# Habitat use by corn mice (*Calomys musculinus*) in cropfield borders of agricultural ecosystems in Argentina

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**Abstract**

   ***Context.*** *Calomys musculinus* (Cricetidae, Sigmodontinae) is a small rodent species widely distributed in Argentina and particularly abundant in agroecosystems of the Pampean region, where it is known to select border habitats over cropfields.
   ***Aims.*** The aim of the present research was to assess habitat use by *C. musculinus* in cropfield borders. Assuming that the number of rodent captures in each border reflects the intensity of use, we intended to identify the habitat characteristics that would account for abundance differences among borders.
   ***Methods.*** Seasonal trapping sessions were carried out in borders of the rural zone of Chucul, Córdoba. Environmental variables were registered from both field surveys and remote-sensing imagery. Generalised linear models were used to identify the habitat variables associated with *C. musculinus* habitat use.
   ***Key results.*** General fit of the models was fairly good; spring, summer and autumn models explained more than 55% of the variation in *C. musculinus* abundance among borders. Individual plant species were significant predictors of *C. musculinus* abundance, but they varied with seasons, whereas tree cover and border width were significant predictors in most seasons studied. In general, rodent abundance was positively associated with peanut and maize crops or maize stubbles and negatively related to soybean or its stubbles. In the coldest seasons, rodent abundance increased with increasing land-surface temperature of the border.
   ***Conclusions.*** Border use by *C. musculinus* appeared to respond to differences in border quality, which seems to be more affected by those environmental characteristics that entail a reduction of the predatory risk rather than by those that involve food supply. Crop-fields may partially afford *C. musculinus* food requirements.
   ***Implications.*** Because *C. musculinus* is the natural reservoir of a zoonotic agent, the identification of the habitat characteristics affecting rodent population numbers in borders may be of crucial importance for the implementation of ecologically based rodent-management strategies aimed at reducing human–rodent contacts. We suggest that wide borders, particularly those contiguous to maize and peanut cropfields, should be understood as priority sites for the implementation of specific control actions.

**Additional keywords:** agroecosystem, AHF, habitat selection, linear habitat, GLM, remote sensing.

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## Introduction

Most ecological studies require an assessment of the relationships between individuals in a population and their environment, both from theoretical and management points of views (Basille *et al.* 2008). Fretwell (1972) identified two factors affecting the distribution of dispersive animals, namely, habitat selection and habitat suitability. Distribution, then, may be considered as the result of a behavioural phenomenon involving stimuli and responses; stimuli include differences in habitat suitability, which give rise, through evolution, to habitat selection, which in turn, determines habitat distribution (Fretwell 1972). Habitat-

selection theory assumes an ideal free distribution in which individuals freely disperse to those habitats where their fitness is optimised (Fretwell and Lucas 1970; Fretwell 1972; Sutherland 1996). The ecological consequence of this process is that population distribution will be uneven in habitats with internal heterogeneity. For any management decision, it is crucial then, to identify the habitat clues which individuals are based on to select patches, i.e. 'what do the organisms search for?' (Morris 1987; Wiens *et al.* 1993; Schaefer and Messier 1995). In this sense, quantitative distribution models and, particularly, generalised linear models, offer simple methods for the

formulation of species–habitat links, and the means for both predicting where species should occur and understanding the factors involved (Rushton *et al*. 2004).

The central Argentine Pampa is mainly formed by agroecosystems that may be defined as heterogeneous mosaics with temporal and spatial variations at diverse scales (Merriam 1988). The pampean landscape is the result of a fragmentation process and mainly consists of monocultures of a few crops, with a network of roadsides, fence lines, railroad rights-of-way and other border habitats (Ellis *et al*. 1997). The expansion of the agricultural area in Argentina and the resulting increase in the proportion of field surface has favoured, at least in certain localities, an increment in *Calomys* species densities (de Villafañe *et al*. 1977).

*Calomys musculinus* is widely distributed in Argentina and it is found in most central and north-western regions (Olrog and Lucero 1981; Redford and Eisenberg 1992). *C. musculinus* is one of the most abundant species of the rodent assemblages in southern Córdoba province (Kravetz and Polop 1983; Polop and Sabattini 1993), contributing up to 80% of rodent community (de Villafañe and Bonaventura 1987). Its ecology has been mainly studied in relation to its role as a reservoir of the Junín virus, etiological agent of the Argentine hemorrhagic fever (AHF). *C. musculinus* shows wider habitat and trophic niches than its co-specifics in rural areas (Polop *et al*. 1985) and has been described as a habitat tolerant (Busch and Kravetz 1992*a*, 1992*b*; Busch *et al*. 1997) and as an opportunistic species (Mills *et al*. 1991; Ellis *et al*. 1998). Although *C. musculinus* has been found in different types of habitat within agroecosystems (cropfields, their borders and natural pastures) (Kravetz and Polop 1983; Mills *et al*. 1992*a*; Busch *et al*. 1997; Ellis *et al*. 1997), it was found particularly to select and inhabit weedy cropfield borders associated with fence lines (Busch *et al*. 2000). Field borders are less disturbed habitats than cropfields, because they are not directly exposed to agricultural practices and offer a year-round suitable habitat for rodents, providing them with food and shelter resources (Mills *et al*. 1991; Busch and Kravetz 1992*a*). Borders, therefore, remain as relatively stable habitats within the highly human-modified landscape that agroecosystems represent.

In a previous study, we reported that pampean field borders are able to sustain a vast rodent assemblage, where some species segregate differently regarding border vegetation features and their surroundings (Simone *et al*. 2010). In the present study, we focus on the habitat use of *C. musculinus* in borders. Under the general hypothesis that variations in *C. musculinus* abundance in borders respond to differences in habitat quality, the aim of the present study was to address the environmental factors that account for that 'quality' (or suitability). We expect that rodent abundance will be related to both border-vegetation (cover and diversity) and border-structure variables. We also expect seasonal variations to occur in border-vegetation, but not in border-structure variables. To identify the habitat features that would explain the differences in border use, we modelled rodent abundance as a function of habitat variables registered in borders and their surroundings. In doing so, we assumed that the number of captures in each border reflects the border-use intensity (Busch *et al*. 2000).

