



## Habitat selection by two sympatric rodent species in the Monte desert, Argentina. First data for *Eligmodontia moreni* and *Octomys mimax*

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### ABSTRACT

Habitat selection in deserts is mainly modulated by the availability of resources. The basic hypotheses regarding coexistence of species in arid environments offer two possibilities: 1) coexisting species partition available resources (each species acting as a specialist) and 2) generalists coexist with specialists because the former use habitats which are underused or not selected by the latter. This study presents the first data on macro- and microhabitat selection by *Eligmodontia moreni* (Cricetidae) and *Octomys mimax* (Octodontidae), two rodent species which coexist in the most arid part of the Monte desert of Argentina. In order to evaluate both hypotheses, animals were trapped during two seasons (humid and dry) in six macrohabitats of the arid Monte (creosote bush scrub, mesquite woodlands, columnar cactus slopes, barrens, chical and saltbush). A multivariate analysis of variance was used to evaluate differences in PCA components of microhabitat (floristic composition and vegetation structure) among capture and control points. The resulting models suggest *E. moreni* to be described as a fine-grained generalist species, which would be segregated from the specialist *O. mimax* in shared macrohabitats by resource partitioning, basically related to substrate type and vegetation cover. Our findings accord with theories of community assembly involving generalist and specialist species.

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### 1. Introduction

In arid environments, the scarcity and clumped distribution of resources has favoured the emergence of two exploitation strategies by rodents. There are generalist species, whose niches overlap widely, whether trophically or structurally, facilitating the processes of competition (Abramsky et al., 2001). There are also specialists, with restricted niches as an outcome of resource partitioning, so that the community is structured not only on diet (Kotler and Brown, 1988) but also on use of space and habitat (Kotler and Brown, 1988; Brown, 1996). Specialist species, which may frequently have similar ecological requirements, may coexist due to differences in behaviour (Abramsky et al., 2001), morphology (see review in Kotler and Brown, 1988) and/or diet (Campos et al., 2001), which translate into differential use of trophic (Behmer and Joern, 2008) and/or spatial resources on different levels of scale (Kotler and Brown, 1988; Brown, 1996; Morris, 1996).

In the case of sympatric rodent species, which tend to differ little in their trophic requirements (Brown, 1989), the determinants of coexistence may be adequately described on the basis of habitat selection patterns on different scales (Rosenzweig, 1981; Morris, 1987; Abramsky et al., 2001; Morris, 2003). Habitat selection is taken to be the active process by which a species chooses between distinct available resources (Johnson, 1980). It is a multiscale process, ranging at least from the level of the macrohabitat: taken here to be the area in which organisms carry out their biological functions (Morris, 1987) though frequently associated with plant community (Coppeto et al., 2006), to that of the microhabitat, a term which refers to the structural and floristic characteristics of those locations actually perceived and finally chosen by an organism (Morales et al., 2008) which affect its behaviour (Morris, 1987). An additional problem involves defining the scales of analysis that allow species which use habitat patches (specialists) to be distinguished from those which do not show a habitat selection pattern on the same scale (generalists) (Coppeto et al., 2006; Morris, 1996). In the particular case of desert rodents, several attempts to link macro and microhabitat selection patterns have been made, although there is disagreement whether the principal factor directing habitat

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selection is the macrohabitat (see for instance Morris, 1987; 1996; Jorgensen and Demarais, 1999; Coppeto et al., 2006) or the microhabitat (Jorgensen and Demarais, 1999; Bowman et al., 2001). In summary, a generalist species, with a fine-grained pattern of macrohabitat selection, could potentially show a greater realized niche at the microhabitat scale. On the other hand, a specialist species showing a coarse-grained macrohabitat selection pattern, would exhibit more restricted preferences on the microhabitat scale.

The majority of studies into habitat selection in arid-zone rodents have been centered on North American deserts, with few dealing with South American species. In the specific instance of South American Cricetidae (cricetid rodents), the few existing studies on describe their habitat selection as more dependent, given their omnivorous character, on structural aspects of the plant cover than their North American congeners (see review in Kotler and Brown, 1988). On the macrohabitat scale, the fundamental factors which explain the abundance, spatial distribution and make-up of the micromammal community have been described, highlighting the importance of vegetation and substrate type (Kravetz and Polop, 1983; Mills et al., 1992; Busch et al., 1997; Ellis et al., 1997; Gonnet and Ojeda, 1998; Corbalán and Ojeda, 2004; Tabeni and Ojeda, 2005; but see Corbalán, 2006). On the microhabitat scale, the existing works have identified the importance of vegetation cover over other variables, rodent feeding activity occurring under plant cover (Taraborelli et al., 2003), where predation risk is reduced (Taraborelli et al., 2003; Corbalán and Ojeda, 2004).

