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Environmental variables and reproductive activity in small rodents of pampean agroecosystems

Abstract: Under the hypothesis that the reproductive activity of a rodent species is influenced by conditions of the environment and by coexistent rodents, we assessed the relationship between environmental variables and reproductive activity of rodents at two spatial scales, field borders and trap sites, during the breeding period (spring, summer and autumn seasons) in pampean agroecosystems of Argentina. We distinguished between active and inactive sites, based on female reproductive condition. We conducted several statistical analyses to compare between active/inactive borders and trap sites for vegetation-rodent and rodent-rodent associations. The environmental variables useful for distinguishing active sites from inactive ones were different for each rodent species. Whereas vegetation cover, at the two habitat scales analyzed, seemed to be important for *Akodon azarae*, the crop types adjacent to borders seemed to be significant for *Calomys musculinus* to differentiate active/inactive sites. In the case of *Calomys venustus*, we could not identify one variable that reflected differences between border types. These associations would be related to the use that each rodent species makes of border and cropfield habitats, together with the resources they need at each moment of the breeding period.

Keywords: cropfield border; habitat conditions; reproductive activity; sigmodontine rodents.

Introduction

Habitat quality differs in heterogeneous environments and likely causes individual reproduction and survival rates to be habitat specific. Thus, measurements of reproductive performance and survival are expected to reflect somehow habitat quality (Arlt and Pärt 2007). The recognition that the location of an organism affects its fitness raises the possibility that the concepts of evolutionary theory could be brought to bear in understanding population dynamics in heterogeneous space (Schauber et al. 2007). Therefore, spatial heterogeneity and limited dispersal interact to cause a passive spatial shift of the population toward suitable locations (Bolker 2003).

Several studies have stressed the occurrence of important changes in land-use patterns and farming practices over the past 2 decades in the pampean region of central Argentina (Ghersa and Martínez-Ghersa 1991, Viglizzo et al. 2001, 2002, Martínez-Ghersa and Ghersa 2005, Paruelo et al. 2005). Pampean agroecosystems can be defined as mosaics, temporally and spatially heterogeneous. They are characterized as monocultural fields, bounded by a network of linear habitats, such as field borders, roadsides and railroad rights-of-way (Ellis et al. 1997). Edge habitats are disturbed less than agricultural fields, sustaining relatively high plant cover throughout the year, thus providing good habitat conditions for small rodent species (Busch and Kravetz 1992, Ellis et al. 1997, Bilenca and Kravetz 1998). Farming practices are known to affect rodent reproduction, survival, dispersion, competition and habitat selection, not only in cropfields but also in their borders (de Villafañe et al. 1977, Kravetz and Polop 1983, Jacob 2003, Jacob and Hempel 2003, Cavia et al. 2005, Bilenca et al. 2007).

Numerous studies on rodent ecology in the pampean region of Central Argentina evidence the role of the different habitat types, driven by the dynamics of agricultural practices, in the distribution and abundances of sigmodontine rodent species (Crespo 1966, Pearson 1967, Crespo et al. 1970, de Villafañe 1970, de Villafañe et al. 1973, Dalby 1975, Kravetz et al. 1975, Kravetz and de Villafañe 1981, de Villafañe and Bonaventura 1987, de Villafañe et al. 1988, Bonaventura et al. 1989, de Villafañe et al.

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1992, Busch et al. 2000). *Akodon azarae* (Fischer, 1829), *Calomys musculinus* (Thomas, 1913) and *Calomys venustus* (Thomas, 1894) are the most abundant species inhabiting the agroecosystems of Córdoba Province, mainly present in cropfield edges, roadsides and fencerows habitats (Kravetz and Polop 1983, Polop et al. 1985, Andreo et al. 2009, Simone et al. 2010). These three species show temporal and spatial variations in abundance: they vary seasonally and among habitats of the agroecosystem. *Akodon azarae* and *C. venustus* are usually found in relatively stable habitats with high vegetation cover, including cropfield edges, roadsides and railway banks and remnant areas of native vegetation (Mills et al. 1991, Priotto and Polop 1997, Bilenca and Kravetz 1998, Polop et al. 2005). *Calomys musculinus* is abundant in field borders but it has been also captured in cropfields (de Villafañe et al. 1988, Ellis et al. 1997, Busch et al. 2000). In a previous study, Simone et al. (2010) described rodent-vegetation associations with certain plant species, varying seasonally. This was in agreement with the assumption that the associations with individual plants respond to species-specific requirements at certain time of the year or of the reproductive cycle (Busch et al. 2000, Bilenca et al. 2007). Cropfield borders do not all show the same physiognomy or vegetation composition during the year, nor even in the same season. These differences could be recognized as distinct places in the “border” habitat type and rodent abundance may differ among them. According to the habitat suitability concept, individuals will have a greater fitness in habitats of higher quality than in poorer habitats (Sutherland 1997). The former habitats may contain potential resources for long-term survival and reproduction as well (Fauske et al. 1997, Bellamy et al. 2000).