Although the present study was not intended to be a longitudinal study (the sampled borders were different from one season to the next one), habitat-use analyses were carried out for each season because the vast evidence of seasonality in *C. musculinus* population dynamics. This seasonal pattern, like that of many other rodent species, seems to be driven by the interaction of the basic processes of recruitment, survival and migration, with both endogenous (intra- and inter-specific competition) and exogenous (climate and environmental) factors (Busch and Kravetz 1992*a*, 1992*b*; Lima *et al*. 1999, 2001, 2002, 2006; Singleton *et al*. 2001; Stenseth *et al*. 2002, 2003; Priotto and Polop 2003; Andreo *et al*. 2009). In particular, agroecosystems are highly variable environments because of seasonal climate conditions and agricultural practices (Ghersa and Martínez-Ghersa 1991; Viglizzo *et al*. 2001, 2002; Paruelo *et al*. 2005). *C. musculinus* populations in agroecosystems of central Argentina increase their abundance from spring to summer, reaching a peak in late summer/early autumn and decline sharply from late autumn to winter (Busch *et al*. 1984; Mills *et al*. 1992*a*, 1992*b*; Simone 2010; Sommaro *et al*. 2010). This annual pattern contributes to the characteristic epidemiology of AHF (Mills *et al*. 1992*b*).

## Study area

The study was carried out in the rural area of Chucul (32°55′06″S, 64°10′09″W; at 395 m asl), in Río Cuarto Department, Córdoba Province, Argentina (Fig. 1). The climate of the region is temperate, with an average annual temperature of 23°C in January and 9°C in July. Annual rainfall is high, especially in summer, averaging 800–900 mm. The study area corresponds to a well drained undulating plain with soft slopes (Bianco *et al*. 1987) and belongs to the phytogeographic District of 'El Algarrobo' in the Province of 'El Espinal' (Cabrera 1953). As a result of agriculture and cattle farming, natural vegetation has undergone marked alterations. At present, the transitional landscape of woodland and pampean native grassland (*Stipa* spp.) persists in small remnants (patches) among cropfields. The fragmented landscape consists mainly of individual cropfield parcels, enclosed by wire fences, with borders dominated by weedy species. These cropfield borders (from now on 'borders') constituted the sampling sites used in the present study.

## Material and methods

### Trapping procedure

Small-mammal trapping in borders was conducted in spring 2005 (December), summer 2006 (March), autumn 2006 (May), winter 2006 (August–September), summer 2007 (February), autumn 2007 (June), winter 2007 (August–September) and spring 2007 (December). A border was defined as the vegetation below cropfield fence lines at both sides of a rural road (Fig. 2). Borders were 80 m long on average and they were, at least, 100 m apart from each other. In total, 24 borders were selected from satellite images in each season, and then localised in the field with a GPS. Location of the borders differed in each season. For rodent trapping, two trap lines of 10 traps each were placed at both sides of the road, alternating Sherman live-traps (23 × 9 × 8 cm) with snap-traps. All traps were baited with a mixture of peanut butter and cow fat. Traps were checked every
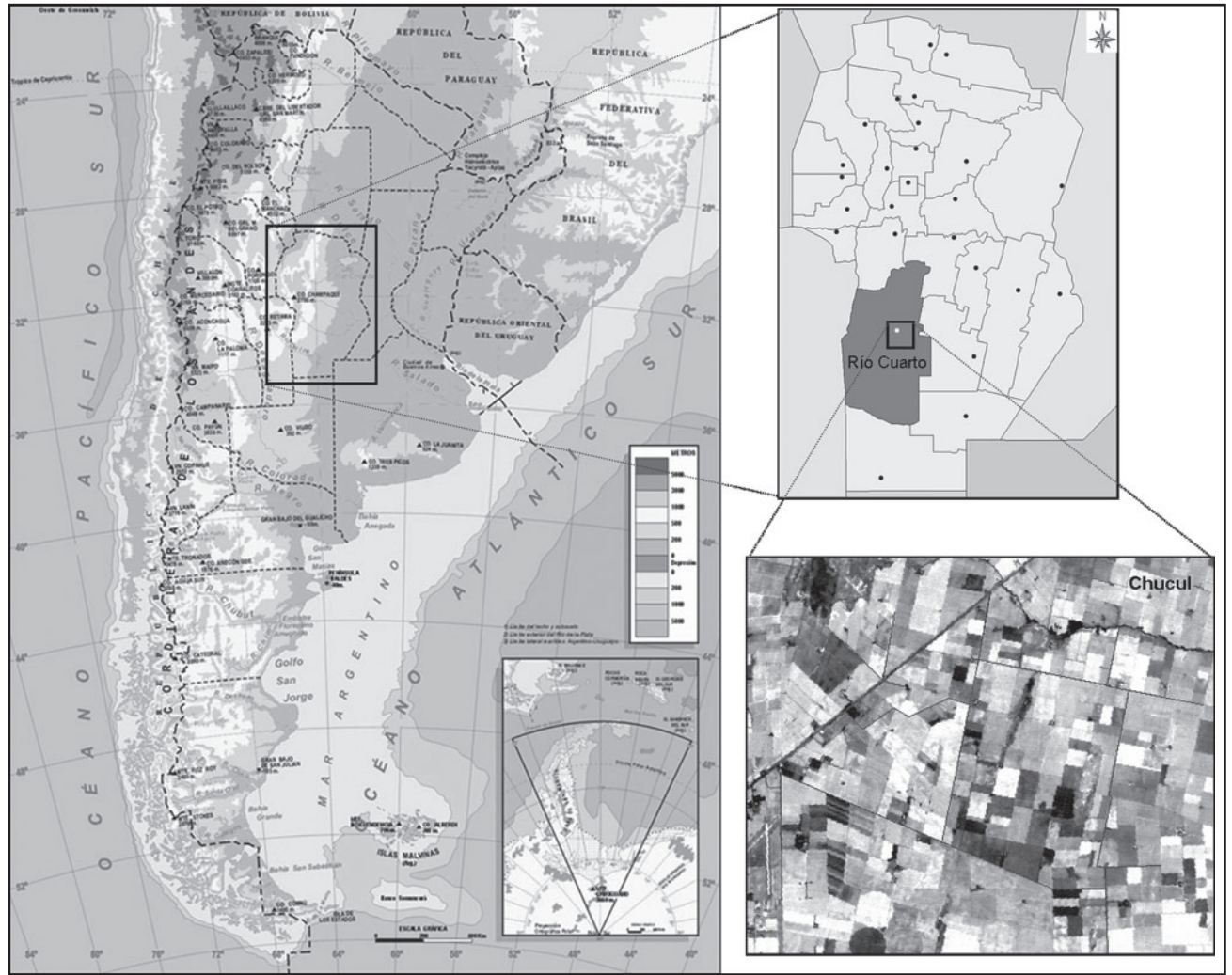
**Fig. 1.**   Political map of Argentina (left), showing the location of Chucul rural area (right, bottom) in Córdoba province (right, top).
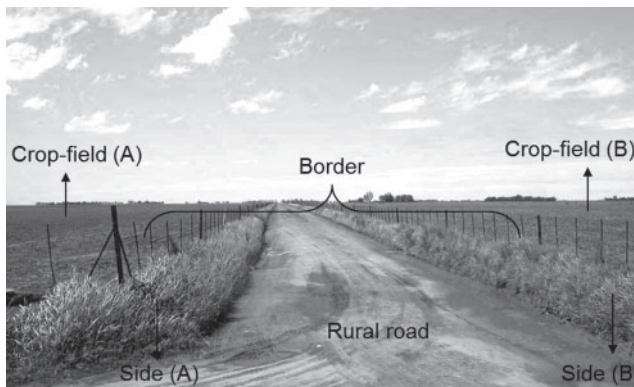


