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Patterns of macro and microhabitat use of two rodent species in relation to agricultural practices

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Abstract Habitat selection may reflect the location of the home ranges or the allocation of shelter and foraging sites within a given habitat. We studied seasonal patterns of habitat use by *Akodon azarae* and *Calomys laucha* at two spatial scales: between maize fields and their weedy edges (macrohabitats), and associations of rodents captures with vegetation variables at the trap site level (microhabitats). We evaluated if the different habitat uses were related to disturbances generated by practices associated to maize cycle. *A. azarae* used mainly field edges, but it showed an increased use of maize fields when the crop reached maturity in summer. Contrarily, *C. laucha* used maize fields in a higher proportion than edges in all seasons. *C. laucha* was more influenced by microhabitat characteristics than *A. azarae*. *C. laucha* was present in sites with abundant dicot weeds when maize was growing up, while it was associated to sites with weeds with scarce cover in stubble maize fields. Before harvesting, both species were segregated at the microscale within maize fields. *A. azarae* was related to sites with high availability of green plant cover and *C. laucha* occupied low-quality sites, probably attributed to differences in their diets. We conclude that the pattern of habitat use by both species is best predicted at the macrohabitat scale, and when they are impoverished and present internal heterogeneity, there is selection at microhabitat scale of those better sites. While *A. azarae*

responds to changes in vegetation cover and habitat structure associated to agricultural practices, *C. laucha* uses cropfields in an opportunistic way, affected by interspecific competition.

Keywords Agroecosystems · *Akodon azarae* · *Calomys laucha* · Habitat use · Spatial scales

Introduction

Habitat selection permits the understanding of the causes of the spatial distribution and abundance of organisms in a certain space and time. Many factors, including the availability of shelters, food, nest sites, mates; the abundance of conspecific and competitors of other species; the risk of predation, parasitism, and disease contribute to habitat selection process (Rosenzweig 1981; Morris 1987b). According to the theory of density-dependent habitat selection, each mobile individual will select the habitat in which its reproductive success is maximized, and habitat quality declines with increasing population density, forcing individuals to change towards alternative poorer habitats (Fretwell 1972).

Morris (1987a) and Bowers (1995) defined macrohabitat as the minimum spatial area in which an individual establishes its home range and spends most of its life. Microhabitats or “foraging patches” are described in terms of environmental variables that affect, directly or indirectly, individual behavior and determine which portions of the area within the home range are more intensively used (Morris 1987a; Bowers 1995). In other words, habitat choice is a function of two decisions: first, where to live and establish the home range; and second, where to shelter and forage within a given habitat.

Organisms often differ in their perception of the scale and degree of heterogeneity within the same landscape and in consequence may differ in the scales of habitat selection (Kotliar and Wiens 1990; Orrock et al. 2000; Coppeto et al. 2006). The scale of habitat selection may depend on the features of the habitat and on individual

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responses in terms of dispersal ability, habitat affinities, assessment of habitat quality by resources availability, and predation risk (Orrock et al. 2000; Williams et al. 2002; Silva et al. 2005). Spatial distribution and species abundance are also closely related to the proportion of available habitats in the environment, habitat size, and shape, and the connectivity among them (Kingston and Morris 2000; Burel and Baudry 2005; Orrock and Danielson 2005).

Small mammals are model organisms for habitat selection studies because they are characterized by small body-size and relatively small individual animal's home ranges. Furthermore, they are mid-way in the food webs because they are predators of soil invertebrates and seeds, and they are preyed upon by larger terrestrial and avian vertebrates. Small mammal species generally respond strongly to both spatial and seasonal aspects of habitat changes in heterogeneous landscapes. In human-dominated ecosystems (i.e., agricultural), habitat changes are associated to the reduction of vegetation cover, which increases small mammals' vulnerability to predation and affects the individual behavior (Macdonald et al. 2000; Todd et al. 2000; Jacob and Hempel 2003; Hodara and Busch 2006).

Habitats modified by land use practices show heterogeneity at different spatial scales that are perceived by small mammals that can respond distributing their daily activities among different patches within home ranges (Jorgensen 2004) or by macrohabitat selection, which in turn translates into population distribution (Pullian and Danielson 1991; Van Horne 1991).