Furthermore, most of this information refers to a few relatively well-studied species (*Graomys griseoflavus*, *Calomys musculus*, *Akodon molinae*), whereas there remain many species for which there is little information on their use of space and habitat selection. With respect to another important family of South American rodents, the Octodontidae (octodont rodents), studies of habitat selection are limited to a single species, *Tympanoctomys barrerae* (Ojeda et al., 1996), whose high degree of trophic specialisation (Giannoni et al., 2000) impedes comparison with closely-related species (Ojeda et al., 1999). Finally, most studies of South American arid-zone rodents have been carried out in the central Monte, where mean annual precipitation is about 325 mm (Ojeda et al., 1998), and practically none of them in the most extremely arid zones, where annual precipitation is below 100 mm.

The present study aims to analyse macro- and microhabitat selection by two hitherto unstudied species, *Eligmodontia moreni* (Cricetidae) and *Octomys mimax* (Octodontidae), in different habitats within the Argentinean arid Monte. In doing so, this study addresses the hypotheses that i) these two coexisting species demonstrate resource partitioning, both acting as generalists or ii) one of them may be a generalist and could coexist with a specialist by exploiting habitats underused or not exploited by the latter. In any event, given the scarce and clumped availability of resources in desert environments, high levels of overlap in trophic and/or structural factors might be expected, relative to classic scenarios of resource partitioning. The resulting selection is also discussed in terms of niche breadth and overlap, these being factors implicated in the coexistence of both rodents.

## 2. Methods

### 2.1. Study area

The study was carried out in Ischigualasto Provincial Park (60 369 ha), 350 km North-East of San Juan, Argentina (29°55' S,

68°05' W), bordering La Rioja province. Most of the park belong to the Monte phytogeographical province and, although plant communities assignable to a range of provinces are present, all are governed by an arid climatic regime. Temperatures range from  $-10^{\circ}\text{C}$  to  $45^{\circ}\text{C}$ , with an annual mean below  $18^{\circ}\text{C}$ . Mean annual precipitation is 80–100 mm, concentrated in spring (November to March) (P. Acebes, unpublished data). Hard substrates predominate, fundamentally Triassic sandstones of variable salt content, dissected by abrupt valleys which drain water during rainy periods. There are also fine-textured substrates (sands, muds and clays) in which the vegetation is drawn to areas where water accumulates after rainfall. Quaternary sediments comprising highly compacted pebbly cover also occur. The landscape is dominated by steppes of shrubby perennials of the family Zygophyllaceae, which are the typical components of the 'jarillal' scrub which extends from the foothills to the flood plain (Márquez et al., 2005; P. Acebes, unpublished data).

### 2.2. Study species

We studied habitat selection in one species of Octodontidae (Vizcacha Rat *O. mimax*; weight:  $120.0 \pm 2.0$  g, Ebensperger et al., 2008) and two species of Cricetidae (silky mouse or Monte gerbil mouse *E. moreni* (weight:  $17.6 \pm 3.3$  g, Lanzone et al., 2007) and gray leaf-eared mouse *G. griseoflavus*), although eventually only the first two were captured in sufficient numbers. Several individuals of a marsupial, *Thylamys pusillus*, were also captured but not enough to include them in the analyses. These are all sympatric species of the central arid Monte and all are nocturnal and omnivorous, with a tendency towards herbivory (Campos et al., 2001). *E. moreni* has elongated hind legs and may hop at times: it is typically distributed in the northern and central Monte (Lanzone and Ojeda, 2005), where it is sympatric with *O. mimax*. This caviomorph shares many adaptive traits with North American desert heteromyids (Mares, 1975) and is listed as Vulnerable in the Red Book of the Mammals of Argentina (Díaz and Ojeda, 2000).