**Fig. 2.**   Scheme of a *border*, showing the fence lines and crop fields at both sides of the rural road, Chucul rural area.

morning for two consecutive weeks (eight nights). All trapped rodents were removed from the field and taken to the laboratory for species identification and biometric measurements.

*Environmental variables*

Habitat variables were recorded in borders and their surrounding cropfields, and were registered both from field surveys and by remote-sensing simultaneously to rodent trapping. Vegetation censuses were carried out using a 1-m² quadrat (modified from Dueser and Shugart 1978) centred over the trap site. Up to 10 trap sites were surveyed in each border. Variables recorded in each quadrat were total vegetation cover, stratum cover (Stratum 1: plants below 10 cm; Stratum 2: plants between 10 and 30 cm; and Stratum 3: plants above 30 cm) and cover of each plant species. Only those plant species covering more than 5% of a single quadrat and present in more than 10% of the surveyed borders were considered for analysis. Values from the 10 quadrats were averaged to obtain a unique border value for total, strata and individual plant-species cover. Presence of seeds was recorded for each vegetation stratum. The percentage of the border covered by trees was estimated from photographs taken during field surveys. Border-diversity measurements were estimated using the surveyed cover data, and included a diversity index (*H'*) (Shannon and Weaver 1962), richness (*S*, total number of plant

species) and evenness (*E*, relative apportionment of abundances among the present species) (Magurran 1991). Border structure was evaluated from border width and height. Border width (cm) was recorded at both sides of the fence line until the border physiognomy changed to that of the crop. Border height was measured from road line, up to the fence line, and it was classified in (1) road line level, (2) up to 1 m and (3) above 1 m. All these measurements were taken at both sides of the road and then combined into a unique value per border.

The composition of the cropfields next to the border was evaluated considering any contiguous monoculture parcel (field) as a sample unit. Because each border was adjacent to two crop fields, sometimes there was more than one crop type registered for each border. Crop types considered were soybean, maize, peanut, alfalfa and wheat. Uncultivated parcels were generally covered by a mixture of weeds or by stubbles. Each crop type, the mixture of weeds and the stubbles were considered unique variables whose values were the phenological stages in which they were observed. Phenological stages were defined as follows: (1) crop stages (1, green plants providing <25% of cover; 2, green plants providing between 25% and 80% of cover; 3, green plants providing >80% of cover; 4, senescent plants (ready to be harvested)); (2) mixture of weeds stages (1, plants shorter than 20 cm and providing <25% of cover; 2, plants shorter than 20 cm and providing >25% of cover; 3, plants higher than 20 cm providing >25% of cover); and (3) stubble stages (1, <50% of the parcel covered; 2, >50% of the parcel covered with fallen stubble; 3, >50% of the parcel surface covered with stood stubble). In winter, stubbles were considered according to the crops they proceeded from. Field variables, when binary, were entered as factors with a category of reference, otherwise they were entered as covariates.

The remote-sensing variables were obtained from Landsat TM satellite images, which were acquired almost simultaneously to the fieldwork dates, namely, 20 November (Spring 2005), 8 February (Summer 2006), 15 May (Autumn 2006), 3 August (Winter 2006), 11 February (Summer 2007), 3 June (Autumn 2007), 21 July (Winter 2007) and 23 September (Spring 2007). Images were processed using ENVI 3.5, System Research. We estimated temperature (land-surface temperature, LST) and vegetation (normalised by difference vegetation index, NDVI) variables. The following two sample units were used to obtain temperature and vegetation-cover estimates: (1) the two or three pixels matching each border (for the estimation of 'NDVI_border' and 'LST' variables) and (2) all pixels fully or partly included in a buffer region of 100-m diameter (created in Arcview 3.2, ESRI, Inc., Redlands, CA) centred in the border (for the estimation of 'NDVI_buffer' variable). NDVI and LST calculations are described in detail in Simone *et al*. (2010).

