte carlo methods in biology. 3rd ed. Chapman and Hall, Florida, USA
- Manly B, McDonald L, Thomas D (1993) Resource selection by animals: statistical design and analysis for field studies. Chapman and Hall, New York
- Manly B, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2002) Resource selection by animals: statistical design and analysis for field studies. Kluwer Academic Publishers, Netherlands
- Martinez Carretero E, Mendez E (1992) La vegetación de la vertiente oriental de la Cordillera Real, Mendoza, Argentina. *Multequina* 1: 99–106
- Méndez E (2011) La vegetación de los altos Andes: El flanco oriental del Cordon del Portillo (Tunuyán, Mendoza, Argentina). *Bol Soc Arg Bot* 46:317–353
- Monjeau JA, Sikes RS, Birney EC, Guthmann N, Phillips CJ (1997) Small mammal community composition within the major landscape divisions of Patagonia, southern Argentina. *Mastozool neotrop* 4:113–127
- Morris DW (1987) Ecological scale and habitat use. *Ecology* 68:362–369
- Morrison ML, Marcot BG, Mannan RW (2006) Wildlife habitat relationships: concepts and applications, 3rd edn. Island Press, Washington, DC
- Neu CW, Randall Byers C, Peek JM (1974) A technique for analysis of utilization – availability data. *J Wildl Manag* 38:541–545
- Novillo A, Ojeda RA (2014) Elevation patterns in rodent diversity in the dry Andes: disentangling the role of environmental factors. *J Mammal* 95:99–107
- Ojeda RA (1989) Small mammal responses to fire in the Monte Desert, Argentina. *J Mammal* 70:416–420
- Ojeda RA, Blendinger PG, Brandl R (2000) Mammals in south American drylands: faunal similarity and trophic structure. *Glob Ecol Biogeogr* 9:115–123
- Ojeda RA, Tabeni S, Corbalán V (2011) Mammals of the Monte Desert: from regional to local assemblages. *J Mammal* 92:1236–1244
- Ostfeld RS, Keesing F (2000) Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends Ecol Evol* 15:232–237
- Price MV (1978) The role of microhabitat in structuring desert rodent communities. *Ecology* 59:910–921
- Rodríguez D, Ojeda RA (2011) Patterns of diversity of the Monte Desert small mammals across multiple spatial scales. *J Arid Environ* 75: 424–431
- Rodríguez D, Lanzone C, Chillo V, Cuello P, Albanese S, Ojeda AA, Ojeda RA (2012) Historia natural de un roedor raro del desierto argentino, *Salinomys delicatus* (Cricetidae, Sigmodontinae). *Rev Chil Hist Nat* 85:13–27
- Roig F (1976) Las comunidades vegetales del piedemonte de la precordillera de Mendoza. *Ecosur* 3:1–45
- Roig, FA (1989) Ensayo de detección y control de la desertificación en el W de la ciudad de Mendoza desde el punto de vista de la vegetación. Detección y Control de la Desertificación. UNEP- IADIZA: 196–232
- Rosenzweig ML (1973) Habitat selection experiments with a pair of coexisting heteromyid rodent species. *Ecology* 54:111–117
- Rosenzweig ML, Winakur J (1969) Population ecology of desert rodent communities: habitats and environmental complexity. *Ecology* 50: 558–572
- Schoener TW (1974) Resource partitioning in ecological communities. *Science* 185:17–39
- Shenbrot GI (1992) Spatial structure and niche patterns of a rodent community in the south Bukhara desert (middle Asia). *Ecography* 15:347–357
- Simonetti JA (1989) Microhabitat use by mammals in central Chile. *Oikos* 56:309–318
- Simonetti JA, Fuentes ER, Otaiza RD (1985) Habitat use by two rodent species in the high Andes of central Chile. *Mammalia* 49:19–25
- Stevens RD, Tello JS (2009) Micro- and macrohabitat associations in Mojave Desert rodent communities. *J of Mammal* 90:388–403

- Tabeni S, Ojeda RA (2005) Ecology of the Monte Desert small mammals in disturbed and undisturbed habitats. *J Arid Environ* 63:244–255
- Tabeni S, Mastrantonio L, Ojeda RA (2007) Linking small desert mammal distribution to habitat structure in a protected and grazed landscape of the Monte, Argentina. *Acta Oecol* 31:259–269
- Taraborelli P, Corbalan V, Giannoni S (2003) Locomotion and scape modes in rodents of the Monte Desert (Argentina). *Ethology* 109:475–485
- Traba J, Acebes P, Campos VE, Giannoni SM (2010) Habitat selection by two sympatric rodent species in the Monte desert, Argentina. First data for *Eligmodontia moreni* and *Octomys mimax*. *J Arid Environ* 74:179–185
- Traba J, Casals P, Broto F, Camprodon J, Giralt D et al (2016) Coexistence and habitat partitioning at micro- and macro-scales of rodent species in a north African desert (Bou-Hedma National Park, Tunisia). *J Arid Environ* 131:46–58
- Whittaker RJ, Willis KJ, Field R (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *J Biogeogr* 2:453–470
- Wiens JA (1977) On competition and variable environments. *J Am Sci* 65:590–597