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Habitat selection and interspecific competition in rodents in pampean agroecosystems

by M. BUSCH, M. R. ALVAREZ, E. A. CITTADINO and F. O. KRAVETZ

*Depto de Biología, Facultad de Ciencias Exactas y Naturales. Universidad de Buenos Aires
Ciudad Universitaria, Pab. II, 4° piso, Lab. 104, Nuñez. (1428) Buenos Aires, Argentina*

Summary. – We analyzed the effect of density-dependent habitat selection and interspecific competition on the use of space by small rodent species in agroecosystems. We studied rodent abundance in cropfields and their borders, weedy margins less disturbed by agricultural activities. We could distinguish two kind of species : those habitat intolerants, *Akodon azarae* and *Oligoryzomys flavescens*, which select the borders, and those habitat tolerants, *Calomys laucha* and *Calomys musculinus*. The two most abundant species in the community, *A. azarae* and *C. laucha*, differ in their habitat use : while the first has a clear preference for borders, the other is more equally distributed between habitats, although it is more abundant in fields. Both species show a shift towards an increased use of fields via density-dependent habitat selection with increasing abundance at some moments of the year. *C. musculinus* does not show habitat preference in any season, overlapping with the other species in both habitats. There is an interspecific effect on habitat use between *A. azarae* and *C. laucha* : While the first species cause a shift in habitat preference of *C. laucha* towards fields, this latter species affects the density-dependent habitat use of *A. azarae*. It is concluded that the pattern of habitat use of the studied species is affected by their differential preferences as well as by intra and interspecific density-dependent processes that change seasonally.

Résumé. – Nous avons analysé l'effet de la sélection de l'habitat densité-dépendante, et de la compétition interspécifique sur l'utilisation de l'espace par les espèces de petits rongeurs qui vivent dans les agroécosystèmes. Nous avons étudié l'abondance des rongeurs dans les champs cultivés et leurs limites, des bordures couvertes d'herbe moins perturbées par les activités agricoles. On distingue deux catégories d'espèces : celles qui ne tolèrent pas de variation de leur habitat, *Akodon azarae* et *Oligoryzomys flavescens* qui choisissent les bordures, et celles qui sont tolérantes, *Calomys laucha* et *Calomys musculinus*. Les deux espèces les plus importantes dans la communauté, *A. azarae* et *C. laucha*, diffèrent dans leur utilisation de l'habitat. La première a une nette préférence pour les bordures, tandis que l'autre est répartie plus également dans les différents habitats, bien qu'elle soit plus abondante dans les champs. Les deux espèces manifestent une tendance à un usage accru des champs par l'intermédiaire d'une sélection de l'habitat densité-dépendante, avec une abondance qui s'accroît à certains moments de l'année. *C. musculinus* ne montre en aucune saison de préférence d'habitat, se trouvant avec l'autre espèce dans les deux habitats. Il y a un effet interspécifique sur l'utilisation de l'habitat entre *A. azarae* et *C. laucha* : tandis que la première espèce cause un changement dans la préférence d'habitat de *C. laucha* vers les champs, cette dernière espèce affecte l'utilisation de l'habitat densité-dépendante de *A. azarae*. On conclut que le schéma d'utilisation de l'habitat par les espèces étudiées est affecté par leurs préférences autant que par les processus intra et interspécifiques dépendant de la densité qui changent selon les saisons.

INTRODUCTION

In a patchy environment, the pattern of habitat use of different related species may be reflecting a differential habitat selection, as well as density-dependent processes (Fretwell and Lucas 1970, Rosenzweig 1981, Morris 1989a). Intra and interspecific competition depressing limited resources forces individuals to expand their range of habitat use from best quality habitats to suboptimal ones.

Rosenzweig (1981) pointed out that habitat selection is a force for achieving species coexistence. While a system with more than one fine grained species will be unstable, differential habitat selection between species may promote equilibrium at lower densities than their carrying capacities.

The relationship between habitat choice and density has been examined theoretically (Morisita 1969 ; Fretwell 1972 ; Rosenzweig 1981 ; Rosenzweig and Abramsky 1985 ; Morris 1987 a and b) as well as in laboratory and field conditions. In the field, when animals are secretive or nocturnal, habitat selection is usually inferred from sampling and counting. Rosenzweig and Abramsky (1985) developed the distributional analysis for assessing habitat selection with census data. Unevenness in the distribution between different types of habitats is considered to be reflecting habitat selection. The evenness in habitat distribution was measured by different kinds of "selectivity indexes" (Rosenzweig and Abramsky 1985) and can be described by the proportion of captures obtained in each habitat. On the other hand, Rosenzweig (1986) applied isoleg models in which habitat choice is mapped onto state spaces where the axes are population sizes of two different species. Regressing selectivity indexes with density provides an empirical way of estimating isoleg equations (Rosenzweig and Abramsky 1986).