Previous studies described intersexual variations in resource use during the breeding season (Bilenca et al. 1992, Bonaventura et al. 1992). Some authors attributed the variations to both differential investments and requirements of each sex in seeking reproductive success (Trivers 1972, Clutton-Brock and Albon 1982). In *Akodon azarae*, *Calomys musculinus* and *C. venustus*, as in many polygynus or promiscuous-polygynus species (Bonaventura et al. 1992, Priotto et al. 2002, Steinmann et al. 2009), each gender has different constraints on reproductive success, leading to sex-specific reproductive tactics (Trivers 1972, Clutton-Brock and Albon 1982, Ostfeld 1985). For females, reproductive performance would rely on their ability to acquire specific resources (such as food and space to rear offspring), whereas the reproductive performance of males would depend on the availability of estrus females and thus would be indirectly related to the distribution and abundance of resources (Zuleta 1989, Bonaventura et al. 1992, Frank and Heske 1992, Zuleta and Bilenca 1992, Wolff 1993, Loughran 2007, Steinmann et al. 2009). The habitat use of *C. musculinus* has been studied by Simone et al. (2012) in Córdoba Province and by Busch et al. (2000) in Buenos Aires Province. The use of space by this rodent species has been widely studied by Steinmann et al. (2005, 2006a,b, 2009). Only some aspects of microhabitat use for *A. azarae* in the breeding period have been dealt with by Bilenca and Kravetz (1998) in Buenos Aires Province. Nevertheless, there are no studies on site (or habitat) selection and the reproductive conditions of the rodent species of this agricultural assemblage.

The knowledge of the abovementioned aspects is very important in species that are responsible for transmitting zoonotic diseases. *Calomys musculinus* is the natural reservoir of Junín arenavirus, the etiological agent of Argentine hemorrhagic fever (AHF) (Vanella 1964, Sabattini et al. 1965). *Akodon azarae* is a reservoir of the virus Pergamino, one hanta genotype virus (Levis et al. 1997, 1998). *Calomys venustus* is a reservoir of the arenavirus Latino (Calderón et al. 2011). Thus, it would be interesting for deciding public health strategies to know if these rodent species respond somehow to different habitat resources, in particular during their reproductive period. The aim of this study was to characterize the relationship between environmental variables and the reproductive activity of rodents at two scales: field borders and trap sites. The underlying hypothesis is that reproductive activity of a rodent species is influenced by environmental conditions and by coexistent rodents.

Materials and methods

Study area

The study area (50 km^2) was located in the rural zone of Chucul, Department of Río Cuarto, Córdoba Province, Argentina (33° 01′ 34″ S; 64° 11′ 21″ W) (Figure 1). The climate is temperate, with an average annual temperature of 23°C in January and 6°C in July. Annual rainfall averages 700–800 mm, with the highest precipitation in summer. This region is a typical undulating pampean plain [600–900 m above sea level (m a.s.l.)] as a result of wind effects and accumulated loess and sandy sediments. Phytogeographically, this region belongs to the Espinal Province, Algarrobo District (Cabrera 1953), and the study area is considered a grassy steppe of the well-drained prairies unit (Bianco et al. 1987). At present, the landscape mainly consists of a matrix of cultivated fields

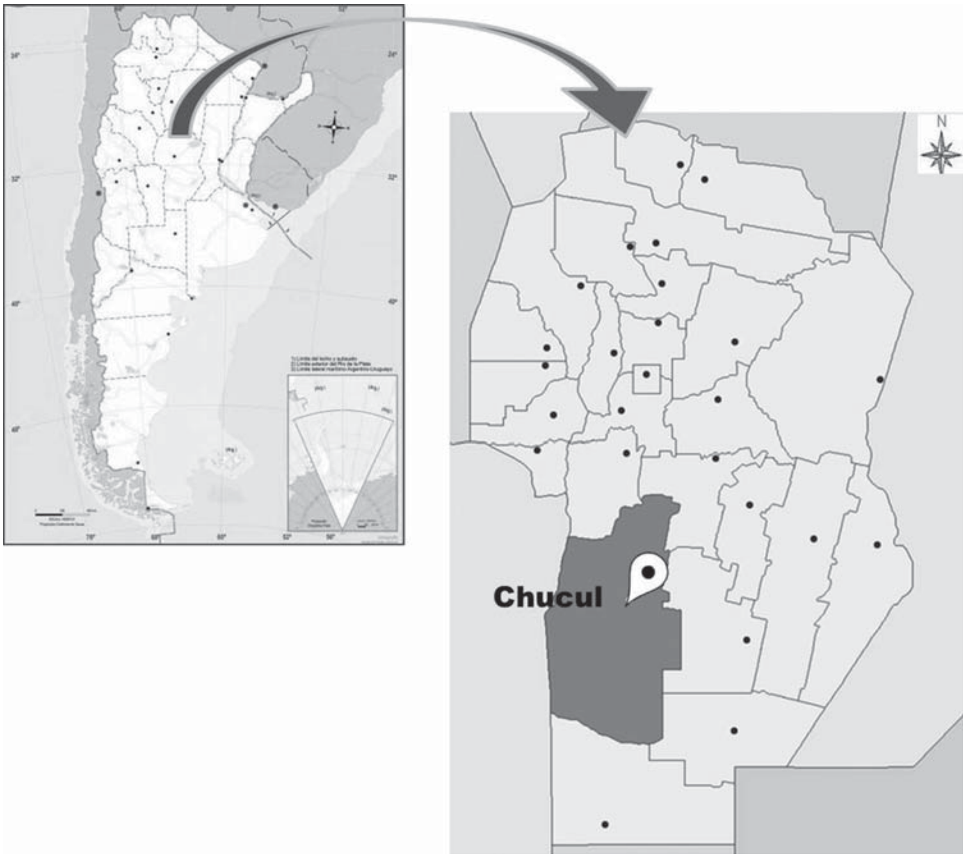

Figure 1 Map of Argentina showing the location of the Chucul rural area in Córdoba Province.