### 2.3. Small mammal captures

Trapping took place in six macrohabitats corresponding with typical plant communities of the Park. Three, the barrens, salt-bush and mesquite woodland, are on fine substrates ranging from clay to sandy. The other three, the creosote bush scrub, columnar cactus slopes and chical, are on progressively firmer and aggregated substrates (P. Acebes, unpublished data). Mesquite woodland is the most heterogeneous macrohabitat and has the greatest plant cover whereas the barrens are the most homogeneous and structurally simplest, given their almost total lack of vegetation. The columnar cactus slopes, creosote bush scrub and chical are characterised by large expanses of rock and by their high variability of plant cover of different heights. Both the saltbush and mesquite woodland have large areas of bare ground (P. Acebes, unpublished data).

Sherman live-capture traps were set up in the six macrohabitats during both the humid season (March–April) and the dry season (August–September) in 2005, on a  $10 \times 6$  grid with 30 m spacing between traps, except in the chical, where we nearly duplicated the grid in order to accommodate it to other experiments (Table 1). The same number of traps was arranged parallel to the drainage line in the mesquite woodland, given the linear character of this macrohabitat. Traps were baited each evening with a mixture of oats and tuna and were visited

**Table 1**  
Sampling intensity (number of trapping nights) at each macrohabitat.

	Wet season	Dry season
Barrens	236	240
Saltbush	223	224
Mesquite woodlands	218	224
Columnar cactus slopes	237	236
Chical	232	428
Creosote bush scrub	208	208
Total	1354	1560

each morning at about 08.00 h. Traps remained in each habitat for four nights resulting in a total of 2918 effective trap/nights, due to the unavailability of some of the initially disposed (Table 1). The most widely separated traps were 10 km apart. Plant communities and microhabitat structure were quantified at all trap-sites with captures and at a variable number (minimum 16, maximum 22) of control points in each habitat, which were randomly selected from the subset of trap-sites with no capture during the sampling period. At each point we established 13  $2 \times 2$  m plots along two perpendicular lines, the first at their intersection and the others two meters apart, giving a total sampling area of 52 m<sup>2</sup> per point, which is sufficient to assess microhabitat (for a review about sampling area, see Jorgensen, 2004). Vegetation cover at 0.5 m, 1 m and canopy height was estimated at each point as well as cover of rock, bare ground and litter. Each variable was estimated independently of the others, such that their sum could exceed 100%, avoiding the so-called unit sum constraint problem, *sensu* Aebischer et al. (1993). We also estimated the cover of each of the plant species present. The mean and coefficient of variation of the 13 plots per sampling point were used for the statistical analyses. This design allows differences in structural and floristic variables between trapping points and control points to be analysed, such that comparisons within a particular habitat allow the microhabitat selection pattern of each species to be determined. Variation in selection patterns of each species between habitats established the breadth of their microhabitat selection and between-species comparisons determined inter-specific overlap.

#### 2.4. Data analysis

Levin's Index (B) (Krebs, 1998) was used to estimate niche breadth of both species on the macrohabitat scale. It is calculated as  $B = 1/\sum p_j^2$ , where  $p_j$  = proportion of individuals using habitat  $j$ . This index is the reciprocal of the Simpson diversity index, so that  $B$  is a maximum when the same number of individuals is found in each habitat type (showing that a species is not discriminating between habitats) and a minimum when all individuals are found in only one habitat type (Krebs, 1998). The index varies from 1 to  $n$ , where  $n$  is the maximum number of habitat types, so that a standardised index ( $B_A$ ) (Krebs, 1998) is calculated, which ranges between 0 and 1:  $B_A = (B - 1)/(n - 1)$ . Niche overlap on the macrohabitat scale was estimated by means of a percentage overlap index,  $P_{jk}$ , which refers to the percentage coincidence in resource utilisation (Krebs, 1998):  $P_{jk} = [\sum(\text{minimum } p_{ij}, p_{ik})] \times 100$ , where  $p_{ij}$  = the proportion of resource  $i$  used by species  $j$  and  $p_{ik}$  = the proportion of resource  $i$  used by species  $k$ . Percent of available traps with captures, i.e. capture index, was also calculated for each macrohabitat. A homogeneity  $\chi^2$  test was used to evaluate differences in capture numbers from random at the macrohabitat scale.

Variables of microhabitat structure were summarised by means of Principal Components Analysis (PCA) on the correlation matrix which permits independent components of maximum explanatory capacity to be obtained, avoiding colinearity problems detected among the original variables in an initial exploratory analysis. The use of PCA components places rodents locations within ecologically meaningful gradients beyond macrohabitats, closer to the effective niche concept, and provides information about habitat selection at small spatial scales. This analytical approach is particularly useful to segregate between generalist and specialist species at microhabitat scale, (for a similar approach, see for instance Morris, 1996; Morales et al., 2008). We included both mean and coefficients of variance in the PCA in order to consider not only the central tendency but also the heterogeneity of the variables, the last being relevant in arid ecosystems. Unrotated components with eigenvalues higher than 1 were selected for further analysis.