Morris (1987c, 1988, 1989a and b) has developed the Multiple Species Isodar model, in which population sizes of one or several species in one habitat are regressed against population densities in the alternative habitat. According to the theory of density-dependent habitat selection densities in each habitat will be such that the fitness is the same in both. Isodars are lines of equal fitness in this state space and can be assessed if we have replicated density estimates in the two habitats. Regressing the numbers of the species in the habitat where it is more abundant against its numbers in the alternative habitat and of competitors in both habitats, we can evaluate : quantitative differences between habitats (intercept), intraspecific (regression coefficient with its own density in the alternative habitat) and interspecific competition (coefficients with densities of the other species) (Morris 1989a). In a recent paper, Ovadia and Abramsky (1995) discussed that isodars fail to detect properly interspecific interaction, but confirmed its usefulness in detecting density-dependent habitat use.

Argentinian pampean agroecosystems represent a complex of heterogeneous habitats where different rodent species show a different habitat use. *Calomys laucha* is more abundant in cropfields whereas *Akodon azarae* and *Oligoryzomys flavescens* are more frequent in cropfield's borders, *Calomys musculinus* shows a variable distribution in these habitats and *Mus musculus* is more abundant around human dwellings (Busch and Kravetz 1992a ; de Villafañe *et al.* 1977 ; Kravetz and Polop 1983). Fields and borders are closely related, and there is interchange of individuals of different species between them. These movements have seasonal variations, partially depending on the condition of each habitat. Some authors (de Villafañe *et al.* 1988 ; Manjón *et al.* 1983) posed that rodents move toward fields during periods of high density, especially if crops are near maturity or in stubble time, thus offering good plant cover. At other times, such as during harvesting or tilling, individuals move from the fields to their

margins. Different relative abundances in each habitat have also been attributed to interspecific segregation, *A. azarae* being competitively dominant in borders compared to *C. laucha* and *O. flavescens* (de Villafañe *et al.* 1973 ; Kravetz *et al.* 1981 ; Busch and Kravetz 1992a and b).

In this paper we want to study the relation between the pattern of habitat use, intraspecific density and interspecific competition in this rodent community.

MATERIALS AND METHODS

Study area

Fieldwork was conducted between 1979-1982 at Diego Gaynor (34° 8' S, 59° 14' W), Province of Buenos Aires, Argentina. The study area is located in the Pampean region, characterized by a temperate climate and pasture type vegetation. The dominant plant species are *Stipa neesiana*, *Stipa brachychaeta*, *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 can be found in Crespo (1966), Bonaventura and Cagnoni (in press) and Busch and Kravetz (1992a and b).

Rodent populations show an annual cycle of density increasing from low levels in spring, to a maximum by the end of autumn. Density declines suddenly after the first frosts (Kravetz *et al.* 1981 ; Busch and Kravetz 1992a).

The landscape shows a predominance of cultivated fields and pastures of about 25 ha, surrounded by weedy longitudinal strips of about two meters in width that are less disturbed by agriculture than fields (borders). Other habitats for rodents are natural pastures, railroad fills and borders along roads and streams.

The most common crops during the study period were : wheat and linen in spring ; sunflower, soybean, maize and some stubbles from winter crops in summer ; and stubbles in winter and autumn. We studied fields and borders that had similar farming labors, implanted crops and associated weeds.

A seasonal analysis was conducted because habitat characteristics, implanted crops and rodent population structure change with season (Kravetz *et al.* 1981 ; Zuleta *et al.* 1988 ; Zuleta 1989). While border characteristics do not significantly change throughout the year, at least with respect to total plant cover, fields show strong variations because of agrarian labors. We expected that quantitative and qualitative differences between habitats will show seasonal variations, independently of density. A pooled analysis was also conducted in order to detect a general trend of variation in habitat use with density.

We considered as replicates the density estimates corresponding to different years, because the main characteristics of the rodent community, population abundances and habitats are similar at the same date in different years.

Sampling of rodents

The number of rodents in each habitat was evaluated through weekly samplings of continuous dead pitfall traps. After every capture the traps were automatically reset. Rodent abundance was simultaneously evaluated in cropfields and in the external border (margin toward the road), on two parallel lines (30 m apart), with 8 traps each, spa-

ced at 20 m intervals. Trap lines were active during one week, at the end of which the traps were checked and the number of rodents of each species present in each line (field and border) recorded. We sampled a total of 15 paired lines in spring, 26 in summer, 18 in autumn and 13 in winter.

Data analysis

* Density estimation.

We used relative density indexes to estimate rodent abundance in each line because in some cases it was not possible to have access to the study area in order to check the traps, and some lines were active for more than a week. Relative density indexes were calculated as :

$$\text{RDI} = (\text{Number of captured rodents/Nr of traps} \times \text{Nr of nights}) \times 1000$$

A global density (in fields and borders) was estimated for each species weighting the relative effects of both habitats according to their size as :

$$\text{Global RDI (GRDI)} = 0.95 \times \text{RDI in fields} + 0.05 \times \text{RDI in borders}$$

* Habitat preference.

Preference for borders was estimated as the ratio of the RDI in the borders to total RDI (RDI in borders + RDI in fields) for each pair of lines. In this case we did not transform the density estimates in each habitat because they represented the magnitude of use (number of captures per trapping effort), since trapping effort was the same in each habitat. Preference indexes higher than 0.5 indicated preference for borders, = 0.5, equal preference for both habitats, and < 0.5, preference for fields.