(corn, wheat, soybean, peanut and sorghum), pastures and their adjacent borders.

Animal sampling

Seasonal samplings were conducted in 48 borders per season that were different from one season to the next. Samples were taken in Summer 2006, Autumn 2006, Summer 2007 and Spring 2007. A total of 10 traps were placed on each border. Seven Sherman live-traps and three snap-traps were alternated and located at 6-m intervals. Traps were baited with a mixture of bovine fat and peanut butter and were checked each morning during two consecutive weeks (eight nights). All trapped rodents were removed from the field and taken to the lab for species identification and biometric measurements. The external reproductive condition was determined for females as dry or lactating nipples or by pregnancy evidence.

Two spatial scales were defined: microhabitat (trap site) and border. Trap sites and borders were classified as “active” or “inactive” in relation to the reproductive condition of the females of each species. At a microhabitat scale, trap sites were classified as active if at least one pregnant or lactating female was captured on it; a perforated vaginal orifice was not used as it is not a reliable indicator of reproductive activity (de Villafañe 1981, Priotto et al. 2006). Trap sites were classified as inactive if no pregnant or lactating females were captured on it through the eight nights. In the same way, at the border scale, a border was classified as active if there was at least one “active trap site” registered on it.

Abundance for each border was estimated from the relative density index (RDI) (Tellería 1986). RDI is defined as the number of individuals captured in relation to the sampling effort (number of trap-nights). RDI was calculated following the formula: RDI=[number of captured individuals/(number of traps×number of nights)]×100. Three values of RDI were estimated: the total RDI (considering all the species), the RDI for each species and the RDI for each species’ females.

The spring (October, November and December), summer (January, February and March), and autumn (April, May and June) seasons were analyzed, considering the length of the breeding period of the studied species (Crespo 1966, Pearson 1967, Dalby 1975, Mills et al. 1991, Polop 1996). All the research on live animals was performed in a humane manner following the national guidelines for the care and use of animals (http://www.sarem.org.ar).

Environmental variables

In each border, vegetation measurements were made using a quadrat of 1 m^2 (modified from Dueser and Shugart 1978) centered over the trap site, and five trap sites were surveyed. Variables registered in each quadrat unit were: total vegetation cover, strata cover (Stratum 1, plants below 10 cm; Stratum 2, plants between 10 and 30 cm; Stratum 3, plants above 30 cm), and the proportional coverage of each plant species present. Only those plant species covering more than 5% of a single quadrat and present in at least two active and two inactive borders were considered for the analyses. The proportional coverage of each plant was considered as an independent variable. Values from the five quadrats were averaged to obtain a unique value per border of each total, strata and plant species covers. The crop type adjacent to the border was recorded as an independent variable.

Data analysis

Comparisons of rodent abundance (total RDI, species RDI and females RDI values) considering the type of border (active/inactive) and season were performed. Analysis of variance (ANOVA) of one factor (type of border), two factors (season and type of border) or three factors (season, type of border and species) were performed when normal distribution and homoscedasticity assumptions were verified, and when not, the non-parametric Mann-Whitney test was used. Comparisons of vegetation variables between active and inactive borders were done, on the one hand, for each season and species, using ANOVA or the Mann-Whitney test. In autumn, the number of inactive borders was much greater than that for active ones. Therefore, to obtain a reliable result, several comparisons with the same number of active and inactive borders were performed. For this, a number of inactive borders were randomly selected until they equaled the number of active borders. This procedure was repeated five times, and the statistical result obtained the greatest number of times was considered the final result (Underwood 1997, Gomez et al. 2007). On the other hand, vegetation variables of only active borders were compared among the three rodent species, using ANOVA or the Kruskal-Wallis non-parametric test, when normality or homogeneity of variance conditions were not satisfied.

For each rodent species, associations between border type (active/inactive) and crop type were also assessed by deriving the association index suggested by Mills et al. (1991). That is, for each rodent species, an expected number of one border type (e.g., active) adjacent to a particular crop was calculated by multiplying the total number of that border type (e.g., total active) by the proportion of borders (relative to total borders) with that crop type. This expected value was then compared with the observed number of borders (e.g., active) with a particular crop type, using a χ^2-test. Deviations of observed from expected values were standardized as percentages of expected values. Significant deviations from expected associations were assessed using 95% Bonferroni confidence intervals (Byers et al. 1984). The association between border type and a particular crop was assessed considering first, the more represented crop (i.e., the crop with the highest percentage), and then those crops for which percentages had a difference in absolute magnitude <10 with respect to the highest one. It should be mentioned here that the proportions of crop types adjacent to sampled borders did not necessarily reflect the actual crop proportions of the study area.

The number of active and inactive borders shared by the three species was analyzed for each season by a coincidence matrix. To determine the proportion of active/inactive borders shared by each pair of species, we used the Cole association index, “C” (Cole 1949). This interspecific association index takes values between -1 and 1 that represent perfect negative and positive associations, respectively, whereas a zero value implies a random association. This index was developed for assessing the association between two species, considering their presence and absence (Cole 1949). In this study, it was used to assess the association between the reproductive conditions of the two species. That is, when both were in the same condition (active or inactive), the index tended to 1; when one species was active and the other inactive, the index tended to -1. When the reproductive conditions of species were randomly associated, the index was near 0.

