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Habitat selection by Calomys musculinus (Muridae, Sigmodontinae) in crop areas of the pampean region, Argentina

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Abstract. Calomys musculinus *(Muridae, Sigmodontinae) is a small rodent species found in most central and northern Argentina. It is the reservoir of the Junin virus, ethiological agent of the Argentine Hemorrhagic Fever (FHA). In the present work we studied habitat selection by* C. musculinus *at different spatial scales in rural habitats where the landscape is mainly formed by cropfields, surrounded by weedy margins (borders). We found that* C. musculinus *selects borders over cropfields, but there were not differences between types of fields or types of borders. The structure of the spatial heterogeneity, which is mainly grouped between macrohabitats due to agrarian labors, did not allow to detect habitat selection, within cropfields and borders, for habitat patches larger than individual trap sites. Distribution between fields and borders was related to the green plant cover in early autumn, probably because of specific requirements of reproductive individuals. Within these habitats, we found differences in captures according to the presence of some plant species, which varied according to the season and the habitat.*

Introduction

Agroecosystems of central Argentina consist of a matrix of cultivated fields (corn, soybean, sunflower, wheat, linen) surrounded by a network of roadsides, fencelines, railways and other border habitats that support a plant community with some remnants of native flora and many introduced weeds, that provide a more stable cover than cropfields (Bonaventura and Cagnoni 1995, Busch and Kravetz 1992 a and b, Busch et al. 1997, Ellis et al. 1997). *Calomys musculinus* (Muridae, Sigmodontinae) is found in most of central and north-western Argentina. It appears to prefer open vegetation formations and is the dominant rodent species in some parts of Argentina (Redford and Eisenberg 1992). Its ecology was mainly studied in relation to its role as reservoir of the Junín virus, ethiological agent of the Argentine Hemorrhagic Fever (AHF). Its abundance showed variation according to the area and year, contributing up to 80% of the rodent communities in areas of Cordoba (de Villafañe and Bonaventura 1987), 17.8 - 25.1 % in Northern Buenos Aires and Southern Santa Fe (Ellis et al. 1997, Mills et al. 1992), 5.8% in Pergamino (de Villafañe et al. 1992), and less than 5 % in Exaltación de la Cruz, Province of Buenos Aires (Busch et al. 1997). The absence of reports of human cases of Hemorrhagic fever in these latter areas is probably related to the low density of *C. musculinus,* since peaks of this disease were associated to high densities of its reservoir (Mills et al. 1992).

The knowledge of the conditions for the circulation of a pathogen in nature is of great importance for epidemiological survey, and geographic distribution and habitat associations of the natural reservoirs are a first step for elucidating possible relationships between ecological variables and the ocurrence of the disease (Kosoy et al. 1997). *Calomys musculinus* shows a wider habitat and trophic niche than other coexisting rodent species in rural habitats of central Argentina. It uses cropfields, their borders and natural pastures, although it shows differences in abundances accordingly to the habitat (Kravetz and Polop 1983, Mills et al. 1992, Ellis et al. 1997, Busch et al. 1997). Lower densities of this species were found in soybean with respect to corn fields (Busch et al. 1984, Mills et al. 1991), suggesting that habitat management could reduce its density and decrease the risk of AHF. However, the potential for this alternative of control is decreased by the fact that in many cases *C. musculinus* lives primarily in border habitats (Ellis et al. 1997).

According to the theory of habitat selection individuals will choose those habitats where their fitness is maximised and population distribution will be uneven in habitats with internal heterogeneity (Fretwell and Lucas 1970). One crucial issue to understand habitat selection is to identify those habitat clues that are used by individuals to select patches, and the scales of spatial heterogeneity that are perceived by them. Habitat associations reflect food and shelter requirements, or combinations between them. The assessment of these requirements needs detailed studies on habitat selection, that should take into account the spatial scale at which processes are taking place (Morris 1987, Senft et al. 1987, Orians and Witterberger 1991, Lavorel et al. 1993, Wiens et al. 1993, Schaefer and Messier 1995). There is an increasing number of studies that take into account scaling effects, most of them are theoretical, and relatively few apply these concepts to specific problems. This fact may be related to the difficulty in defining non arbitrary scales, which may take in account both habitat heterogeneity at different spatial scales as well as animal characteristics as movements and habitat requirements (Wiens et al. 1993). Macrohabitats may include suitable microhabitats for foraging, but their characteristics are not necessary or sufficiently described by the sum or the average of the characteristics of microhabitats. Selection at every scale may be a response to different factors that operates at different spatial scales (Wiens et al. 1993, Schaefer and Messier 1995).