Intra and interspecific effects on habitat preference were estimated by regressing preference indexes against GRDI. Since true selectivity is expressed when competitors are rare or absent (Rosenzweig and Abramsky 1985 and 1986 ; Abramsky *et al.* 1990) we examined the y intercepts of the regressions in order to detect preferences, while the slopes described the relation between preference and density. We calculated the confidence intervals (C.I.) of the intercepts and slopes in order to test if they statistically differ from some specified values (e.g. : for testing if the intercepts of the regression of the preference index on density differ from 0.5). C.I. = Parameter \pm SE $\times t_{0.05, n-2}$. Where SE = Standard error of the estimate, $t_{0.05, n-2}$ = Student t value.

In order to estimate the effect of interspecific competition on the intraspecific density-dependent effect of the two most abundant species, we conducted regressions of the preference index on intraspecific density separately in lines where the other species was present and in lines where it was absent.

Rosenzweig and Abramsky (1985) showed that many selectivity indexes are density dependent in themselves, thus providing a measure of apparent selectivity when they decrease as population density increases. They provide an alternative method for estimating density dependence of selectivity, with the regression of the transformed Simpson index (y') on population density minus one. In this regression, the slopes represent selectivity indexes. In absence of selectivity what is expected is a slope equal to zero, while different slopes represent different degrees of selectivity. Hyperdispersion is inferred from negative slopes. If selectivity does not change with density there will be a linear relation between y' and GRDI-1, while if selectivity decreases with increasing density, there will be a negative quadratic term of the regression (Rosenzweig and Abramsky 1985). We conducted regressions of the transformed Simpson index on GRDI-1 for *A. azarae* and *O. flavescens*, but not for *C. laucha* and *C. muscu-*

linus. For the latter two species, which sometimes use more the borders and at other moments are more abundant in fields, the transformed Simpson index will not discriminate between these two situations, because it only measures unevenness in the distribution, but does not give information about which habitat is preferred.

In order to detect density-dependent habitat use and fitness rewards in the two habitats we used multiple regressions to estimate the corresponding coefficients of isodar equations as described by Morris (1988, 1989b). The dependent variable was the density of each species in the habitat where it was more abundant. The independent variables were the densities of the same species in the other habitat, and of the other species in both habitats.

Intraspecific density-dependent habitat selection was confirmed for any species when there was a positive and significant coefficient between its own densities in both habitats. Quantitative differences between habitats were inferred from significant intercepts. After Morris (1988), we didn't consider to exist density-dependent habitat selection when the slope of the isodar was significant but the intercept did not significantly differ from zero, because this implies absence of selection at low densities. Significant negative coefficients with the density of other species in the preferred habitat, or positive coefficients with RDI values in the alternative habitat in the regression were taken as evidence of interspecific competition. Sample numbers did not allow to evaluate interference coefficients.

The character of the variables used (relative density estimates) which were all measured with some error, and in which there were not strictly dependent and independent variables, does not allow to use Model I regression equations for quantitative prediction. We used this model only to assess the sign and significance of species interaction and the pattern of habitat use.

RESULTS

Species and relative abundances

Five rodent species were trapped, *A. azarae*, *C. laucha*, *C. musculus*, *O. flavescens* and *M. musculus*. The last species occurred at low abundance during most of the study (Table 1), so it was not considered in the analysis. For *C. musculus*, we only

TABLE 1. – Total number of rodents captured in each season (spring, summer, autumn and winter).

	spring	summer	autumn	winter
<i>A. azarae</i>	27	34	148	131
<i>C. laucha</i>	38	98	618	263
<i>C. musculus</i>	8	25	591	11
<i>O. flavescens</i>	2	9	33	18
<i>M. musculus</i>	3	8	2	0
Number of paired trap lines	15	26	18	13

conducted regressions for the pooled data, in spring, summer and autumn, because in winter the number of paired lines in which it was captured was not sufficient to conduct a regression. For *O. flavescens* low numbers allowed to perform only the global analysis. Densities of all species were included as independent variables when analyzing habitat use of the remaining species, in order to evaluate competitive effects.

Rodent abundance varied throughout the study with an annual pattern similar to that described elsewhere (Kravetz *et al.* 1981 ; Zuleta *et al.* 1988). Rodent densities were at a minimum in spring – summer, increasing toward a peak in autumn – early winter.

Habitat preference

A. azarae used the border in a greater proportion than the field throughout the year, the mean proportion of habitat used ranged from 0.87 to 0.92.

The preference of this species for borders was detected by both the regression of the preference index on density and by the isodars. The y intercepts of the regression of the preference index on intra and interspecific density ranged between 0.89 and 1.03. They were significantly higher than 0.5 in all seasons, ($P < 0.005$, Table 2). The y intercepts of the regression of the preference index on intraspecific density did not differ from 1 both in absence (Fig. 1a) and in presence of *C. laucha* (Fig. 1b) (Confidence Intervals = 1-1, 1.056-0.846 ; respectively), while the slope was not significantly different from 0 in the first case and negative in the second ($P < 0.05$).