This index is differently calculated, depending on the values of the formulas’ parameters. Thus, if it is true that:
Case 1: $a\times d\geq b\times c$, then $C=[(a\times d)-(b\times c)]/[(a+b)\times(b+c)]$
Case 2: $a\times d<b\times c$ and $a\leq d$, then $C=[(a\times d)-(b\times c)]/[(a+b)\times(a+c)]$
Case 3: $a\times d<b\times c$ and $a>d$, then $C=[(a\times d)-(b\times c)]/[(b+d)\times(c+d)]$,

where a is the number of borders where both species were captured active, b is the number of borders where species

1 was active and species 2 inactive, c is the number of borders where species 2 was active and species 1 inactive and d is the number of borders where both species were captured inactive.

All previous analyses were conducted by season, and data from both summers (2006, 2007) were analyzed together. Because of the low amount of data for spring and autumn, only summer seasons were used for microhabitat analyses. Thus, at a microhabitat scale, the vegetation variables were compared between active and inactive trap sites by ANOVAs or the Mann-Whitney test.

Results

Captured rodents

A total of 1188 rodents were captured in the studied seasons. There were 325 *Akodon azarae* (137 females and 188 males), 529 *Calomys musculinus* (215 females and 314 males) and 334 *C. venustus* (117 females and 217 males). The number of active and inactive borders by species, by season, is shown in Figure 2. The number of active borders was higher than inactive borders for *A. azarae* and *C. musculinus* in summer, whereas the opposite was observed in autumn, showing the spring as an intermediate situation.

The three-factors ANOVA (season, type of border and species) for total RDI showed that season was the only significant factor (F2,212=18.85, p<0.001), with the differences between autumn-summer and autumn-spring being significant (p<0.001 and p<0.001, respectively), but not being significant between spring-summer (p=0.292). Autumn abundances were higher than the abundances of the other two seasons. When considering individual rodent species, i.e., species RDI and females' RDI, two-factors ANOVA (season and type of border), could not be performed as the data did not fit normal distribution and homoscedasticity. We observed that the abundances of *Calomys musculinus* males and *C. musculinus* females were significantly different between active and inactive borders in summer Q (U=153, N_{active}=36, $N_{inactive}$=14, p=0.032 and U=121, N_{active}=36, $N_{inactive}$=14, p=0.004, respectively), with higher RDI values in active borders than in inactive ones. The other species did not show any differences (p>0.05).

Habitat analyses at border scale

The sampled borders showed high vegetation richness, independent of if they were active or inactive for each rodent species (Supplemental Tables 1, 2 and 3 for spring, summer and autumn data, respectively). Nevertheless, those plant species exclusive of active borders and those exclusive of inactive borders were present only in a few borders and in a low proportion that varied seasonally. Total border cover was higher than 70% for all borders in all seasons. The cover was mainly represented by the vegetation of the third stratum. Two plant species, *Cynodon dactylon* and *Sorghum halepense*, predominantly contributed to the total cover during the study. In spring, only

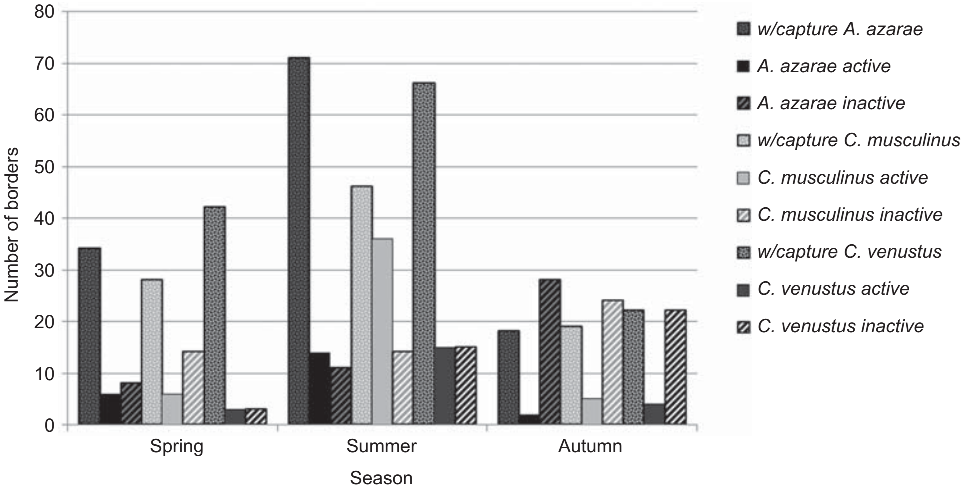

Figure 2 Number of borders per season classified as *with no captures* (w/capture), *active* and *inactive* for the three rodent species *Akodon azarae, Calomys musculinus* and *C. venustus*. Rural zone of Chucul, Córdoba, 2006–2007.

C. dactylon and the coverage of the second stratum were significantly higher for active borders than for inactive ones for *Akodon azarae* (F1,10=8.20, p=0.017 and U=2, N_{active}=6, $N_{inactive}$=8, p=0.004, respectively). Other vegetation variables showed no significant differences between active and inactive borders for any of the other two rodent species (p>0.05). Finally, when comparing the vegetation variables among the active borders for the three rodent species, no significant differences were registered for any season (p>0.05).