In the agrarian systems, heterogeneity is not randomly distributed, and the greatest contrast is between cropfields and borders, decreasing between different types of borders or cropfields, between different habitat patches within cropfields or borders and between individual trap sites. Cropfields and borders differ in the levels of perturbation, which influence on plant and rodent communities. Differences in suitability between these habitats change according to the season, being greatest after plowing and sowing, when fields lack plant cover. Different crops differ in their associated weeds and in the moments when agrarian labors take place. Population dynamics of *C. musculinus* and of its congeneric *C. Laucha* are well synchronized with the summer crops, specially corn, but they show variations according to the implantation distance and with grazing history (Busch et al. 1984). The borders, weedy margins that surround the cropfields, are developed between neighbour cropfields (internal borders) and between cropfields and roads (external borders). Rodents probably move between cropfields through internal borders. Another level of heterogeneity is found within cropfields and borders, due to edaphic and topographic conditions that generate patches which can be used diferentially by the rodent species (Bonaventura et al. 1988). *Calomys musculinus* distribution between cropfields and borders was studied by Busch et al. (1984), Mills et al. (1991), Busch et al. (1997) and Ellis et al. (1997). Differences according to types of cropfields were studied by Busch et al. (1984) and Ellis et al. (1997), however, these studies were based on differences in densities between non neighbour fields, which may have been caused by different factors, as habitat selection, differential reproductive success, history, among others. The relation between the uneven distribution of rodent captures and vegetation variables were at present only studied at the patch and microsite level (Bonaventura et al. 1988, Ellis et al. 1997).

In the present work we want to study habitat selection by *C. musculinus* at different spatial scales: between cropfields and borders, among types of fields and borders, and within fields and borders for habitat patches and for individual vegetation variables. Our specific goals were:

- Identify those spatial scales at which *C. musculinus* selects habitat.
- Identify those variables that influence habitat selection by *C. musculinus* at different spatial scales.

Materials and Methods

Study area

Fieldwork was conducted between the end of July 1993 and the beginning of August 1994 at Diego

Gaynor (34°8’S, 59°14’W), Buenos Aires Province, Argentina. These area is located in the Pampean region, characterised by a temperate climate and pasture type vegetation. The dominant plant species are *Stipa neesiana, Stipa hyalina, Stipa papposa, Paspalum dilatatum, Lolium multiflorum, Lolium perenne, Bromus unioloides, Senecio sp, Solidago chilensis, Cirsium vulgare, Carduus achantoides, Cynara cardunculus, Cichorium sp, Taraxacum officinale* and *Poa annua,* among others. A more detailed description of the vegetation of the area can be found in Bonaventura and Cagnoni (1995) and Ellis et al. (1997).

We conducted four samplings corresponding to different phases of rodent population abundance: decrease (24 July - 3 August 1993, winter 1993), minimum (8 - 15 November 1993, spring 1993), increase (24 March - 2 April 1994, early autumn 1994), and peak (3 - 10 July 1994, early winter 1994). These phases of population abundance were described by Zuleta et al. (1988) and Busch and Kravetz (1992a), and correspond to changes in population social structure, intra and interspecific competition, dispersion rates (Cittadino et al. 1999), as well as strong variations in the conditions of habitats, and in the contrast between cropfields and borders (Hodara 1997). Six grids of 15x15 Sherman live traps were set in each sampling date. Distance between Sherman traps was 10 meters. Each grid covered two neighbour cropfields (with different implanted crops), the internal border between them and the external border (Figure 1). This design permitted to assess habitat selection between neighbour habitat patches, since for active selection animals may have accessibility to the different alternatives (Morris 1996). The trapping effort was greater in cropfields than in borders, because of differences in areas and because rodent density is generally lower in fields than in borders. These differences in trapping effort were taken into account when assessing relative densities in each habitat.

Traps were baited with peanut butter. During cool weather traps were wrapped in paper and nylon bags and bedding was provided to prevent mortality from hypothermia. Each trapping session ran for three consecutive nights. Traps were checked each morning. Captured animals were identified to species, sexed, weighed and measured (total and tail length). Animals were given an individual mark by toe clipping and released at the site of capture. Location on the grid was recorded for each capture occasion.