The y intercepts of the isodar regression for *A. azarae* were significantly higher than 0 for the global analysis, in summer and in autumn, but they were not significant in spring ($P = 0.069$) and winter ($P = 0.318$, Table 3). According to the results, *A. azarae* perceives quantitative differences between habitats along most of the year, but except in spring, there were no qualitative differences (slopes do not significantly differ from 1, Table 3).

C. laucha was more abundant in fields than in borders throughout the year, and the preference index ranged from 0.20 to 0.39. The y intercepts of the regression of preference index on intra and interspecific density did not significantly differ from 0.5 (range 0.407-0.571, Table 4). When regressing *C. laucha* preference index only on intraspecific density, in absence of *A. azarae* the y intercept did not differ significantly from 0.5 (Confidence interval = 0.651-0.309, Fig. 2a), while in presence of this species it was significantly less than 0.5 (Confidence interval = 0.451-0.208, $P < 0.05$, Fig.

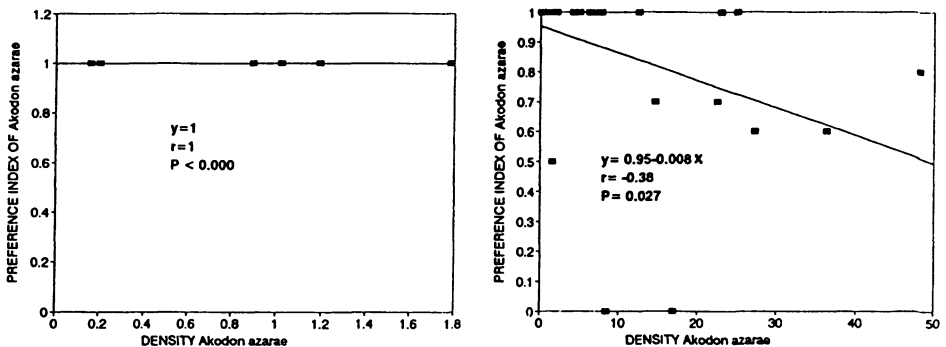


Fig. 1. – The relationship between preference of *Akodon azarae* for borders and its own intraspecific density when *Calomys laucha* was absent (a) or present at various densities (b).

2b). As can be seen in Fig. 1 and 2, preference indexes for *C. laucha* showed more variation than those of *A. azarae* at any density level.

C. laucha isodar intercepts were significantly higher than 0 in spring and summer (when using *C. laucha* density in fields as the dependent variable, Table 5), suggesting that this species perceives quantitative differences between habitats in these seasons, while in autumn there were not detected differences between habitats (the intercept of

TABLE 2. – The relationship between the preference of *A. azarae* (*PAa*) and intra and interspecific density (*C. laucha*, *C. musculus* and *O. flavescens* densities). The confidence intervals (C.I.) for the y intercepts are given. B = coefficients.

A) GLOBAL

$$PAa = 0.996 - 1.386 Aa + 0.022 CI \quad F = 9.3287 \quad P < 0.001$$

	B	C.I.	SE	t-value	P
Intercept	0.996	0.849-1.143	0.072	20.71	0.0000
<i>Aa</i> density	-1.386		0.032	-4.30	0.0001
<i>CI</i> density	0.022		0.012	1.79	0.0806

B) SPRING

$$PAa = 0.959 \quad F = 1.5465 \quad P = 0.32$$

	B	C.I.	SE	t-value	P
Intercept	0.959	0.723-1.195	0.096	9.963	0.0006

C) SUMMER

$$PAa = 1.033 - 0.061 Aa \quad F = 273.43 \quad P = 0.0000$$

	B	C.I.	SE	t-value	P
Intercept	1.033	0.995-1.071	0.017	60.027	0.0000
<i>Aa</i> density	-0.061		0.002	-23.258	0.0000

D) AUTUMN

$$PAa = 0.89 \quad F = 0.318 \quad P = 0.73$$

	B	C.I.	SE	t-value	P
Intercept	0.891	0.606-1.175	0.131	6.824	0.0000

E) WINTER

$$PAa = 1.031 - 0.017 Aa + 0.00027 CI \quad F = 11.25 \quad P = 0.0093$$

	B	C.I.	SE	t-value	P
Intercept	1.031	0.936-1.127	0.0413	24.987	0.0000
<i>Aa</i> density	-0.017		0.0034	-5.021	0.0024
<i>CI</i> density	0.00027		0.00007	3.772	0.0093