Differences in microhabitat structure between control and capture points for the two species were tested by means of a multivariate analysis of variance (MANOVA) of the first three components of the PCA. Macrohabitat and season were included as fixed factors, the null hypothesis being that mean values of the component scores for different levels did not differ (season having two levels: humid and dry and macrohabitat having six levels: barrens, saltbush, mesquite woods, creosote bush, chical and columnar cactus slopes). 'Season' was subsequently eliminated since it showed no significant differences in the entire model. In addition, model without 'season' showed the best fit according to Adjusted  $r^2$ , the Akaike Information Criterion (AIC) and the Schwarz Bayesian Information Criterion (BIC) combined (Quinn and Keough, 2002). 'Capture' was included as a random factor (with three levels: control, capture of *E. moreni* and capture of *O. mimax*), nested in macrohabitat, under the premise that there is no variation for the capture factor among the different levels of the macrohabitat factor (Quinn and Keough, 2002).

Variation in floristic selection was analysed by searching for differences in plant cover among the six macrohabitats and among trapping points of each species versus control points using MANOVA. The Fisher LSD test was used to compare pairs of means *a posteriori*, both for the structural and the floristic analyses.

All analyses employed Statistica 6.0 (Statsoft, Inc., 2002). However, degrees of freedom and  $F$ -ratios were calculated manually (Quinn and Keough, 2002) given the lack of a square design, since both species were not captured at all locations and neither was captured in the creosote bush scrub.

### 3. Results

#### 3.1. Small mammal captures and macrohabitat selection

In total, 41 individuals were captured across the two seasons. They comprised 17 *E. moreni*, 15 *O. mimax*, 6 *G. griseoflavus* and 3 *T. pusillus*. The microhabitat analysis used all the *E. moreni* captures and 10 of the *O. mimax* captures for which complete data were available. Table 2 shows the capture indices (as percentages relative to trapping effort) for the four species in the six habitats considered. The habitats with most captures were the chical and the columnar cactus slopes. The highest capture index (2.1%) was obtained in the columnar cactus slopes in the dry season. No animals at all were captured in the creosote bush scrub.

Levin's standardised index for estimating niche breadth gave higher mean values for *E. moreni* (0.48) than for *O. mimax* (0.25).

**Table 2**

Capture indices (percentages relative to sampling intensity) for the four species, and number of control points where microhabitat was sampled, in the six macrohabitats considered.

	<i>Eligmodontia moreni</i>	<i>Octomys mimax</i>	Number of control points
Barrens	0.83	0.21	17
Saltbush	1.57	0.00	16
Mesquite woodlands	0.45	0.00	17
Columnar cactus slopes	0.00	1.69	16
Chical	0.61	0.91	22
Creosote bush scrub	0.00	0.00	20
Total	0.58	0.51	108

Niche overlap between the two species at the macrohabitat scale was low (30%), slightly lower in the humid season (31%) than in the dry season (38%).

The capture distribution for *E. moreni* in the various macrohabitats did not diverge from chance during both seasons (humid season:  $\chi^2 = 7.67$ ;  $p = 0.175$ ; dry season:  $\chi^2 = 8.50$ ;  $p = 0.131$ ). For *O. mimax*, capture distribution on the macrohabitat scale was also random during the humid season ( $\chi^2 = 8.20$ ;  $p = 0.146$ ) but significantly different from chance during the dry season ( $\chi^2 = 20.0$ ;  $p < 0.01$ ).

**3.2. Microhabitat selection**

The first three axes of the PCA performed on structural variables accounted for 81.3% of the common variance (Table 3). The first component (32.1% of the variance) was related positively to area of bare ground and negatively to area of rock and to heterogeneity (coefficient of variation) in the surface of bare ground, indicating a gradient of substrate type. The second component (28.2%) was associated with a gradient of increasing plant cover, whereas the third component, which was only slightly less explicative (20.9%), was associated with a gradient of heterogeneity of plant cover (Table 3).