### Statistical analysis

Differences in the seasonal captures of *C. musculinus* for the two studied years were assessed with a Mann–Whitney test. Habitat features related to the habitat use by *C. musculinus* were identified using generalised linear models (GLMs). In GLMs, the predicted values are determined by discrete and continuous predictors and by the link function (Bolker *et al*. 2009). Rodent abundance (assumed as a proxy for habitat use) was defined as the response

variable, and several environmental factors were included as explanatory variables. Because rodent abundance was a count variable, we performed GLMs with Poisson distribution and we used the log-link function. The environmental variables were evaluated for bivariate correlation and only non-correlated variables were included in the models. We contrasted several models for each season. The general fit of the models was assessed using a measure of deviance reduction ($D^2$-value), Akaike information criterion corrected for small sample size (AICc), difference in AICc (ΔAICc) with respect to the best model, log-likelihood, residual deviance and an overdispersion index (residual deviance/degrees of freedom). In GLMs, the fit of the model is optimised through deviance reduction, which can be easily converted into an estimated $D^2$ – equivalent to $R^2$ – by the formula

$$D^2 = (\text{null deviance} - \text{residual deviance})/\text{null deviance},$$

where the null deviance is the deviance of the model with the intercept only, and the residual deviance is the deviance that remains unexplained by the model after all final variables have been included (Guisan and Zimmermann 2000). AICc value is extensively used for ranking candidate models because $D^2$ – as $R^2$ – is useful as a descriptive statistic but not in model selection when considered alone (Burnham and Anderson 2002). Residual deviance is defined as –2 times the difference in log-likelihood between the current model and a saturated model (i.e. a model that fits the data perfectly) (Crawley 2007). Overdispersion is present when the deviance is at least twice the number of degrees of freedom and, if larger than five units, something is probably missing in the model and needs to be added (Lindsey 1999). Only models having ΔAICc within one or two units were considered for drawing inferences on border use by *C. musculinus* (Burnham and Anderson 2002). Variables included in each selected model were evaluated for significance by means of chi-square test. The best final model (most parsimonious) for each season was selected balancing AICc, $D^2$, overdispersion index and the number of predictors involved (Crawley 2007; Logan 2010). GLMs were implemented in PASW 18 (SPSS 18) statistical software (IBM, Armonk, NY).

### Results

We captured a total of 838 *C. musculinus* individuals. There were not significant differences in rodent captures between the two studied years ($U_{(1)} = 4567.0$, $P = 0.915$). During the first year, we captured 397 individuals of *C. musculinus* and during the second year, 441. The sex ratio (males : females) was 1.64 in the first year and 1.46 in the second one. The seasonal pattern of variation in the number of captures was also very similar between years (Fig. 3). Population peaks were observed in autumn, whereas the lowest values were registered in winter.

Several generalised linear models were fitted for each season data to evaluate the variables associated with border use by *C. musculinus*. The best five models for each season are shown in Table 1. These models involved different categories of variables referred to as border vegetation, border structure, cropfields and/or remote sensing. From these five models, we selected the best one for each season to analyse in detail *C. musculinus* habitat use in borders. In some seasons, the best
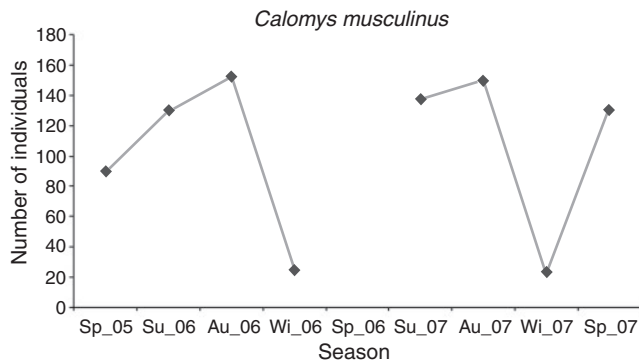
**Fig. 3.** Seasonal pattern of variation in the number of captures of *Calomys musculinus* for the two studied years in the rural area of Chucul.

model was clearly identifiable, whereas in others, more than one model was equally acceptable (e.g. Winter 2007). The selected habitat-use models per season are presented in Table 2. Summer and autumn models reached quite high explanatory levels as measured by $D^2$; more than 70% of the variation in *C. musculinus* abundance in borders was explained by the environmental variables considered by the GLMs. Whereas the model for Spring 2005 reached 50% of explanatory power, the model for Spring 2007 was the best model obtained, explaining >80% of *C. musculinus* variation in abundance. Winter models showed <45% of explanatory power. Most variables included in the different models were significant at a confidence level of 95% (Table 2).

The fitted model for Spring 2005 explained almost 60% of the variation in *C. musculinus* abundance among borders (Table 1). This model included six significant environmental variables corresponding to the categories border vegetation and border structure, obtained from field survey, and remote sensing, related to border surroundings (Table 2). *C. musculinus* was positively related to *D. uninervia* cover and to border width. Also, rodent abundance was significantly related to NDVI_buffer and negatively associated with *C. montevidensis*, *S. halepense* and tree cover. The model for Spring 2007 was the best model obtained. It explained 83% of the variation in *C. musculinus* abundance (Table 1). This model, like the previous one, included border variables but also some others related to cropfields (Table 2). *C. musculinus* abundance was higher in borders where the third stratum, *B. subalternans* and *C. montevidensis* cover were high. However, it varied negatively with increases of *B. catharticus* cover. Regarding cropfields, rodent abundance was positively related to borders adjacent to peanut or maize crops and to those fields covered by stubbles.