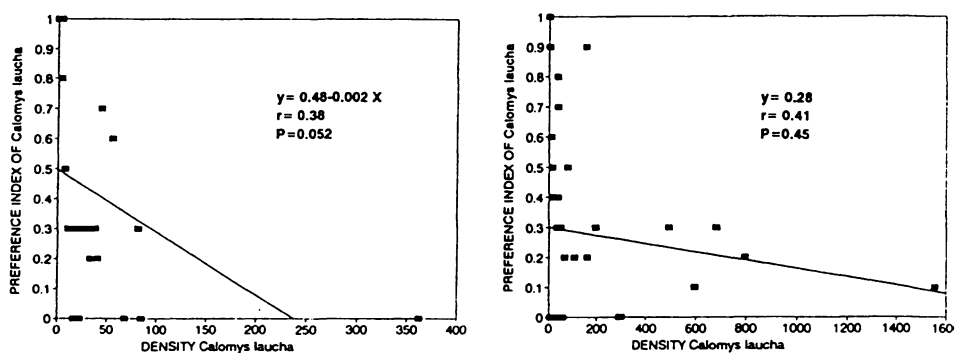


Fig. 2. – The relationship between preference of *Calomys laucha* for borders and its own intraspecific density when *Akodon azarae* was absent (a) or present at various densities (b).

the isodar was not significant and the slope did not differ significantly from 1, Confidence interval = 0.8833-3.3967), and in winter results did not support the isodar model (Table 5).

C. musculus mean preference indexes ranged from 0.20 to 0.81. While the y intercept of the regression of preference indexes versus density did not significantly differ from 0.5 for the global data in spring and in autumn, in summer it was shifted toward borders (Table 6). Isodar intercept confirms the preference for borders in summer (significantly different from 0, $P < 0.05$, Table 7).

The regression analysis conducted on the preference indexes of *O. flavescens* showed a clear preference for borders (y intercept = 0.997, $P < 0.05$, Table 8). According to the isodars, the borders were qualitatively better than fields (slope of the regression = 4.07, $p = 0.037$), but did not differ quantitatively (non significant intercept, Table 9).

Habitat preference in relation to intra and interspecific density

The results of the regression analysis conducted on the preference of *A. azarae* as a function of intra and interspecific densities support the hypothesis that *A. azarae* preference changes according to both intraspecific (decreasing) and interspecific (increasing) density. Density dependent habitat use was expressed in summer (only intraspecific effect) and winter (both intra and interspecific effect, Table 2). The change in the slope of the regression of the preference index of *A. azarae* on intraspecific density in absence and presence of *C. laucha*, suggests that this latter species is favouring the use of fields as an alternative habitat by individuals of *A. azarae* when density of this species increases (Fig. 1a and b).

Density-dependence of habitat use was not detected for *A. azarae* by the isodar analysis, since there were no significant relations between border's and field's densities, except in spring (Table 3). When regressing the transformed Simpson index (y') on population density (GRDI) minus one, a significant linear term (coefficient = 0.687, $P = 0.000$) was found. The quadratic term was positive, significant and very small (coefficient = 0.0006, $P = 0.01$), while for the hypothesis of density-dependent habitat use, a negative quadratic term was expected.

The results obtained when regressing the preference index of *C. laucha* against intra and interspecific densities, when considering all data pooled, support the hypo-

TABLE 3. – Multiple species regression summary and Anova table for *A. azarae* in the different seasons. *A. azarae* density in borders is the dependent variable. *Aa* : *A. azarae*, *Cl* : *C. laucha*, *Cm* : *C. musculus*, *Of* : *O. flavescens*, *Mm* : *Mus musculus*.

	Regression summary			ANOVA Table		
	Variable	Coefficient	Sig. Level	Source	DF	P
Global (intraspecific)	Constant	36.54	0.002	Model	1	0.42
				Error	67	
Spring	Constant	6.04	0.069	Model	1	0.004
	<i>Aa</i> density in fields	1.16	0.004	Error	13	
Summer	Constant	4.96	0.043	Model	1	0.022
	<i>Cm</i> density in borders	0.36	0.022	Error	24	
Autumn	Constant	45.75	0.027	Model	3	0.000
	<i>Cm</i> density in fields	1.59	0.000	Error	14	
	<i>Cm</i> density in borders	-2.73	0.041			
	<i>Mm</i> density in borders	8.64	0.023			
Winter	Constant	16.9	0.318	Model	4	0.000
	<i>Of</i> density in borders	3.67	0.000	Error	6	
	<i>Cm</i> density in borders	-8.16	0.003			
	<i>Cl</i> density in fields	0.26	0.000			
	<i>Cl</i> density in borders	0.27	0.003			

Values of the constants (significant and non significant) were always included, while for the other variables only those with significant coefficients were included.

thesis of constant selectivity (the slope is not statistically significant, Table 4). When analyzing each season separately, it was seen that in summer and autumn there was a trend to intraspecific density-dependent habitat selection ($P < 0.05$ in the first case, and

TABLE 4. – The relationship between the preference of *C. laucha* (PCI) and intra and interspecific density (*A. azarae*, *C. musculus*, and *O. flavescens* density). The confidence intervals (C.I.) of the y intercept are given. B = coefficients.