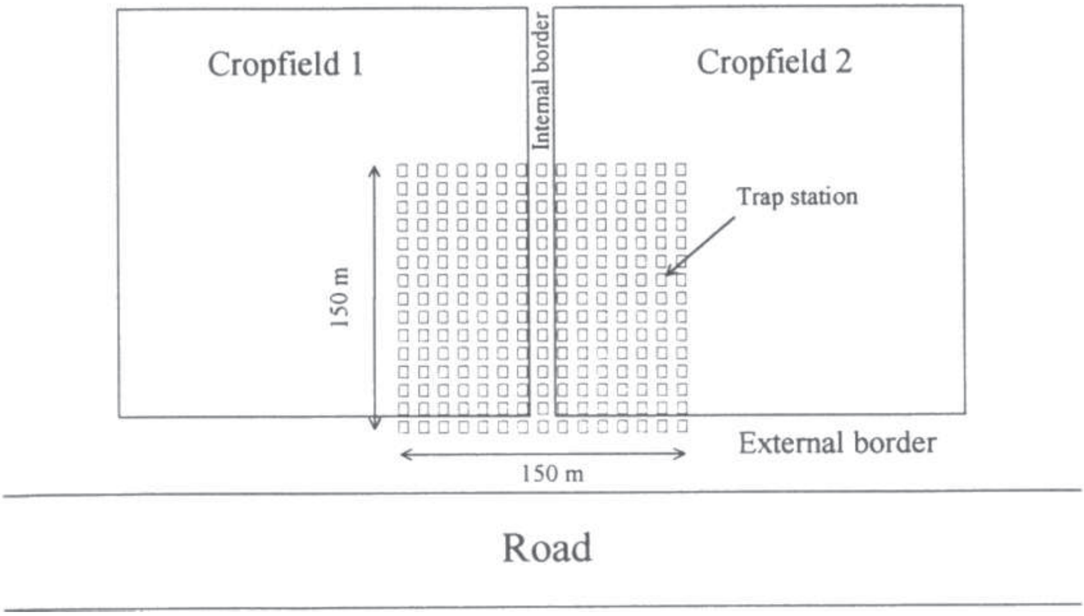

Figure 1. Scheme of localization of trapping grids in cropfields and borders. Each trapping grid was a 15x15 trap quadrat covering two types of cropfields, the border between them (internal) and the border to the road (external). Six grids were sampled at each season.

Vegetation measurements

Sampling grids were all located in cropfields with similar labour history, topography and edaphic conditions. We assumed that habitat heterogeneity among trapsites was mainly accounted by variations in plant cover and species composition. In an area covering one meter around each trap-site we registered: total plant cover, green plant cover, presence of plant species that cover more than 5 % of the area, and vegetation strata. We recorded the presence of plant cover at three height intervals: stratum 1 (Hl): below 0.05 m; stratum 2 (H2), between 0.05 and 0.5 m and stratum 3 (H3), above 0.5 m. Total and green plant cover were expressed as the percentage of total area covered, while for the other vegetation variables we recorded presence or absence. In order to identify habitat patches we performed a cluster analysis joining trap sites according to their euclidean distance, using the average linkage method (Pielou 1984). This analysis was conducted separately for each grid and in each sampling date. We considered belonging to the same microhabitat patch all trap sites that were at Euclidean distances less than 0.25. Capture data were not included in this analysis. Clustering was also used to identify groups of variables, including both vegetation and rodent data. For clustering we used a matrix of presence-absence data for all variables, standardising all variables by defining categories for those data which were not binary, as plant cover and number of captures. We defined four plant cover categories: 1- cover between 0 and 25%, 2- cover between 26 and 50%, 3- cover between 51 and 75%, and 4- cover between 76 and 100%. For rodent captures we considered the presence or absence of 0, 1, 2 or 3 individuals at each capture site.

Comparison of rodent captures in different habitat units

We compared the number of individual captures in fields and borders by means of the Wilcoxon paired- sample test, while differences in captures between autumn and winter samplings were assessed by means of a Kruskal- Wallis test (Sokal and Rohlf 1981). In both cases captures were standardised according to the number of traps and days of capture calculating a Relative density index (RDI = Number of captures/ Number of traps x number of nights). Captures according to type of cropfield or border were compared with the expected frequencies according to the binomial distribution (Sokal and Rohlf 1981), taking into account the number of traps located at each habitat.

In order to assess the relationship between *C. musculinus* captures and plant variables at the trap site level, we conducted a preliminar univariate analysis (G or binomial tests), for preselecting those variables that appear to be associated. Then we used a logistic multiple regression (Norman and Streiner 1996) to assess the contribution of these variables to the prediction of *C. musculinus* presence or absence. In the final model we included those variables whose coefficients were statistically significant at $P<0.05$, and those for which the P-value of the coefficient was higher than 0.05 but less than 0.2, and contributed to an improvement in the predictive power of the model. For the multivariate analysis we considered a sub sample of the total sites studied, taking into account all sites with rodent presence, and a random selection of a similar number of sites without capture. For the univariate analysis the observed frequency of co-ocurrence between rodents and plant variables was compared with the frequency expected according to the total frequencies of rodent captures and the plant variable: Expected frequency = frequency of captures x frequency of the plant variable/ total number of trap sites.

The effect of other rodent species *(Calomys laucha, Akodon azarae* and *Oligoryzomys flavescens)* on *Calomys musculinus* numbers at the trap site level was assessed by a non parametric correlation (Kendall rank correlation, Zar 1996). Winter data were pooled because of sample size (number of captures). We did not consider in the analysis those sites where there were not any rodent capture.

We considered that succesive captures of an animal in the same location were not independent. In order to avoid comitting pseudorreplication (Hurlbert 1984), we did not consider the recaptures if they were produced in the same location as the first time, but they were taken into account when the animal changed its habitat between captures.

The percentages of total and green plant cover in sites with and without *C. musculinus* captures in the different sampling periods were compared by a Kruskal-Wallis ANOVA by ranks, considering all sites of all grids at each season.