Models for both summer seasons explained more than 70% of the variation in *C. musculinus* abundance (Table 1). The model for Summer 2006 included five significant predictors (Table 2). Rodent abundance was positively related to *S. halepense* cover and border richness. As in the previous season, it was positively related to border width and negatively related to tree cover. Rodent abundance in borders was also positively affected by the adjacency of maize crops. The model for Summer 2007 explained 80% of rodent abundance variation (Table 1) and it included five different variables (Table 2). As in the previous summer, *C. musculinus*

abundance was positively related to border richness and also to *O. conorriza* and *Setaria* sp., and negatively related to *D. uninervia*. *C. musculinus* abundance was lower in those borders contiguous to soybean crops.

In Autumn 2006, 70% of the variation in rodent abundance was significantly explained by six variables (Table 1). The model for Autumn 2006 did not include any plant species (Table 2). *C. musculinus* was negatively associated with border-vegetation evenness. Once again, it was significantly more abundant in wide borders and in borders contiguous to cropfields covered by stubbles. Regarding remote-sensing variables, rodent abundance was negatively associated with both NDVI indexes and positively related to LST. For Autumn 2007, the fitted model explained almost 80% of the variation in rodent abundance (Table 1) and it included seven different variables (Table 2). Rodent abundance increased with the cover of *B. subalternans*. On the contrary, abundance decreased as *C. dactylon*, *D. uninervia* and tree cover increased. Regarding cropfields, *C. musculinus* abundance was positively associated with maize stubbles. Finally, *C. musculinus* was also positively related to the NDVI index of the buffer region and LST.

Models for both winters showed lower explicative power than models for all other seasons. On the one hand, the model for Winter 2006 explained almost 30% of variation in rodent abundance (Table 1). This model included only two variables (Table 2). *C. musculinus* was positively related to *S. halepense* cover and it was more abundant in those borders contiguous to fields with maize stubbles. On the other hand, the model for Winter 2007 explained almost 45% of variation in *C. musculinus* abundance (Table 1), with four different variables belonging to border-vegetation, cropfields and remote-sensing categories (Table 2). *C. musculinus* was more abundant in borders with higher total cover but lower richness. It also appeared to be more abundant in borders contiguous to fields without soybean stubbles. Finally, as in autumn, rodent abundance was positively related to the LST variable.

## Discussion

Although *C. musculinus* is defined as a generalist species that shows a wider habitat and trophic niche than its co-specifics, it is well documented that it shows differences in abundances according to habitat type (Kravetz and Polop 1983; Mills *et al*. 1992*a*; Busch *et al*. 1997; Ellis *et al*. 1997). Moreover, previous studies performed in agroecosystems have shown that *C. musculinus* selects borders over cropfields (Busch *et al*. 2000) and that it segregates differently from the other more abundant rodent species of the assemblage when assessing the structure of the borders of rodent community (Simone *et al*. 2010). In the present study, we modelled *C. musculinus* abundance in borders against a variety of habitat characteristics to determine which of them would better explain the habitat use by *C. musculinus*.

All the resulting models significantly explained the variations in *C. musculinus* abundance among borders. Model fit was high in all seasons, except in winter. The low fit of winter models may be due to the generally low captures registered in this season. Because GLMs – as regression techniques – are designed to identify those variables causing the differences among units, and

**Table 1.**  **Best five seasonal generalised linear models for *Calomys musculinus* habitat use in borders (*n* = 24) of the rural area of Chucul (from Spring 2005 to Spring 2007)**

Model structure: Cm, *Calomys musculinus* abundance; {type of habitat variable and number of ≠ variables of each type (in parenthesis)}; RS, remote sensing. $D^2$, goodness of fit index; $AIC_c$, Akaike information criterion corrected for small sample bias; $\Delta AIC_c$, difference in $AIC_c$ with respect to the best model; v, number of variables; Deviance/d.f., overdispersion index. Models with $\Delta AIC_c \leq 2$ are in **bold**