A) GLOBAL

PCI= 0.419 F= 1.066 P= 0.35

	B	C.I.	SE	t-value	P
Intercept	0.419	0.071	0.064	6.055	0.0000

B) SPRING

PCI= 0.407 F= 1.207 P= 0.348

	B	C.I.	SE	t-value	P
Intercept	0.407	0.039-0.775	0.165	2.466	0.0389

C) SUMMER

PCI= 0.571 - 0.0099 CI F=4.714 P= 0.0415

	B	C.I.	SE	t-value	P
Intercept	0.571	0.332-0.810	0.115	4.947	0.0001
CI density	-0.010		0.005	-2.120	0.047

D) AUTUMN

PCI= 0.43 - 0.0005 CI F= 3.25 P= 0.0915

	B	C.I.	SE	t-value	P
Intercept	0.4323	0.206-0.658	0.1066	4.055	0.0012
CI density	-0.0005		0.0003	-1.796	0.094

E) WINTER

The model is not significant for all variables

P < 0.1 in the second), with an increase in the use of fields at increasing densities (Table 4). This effect was also revealed by the isodar slopes, which were statistically significant for the global analysis, in summer and in autumn (Table 5). The isodar of *C. laucha* in trap lines where *A. azarae* was absent had a significant intercept (coefficient = 40.07, P = 0.039) and a non significant slope (coefficient = 0.066, P = 0.910), while in trap lines where *A. azarae* was present *C. laucha* densities in fields and borders were positively related (slope = 0.93, P = 0.016) and the intercept was also significant (coefficient = 114.51, P = 0.05).

TABLE 5. – Multiple species regression summary and Anova table for *C. laucha* in the different seasons. *C. laucha* density in fields was the dependent variable. *Aa* : *A. azarae*, *Cl* : *C. laucha*, *Cm* : *C. musculus*, *Of* : *O. flavescens*.

	Regression summary			ANOVA Table		
	Variable	Coefficient	Sig. Level	Source	DF	P
Global (intraspecific)	Constant	62.75	0.000	Model	1	0.000
	Slope	1.04	0.034	Error	67	
Spring	Constant	24.03	0.007	Model	1	0.000
	<i>Aa</i> density in fields	7.90	0.00	Error	13	
Summer	Constant	9.32	0.011	Model	2	0.005
	<i>Cl</i> density in borders	0.46	0.008	Error	23	
	<i>Cm</i> density in borders	0.48	0.017			
Autumn	Constant	55.64	0.420	Model	1	0.003
	<i>Cl</i> density in borders	2.14	0.003	Error	16	
Winter	Constant	-49.50	0.442	Model	4	0.000
	<i>Cl</i> density in borders	-0.94	0.010	Error	6	
	<i>Cm</i> density in bordes	29.24	0.008			
	<i>Aa</i> density in borders	3.62	0.000			
	<i>Of</i> density inborders	-13.33	0.000			

Values of the constants (significant and non significant) were always included, while for the other variables only those with significant coefficients were included.

The regression of the preferences index of *C. musculus* against intra and inter-specific densities showed a trend to a density-dependent use of borders for the pooled data ($P < 0.1$), in summer ($P < 0.05$) and in autumn ($P < 0.1$), while in spring habitat use was independent of density (significant intercept, Table 6). The low number of trap lines where this species was captured in winter did not allow to perform regression analysis. Intraspecific density dependent effect was not detected by the isodar analysis in any season (Table 7).

TABLE 6. – The relationship between the preference of *C. musculus* (PCm) and intra and interspecific density (*A. azarae*, *C. laucha* and *O. flavescens* densities). The confidence intervals (C.I.) of the y intercepts are given. B = coefficients.

A) GLOBAL

$$PCm = 0.58 - 0.003 Cm \quad F = 3.66 \quad P = 0.0677$$

	B	C.I.	SE	t-value	P
Intercept	0.603	0.421-0.784	0.090	6.842	0.000
Cm density	-0.0036		0.002	-1.999	0.057

B) SPRING

$$PCm = 0.680 \quad F = 3.416 \quad P = 0.1383$$

	B	C.I.	SE	t-value	P
Intercept	0.680	0.024-1.337	0.255	2.664	0.0561

B) SUMMER

$$PCm = 1.028 - 0.102 Cm \quad F = 7.887 \quad P = 0.0262$$

	B	C.I.	SE	t-value	P
Intercept	1.028	0.743-1.313	0.124	8.323	0.0001
Cm density	-0.102		0.036	-2.808	0.0262

C) AUTUMN

$$PCm = 0.625 - 0.003 Cm \quad F = 5.203 \quad P = 0.0777$$

	B	C.I.	SE	t-value	P
Intercept	0.626	0.349-0.903	0.120	5.203	0.0012
Cm density	-0.003		0.001	2.065	0.078

Preference indexes of *O. flavescens* decreased with intraspecific and *C. musculus* densities, while they showed a positive relation with *C. laucha* and *A. azarae* densities ($P < 0.05$, Table 8). The isodar slope also supported the hypothesis of intraspecific density dependent habitat use (slope = 4.07, $P < 0.05$, Table 9).