To compare selection for some individual variables across different scales we assigned at each level the sum or the mean of the values obtained for the corresponding units at the level below (Schaefer and Messier 1995). We compared the proportions of rodent captures in each type of habitat to the expected proportion estimated according to the frequencies of each habitat variable (except total and green plant cover) by means of a goodness of fit Chi square test. We considered evidence of association when these proportions did not differ significantly (ata > 0.1), and when the power (1-β) of the test was higher than 0.9. The values of β were estimated using the normal transformation of the Chi square (Zar 1996).

In order to analyse the effect of total and green plant cover on rodent distribution between cropfields and borders, and between types of them, we estimated the Kendall rank correlation coefficient (Zar 1996) between the proportion of captures in one habitat type (numbers in habitat type 1/ total numbers) and the differences in the percentages of plant cover between habitats (mean total or green plant cover in habitat type 1 - mean total or green plant cover in habitat 2). Grids were considered as replicates. Winter data were pooled because of insufficient captures to conduct the correlations.

Results

Calomys musculinus abundance and distribution

During the sampling period we recorded a total of 85 captures of 79 different *C. musculinus*. Abundance was significantly higher in autumn than in winter (Kruskall-Wallis ANOVA, H=4.45, P=0.035), while in spring it was practically nil (Table 1). Due to the low densities observed in spring, this season was not included in the subsequent analyses . Borders showed significantly higher densities than neighbour fields (Wilcoxon matched paired test, T=12, Z=2.34, P=0.019, N=13). External and internal borders showed no significant differences in *C. musculinus* captures (Wilcoxon matched paired test, T=13, Z=0.70, P=0.484, N=9). This species showed significant differences in abundance between neighbour cropfields in only one out of 10 grids (Binomial test, P < 0.001).

Identification of habitat patches and rodent distribution between them.

in most of the grids and sampling dates (15/18), the cluster analysis first identified two groups of trap sites, corresponding to those located in cropfields and borders, with mean euclidean distances ranging between 30.7 in early autumn and 40.7 in winter. Cropfields were characterised by a low plant cover (less than 25 %), the presence of stratum 1 and of *Stellaria media, Datura ferox, Rumex crispus, Coronopus didymus, Carduus achantoides, Cirsium vulgare, Cynara cardunculus, Lolium multiflorum, Cynodon dactilon, Lepidium sp., Raphanus sativa* and *Senecio grisebachii.* Borders were characterised by abundant plant cover (over 70%), and presence of stratum 3, *Stipa spp. (S. hyalina, S. papposa* and S. *neesiana), Baccharis spp.* (including *B. leptophyllum* and *B. pingraea), Dipsacus sativa, Conium maculatum, Phalaris sp., Coniza bonariensis* and *Wedelia glauca.* (Appendix 1). Internal and external borders were separated at mean euclidean distances ranging from 5.6 in early winter and 24.7 in early autumn. Mean euclidean distances between neighbour fields ranged between 18.1 in winter and 69.1 in early winter. The number and size of patches identified in each grid was variable. In winter the number of patches ranged between 1 and 8, with sizes between 1 and 26 trap sites. In early autumn we found 1 and 2 patches within cropfields, with sizes ranging between 7 and 98 trap sites. In early winter the number of patches ranged between 1 and 38, with sizes between 1 (the most frequent) and 98 trap sites.

In early winter, *C. musculinus* used a patch within a grid with sunflower and sunflower stubble fields in greater proportion than expected when comparing to the abundances observed in both fields and the total grid (Binomial test, P=0.050 and P=0.042, respectively). In the other seasons and grids there was not differential use of habitat patches, probably because patches were not of sufficient size or number to allow the detection of differences in rodent abundance.

Table 1. Relative density Index (RDI = Number of individuals caught/(number of traps* number of nights)) of *Calomys musculinus* according to macrohabitat type. The number of traps per grid was 225. In early autumn there was a significantly higher density than in the other seasons (H=4.45, P=0.035, according to the Kruskal-Wallis test), and densities were higher in borders than in cropfields (T=12.0, Z=2.34, P=0.019, Wilcoxon matched paired test).

	Spring		Early Autumn		Early Winter		Winter	
Grid	Fields	Borders	Fields	Borders	Fields	Borders	Fields	Borders
1	0.000	0.034	0.046	0.340	0.000	0.482	0.000	0.034
2	0.000	0.000	0.000	0.000	0.112	0.034	0.005	0.000
3	0.000	0.000	0.025	0.310	0.000	0.000	0.000	0.034
4	0.000	0.000	0.031	0.000	0.015	0.103	0.005	0.241
5	0.000	0.000	0.005	0.103	0.000	0.000	0.000	0.000
6	0.000	0.000	0.005	0.207	0.005	0.000	0.000	0.000

Table 2. Goodness of fit test between the distribution of *Calomys musculinus* and plant variables between cropfields and borders, between types of borders and between types of fields. We considered evidence of association when both distributions did not differ at P>0.1, and with a power of the test (1-ß) of 0.9. Values of ß were estimated with the normal aproximation of the Chi square (Zar, 1996). Significant values are resalted in bold letter.