| Season | Model ID | Model structure | $D^2$ | $AIC_c$ | $\Delta AIC_c$ | v | Log-likelihood | Residual deviance | Deviance/d.f. |
|---|---|---|---|---|---|---|---|---|---|
| Spring 2005 | A | **Cm ~{border vegetation (4)+border structure (1)+RS (1)}** | **0.57** | **113.079** | **0.000** | **6** | **−46.040** | **28.530** | **1.678** |
| | B | **Cm ~{border vegetation (4)+border structure (1)}** | **0.50** | **113.357** | **0.278** | **5** | **−48.208** | **32.867** | **1.826** |
| | C | Cm ~{border vegetation (5)+border structure (1)} | 0.53 | 115.852 | 2.773 | 6 | −47.426 | 31.303 | 1.841 |
| | D | Cm ~{border vegetation (6)+border structure (1)} | 0.58 | 117.130 | 4.051 | 7 | −45.765 | 27.981 | 1.749 |
| | E | Cm ~{border vegetation (7)+border structure (1)} | 0.64 | 118.149 | 5.070 | 8 | −43.646 | 23.742 | 1.583 |
| Spring 2007 | A | **Cm ~{border vegetation (4)+cropfields (3)}** | **0.83** | **114.586** | **0.000** | **7** | **−44.493** | **19.788** | **1.237** |
| | B | Cm ~{border vegetation (4)+border structure (1)+cropfields (3)} | 0.85 | 117.996 | 3.410 | 8 | −43.569 | 17.941 | 1.196 |
| | C | Cm ~{border vegetation (4)+border structure (1)+cropfields (3)} | 0.74 | 129.652 | 15.066 | 8 | −49.398 | 29.597 | 1.973 |
| | D | Cm ~{border vegetation (3)+border structure (1)+cropfields (3)} | 0.63 | 138.297 | 23.711 | 7 | −56.349 | 43.499 | 2.719 |
| | E | Cm ~{border vegetation (2)+border structure (1)+cropfields (3)} | 0.55 | 141.926 | 27.340 | 6 | −60.463 | 51.728 | 3.043 |
| Summer 2006 | A | **Cm ~{border vegetation (3)+border structure (1)}** | **0.71** | **118.743** | **0.000** | **4** | **−52.705** | **33.870** | **1.783** |
| | B | **Cm ~{border vegetation (3)+border structure (1)+cropfields (1)}** | **0.73** | **119.940** | **1.197** | **5** | **−51.499** | **31.459** | **1.748** |
| | C | Cm ~{border vegetation (3)+border structure (1)+RS (1)} | 0.71 | 121.904 | 3.161 | 5 | −52.481 | 33.423 | 1.857 |
| | D | Cm ~{border vegetation (3)+border structure (1)+cropfields (1)+RS (1)} | 0.73 | 123.142 | 4.399 | 6 | −51.071 | 30.603 | 1.800 |
| | E | Cm ~{border vegetation (3)+border structure (1)+RS (2)} | 0.72 | 124.835 | 6.092 | 6 | −51.918 | 32.296 | 1.900 |
| Summer 2007 | A | **Cm ~{border vegetation (3)+cropfields (1)}** | **0.75** | **109.827** | **0.000** | **4** | **−48.247** | **14.819** | **0.780** |
| | B | **Cm ~{border vegetation (4)+cropfields (1)}** | **0.80** | **110.433** | **0.606** | **5** | **−46.746** | **11.817** | **0.657** |
| | C | **Cm ~{border vegetation (2)+cropfields (1)}** | **0.67** | **111.498** | **1.671** | **3** | **−50.697** | **19.719** | **0.986** |
| | D | Cm ~{border vegetation (4)+border structure (1)+cropfields (1)} | 0.83 | 113.209 | 3.382 | 6 | −46.105 | 10.535 | 0.620 |
| | E | Cm ~{border vegetation (4)+border structure (1)+cropfields (1)+RS (1)} | 0.84 | 116.697 | 6.870 | 7 | −45.549 | 9.423 | 0.589 |
| Autumn 2006 | A | **Cm ~{border vegetation (1)+border structure (1)+cropfields (1)+RS (3)}** | **0.70** | **127.116** | **0.000** | **6** | **−53.058** | **23.686** | **1.393** |
| | B | Cm ~{border vegetation (1)+border structure (1)+cropfields (1)+RS (3)} | 0.66 | 129.546 | 2.430 | 6 | −54.273 | 26.116 | 1.536 |
| | C | Cm ~{border structure (1)+cropfields (1)+RS (3)} | 0.63 | 130.868 | 3.752 | 5 | −56.964 | 28.427 | 1.750 |
| | D | Cm ~{border vegetation (1)+border structure (1)+cropfields (1)+RS (3)} | 0.62 | 133.064 | 5.948 | 6 | −56.032 | 29.633 | 1.743 |
| | E | Cm ~{border vegetation (2)+border structure (1)+cropfields (1)+RS (3)} | 0.68 | 133.172 | 6.056 | 7 | −53.786 | 25.142 | 1.571 |
| Autumn 2007 | A | **Cm ~{border vegetation (4)+cropfields (1)+RS (2)}** | **0.79** | **135.517** | **0.000** | **7** | **−54.959** | **43.739** | **2.734** |
| | B | Cm ~{border vegetation (4)+RS (2)} | 0.75 | 139.052 | 3.535 | 6 | −59.026 | 51.874 | 3.051 |
| | C | Cm ~{border vegetation (4)+border structure (1)+RS (2)} | 0.76 | 142.357 | 6.840 | 7 | −58.378 | 50.579 | 3.161 |
| | D | Cm ~{border vegetation (3)+RS (2)} | 0.72 | 143.193 | 7.676 | 5 | −63.126 | 60.074 | 3.337 |
| | E | Cm ~{border vegetation (2)+RS (2)} | 0.63 | 158.737 | 23.220 | 4 | −72.702 | 79.226 | 4.170 |
| Winter 2006 | A | **Cm ~{border vegetation (1)+cropfields (1)}** | **0.28** | **61.159** | **0.000** | **2** | **−26.980** | **17.521** | **0.834** |
| | B | Cm ~{border vegetation (1)+border structure (1)+cropfields (1)} | 0.29 | 63.898 | 2.739 | 3 | −26.897 | 17.355 | 0.868 |
| | C | Cm ~{border vegetation (1)+cropfields (1)+RS (1)} | 0.28 | 63.915 | 2.756 | 3 | −26.905 | 17.371 | 0.869 |
| | D | Cm ~{border vegetation (2)+cropfields (1)+RS (1)} | 0.31 | 66.630 | 5.471 | 4 | −26.648 | 16.858 | 0.887 |
| | E | Cm ~{border vegetation (1)+border structure (1)+cropfields (1)+RS (1)} | 0.29 | 67.099 | 5.940 | 4 | −26.883 | 17.328 | 0.912 |
| Winter 2007 | A | **Cm ~{border vegetation (1)+cropfields (1)+RS (1)}** | **0.38** | **64.516** | **0.000** | **3** | **−27.205** | **23.921** | **1.196** |
| | B | **Cm ~{border vegetation (2)+cropfields (1)+RS (1)}** | **0.43** | **65.685** | **1.169** | **4** | **−26.176** | **21.862** | **1.151** |
| | C | **Cm ~{border vegetation (1)+border structure (1)+cropfields (1)+RS (1)}** | **0.42** | **66.125** | **1.609** | **4** | **−26.396** | **22.302** | **1.174** |
| | D | **Cm ~{cropfields (1)+RS (1)}** | **0.25** | **66.486** | **1.970** | **2** | **−29.643** | **28.796** | **1.371** |
| | E | Cm ~{border vegetation (1)+cropfields (1)+RS (2)} | 0.41 | 66.527 | 2.011 | 4 | −26.597 | 22.703 | 1.195 |