Experiments conducted in small mammals demonstrated that most farming and agricultural practices affect the distribution and habitat use of small mammals, but their response differs depending on the type and intensity of the disturbance (Millán de la Peña et al. 2003; Butet et al. 2006; Michel et al. 2006). Rodent populations diminished by ploughing effects on arable lands (Jacob 2003) as a response to decreased vegetation height (Macdonald et al. 2000), and in consequence caused restricted spatial activity (Todd et al. 2000; Jacob and Hempel 2003).

Agroecosystems of the Pampean region in central Argentina are human-dominated landscapes derived from native grasslands since the last two centuries, and they are mosaics of cultivated fields, pastures, and a network of weedy edges that surround them below wire fences (Viglizzo et al. 2001). These habitats show seasonal changes in plant cover, height of vegetation, and availability of resources according to the climatic conditions, as well as to the calendar of agrarian labors. These changes affect the pattern of habitat use and movements of rodents among habitats (Busch and Kravetz 1992a; Ellis et al. 1997; Hodara and Busch 2006), especially in response to harvest and plough when crop areas are low-quality habitats for rodent survival (de Villafañe et al. 1988; Cavia et al. 2005).

Akodon azarae (Pampean grassland mouse) and *Calomys laucha* (small vesper mouse) (Rodentia, Crice-

tidae) are two of the most abundant rodent species inhabiting the Pampean agroecosystems. Both species differ in habitat associations (Mills et al. 1991; Hodara et al. 2000; Busch et al. 2001). This habitat segregation between species is directly related to interspecific competition, with the dominance of *A. azarae* over *C. laucha* in weedy edge habitats (Busch and Kravetz 1992b; Hodara et al. 2000). Both species also differ in nesting behavior and dietary habits. While *A. azarae* digs burrows in compacted soils from edges and consumes high quantities of arthropods, *C. laucha* builds surface nests in the cropfields and is mainly granivorous-herbivorous (Hodara et al. 1997; Ellis et al. 1998). Although both rodent species were intensively studied regarding ecological and behavioral attributes in agrarian Pampean systems, the spatial and temporal effects generated by the crop type (maize) and the major agricultural events of corn (sowing, crop up, harvest, ploughing) on their patterns of habitat use and movements are little known.

The goal of this study was to evaluate the patterns of habitat use by *Akodon azarae* and *Calomys laucha* at macrohabitat (maize fields versus their adjacent edges) and microhabitat scales (association of rodents captures with vegetation variables at the trap site level) in different moments of the maize cycle. Specifically, we asked two questions. First, do rodents select habitats at both macro and microhabitat scales in maize fields? Second, are the changes in the pattern of habitat use related to variations generated by disturbances associated to the maize culture?

Methods

Study area

Fieldwork was conducted in Diego Gaynor (34°18'S, 59°14'W), North-western Buenos Aires Province, central Argentina. The study area is a temperate grassland in the Rolling Pampa of the Pampean phytogeographic province (Hall et al. 1992). The climate is temperate and humid with a mean summer temperature of 22.5°C and a mean winter temperature of 9.8°C. The annual average rainfall is 950 mm with higher values in summer than in winter (Hall et al. 1992).

During the last two centuries, the original grassland was intensively transformed by farming and grazing activities to an agricultural landscape of pastures and cultivated fields. However, from the late 1980s, natural rangelands and pastures were progressively replaced by crops and cattle breeding was restricted to marginal areas (Viglizzo et al. 2001; Paruelo et al. 2005). Along cropfield edges, roadsides, and fencerows, there is a plant community dominated by some native grasses of 0.5–1.0 m high and introduced weeds. Dominant species are the grasses *Stipa neesiana*, *Stipa papposa*, *Bromus unioloides*, and *Cynodon dactylon*, forbs as *Solidago chilensis* and *Senecio grisebacchi*, and thistles (*Carduus*

acanthoides, *Cirsium vulgare*, and *Cynara cardunculus*) (Ellis et al. 1997; Busch et al. 2001). Field edges provide better habitat conditions than cropfields for many small mammals because they are less affected by agricultural practices (Busch and Kravetz 1992a; Cavia et al. 2005), but the relative qualities of edges and cropfield habitats depend on the moment of the year and the temporal variation generated by the developing of the crop and the agricultural practices (Hodara et al. 2000; Cavia et al. 2005). In Pampean agroecosystems, the removal of vegetation cover decreases the food availability but increases the predation pressure upon rodents (de Villafañe et al. 1988; Hodara and Busch 2006). In these agrarian landscapes, small rodents are exposed to avian predators as owls (*Tyto alba*, *Speotyto cunicularia*, and *Asio flammeus*) and terrestrial vertebrates as opossums, grisons, and foxes (Pardiñas and Cirignoli 2000; Barquez et al. 2006).