The MANOVA performed on the first three PCA components showed significant differences in microhabitat characteristics among macrohabitats (nested MANOVA,  $F_{5,7} = 7.21$ ;  $p < 0.05$ ) and for the factor capture nested in macrohabitat ( $F_{7,122} = 2.35$ ;  $p < 0.05$ ; Adjusted  $r^2 = 0.573$ ), this explaining differences between habitat use and availability. Interaction between factors is not evaluable due to nesting.

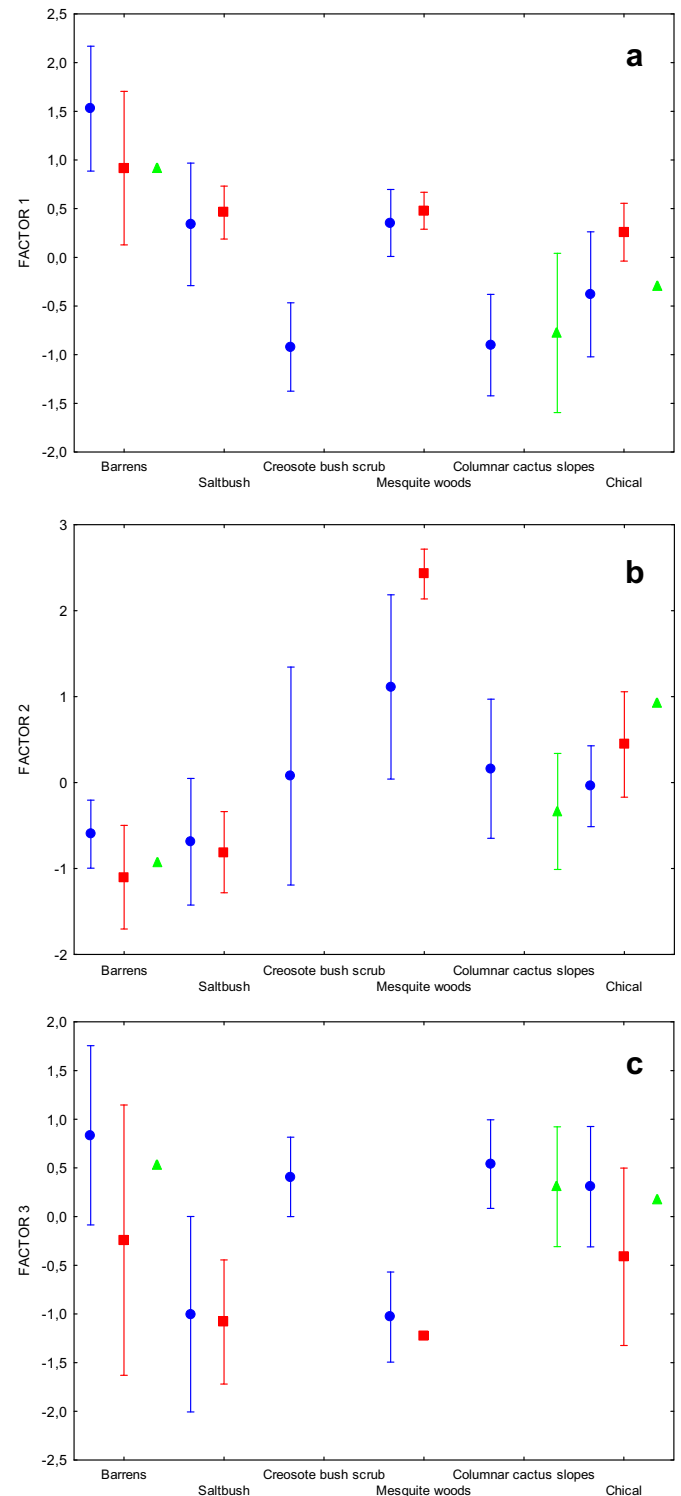
The Fisher LSD tests performed subsequently on the three levels of the capture factor (control, capture of *E. moreni*, capture

**Table 3**

Results of the principal component analyses carried out to synthesise the variation in environmental and structural characteristics at the sampling points. Asterisks indicate the highest component scores.