**Table 2.   Best generalised linear model fitted for *Calomys musculinus* seasonal abundance in cropfield borders (*n* = 24) of Chucul rural area**
Description of the variables in the model, *B* parameter values and their significance (*P*). Model ID from Table 1. LST, land-surface temperature; NDVI, normalised by difference vegetation index

| Variable | B | P | Variable | B | P |
|---|---|---|---|---|---|
| **Spring 2005 (Model A)** | | | **Spring 2007 (Model A)** | | |
| Intercept | 0.739 | 0.014 | Intercept | −0.770 | 0.052 |
| *Clematis montevidensis* | −0.315 | 0.000 | Stratum_3 | 0.024 | 0.000 |
| *Diplachne uninervia* | 0.072 | 0.000 | *Bidens subalternans* | 0.090 | 0.001 |
| *Sorghum halepense* | −0.017 | 0.013 | *Bromus catharticus* | −0.031 | 0.001 |
| Trees | −0.047 | 0.000 | *Clematis montevidensis* | 0.083 | 0.000 |
| Width | 0.138 | 0.001 | Crop_maize | 0.246 | 0.010 |
| NDVI_buffer | 4.046 | 0.036 | Crop_peanut | 0.724 | 0.000 |
| | | | Stubbles | 1.071 | 0.002 |
| **Summer 2006 (Model B)** | | | **Summer 2007 (Model B)** | | |
| Intercept | −0.865 | 0.114 | Intercept | 0.635 | 0.043 |
| *Sorghum halepense* | 0.027 | 0.000 | *Diplachne uninervia* | −0.022 | 0.056 |
| Richness (S) | 0.081 | 0.005 | *Oxalis conorriza* | 0.033 | 0.018 |
| Width | 0.226 | 0.000 | *Setaria* sp. | 0.020 | 0.080 |
| Trees | −0.028 | 0.000 | Richness (S) | 0.091 | 0.009 |
| Crop_maize | 0.353 | 0.125 | [Crop_soybean = 0] | 0[A] | |
| | | | [Crop_soybean = 1] | −0.459 | 0.039 |
| **Autumn 2006 (Model A)** | | | **Autumn 2007 (Model A)** | | |
| Intercept | −5.907 | 0.009 | Intercept | −19.837 | 0.000 |
| Eveness (E) | −1.414 | 0.005 | *Bidens subalternans* | 0.076 | 0.000 |
| Width | 0.214 | 0.013 | *Cynodon dactylon* | −0.031 | 0.000 |
| Stubbles | 0.345 | 0.001 | *Diplachne uninervia* | −0.023 | 0.002 |
| NDVI_border | −5.594 | 0.001 | Trees | −0.052 | 0.000 |
| NDVI_buffer | −2.842 | 0.001 | Stubble_maize | 0.454 | 0.006 |
| LST | 0.511 | 0.000 | NDVI_buffer | 20.738 | 0.000 |
| | | | LST | 1.095 | 0.000 |
| **Winter 2006 (Model A)** | | | **Winter 2007 (Model B)** | | |
| Intercept | 0.054 | 0.880 | Intercept | −22.028 | 0.001 |
| *Sorghum halepense* | 0.029 | 0.106 | Richness (S) | −0.256 | 0.158 |
| [Stubble_maize = 0] | 0[A] | | Total cover | 0.057 | 0.019 |
| [Stubble_maize = 1] | 0.793 | 0.060 | [Stubble_soybean = 0] | 0[A] | |
| | | | [Stubble_soybean = 1] | −1.506 | 0.003 |
| | | | LST | 1.350 | 0.002 |

[A]Redundant parameter.

all borders registered generally low captures in winter, then, differences in rodent abundances would not be adequately modelled in this season. The environmental characteristics that appeared as significant predictors of *C. musculinus* abundance varied with seasons. It is well known, in this sense, that habitat-use pattern may vary temporally as a function of the distribution and seasonality of critical resources or even as a response to the biological condition of the individuals (Van Horne 1982; Bright and Morris 1991, 1992; Lurz *et al*. 2000). Although there were no two identical models, we did observe some habitat characteristics that were shared among models of the same season in the two studied years. Moreover, in some cases, the same habitat variables were included in models of different seasons. In this sense, border width – referred to as border structure – and tree cover were identified as significant predictors of *C. musculinus* abundance in several models. Whereas the first one was positively related to rodent abundance, the latter was negatively associated with *C. musculinus* abundances. Regarding cropfields, maize crop and its stubbles were positive predictors of *C. musculinus* abundance in borders, whereas the presence of soybean and its stubbles were negative ones. In three of the selected models, i.e. precisely those

of the coldest seasons, the land-surface temperature was positively related to *C. musculinus* abundance.

Several vegetation variables were significant predictors of *C. musculinus* abundance in borders. Individual plant species associated with rodent abundance varied according to the season. With the exception of *S. halepense*, the other plant species positively related to *C. musculinus* abundance were not recognised as food items for this species (Dellafiore and Polop 1994; Ellis *et al*. 1998; Castellarini *et al*. 2003). In fact, the abundance of seeds in the border was not identified as a significant predictor in any of the obtained models. *C. musculinus* abundance decreased as tree cover increased in spring, summer and autumn. This negative association with the arboreal cover of the border could be related to the high probability of aerial-predator settlement in trees. Birds, along with reptiles and larger mammals, are the main predators of *C. musculinus* and other small rodents (Bellocq and Kravetz 1994; Kittlin 1997; Orrock *et al*. 2003; Smith *et al*. 2005). Besides, a larger arboreal cover could entail lower ground cover and, somehow, reduce habitat complexity. It is generally assumed that the perceived predation risk is related to total habitat complexity, rather than specific

habitat characteristics (Newsome and Catling 1979). These observations allow us to suspect that for *C. musculinus*, the most generalist and opportunistic species of the rodent assemblage (Mills *et al.* 1991; Ellis *et al.* 1998; Busch *et al.* 2000), the dietary constraints may be less crucial than those structural habitat characteristics that reduce predatory risk.