Border-cropfield associations

Regarding the vegetation of cropfields, the type and proportion of crops adjacent to active and inactive borders varied seasonally. The percentage of active and inactive borders contiguous with each crop type is shown in Table 1. For *Akodon azarae* in spring, a significant association between border type and crop vegetation was registered (X^2=33.5, d.f.=4, p<0.001 for active borders, and X^2=12.4, d.f.=2, p=0.020 for inactive borders). Active borders were mainly associated with soybean crops, and inactive borders were associated with corn crops (Table 1). In summer, a significant association for *A. azarae* was registered for both active (X^2=42.6, d.f.=4, p<0.001) and inactive borders (X^2=34.8, d.f.=4, p<0.001). Both border types were more associated with soybean crops (Table 1). In autumn, there was also a significant association between active and inactive borders for *A. azarae*, with cropfield vegetation (X^2=4.5, d.f.=1, p=0.030 and X^2=123.1, d.f.=5, p<0.001, respectively). Nevertheless, in this season, only two borders were classified as active for *A. azarae;* one border was adjacent to soybean and the other to peanut. Inactive borders were associated in the same proportion with corn and soybean crops (Table 1).

For *Calomys musculinus* in spring, the associations between crop vegetation and both active and inactive borders were significant (X^2=18.7, d.f.=2, p<0.001 and X^2=47.8, d.f.=4, p<0.001, respectively). Active borders were associated with peanut crops, whereas inactive borders were associated with corn (Table 1). In summer, the association index was statistically significant for active (X^2=124.4, d.f.=5, p<0.001) and inactive borders (X^2=87.1, d.f.=5, p<0.001). Active borders were associated with corn and soybean, whereas inactive borders were associated with soybean and peanut crops (Table 1). In autumn, the associations for both active and inactive borders were also statistically significant (X^2=10.6, d.f.=2, p=0.005 and X^2=85.8, d.f.=4, p<0.001, respectively). Active borders

Table 1 Percentage of active and inactive borders of *Akodon azarae*, *Calomys musculinus* and *C. venustus* associated with each crop type.

	A. azarae		***C. musculinus***		***C. venustus***	
Crops	**Active borders**	**Inactive borders**	**Active borders**	**Inactive borders**	**Active borders**	**Inactive borders**
Spring						
Corn	16.7	62.5	33.3	57.1	66.7	66.7
Peanut	16.7	25	50	7.1	33.3	0
Soybean	33.3	12.5	16.7	7.1		
Weeds	16.7	0				
Wheat	16.7	0	0	21.4	0	33.3
Without crop			0	7.1		
Summer						
Alfalfa			5.9	7.1	7.1	6.7
Corn	21.4	10	35.3	14.3	28.6	20
Peanut	21.4	20	23.5	21.4	21.4	26.7
Soybean	35.7	30	26.5	28.6	28.6	33.3
Weeds	7.1	20	5.9	14.3	7.1	6.7
Without crop	14.3	20	2.9	14.3	7.1	6.7
Autumn						
Barley	0	10.7	0	4.2	0	4.5
Corn	0	32.1	40	25	0	27
Peanut	50	17.9	40	16.7	50	9.1
Sorghum	0	3.6			25	0
Soybean	50	32.1	20	50	25	54.5
Weeds	0	3.6	0	4.2	0	4.5

Spring, summer and autumn seasons in the rural zone of Chucul (Córdoba).

were associated with corn and peanut crops and inactive ones with soybean (Table 1).

For *Calomys venustus* in spring, the associations between crop vegetation and both active and inactive borders were significant (X^2=6.5, d.f.=1, p=0.01, and X^2=7.4, d.f.=1, p=0.007, respectively). Both border types were mainly associated with corn crops (Table 1). In summer, a significant association for *C. venustus* was registered for both active (X^2=60.5, d.f.=5, p<0.001) and inactive borders (X^2=62.1, d.f.=5, p<0.001). Active borders were associated with corn, soybean and peanut crops, whereas inactive borders were associated with soybean and peanut (Table 1). In autumn, there was also a significant association between active and inactive borders for *C. venustus* with cropfield vegetation (X^2=38.5, d.f.=2, p<0.001 and X^2=78.8, d.f.=4, p<0.001, respectively). In autumn, active borders were adjacent to peanut crops as frequently as inactive borders were to soybean crops (Table 1).

Rodent-rodent associations

From the comparisons of active and inactive borders using the coincidence matrix, *Akodon azarae* and *Calomys musculinus* were shown to be alone rather than sharing the borders (both active and inactive) with other rodent species in spring and summer. In autumn, the same pattern was registered for active borders but not for inactive ones. In the latter, *A. azarae*, *C. musculinus* and *C. venustus* were present in a higher number of shared borders rather than alone (Table 2).

Calomys musculinus shared proportionally more borders with *C. venustus*, and *vice versa*, than those they each shared with *Akodon azarae*. This was particularly observed at the beginning and middle of the reproductive cycle, i.e., the spring and summer seasons.

The pairwise comparisons represented by the Cole index showed that, in spring, the three interactions (*Akodon azarae-Calomys musculinus*, *A. azarae-C. venustus* and *C. musculinus-C. venustus*) were negative but not <-0.38 (Table 3). In summer, the interactions between *A. azarae-C. musculinus*, and between *A. azarae-C. venustus* were negative, with the former being stronger than the latter. Meanwhile, the interaction between *C. musculinus-C. venustus* was also negative but near zero, suggesting a random association (Table 3). Finally, in autumn, the value of the Cole index varied for the three pairs of interactions: it was positive for *A. azarae-C. musculinus* and negative for *C. musculinus-C. venustus*. A perfect positive association was obtained for *A. azarae-C. venustus* species (Table 3).

Table 2 Number of active and inactive borders (defined for each particular rodent species in lines) where another or the same species was captured (in column) by season.