	Component 1	Component 2	Component 3
Canopy (Mean)	-0.27	0.90*	-0.16
Canopy (CV)	-0.54	-0.41	-0.65*
Vegetation at 1 m (Mean)	-0.40	0.86*	-0.06
Vegetation at 1 m (CV)	-0.56	-0.40	-0.69*
Vegetation at 0.5 m (Mean)	-0.43	0.80*	-0.07
Vegetation at 0.5 m (CV)	-0.50	-0.35	-0.68*
Rock cover (Mean)	-0.77*	-0.13	0.56
Rock cover (CV)	0.54	0.29	-0.51
Bare ground (Mean)	0.84*	0.01	-0.44
Bare ground (CV)	-0.80*	-0.10	0.38
Leaf litter cover (Mean)	-0.11	0.79*	-0.36
Leaf litter cover (CV)	-0.58	-0.08	-0.30
Variation explained (%)	32.1	28.2	20.9

of *O. mimax*), for the three PCA components indicated that points where *E. moreni* was captured had significantly higher values for component 1 (areas with more bare ground) than control points in the chical, whereas the opposite was the case in the barrens.



**Fig. 1.** Means and confidence intervals (95%) for the three dependent variables in the MANOVA test to detect differences between sites and captures (three levels: two species and control) in the scores of the Principal Components Analysis performed on the vegetation structure variables at the six site locations. Fig. 1a–c correspond to components 1, 2 and 3. In all figures, filled circles correspond to Control samples, filled squares to *E. moreni* captures and filled triangles to *O. mimax* captures.

In the other two macrohabitats where this species was captured (mesquite woodland and saltbush), capture points did not differ significantly from controls, indicating that animals used the available substrate (Fig. 1a). Furthermore, this species showed no significant differences between macrohabitats, indicating that it did not change its habitat selection in any of the environments where it was captured (Fig. 1a). In the case of component 2, *E. moreni* selected significantly higher values (greater plant cover) than at control points in the mesquite woodland (Fig. 1b). When comparing habitat selection by this species between the four macrohabitats in which it was caught significant differences were noted in all cases except between the barrens and the saltbush (Fig. 1b). Regarding component 3, capture points for *E. moreni* showed significant differences from the control points in the chical and the barrens, where the values selected by the species were lower than those available i.e. it was caught in the more heterogeneous zones (Fig. 1c). *O. mimax* showed significant differences from the control points only for component 2 in the columnar cactus slopes, which seems to suggest that it used the available habitat (Figs. 1a–c).

The nested design did not permit possible differences between the species for the three components to be detected in any of the macrohabitats in which both were captured. A one-way ANOVA with an *a posteriori* Fisher test showed significant differences between both species for component 1 ( $p < 0.0001$ ) and component 3 ( $p < 0.001$ ).

### 3.3. Floristic composition

Sampling of the six macrohabitats found 69 species in total. Of these, 15 species belonging to seven families showed significant differences in cover under the capture factor (MANOVA with 15 species;  $F_{7,121} = 6.256$ ;  $p < 0.0001$ ). The *a posteriori* analysis allowed the detection of those species which were selected or avoided, in relation to their availability at the control points, by the two rodents studied (Appendix).

In the barrens, *E. moreni* selected points with greater cover of *Halophytum ameghinoi*. In the chical it selected points with the most cover of *Trichocereus strigosus* and *Senna aphylla*, whereas it avoided points with the highest cover of *Mimosa ephedroides*. These latter two plants, as well as *Denmoza rhodacantha*, were nevertheless positively selected by *O. mimax*. In the saltbush, where only *E. moreni* was captured, it chose points with greatest cover of *Sporobolus rigens* and *Atriplex lampa*. This latter plant was also positively selected by *E. moreni* in the mesquite woodland and was the only species chosen by a rodent in more than one macrohabitat. *Prosopis chilensis*, *Tessaria dodoneifolia* and *Aristida mendocina* stand out for their high cover values among the other species chosen by *E. moreni* in the mesquite woodland. Finally, in the columnar cactus slopes, *O. mimax* only selected *Monttea aphylla*.

## 4. Discussion

Our results are the first to describe capture rates and habitat selection for *E. moreni* and *O. mimax*. They also comprise new data for the Ischigualasto Provincial Park, one of the most arid regions of the Monte phytogeographical province. The results show low capture rates, similar to those reported from comparable zones in the arid Monte (Mares et al., 1977), although lower than those reported for other zones of the Monte and for other deserts, which probably reflects the low density of animals (Mares et al., 1977). Micromammal density in the Monte has been directly related to habitat type (Corbalán and Ojeda, 2004; Corbalán et al., 2006),

which would be due to a process of selection on the macrohabitat scale (Morris, 1987; Jorgensen and Demarais, 1999). This low animal density could be related to the low number of high quality sites for breeding (actual fitness) of the different macrohabitats (Morris, 2003).