Major cultivated crops in the region are wheat, maize, sunflower, and soybean, and according to recent estimates in the Rolling Pampas nowadays approximately 90% of the land is devoted to agricultural use (Viglizzo et al. 2001; Paruelo et al. 2005). Maize is a warm-season crop that provides good-quality habitats for rodents during the reproductive period of them, which begins in spring when the crop is sown. There is an improvement in plant cover, vertical vegetation density, productivity, food, and refuge availability from this moment up to maize harvest time, along with an increase in rodent abundance (end of March–April). After harvesting, the stubble fields impoverish in habitat cover, which coincide with a peak of high rodent density (Busch et al. 1984; Busch and Kravetz 1992a).

Study species

In Pampean agroecosystems, the rodent assemblage includes at least 12 rodent species. The most abundant species are five native sigmodontines (*Akodon azarae*, *Calomys laucha*, *C. musculus*, *Oligoryzomys flavescens*, and *Oxymycterus rufus*), the native caviid *Cavia aperea* (Pampa's cavy) and the introduced murine *Mus musculus* (Mills et al. 1991; Busch and Kravetz 1992a; Ellis et al. 1997).

Studies of habitat selection showed that both species considered in this study present different patterns of spatial distribution. While *A. azarae* uses differentially linear undisturbed habitats (i.e., cropfield edges) or remnants of grasslands, *C. laucha* is numerically dominant in cultivated areas (Ellis et al. 1997; Hodara et al. 2000; Busch et al. 2001). At a smaller scale (microhabitat), *A. azarae* individuals are associated to sites with abundant green plant cover of grasses during the breeding season and with green forbs in winter, while *C. laucha* individuals are related to green plant cover, except in winter when they are more frequently caught in grassy sites (Ellis et al. 1997; Bilenca and Kravetz 1998; Busch et al. 2001).

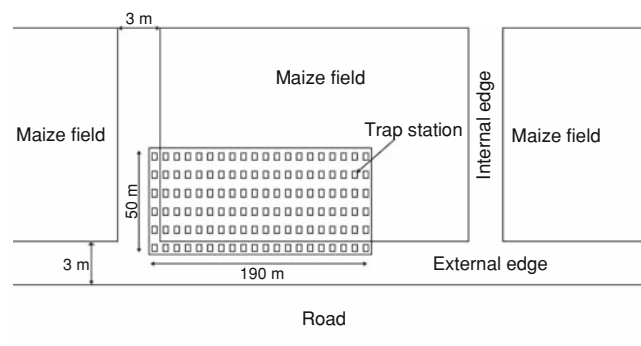


Fig. 1 Schematic of trapping grid in maize fields and their adjacent internal and external edges. Each trapping grid was composed of six lines of 20 traps at 10-m intervals (0.95 ha)

Rodent sampling

We conducted four live-trapping sessions in both 1993 and 1994 in three maize fields and their adjacent edges (internal edges developed between contiguous fields and external ones between fields and roads, Fig. 1). Distances between trapping sites were approximately 500 m. Rodent samplings were conducted at different phases of rodent population density and crop cycle: (1) low rodent density and recently sown maize in October and November (spring), (2) increasing density and mature crop in February (summer), (3) peak density and crop stubble after harvest in April and May (late autumn), and (4) decreasing density and ploughed fields in July and August (winter). All samplings were conducted in the same three maize fields and their surrounding weedy edges (experimental plots) to assess the changes in the patterns of habitat use of rodents in relation to the seasonal changes in habitat structure (plant phenology and disturbances by agricultural practices). We set 120 single-capture Sherman live-traps (spaced at 10-m intervals) in each experimental plot: 95 traps placed in the crop habitat and 25 traps set along the field edges (Fig. 1). We placed one trap at each trap station and we baited traps with rolled oats mixed with peanut butter, wrapped in paper and nylon bags, and supplied with cottonwood for nesting to reduce mortality from hypothermia during cold periods. In each trapping session, we checked each trap every morning during three consecutive days. Individuals captured were individually marked, and species, sex, body mass, corporal and tail length, and reproductive condition were recorded before release at the site of capture. We recorded location and habitat of capture for each capture occasion.