Relative effects of intra and interspecific competition

The relation between the intraspecific coefficient and the effect of *C. laucha* on *A. azarae* preference index is 63 : 1 for both the global data (intraspecific = - 1.386, interspecific = 0.022, Table 2) and in winter (intraspecific = - 0.017, interspecific = 0.00027, Table 2). According to the isodars there is competition between *A. azarae*

TABLE 7. – Multiple species regression summary and Anova table for *C. musculus* in the different seasons. *C. musculus* density in fields was the dependent variable in spring while for the global analysis, in summer and autumn the dependent variable was the density in borders.

Global: Dependent variable: *Cm* density in borders

Regression summary			ANOVA Table		
Variable	Coefficient	Sig. Level	Source	DF	P
Constant	16.402	0.0016	Model	1	0.597
<i>Cm</i> density in fields	-0.048	0.5970	Error	25	

Spring: Dependent variable: *Cm* density in fields

Regression summary			ANOVA Table		
Variable	Coefficient	Sig. Level	Source	DF	P
Constant	11.1538	0.034	Model	1	0.158
<i>Cm</i> density in borders	-0.563	0.158	Error	4	

Summer: Dependent variable: *Cm* density in borders

Regression summary			ANOVA Table		
Variable	Coefficient	Sig. Level	Source	DF	P
Constant	19.801	0.050	Model	1	0.387
<i>Cm</i> density in fields	-2.374	0.387	Error	7	

Autumn: Dependent variable: *Cm* density in borders

Regression summary			ANOVA Table		
Variable	Coefficient	Sig. Level	Source	DF	P
Constant	27.384	0.047	Model	1	0.517
<i>Cm</i> density in fields	-0.091	0.510	Error	7	

Values of the constants (significant and non significant) were always included, while for the other variables only those with significant coefficients were included.

and *C. musculus* in both habitats in autumn, and only in borders in winter. In these last two cases no intraspecific effect on habitat use was detected (Table 3).

There was not effect of any species on *C. laucha* preference index (Table 4), while the isodars suggest that there is competition with *C. musculus* in summer and winter in borders. The interspecific and intraspecific coefficients in summer were very similar (0.48 and 0.46, respectively, Table 5), while in winter there was not intraspecific effect. No effect of any species on *C. musculus* habitat use was detected by either method (Tables 6 and 7). The preference index for borders of *O. flavescens* decreased with *C. musculus* density (the ratio between inter and intraspecific competition was 0.59), but there was no competition detected between these two species by the isodar analysis (Tables 8 and 9).

TABLE 8. – The relationship between the preference of *O. flavescens* (*Pof*) and intra and interspecific density (*A. azarae*, *C. laucha*, *C. musculus* and *O. flavescens* densities). The confidence intervals (C.I.) of the y intercept are given. B = coefficients.

$$Pof = 0.997 - 0.056 Of + 0.012 Aa + 0.004 CI - 0.03 Cm \quad F = 137.156 \quad P = 0.0000$$

	B	C.I.	SE	t-value	P
Intercept	0.997	0.959-1.035	0.017	57.1759	0.0000
<i>Of</i> density	-0.056		0.004	-15.3900	0.0000
<i>Aa</i> density	0.012		0.002	7.6856	0.0000
<i>CI</i> density	0.004		0.000	17.6433	0.0000
<i>Cm</i> density	-0.033		0.002	-14.8745	0.0000

TABLE 9. – Multiple species regression summary and Anova table for *O. flavescens*. *O. flavescens* density in borders was the dependent variable. *Aa* : *A. azarae*, *Of* : *O. flavescens*.

Regression summary			ANOVA Table		
Variable	Coefficient	Sig. Level	Source	DF	P
Constant	4.79	0.5472	Model	3	0.046
<i>Of</i> density in fields	4.07	0.037	Error	8	
<i>Aa</i> density in borders	0.65	0.011			
<i>Aa</i> density in fields	- 2.48	0.038			

The value of the constant was included, although it was not significant, while for the other variables only those with significant coefficients were included.

DISCUSSION

Our results confirmed previous works that described a differential habitat selection in the studied species (Crespo 1966 ; Busch and Kravetz 1992a and b). We also found that there are two kind of species in this rodent community : two habitat intolerants (*A.azarae* and *O. flavescens*), and two habitat tolerants (*C. laucha* and *C. musculus*).

The effect of density on habitat selection for *A. azarae* is still not clear. According to the isodars, *A. azarae* uses the borders in a density independent form, while the preference index decreases with intraspecific and increases with interspecific density at some moments of the year (for the global data, in summer and autumn). The regression of the transformed Simpson index (*y'*) on GRDI-1 also agrees with the hypothesis of constant selectivity. This disagreement in the results of different methods can be related to the habitat configuration, since in order to relate the preference indexes to density we needed to estimate a global density, weighting each habitat according to its

size (stratified sampling, Poole 1974). This approach gives more weight to density estimates in fields than in borders, and implies the assumption that animals are distributed between the two habitats according to the global density. On the other hand, when applying the isodar method, we considered abundances in each habitat separately, without weighting them differently.

A priori, we expected that density dependence in species that prefer borders should be detected first by the isodar method, or regressing preference indexes with untransformed global density (which gives more weight to border's densities), but in the case of *A. azarae*, preference indexes were not significantly related to untransformed intra and interspecific densities. Further experimental research, in which both habitats should be offered in a similar proportion, is needed in order to clarify these results.