### 4.1. Macrohabitat selection

The capture indices, which may be interpreted as selection indices since they are directly dependent on local rodent densities, as well as the niche breadth index and the analysis of the distribution of captures, have demonstrated only a certain level of selectivity on the macrohabitat scale by *O. mimax*. This species was basically captured in habitats dominated by hard substrates (sandstones), while *E. moreni* was captured in four of the six macrohabitats considered, showing less large-scale habitat specificity, as indicated by its higher niche breadth index and the analysis of capture distribution. Both patterns are consistent with the habitat preferences described for a well-studied neighbouring species, *E. typus*, to which a preference for open environments, where it demonstrates higher fitness, has been attributed (Corbalán and Ojeda, 2004; Corbalán et al., 2006), although its ecological plasticity allows it to occupy other habitats (Corbalán and Debandi, 2006; Tabeni et al., 2007). The low overlap at the macrohabitat scale shown by both species (around 30%) seems to be related to the higher selectivity shown by *O. mimax* in contrast to the more generalist character of *E. moreni*.

No captures were made in the creosote bush scrub despite this having been frequently described as the richest habitat and the one with the highest abundance of micromammals (see e.g. Corbalán et al., 2006). The creosote bush scrub in the study area was located on poorly compacted substrates lacking cavities, which could impede its colonisation by caviomorph species.

### 4.2. Microhabitat selection

Although the importance of microhabitat in defining patterns of distribution and abundance in micromammals has been questioned (Morris, 1984; 1987; 1996; Corbalán and Ojeda, 2004; Corbalán, 2006; see review in Jorgensen, 2004), our results have shown certain level of selectivity at microhabitat scale by differences between capture and control points. This hierarchical selection pattern has frequently been described for other animal groups (Schaefer and Messier, 1995), and has come to be considered as the main factor over macroscale aspects (Morales et al., 2008). In spite of the low number of captures, the results of the microhabitat comparisons seem to indicate resource partitioning between the species, at least relating to selection of substrate type, from fine material to bare rock. This may be related to the ability to excavate burrows versus the availability of rock crevices, given that *E. moreni* is principally a burrower while *O. mimax* is a saxicolous species (Mares, 1975). Indeed, the two species showed preferences for different substrates: *E. moreni* always preferred fine substrates and thus positively selected them in the chical, whereas it did not show active selection in the mesquite woodland and saltbush, where all the microhabitats seem to be optimal. These latter two habitats transpired to be optimal for the species (macrohabitat selection) since it could occupy more terrain than in the strictly sandy areas, which is where it appears in the sandstones of the chical (microhabitat selection). *O. mimax* apparently prefers more rocky environments, perhaps in order to take advantage of

fissures and crevices in the rock before burrowing (Ebensperger et al., 2008; Mares, 1975).

In relation with plant cover (explaining food and shelter availability), the response of *E. moreni* was more flexible than the *O. mimax* one, indicating a greater potential breadth of selection which adapts to the characteristics of each environment without changing the selection pattern (Coppeto et al., 2006; Tabeni et al., 2007), although low capture rates must be in mind. Moreover, floristic selection, in spite of the low sample size, may also indicate coexistence based on resource partitioning in shared environments (see Appendix). For example, *O. mimax* positively selected some species which *E. moreni* avoided, and both species showed segregated floristic selection with respect to cacti. In general, *E. moreni* showed low selectivity in plant species selection, except in the case of *A. lampa*. The selection pattern detected is novel and consistent with what has been described of the diet of a related species (*E. typus*; Campos et al., 2001), although it does not allow the trophic behaviour of the species to be predicted.

#### 4.3. Conclusions

Although our results are depending on a low number of captures, they apparently have shown the low level of overlap between both species at the macrohabitat scale, which could provide more evidence of the hypothesis of micromammal segregation by macrohabitat (Morris, 1987). Nevertheless, microscale segregation detected in habitats where the two species coexist support the idea that resource partitioning and microhabitat spatial selection are the mechanisms which drive the composition of rodent communities in arid systems (Kotler and Brown, 1988). In this sense, *E. moreni* and *O. mimax* will share resources linked to trophic availability and shelter but will segregate on the basis of features such as burrow location and heterogeneity of plant cover. In addition, the microhabitat results show *E. moreni* to have a generalist character and *O. mimax* to be more of a specialist. Previously 'inconsistencies' have been reported between the variables selected by a given species in different habitats (Corbalán, 2006), these being interpreted as showing the non-existence of microscale patterns of selection rather than indicating a greater breadth of specific response. Nonetheless, lower selectivity in any level of the variables, can indicate more flexibility in the use of resources, given that individuals carry out their selection as an immediate adaptive response rather than in fulfillment of an evolutionary constraint. In this respect, *O. mimax* would behave as a species linked to coarse-grained selection, whereas *E. moreni* would be an opportunist showing fine-grained selection (Morris, 1987; 1996).