Patterns of habitat use

In order to evaluate the patterns of habitat use, we considered two levels of spatial heterogeneity. We considered maize fields and their weedy edges as two different macrohabitats. At the microhabitat scale, we

recorded a set of vegetation variables: total plant cover, green plant cover, height of vegetation, and all plant species covering more than 5% (listed in Appendix 1) within a circular area of 1 m radius (3.14 m²) centered at every trap station. These variables were registered at each trapping period. The height of the vegetation was quantified according to the presence of plant cover at three height intervals: stratum 1, below 0.10 m; stratum 2, between 0.10 and 0.50 m; and stratum 3, above 0.50 m. For both total and green plant cover were registered the percentage of coverage in the circular area, while for the dominant plant species we assigned categorical values from 0 to 4, according to their relative contribution to the total plant cover.

Data analysis

We examined the pattern of habitat use between maize fields and their edges (macrohabitat scale) considering the first capture of each individual because successive captures of an animal in the same location were not independent, but we considered the different captures of the same individual in different locations. We estimated rodent abundance as relative density index (RDI) by the trapping success (number of captures/number of trap-nights) \times 1,000 (Mills et al. 1991). For each species, we assessed the effect of habitat and seasons on abundance by a two-way within-subjects (repeated-measures) analysis of variance model. Multiple observations of rodent abundances on the same experimental plots (habitat pairs) along seasons constitute the two within-subjects factors. Post hoc pairwise comparisons among mean abundances were performed by Tukey HSD tests (honestly significant differences). The sphericity assumption was tested by the Mauchly's sphericity test.

Because microhabitat use is related to foraging activity, we considered all captures as an activity-density measurement for assessing the associations between vegetation variables and rodent captures, as suggested by Abramsky et al. (1990) and Morris (1997).

For each rodent species and at each trapping period we conducted logistic regressions between the presence or absence of a rodent (dependent variable) and vegetation data as explanatory variables at each trap site. We assessed multicollinearity among explanatory variables by the Spearman correlation matrix, and we entered into the logistic regression only uncorrelated variables. From pairs of correlated variables we selected those that were most strongly related to the dependent variable (Schadt et al. 2002). We conducted a stepwise backward regression and we considered the best-fit logistic regression model with the lowest Akaike information criterion (AIC) and the smallest number of significant explanatory variables as predictors. For each rodent species we constructed two-by-two contingency tables of the observed frequencies of presences and absences versus the predicted values derived from logistic regression models

for different cut-off values. We calculated the proportion of correctly predicted presences (sensitivity) and the proportion of correctly predicted absences (specificity) from contingency tables. We tested the accuracy of predictive models using receiver operating characteristic (ROC) curves (Pearce and Ferrier 2000). A ROC curve was obtained by plotting the proportion of presences correctly predicted (sensitivity) on the y-axis against the proportion of false presences (proportion of absences incorrectly predicted, 1-specificity) on the x-axis. The area under the ROC curve (AUC) is the best discrimination measurement between proportions of correctly and incorrectly classified predictions over a range of threshold probabilities. The AUC ranges from 0.5 for models with no discrimination ability, to 1 for models with perfect discrimination (Pearce and Ferrier 2000; Schadt et al. 2002). Statistical analyses were conducted using the R Statistics System (<http://www.cran.r-project.org/>, version R-2.7.2 tar.gz, Department of Statistics and Mathematics, Wirtschaftsuniversitaet Wien, Austria). We considered statistically significant values of $P < 0.05$ in all analyses.