	Aa	Cm	Cv
Spring			
Active border			
Aa	**4**	2	1
Cm	2	**5**	1
Cv	1	1	**2**
Inactive border			
Aa	**5**	3	1
Cm	3	**9**	2
Cv	1	2	**1**
Summer			
Active border			
Aa	**10**	2	3
Cm	2	**26**	9
Cv	3	9	**4**
Inactive border			
Aa	**10**	0	1
Cm	0	**9**	5
Cv	1	5	**9**
Autumn			
Active border			
Aa	**1**	1	1
Cm	1	**4**	1
Cv	1	1	**3**
Inactive border			
Aa	**6**	12	13
Cm	12	**7**	10
Cv	13	10	**3**

Spring, summer and autumn seasons in the rural zone of Chucul (Córdoba).
Aa, *Akodon azarae*; Cm, *Calomys musculinus*; Cv, *C. venustus*.

Table 3 Cole association index for the pairs of species *Akodon azarae-Calomys musculinus*, *A. azarae-C.venustus* and *C. musculinus-C. venustus*, analyzed in the spring, summer and autumn seasons.

Pair of species	Cole index
Spring	
Aa-Cm	-0.26
Aa-Cv	-0.36
Cm-Cv	-0.38
Summer	
Aa-Cm	-0.89
Aa-Cv	-0.63
Cm-Cv	-0.04
Autumn	
Aa-Cm	0.56
Aa-Cv	1
Cm-Cv	-0.43

Rural zone of Chucul, Córdoba.
Aa, *Akodon azarae*; Cm, *Calomys musculinus*; Cv, *C. venustus*.

Habitat analyses at microhabitat scale

Sorghum halepense was the only vegetation variable that showed significant differences between active and inactive trap sites for *Akodon azarae* (F1,17=5.92, p=0.026). Active trap sites had a higher average cover (mean=62.7±35.5) than inactive ones (mean=27.5±23.7). For *Calomys musculinus*, *Bidens subalternans* cover was the only variable significantly different among active and inactive trap sites (F1,23=13.28, p=0.001), with higher coverage in inactive trap sites than in active ones. Finally, for *C. venustus* species, no vegetation variable showed differences between active and inactive trap sites.

Discussion

The proportional number of active/inactive borders increased from spring to summer and declined in autumn, consistent with the length of the breeding period of the species considered, which lasts from spring to autumn with a peak in summer (Crespo 1966, Pearson 1967, Dalby 1975, Mills et al. 1991, Polop 1996). The methodology used to define active/inactive borders was based on pregnant and lactating females. Although the probability of detecting them may be low because lactating females tend to remain in nests taking care of the offspring, the possible underestimation of active borders would have been systematically committed along the studied period.

Rodent total abundance did not vary between active and inactive borders in any season. If the reproductively active condition was related to high quality habitat, abundance would be higher in better habitats. This was registered for *Calomys musculinus*, which was more abundant in active than in inactive borders in summer. The summer season could reflect a particular meaning of habitat quality at the peak of *C. musculinus* breeding season (de Villafañe and Bonaventura 1987, Mills et al. 1991, 1992, Mills and Childs 1998, Simone et al. 2010). The same response was expected for *C. venustus* (Polop et al. 2005). For *Akodon azarae*, for which the highest reproductive effort is observed in overwintering animals (Zuleta et al. 1988), it would be expected to find different abundances between border types in spring. However, for these two latter species, we did not find any significant differences in abundance between active and inactive borders.

Although the association with vegetation cover in the period of reproductive activity may be related to specific food requirements of reproductive females (Bonaventura et al. 1992, Mills et al. 1992, Bilenca and Kravetz 1998, Busch et al. 2000), we found no differences for most of the plant species between active/inactive border types. This could be related to the situation that both border types showed a total cover higher than 70% in all seasons. We detected only some differences for *Akodon azarae* in spring. Also, at the microhabitat scale, the higher cover of *Sorghum halepense* registered at active trap sites, in comparison with inactive ones during summer, would be in agreement with other results that have shown a high green cover associated with the reproductive condition of *A. azarae* females (Bonaventura et al. 1992, Bilenca and Kravetz 1998). For this sex, reproductive performance would rely on its ability to acquire specific resources (green cover, insects) (Bilenca and Kravetz 1998, Castellarini et al. 2003). In our study, the vegetation cover would be an important resource for protection rather than for alimentary supply.

Calomys musculinus showed similar associations with crop types in summer and autumn: it was active in borders contiguous mainly to corn and inactive in borders contiguous to soybean. In autumn, *C. musculinus* was also active in borders contiguous to peanut crops. *Calomys musculinus* occupies “border” habitats throughout the year. From these habitats, it colonizes the fields when crops offer a good cover and settles there until harvest, when plowing destroys the habitat, causing high mortality and the dispersion of individuals back to the border habitats (de Villafañe et al. 1988, Ellis et al. 1997). Corn has been described as an alimentary item for *C. musculinus* (Dellafiore and Polop 1994), and may be important as alimentary item for a generalist species (that have access to fields) in the peak of its reproductive period. In the southern region of Córdoba Province, peanut is the second summer crop, following corn. Because of its similar agricultural cycle, it could also offer shelter and a food supply to *C. musculinus*, but there are no previous studies about this. *Calomys venustus* was active in borders contiguous to different crops, with the association with peanut crops being registered in summer and autumn. It is difficult to interpret this result as *C. venustus* has been characterized as omnivorous with a tendency toward granivory during summer, but peanut was not identified as one of its alimentary items (Castellarini et al. 1998). However, unlike *C. musculinus*, which may make incursions into cropfields, *C. venustus* almost exclusively inhabits relatively stable habitats (Kravetz and Polop 1983, Priotto and Polop 1997, Polop et al. 2005). *Akodon azarae* was, in general and in comparison to the other two rodent species, more associated to soybean crops in spring and summer seasons. It is known that soybean is not consumed by this rodent (Bilenca and Kravetz 1998, Castellarini et al. 2003). Bilenca and Kravetz

(1998) stated that borders are the only type of habitats that can provide year-round favorable conditions for *A. azarae*, and Busch et al. (2001) concluded that this rodent species prefers borders despite the high selection cost of continuously rejecting cropfields.