	Distribution between cropfields and borders			Distribution between borders			Distribution between fields		
	Chi-square		1-ß	Chi–square		1-ß	Chi-square		1-ß
Winter 1993									
Brassica campestris	-	-	-	**1.67**	**0.19**	**0.901**	-	-	-
Chenopodium alba	**1.83**	**0.170**	**0.915**	0.71	0.390	0.800	-	-	-
Lolium multiflorum	**2.39**	**0.120**	**0.939**	3.5	0.06	0.963	-	-	-
Wedelia glauca	0.04	0.840	0.573	**1.55**	**0.21**	**0.900**	-	-	-
Early Autumn 1994									
Paspalum dilatatum	32.4	0.000	0.999	**1.79**	**0.18**	**0.91**	210	0.000	0.999
Phalaris aquatica	15.18	0.000	0.999	**2.14**	**0.14**	**0.93**	-	-	-
Solidago chilensis	6.9	0.009	0.997	**1.5**	**0.21**	**0.90**	76.3	0.000	0.999
Stratum 2	33	0.000	0.999	0.49	0.48	0.76	**1.4**	**0.23**	**0.90**
Early Winter 1994									
Cynodon dactilon	47.10	0.000	0.999	0.16	0.69	0.800	**1.48**	**0.224**	**0.900**
Senecio sp	40.13	0.000	0.999	**1.48**	**0.22**	**0.900**	0.81	0.367	0.816

Rodent and plant variables associations

Sites where *Calomys musculinus* was captured had higher plant cover than sites without rodent captures (Kruskal-Wallis ANOVA, H=8.01, P=0.005 in winter 1993, H=3.82, P=0.051 in early autumn 1994 and H=14.25, P=0.000 in early winter 1994). Sites with captures showed higher green plant cover than not capture sites only in early autumn (Kruskall-Wallis ANOVA, H=1.41, P=0.236 in winter, H=5.005, P=0.025 in early autumn and H=3.67, P=0.056 in early winter).

In winter 1993 the distribution of *C. musculinus* between cropfields and borders was associated ro the distribution of *Ch. alba* and *L. multiflorum*. The distribution between borders was associated to those of *B. campestris* and *W. glauca* (Table 2). *Stellaria media* was agood predictor of the presence of *C. musculinus* at the trap site level withia borders (Table 3). In fields there were not sufficient captures to perform comparisons.

In early autumn there were not significant associations between rodent captures and plant variables distribution between fields and borders. Between borders, *C. musculinus* distribution was associated to those of S. *chilensis*, *P. dilatatum* and P. *aquatica*. Between fields *C. musculinus* distribution was associated to those of the stratum 2 (Table 2). At the trap site level, the presence of *Carduus sp* was a good predictor of *C. musculinus* presence within borders (Table 3), while in fields this rodent species was negatively related to *C. dactilon* (Table 4).

Table 3. Logistic regression between habitat variables (height of vegetation and plant species) and *C. musculinus* presence in borders. For the regression we selected those variables that showed significant relations with rodent captures in a previous univariate analysis. In the regression we included all trap sites where rodents were captured and a similar number of random selected sites with 0 captures.

a) Winter 1993		
Predictive Variable	Coefficients	P
Constant	- 2.07938	0.0488
Stellaria media	4.15876	0.0053
Deviance: 12.56	P-value: 0.7048	gl: 16
% of 0 classified correctly = 0.889	% of 1 classified correctly = 0.889	Overall cases correctly classified = 0.889
b) Early Autumn 1994		
Predictive Variable	Coefficients	P
Constant	- 1.60944	0.0109
Carduus achantoides	1.85060	0.0136
Deviance: 50.52	P-value: 0.1465	gl: 41
% of 0 classified correctly = 0.577	% of 1 classified correctly = 0.824	Overall cases correctly classified = 0.674
c) Early Winter 1994		
Predictive Variable	Coefficients	P
Constant	1.38629	0.2148
Sratum 3	-2.07944	0.0947
Deviance: 24.10	P-value: 0.1518	gl: 18
% of 0 classified correctly = 0.909	% of 1 classified correctly = 0.444	Overall cases correctly classified = 0.700

Table 4. Logistic regression between habitat variables (height of vegetation and plant species) and *C. musculinus* presence in fields. For the regression we selected those habitat variables that showed significant relations with rodent captures in a previous univariate analysis. In the regression we included all trap sites where rodents were captured and a similar number of random selected sites with 0 captures.

a) Early Autumn 1994		
Predictive Variable	Coefficients	P
Constant	0.69315	0.2055
Cynodon dactilon	-1.20397	0.0673
Deviance: 61.44	P-value:0.0.052	gl: 45
% of 0 classified correctly = 0.80	% of 1 classified correctly = 0.455	Overall cases correctly classified = 0.638
a) Early Autumn 1994		
Predictive Variable	Coefficients	P
Constant	-1.18885	0.0073
Brassica campestris	1.56279	0.0380
Matricaria chamomilla	1.37896	0.0654
Trifolium repens	1.52986	0.0321
Deviance:64.91	P-value: 0.1264	gl: 53
% of 0 classified correctly = 0.667	% of 1 classified correctly = 0.810	Overall cases correctly classified = 0.737