Intraspecific differences in habitat use may also make it difficult to detect a significant relation with population density. Bilenca (1993) found that habitat use in *A. azarae* changes according to the sex and reproductive status of individuals, while competitive interactions are also affected by population structure (Busch and Kravetz 1992a).

Although *C. laucha* uses both habitats in a similar proportion to their availability (preference indexes did not differ from 0.5) along most of the year, fields may contribute more than borders to the determination of population numbers because of their large size. It seems that *A. azarae* affects *C. laucha* habitat selection, changing the intercept of the regression of the preference index in lines with and without *A. azarae* (Fig. 2a and 2b). *C. laucha* isodar's slopes also change when comparing lines in which *A. azarae* is absent with lines in which this species is present: while in the first case there is no significant relationship between *C. laucha* densities in fields and borders, when *A. azarae* is present there is an intraspecific density-dependent habitat use by *C. laucha* (slope = 0.046, $P = 0.938$ and slope = 3.38, $P = 0.000$, respectively). Changes in isodar intercepts and slopes in sympatry and allopatry have been related to interference competition (Morris 1989b). Busch and Kravetz (1992a and b) postulated that interference competition between *A. azarae* and *C. laucha* in borders contributes to habitat segregation. Cueto *et al.* (1995) and Alvarez (1995) also found evidences of interference competition between these two species. It is the first work where a reciprocal effect of *C. laucha* on *A. azarae* is detected, but the kind of interspecific effect differs in both species: while *A. azarae* causes a change in *C. laucha* habitat use at low densities (change in preference), *C. laucha* contributes to the *A. azarae* density-dependent habitat selection.

While the y intercept of the regression of the preference index of *O. flavescens* on density suggests a strong preference for borders (Table 7), the isodar intercept is not significant (Table 8). Since the isodar intercept represents the density in borders when density in fields is zero, the absence of significance may be related to the analysis of pooled data, which generates a great variance in borders data, while in fields most of them are zeros.

Community organization

Habitat use of the two most abundant species, *A. azarae* and *C. laucha*, partially agrees with that expected from the model of differential preferences, in which species differ in the perception of differences between habitats (Morris 1988). While for *A. azarae* habitats are very different, for *C. laucha* they are more similar. For the first species there are quantitative differences between habitats, while for *C. laucha* there are only quantitative differences if we consider the global data. The effect of *C. laucha*

density on *A. azarae* preference index (increasing the use of borders with respect to fields) agrees with that expected from a distinct preference model, since *C. laucha* is limiting an increase in the use of fields by *A. azarae*. However, the changes in the y intercepts of the preference index of *C. laucha* on density, suggest that this species does not prefer the fields when alone, but this preference appears when *A. azarae* is present. This result is consistent with the laboratory experiments of Hodara *et al.* (unpubl. data) who observed that in laboratory experiments solitary individuals select sods of borders to nest, while under field conditions most *C. laucha* nests are located in the fields, and with the observed increase in the use of borders by *C. laucha* when *A. azarae* is removed (Busch and Kravetz 1992b). These authors also observed that there is a threshold density of *A. azarae* above which there are not *C. laucha* in borders. A similar situation was observed by Abramsky *et al.* (1990, 1991, 1992, 1994), studying two gerbil species. They found that the presence of very few individuals of the dominant species caused a shift of the subordinate to the alternative habitat, and an apparent preference for this latter habitat.

The relative effects of interspecific and intraspecific competition on habitat use differ according to the pair of species considered, and with the method used. Ovadia and Abramsky (1995) found that the isodar method was not able to detect interspecific competition between two gerbil species, while they were found to compete according to the results of intensive manipulative experiments. In our case, interspecific competition is either detected by one of the two methods, by both or none, depending the case. Both methods detected an interaction between *C. laucha* and *A. azarae*, and the relative effects of intra and interspecific competition (63 : 1) are in agreement with the possibility of stable coexistence. The more similar effect of intra and interspecific competition between both species of *Calomys* may be related to their similarity in both diet and habitat use. While *A. azarae* is omnivorous-insectivorous, both species of *Calomys* feed mainly on green parts of plants and seeds (Bilenca *et al.* 1992 ; Bilenca 1993). The stronger effect of interspecific competition was that of *C. musculinus* on *O. flavescens*.

The coexistence of these species in agroecosystems may be related to both the possibility of spatial segregation at different spatial scales, as well to dietary differences. While *A. azarae* and *O. flavescens* overlap in macrohabitat use, they segregate at microhabitat scale (Busch and Kravetz 1992a), and they show a lower overlap in diet than the other species (Bilenca *et al.* 1992 ; Bilenca 1993). The coexistence between *C. laucha* and *C. musculinus*, which overlap in macrohabitat use and diet, may be favoured by microhabitat segregation within fields and borders (Bonaventura *et al.* 1988).

In conclusion, the pattern of habitat use of the studied species is affected by their differential preferences as well as by intra and interspecific density-dependent processes that change seasonally.

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