In relation to the results of the coincidence matrix, the comparisons made for active and inactive borders among species showed that, in spring and summer seasons, *Akodon azarae* and *Calomys musculinus* were present in a greater number of borders where they were alone than in borders that they shared with other species, independent of their reproductive condition. Therefore, exclusivity was observed at the beginning and peak of the breeding season; in autumn, it seemed to relax. *Akodon azarae*, *C. musculinus* and *C. venustus* are sympatric species in cropfield borders, but the former exert a strong effect of dominance over the other two (Busch and Kravetz 1992, Busch et al. 2005). Regarding the reproductive condition of species, the Cole index revealed that in spring and summer, *A. azarae* and *C. musculinus* were reproductive in different borders, whereas in autumn, they were reproductive in the same borders. This would be in agreement with the observation made by Busch and Kravetz (1992) that these two rodents were negatively related in spring and summer because of interspecific competition during the breeding period. A similar situation was observed for *A. azarae* and *C. venustus*, which were reproductive in different borders in spring and summer. However, they were reproductive in all the same borders in autumn (the Cole index revealed a perfect positive association). The latter result differs from what Priotto and Polop (1997) observed for these two rodents: their association was defined as random as the Cole index was near a zero value. Nevertheless, these authors assessed the association of rodent co-occurence, whereas in this study we assessed the association of the reproductive condition of rodents. Finally, *C. musculinus* and *C. venustus* were reproductive in different borders in spring and autumn, but they were randomly distributed in borders, with regard to reproductive condition, in summer.

In summary, the environmental variables useful for distinguishing active borders from inactive ones were different for each rodent species. In this sense, vegetation cover seemed to be important for *Akodon azarae* at the two habitat scales analyzed, i.e., border and microhabitat. However, the crop type adjacent to the border habitat would allow differentiating active/inactive borders for *Calomys musculinus*. In the case of *C. venustus*, we could not identify a variable that reflected differences between border types. The interspecific association analyses, considering the reproductive condition, would suggest interference by competition, which would be reflected at the beginning of the breeding season and markedly accentuated at the peak of it. The mentioned associations would be related to the use that each rodent species makes of border and cropfield habitats, together with the resources (food and refuge) that these offer in each moment of the breeding period. Nevertheless, to support these results, experimental approaches should be conducted that consider the manipulation of vegetation cover and crop types and assessment of the reproductive performance of different rodent species.

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Appendix I

Floristic composition of cropfield borders classified as active and inactive for *Akodon azarae*, *Calomys musculinus* and *C. venustus* rodent species in spring. Rural zone of Chucul (Córdoba). ** indicates exclusivity of that plant species for that border type.

Rodent species	Border	Plant species	
Akodon azarae	Active	*Bidens subalternans*** *Briza subaristata*** *Bromus catharticus* *Cynodon dactylon* *Diplachne uninervia***	*Hirschfeldia incana* *Oenothera indecora*** *Solidago chilensis*** *Sorghum halepense* *Stipa papposa***
	Inactive	*Bromus catharticus* *Cenchrus myosuroides*** *Cestrum parqui*** *Chenopodium album*** *Clematis montevidensis*** *Cynodon dactylon*	*Eleusine indica*** *Hirschfeldia incana* *Ligustrum lucidum*** *Sorghum halepense* *Stipa neesiana*** *Ulmus pumila***
Calomys musculinus	Active	*Bidens subalternans* *Bromus catharticus* *Clematis montevidensis* *Cynodon dactylon* *Diplachne uninervia***	*Foeniculum vulgare*** *Hirschfeldia incana* *Oenothera indecora*** *Sorghum halepense* *Stipa papposa*
	Inactive	*Bidens subalternans* *Bromus catharticus* *Cenchrus myosuroides*** *Cestrum parqui*** *Chenopodium album*** *Clematis montevidensis* *Cynodon dactylon*	*Digitaria sanguinalis*** *Gleditsia triacanthos*** *Hirschfeldia incana* *Ligustrum lucidum*** *Solidago chilensis*** *Sorghum halepense* *Stipa papposa*
Calomys venustus	Active	*Cynodon dactylon* *Diplachne uninervia***	*Foeniculum vulgare*** *Sorghum halepense***
	Inactive	*Bidens subalternans*** *Bromus catharticus***	*Cynodon dactylon* *Sorghum halepense*

Appendix II

Floristic composition of cropfield borders classified as active and inactive for *Akodon azarae*, *Calomys musculinus* and *C. venustus* rodent species in summer. Rural zone of Chucul (Córdoba). ** indicates exclusivity of that plant species for that border type.