In early winter the distribution of *C. musculinus* between cropfields and borders was not associated to any plant variable, while the distribution between borders was related to that of *Senecio sp.* The distribution of *C. musculinus* between cropfields was related to the distribution of *Cynodon dactilon* (Table 2). The presence of *C. musculinus* in individual trap sites within borders was negatively related to the presence of stratum 3 (Table 3), while within fields it was positively related to *B. campestris, M. chamomilla* and *T. repens* (Table 4).

Total plant cover was neither associated to rodent distribution between cropfields and borders, nor between types of them in the two periods considered (early autumn and winter). Green plant cover was significantly correlated to rodent distribution between cropfields and borders only in early autumn (Table 5).

Calomys musculinus captures were negatively related to *C. Laucha* and *A. azarae* in borders in early auturnn, while in winter there were not significant relationships between species (Table 6). Within cropfields there were significant negative relationships between species both in autumn and winter (Table 7).

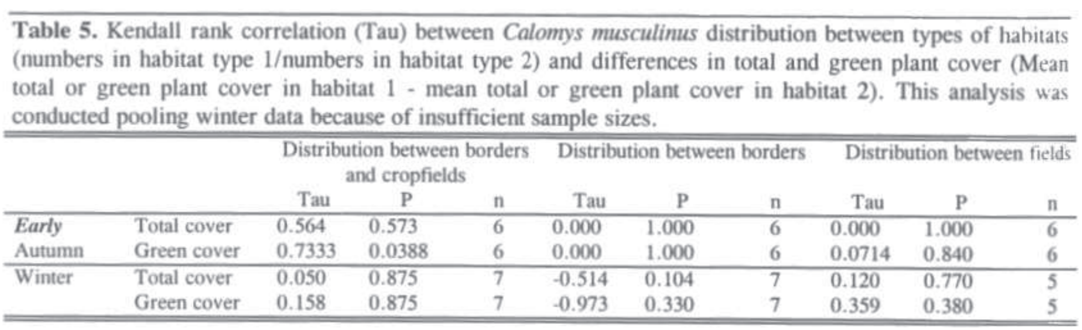

Table 5. Kendall rank correlation (Tau) between *Calomys musculinus* distribution between types of habitats (numbers in habitat type 1/numbers in habitat type 2) and differences in total and green plant cover (Mean total or green plant cover in habitat 1 - mean total or green plant cover in habitat 2). This analysis was conducted pooling winter data because of insufficient sample sizes.

		Distribution between borders and cropfields			Distribution between borders			Distribution between fields		
		Tau	P	n	Tau	P	n	Tau	P	n
Early Autumn	Total cover	0.564	0.573	6	0.000	1.000	6	0.000	1.000	6
	Green cover	0.7333	0.0388	6	0.000	1.000	6	0.0714	0.840	6
Winter	Total cover	0.050	0.875	7	-0.514	0.104	7	0.120	0.770	5
	Green cover	0.158	0.875	7	-0.973	0.330	7	0.359	0.380	5

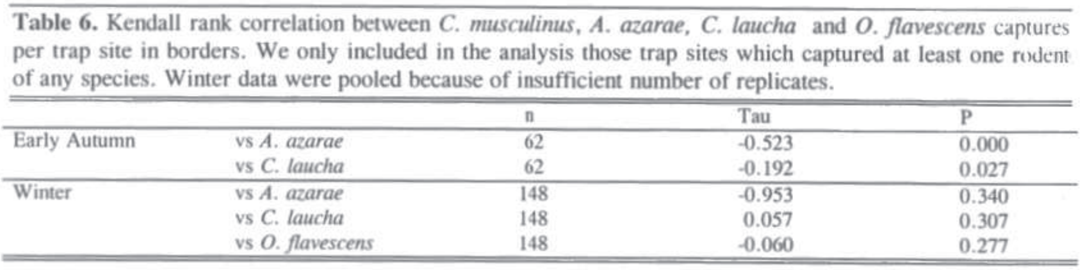

Table 6. Kendall rank correlation between *C. musculinus*, *A. azarae*, *C. laucha* and *O. flavescens* captures per trap site in borders. We only included in the analysis those trap sites which captured at least one rodent of any species. Winter data were pooled because of insufficient number of replicates.

		n	Tau	P
Early Autumn	vs *A. azarae*	62	-0.523	0.000
	vs *C. laucha*	62	-0.192	0.027
Winter	vs *A. azarae*	148	-0.953	0.340
	vs *C. laucha*	148	0.057	0.307
	vs *O. flavescens*	148	-0.060	0.277