Habitat use by *C. musculinus* in borders also varied according to the crop types surrounding them. Although crop types and their phenology varied seasonally; in general, rodent abundance was positively associated with peanut and maize crops or with the stubbles of the latter one, and negatively related to soybean crop or its stubbles. Even though we conducted all the captures in borders, our results may be consistent with two previous studies in which higher densities of *C. musculinus* were recorded in maize crops compared with soybean crops (Busch *et al.* 1984; Ellis *et al.* 1997). It has been shown that cropfield habitats may function as seasonal food sources for the rodent species of the pampean assemblage, being predominantly used in autumn and winter. In particular, *C. musculinus* seems to prefer maize and avoid soybean as food plants in cropfield habitats (Ellis *et al.* 1998).

Habitat variables obtained from remote sensing complemented field-surveyed data. Some of the remote-sensing variables considered were significant predictors of rodent abundance in spring, autumn and winter. On the one hand, *C. musculinus* abundance was negatively associated with the vegetation index of the border. This border index may be mainly influenced by tree cover, which was negatively related to rodent abundance. On the other hand, in the coldest periods – autumn and winter – *C. musculinus* was more abundant in borders where higher land-surface temperature was registered. NDVI of the buffer region was also a significant predictor of *C. musculinus* abundance. However, it is difficult to clearly interpret the meaning of this relationship because this index is calculated from the compound reflectance of the fields contiguous to the border, which may have different crop types and crop phenologies. NDVI as a proxy for vegetation has been more often used to assess seasonal or inter-annual variations in rodent abundance (Porcasi *et al.* 2005; Andreo *et al.* 2009). In particular, for some species of the studied agroecosystem, NDVI appeared as an important predictor of abundance variations (Andreo *et al.* 2009). In our study – aimed at assessing spatial variations in rodent abundance – the remote-sensed variables should be carefully considered because of their spatial resolution. The satellite images we used have a 30-m pixel that includes several field components: the border, the rural road and the cropfield. It would be optimal then to compare these results with those obtained from higher-resolution remote information, so as to improve the correspondence between each field component and its reflectance detected by sensors.

As it was mentioned before, *C. musculinus* abundance was related to border width in almost every season. It has been suggested that widening field margins would increase their suitability as habitats for some small mammal species (Bellamy *et al.* 2000; Shore *et al.* 2005). In the present study, the border width may be directly related to habitat quality. This would be in agreement with the results of a previous study performed in the same agroecosystem, in which it was observed that *C. musculinus* moved longer distances in narrow

borders (Sommaro *et al.* 2010). The length of movements – recognised as a good index of home-range size in small mammals (Slade and Russell 1998) – is considered to affect not only the energetic costs of food acquisition but also the risk for an individual to be preyed on (Norrdahl and Korpimäki 1998; Banks *et al.* 2000). Therefore, both large home ranges and long movement distances have been used as indicators of low-quality habitats (Tufto *et al.* 1996; Yletyinen and Norrdahl 2008). Because the maximum diameter of a given habitat area (e.g. a home range) is affected by the habitat shape, so that the diameter increases as the habitat becomes more linear (Yletyinen and Norrdahl 2008), then the habitat shape determines the habitat quality. In the present study, the more similar a cropfield border was to natural bi-dimensional habitats, the better the border quality was for *C. musculinus*. Wide borders may entail shorter foraging trips (Sommaro *et al.* 2010), thus reducing predation risk or home-range overlap.

Understanding the basis of habitat use by rodent species associated with rodent-borne diseases may become very important for the implementation of effective management actions, given its significant implications for distinguishing among habitats of different quality (Chalfoun and Martin 2007). This should be the case of any intended management action over *C. musculinus* populations aimed at reducing rodent–human contacts and, therefore, AHF risk. Within the framework of an ecologically based rodent management, if any control measure is to be applied cost-effectively, a process is required by which to decide when and where to apply it (Buckle 1999). Decision makers should implement their strategies at those sites identified as priority (Buckle and Smith 1994), on the basis of models provided by ecologists (Akçakaya *et al.* 1999). We consider our results – which tended to answer the 'where' question – represent a significant advance in the identification of the habitat keys that *C. musculinus* perceives and selects within cropfield borders, a habitat that has not been studied previously even though it is known to be relevant for *C. musculinus* populations (Mills 1999). In the present study, the differences in border use by *C. musculinus* revealed differences in border quality, which for this rodent species, mainly seems to rely on border complexity. Border complexity was mostly related to border width (related to the resemblance of natural bi-dimensional habitats) and to border vegetation as a refuge source (rather than as a food source). In fact, all the characteristics of border habitats that involve a reduction of the predatory risks appeared to be more important than food supply, independently of the season. Besides, *C. musculinus* may partially afford its dietary requirements by consuming grains from cornfields. Last, but not least, *C. musculinus* perception of border quality may be also influenced by the presence and abundance of other rodent species of the assemblage (Simone *et al.* 2010). Considering the arguments exposed above, we suggest that wide borders, particularly those contiguous to maize or peanut cropfields, should be considered as priority sites for the implementation of specific control actions. On the contrary, minor or no effort should be directed to borders contiguous to soybean crops. To control rodent populations, it would also be important to consider management strategies that aim at reducing habitat complexity, for example, by reducing vegetation cover. Finally, any non-specific control measure should take into account the probable

damage to the other rodent species of the assemblage that may be regulating *C. musculinus* abundance in borders.

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