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#### Appendix

Cover (mean ± SE) of plant species with significant differences between rodent species and control points in the MANOVA, with the capture factor nested in the macrohabitat factor and the season factor (the latter two constant). Different superscripts indicate significant differences in the  $\alpha$  posteriori Fisher LSD test among capture-control points for a shared location.

Species	Family	Chical		Barrens		Saltbush		Mesquite woods		Columnar cactus slopes	
		Control	<i>E. moreni</i>	Control	<i>E. moreni</i>	Control	<i>E. moreni</i>	Control	<i>E. moreni</i>	Control	<i>O. mimax</i>
<i>Denmoza rhodacantha</i>	Cactaceae	0.06 + 0.04 <sup>a</sup>	0.00 + 0.00 <sup>a</sup>	-	-	-	-	-	-	0.10 + 0.06	0.06 + 0.06
<i>Trichocereus strigosus</i>	Cactaceae	0.40 + 0.13 <sup>a</sup>	0.69 + 0.38 <sup>b</sup>	-	-	-	-	-	-	0.202 + 0.09	0.39 + 0.26
<i>Halophytum arnegitinoi</i>	Chenopodiaceae	-	-	0.00 + 0.00 <sup>a</sup>	0.04 + 0.02 <sup>b</sup>	-	-	-	-	-	-
<i>Atriplex lampa</i>	Chenopodiaceae	0.33 + 0.18	0.52 + 0.35	-	-	0.14 + 0.14 <sup>a</sup>	0.77 + 0.56 <sup>b</sup>	0.3 + 0.20 <sup>a</sup>	1.15 + 0.00 <sup>b</sup>	-	-
<i>Atriplex litophila</i>	Chenopodiaceae	0.23 + 0.15 <sup>a</sup>	0.29 + 0.29 <sup>a</sup>	-	-	-	-	-	-	-	-
<i>Senna apiphylla</i>	Fabaceae	0.24 + 0.14 <sup>a</sup>	2.46 + 0.93 <sup>b</sup>	-	-	0.10 + 0.10	-	-	-	0.46 + 0.32	0.63 + 0.57
<i>Mimosa ephedroides</i>	Fabaceae	0.54 + 0.20 <sup>a</sup>	0.06 + 0.06 <sup>b</sup>	-	-	-	-	0.01 + 0.00	-	0.11 + 0.08	-
<i>Prosopis chilensis</i>	Fabaceae	-	0.06 + 0.06	-	-	-	-	11.64 + 2.77 <sup>a</sup>	33.69 + 7.85 <sup>b</sup>	-	-
<i>Hoffmannseggia sp.</i>	Fabaceae	-	-	-	-	-	-	0.01 + 0.00 <sup>a</sup>	0.04 + 0.04 <sup>b</sup>	-	-
<i>Grabowskia obtusa</i>	Solanaceae	-	-	-	-	-	-	0.05 + 0.05 <sup>a</sup>	0.38 + 0.38 <sup>b</sup>	-	-
<i>Lycium ciliatum</i>	Solanaceae	-	-	-	-	-	-	0.068 + 0.04 <sup>a</sup>	0.96 + 0.96 <sup>b</sup>	-	-
<i>Monttea apiphylla</i>	Scrophulariaceae	0.56 + 0.20	-	-	-	-	-	-	-	0.14 + 0.14 <sup>a</sup>	0.82 + 0.59 <sup>b</sup>
<i>Tessaria dodoneifolia</i>	Asteraceae	-	-	-	-	-	-	0.52 + 0.35 <sup>a</sup>	2.31 + 2.31 <sup>b</sup>	-	-
<i>Sporobolus rigens</i>	Poaceae	-	-	-	-	0.00 + 0.00 <sup>a</sup>	0.10 + 0.10 <sup>b</sup>	-	-	-	-
<i>Aristida mendocina</i>	Poaceae	-	-	-	-	-	-	1.25 + 0.79 <sup>a</sup>	5.35 + 5.35 <sup>b</sup>	-	-
N		22	4	17	4	16	7	17	2	16	8

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