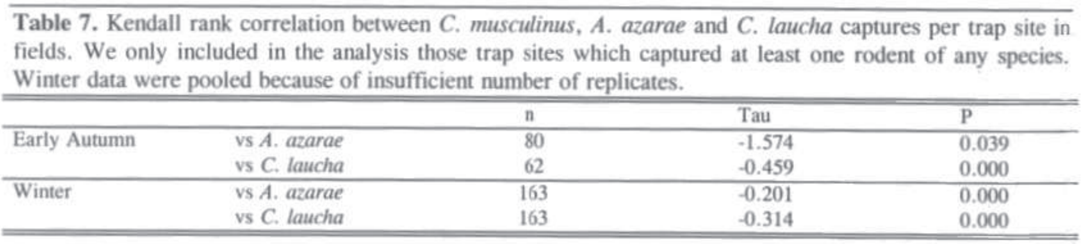

Table 7. Kendall rank correlation between *C. musculinus*, *A. azarae* and *C. laucha* captures per trap site in fields. We only included in the analysis those trap sites which captured at least one rodent of any species. Winter data were pooled because of insufficient number of replicates.

		n	Tau	P
Early Autumn	vs *A. azarae*	80	-1.574	0.039
	vs *C. laucha*	62	-0.459	0.000
Winter	vs *A. azarae*	163	-0.201	0.000
	vs *C. laucha*	163	-0.314	0.000

Discussion

We considered that macrohabitat scale in the pampean agroecosystems correspond to the differences between the cropfields and their weedy margins, the borders, as was confirmed by the cluster analysis performed with habitat variables. *Calomys musculinus* showed a significant response in abundance to this level of habitat heterogeneity, being significantly more abundant in borders than in fields, as was previously observed by Mills et al. (1992) and Busch et al. (1997). This response to structural features of habitats at scales larger than microhabitat patches is expected in omnivorous species (Dooley and Bowers 1996) as C. musculinus, which is opportunistic, although it includes few arthropods in its diet (Ellis et al. 1998). Differences between cropfields and borders are probably related to the need of protection of the superficial nests (Busch et al. 1984, Ellis et al. 1997), which are more exposed in cropfields.

The second level of heterogeneity considered was that between types of cropfields and borders. *Calomys musculinus* did not show significant responses in abundance at this spatial scale, although previous studies reported differences in *C. musculinus* abundance between maize and soybean fields (Busch et al. 1984, Ellis et al. 1997), but, as it was previously mentioned, these differences can not be attributed to habitat selection because the studied fields were not adjacent. In the present study the evaluation of selection at this level was complicated by the absence of replicates for the pairs of neighbour crops. Each grid was implanted with different neighbour crops, and we only could compare individual pairs of fields.

The third level of heterogeneity considered was among habitat patches within borders and fields. The homogeneity of conditions within macrohabitats did not favour the formation of patches of sufficient size to detect differences in rodent captures, and, as was quoted by Morris (1987), even if there were local patches of good quality within macrohabitats, if their size is less than the home range size of the foragers, it is unlikely to lead to predictable changes in local abundance. Small sized patches of good quality may also cause a spillover of surplus individuals and produce higher densities in the surrounding poorer patches than it may be expected according to their quality (Morris 1997). Agrarian labors and seasonal effects within fields produce ephemeral microhabitat conditions, and probable mitigate against consistent patch trends in abundance (Morris 1987).

Individual plant species were significant predictors of *C. musculinus* presence at a trap site level, suggesting that there are differences in habitat use at this habitat scale (trap sites are distanced by 10 meters). The low number of recaptures did not allow to compare habitat selection estimates taking in account the successive captures of an individual with those obtained by the captures of different individuals, but we assumed that the number of captures in each site was reflecting both the presence at this site as well as a higher intensity of use.

At the trap site level, *Calomys musculinus* showed a negative correlation to *A. azarae* and *Caloinys laucha,* both within borders and cropfields. This was previously observed in studies that reported competition between them (Busch and Kravetz 1992a, Ellis et al. 1997). We could not assess if habitat associations of *C. musculinus* changed between sites with and without captures of the other species, because of insufficient sample sizes, but it remains as an open question. Species coexistence involves an axis of environmental heterogeneity along which species might exhibit niche partitioning, which may involve space (at different scales), time and diet (Brown et al. 1994). In the case of the cropfield- border system, there is spatial segregation between *C. Laucha* and *C. musculinus* between fields and borders and among habitat patches within fields (Bonaventura et al. 1988), but they show a great dietary overlap (Ellis et al. 1998). *Calomys musculinus* and *A. azarae* are overlapped in microhabitat use, but the use of borders by *C. musculinus is* probably restricted by the presence of *A. azarae* , as was observed with *Akodon dolores* in agroecosystems of Río Cuarto, Córdoba (Kravetz and Polop 1983). These species showed spatial segregation at the trap site level (Busch and Kravetz 1992a), and showed less dietary overlap than the two species of *Calomys* (Ellis et al. 1998). The time axis remains as a question, although there are preliminar evidences that *C. musculinus* and *A. azarae* densities in different years exhibit negative correlations (Busch et al. 1991), and they also differ in the peaks of daily activity *(A.azarae is* more crepuscular and *C. musculinus* nocturnal, Busch pcrs. comm).