Rodent species	**Border**	**Plant species**	
Akodon azarae	Active	*Bidens subalternans* *Bromus catharticus*** *Cenchrus myosuroides* *Clematis montevidensis* *Comelina erecta*** *Cynodon dactylon*	*Gleditsia triacanthos*** *Oxalis conorriza* *Sorghum halepense* *Stipa sp.* *Stipa tenuis*** *Zinnia peruviana***
	Inactive	*Bidens subalternans* *Cenchrus myosuroides* *Clematis montevidensis* *Cynodon dactylon* *Diplachne uninervia*** *Gleditsia triacanthos* *Hirschfeldia incana*** *Oxalis conorriza*	*Paspalum quadrifarium*** *Setaria parviflora*** *Setaria verticillata*** *Sorghum halepense* *Stipa sp.* *Ulmus pumila*** *Valeriana effusa***
Calomys musculinus	Active	*Baccharis ulicina*** *Bidens subalternans* *Carduus nutans*** *Cenchrus myosuroides* *Clematis montevidensis* *Comelina erecta* *Coniza bonariensis*** *Cotula australis*** *Cynodon dactylon* *Dichondra microcalix* *Digitaria sanguinalis*** *Diplachne uninervia* *Gleditsia triacanthos***	*Hordeum stenostachys*** *Lippia turbinata*** *Oxalis conorriza* *Paspalum quadrifarium*** *Pfaffia gnaphaloides*** *Setaria parviflora*** *Setaria verticillata*** *Sorghum halepense* *Stipa neesiana*** *Stipa sp.*** *Stipa tenuis* *Ulmus pumila*
	Inactive	*Bidens subalternans* *Bromus catharticus*** *Cenchrus myosuroides* *Chenopodium album*** *Clematis montevidensis* *Comelina erecta* *Cynodon dactylon* *Dichondra microcalix*	*Diplachne uninervia* *Eleusine indica*** *Oxalis conorriza* *Sorghum halepense* *Stipa tenuis* *Ulmus pumila* *Valeriana polybotrya*** *Zinnia peruviana***
Calomys venustus	Active	*Baccharis ulicina*** *Bidens subalternans* *Cenchrus myosuroides* *Clematis montevidensis* *Cynodon dactylon* *Dichondra microcalix* *Diplachne uninervia* *Gleditsia triacanthos*** *Ulmus pumila*	*Lippia turbinata*** *Oxalis conorriza* *Paspalum quadrifarium*** *Prunus persica*** *Setaria parviflora*** *Setaria verticillata* *Sorghum halepense* *Stipa sp.* *Stipa tenuis*
	Inactive	*Baccharis pingraea*** *Bidens subalternans* *Bromus catharticus*** *Cenchrus myosuroides* *Chenopodium album*** *Clematis montevidensis* *Cotula australis*** *Cynodon dactylon* *Dichondra microcalix* *Diplachne uninervia*	*Lippia turbinata* *Oxalis conorriza* *Setaria verticillata* *Sorghum halepense* *Stipa neesiana*** *Stipa sp.* *Stipa tenuis* *Ulmus pumila* *Valeriana effusa*** *Zinnia peruviana***

Appendix III

Floristic composition of cropfield borders classified as active and inactive for *Akodon azarae*, *Calomys musculinus* and *C. venustus* rodent species in autumn. Rural zone of Chucul (Córdoba). ** indicates exclusivity of that plant species for that border type.

Rodent species	Border	Plant species	
Akodon azarae	Active	*Cynodon dactylon* *Diplachne uninervia*	*Sorghum halepense* *Stipa tenuis*
	Inactive	*Acaena miriophylla*** *Baccharis pingraea*** *Bidens subalternans*** *Bromus catharticus*** *Cenchrus myosuroides*** *Clematis montevidensis*** *Cortaderia selloana*** *Cynodon dactylon* *Diplachne uninervia* *Hirschfeldia incana*** *Ligustrum lucidum*** *Lippia turbinata***	*Melia azederach*** *Oxalis conorriza*** *Salsola kali*** *Schizachyrium c.*** *Setaria parviflora*** *Setaria sp*** *Setaria verticillata*** *Sorghum halepense* *Stipa papposa*** *Stipa tenuis* *Ulmus pumila***
Calomys musculinus	Active	*Acaena miriophylla*** *Bidens subalternans* *Cynodon dactylon* *Hirschfeldia incana*	*Setaria sp*** *Sorghum halepense* *Stipa tenuis***
	Inactive	*Bidens subalternans* *Bowlesia incana*** *Cenchrus myosuroides*** *Clematis montevidensis*** *Cynodon dactylon* *Diplachne uninervia***	*Hirschfeldia incana* *Lippia turbinata*** *Melia azederach*** *Oxalis conorriza*** *Sorghum halepense*
Calomys venustus	Active	*Bidens subalternans* *Cenchrus myosuroides* *Clematis montevidensis* *Cynodon dactylon* *Diplachne uninervia* *Oxalis conorriza***	*Setaria parviflora*** *Setaria verticillata*** *Sorghum halepense* *Stipa papposa* *Stipa tenuis*
	Inactive	*Bidens subalternans* *Bromus catharticus*** *Cenchrus myosuroides* *Clematis montevidensis* *Cortaderia selloana*** *Cynodon dactylon* *Diplachne uninervia* *Hirschfeldia incana*** *Lippia turbinata***	*Melia azederach*** *Salsola kali*** *Schizachyrium c.*** *Setaria sp*** *Sorghum halepense* *Stipa papposa* *Stipa tenuis* *Ulmus pumila***