Rodent associations to individual variables changed depending on the habitat scale considered and in different moments of the year, as was observed by Schaefer and Messier (1995) for muskoxen. For *C. musculinus,* these changes probably reflect seasonally changes in the vegetation composition, as well as variations in the phenology of crops and the agrarian labors. Variations in rodent- plant variables associations at different scales may influence their evaluation when different habitat types are not equally sampled or represented in the landscape, or when higher spatial hierarchies are not considered when evaluating microhabitat use.

The association between rodent captures and habitat variables may be reflecting the compromise between the selection of habitats of the highest harvest rate and the lowest predatory risk (Ziv et al. 1995, Abramsky et al. 1997, Kotler 1997). For *C. musculinus,* structural characteristics which reduce predatory risk may be more important than dietary constraints, since it is a generalist and opportunistic species (Ellis et al. 1998), although the association with the green plant cover in the period of reproductive activity may be related to specific food requirements of reproductive females and agrees with that observed for *A. azarae* by Mills et al. (1992), Bonaventura et al. (1992) and Bilenca and Kravetz (1998).

In summary, *C. musculinus* showed microhabitat selection, and used differentially microsites with different plant species. Its distribution within cropfields and borders was related to the presence of individual plant species as well as negatively associated to the distribution of two other rodent species, *Akodon azarae* and *Calomys laucha.* Associations to habitat variables changed according to the habitat and the scale considered, showing that this species perceives different scales of habitat heterogeneity, and the relative qualities of habitats change according to the season, probably because of changes in plant composition and phenology as well as changes in specific requirements of rodents.

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Appendix 1. List of plant species recorded in each season. Numbers are the frequencies observed in each type of habitat (B: borders, F: fields). Total number of field sites: 1176. Total number of border sites: 174. Ubiq.: ubiquitous, in general they are in similar frequency in both habitats. (Classification of functional groups, growth season and habitat affinities were made after Ellis et al. 1997, Rusch and Oesterheld 1997, with some modifications according to our data).

Plant variable	Growth season	Typical habitat	Winter 1993		Spring 1993		Early Autumn 1994		Early Winter 1994	
Annual Dicot			B	F	B	F	B	F	B	F
Amaranthus quitensis	Warm	Ubiq.					31	114	3	28
Bidens sp	Cool	Ubiq.			13	97	43	252		
Bowlesia incana	Cool	Field	16	0					31	3
Brassica campestris	Cool	Ubiq	14	198	11	106	18	98	51	150
Carduus achantoides	Cool	Border	68	304	52	211	83	204	97	268
Conium maculatum	Warm	Ubiq.			28	1	27	196	0	5
Coronopus didymus	Cool	Field			0	98			0	23
Chenopodium alba	Warm	Field	9	5	0	39				
Datura ferox	Warm	Field			16	187	0	188	1	98
Dichondra microcalyx	Cool	Field	12	3						
Dipsacus sativa	Warm	Border	30	1	26	0	32	0	27	0
Matricaria chamomilla	Warm	Field	2	114	13	242			1	113
Physalis viscosa	Cool	Field	13	337						
Raphanus sativa	Cool	Field			0	99				
Rumex crispus	Cool	Field			10	359			22	45
Solanum bonariensis	Warm	Border			24	98	31	0	8	14
Solidago chilensis	Warm	Border	10	99	10	21	39	98	45	7
Stellaria media	Cool	Field	45	433	0	205	0	105	0	514
Tagetes minuta	Cool	Ubiq	9	98	7	107	30	190		
Trifolium repens	Warm	Ubiq	20	196	5	153	14	98	3	180
Annual monocot										
Bromus unioloides	Cool	Ubiq.	31	118					11	16
Digitaria sanguinalis	Warm	Ubiq.	8	124						
Lolium multiflorum	Cool	Border	13	0	39	201			4	9
Poa annua	Cool	Field	11	207			17	309	2	58
Perennial Dicot										
Althernantera philoxeroides	Warm	Field			0	194				
Baccharis sp	Warm	Border	61	8	9	0	68	1	78	2
Dichondra microcalyx	Cool	Ubiq.	12	3						
Eryngium sp	Warm	Border	18	0			29	0	7	0
Senecio sp	Warm	Ubiq.	14	189	21	116	9	98	48	276
Wedelia glauca	Warm	Ubiq.	38	7						
Perennial monocot										
Cynodon dactilon	Warm	Ubiq.	48	60	14	292	62	694	50	308
Paspalum dilatatum	Warm	Ubiq.	1	108			50	294	3	101
Phalaris aquatica	Cool	Border			26	95	13	1	10	0
Sorghum halepense	Warm	Ubiq.	17	152	18	365	25	378	26	35
Stipa sp	Cool	Border	78	13	53	95	81	98	84	0