Results

We captured 397 individuals of 5 rodent species (626 captures). *Akodon azarae* was the most common species captured (207 individuals), followed by *Calomys laucha* (155 individuals), *C. musculus* (19 individuals), *Oligoryzomys flavescens* (8 individuals), and *Mus musculus* (8 individuals). The last three species were not included in the analyses because of the low number of captures.

Patterns of habitat use at macrohabitat scale

A. azarae abundance varied significantly between habitats depending on the sampling periods ($F_{\text{interaction}} = 85.08$; $df = 3, 6$; $P < 0.001$), because it was captured more frequently in field edges than maize fields in spring, late autumn and winter (Tukey HSD test, for the three pairwise comparisons $P < 0.01$), but in summer, both habitats were used similarly (Tukey HSD test, $P = 0.351$, Fig. 2). *A. azarae* showed significant variations in abundance among trapping periods in edge habitat (Tukey HSD test, for all pairwise comparisons $P < 0.01$, except in the comparison between spring and summer $P = 0.532$, Fig. 2), but not in maize fields (Tukey HSD test, for all pairwise comparisons $P > 0.05$, Fig. 2).

C. laucha used maize fields in a higher proportion than edges habitat in all seasons ($F_{\text{habitat}} = 66.22$; $df = 1, 2$; $P = 0.014$, Fig. 3), but there was no significant interaction between habitat use and season ($F_{\text{interaction}} = 0.81$; $df = 3, 6$; $P = 0.531$). We did not detect significant variations in *C. laucha* abundance among seasons in any habitat ($F_{\text{season}} = 2.98$; $df = 3, 6$; $P = 0.118$, Fig. 3).

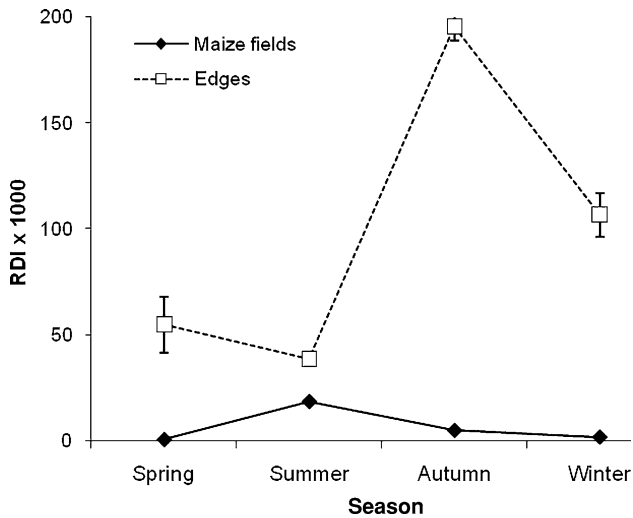


Fig. 2 Abundance of *Akodon azarae* expressed as relative density index (RDI) \times 1,000 \pm SE in maize fields and their edges by season

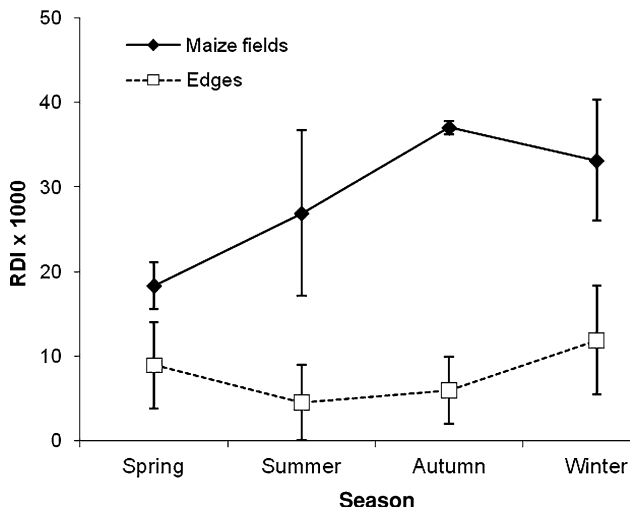


Fig. 3 Abundance of *Calomys laucha* expressed as relative density index (RDI) \times 1,000 \pm SE in maize fields and their edges by season

Patterns of habitat use at microhabitat scale

We registered 18 dominant plant species during the study period in both habitat types (Appendix 1). *A. azarae* captures within field-edge habitat were not associated to any plant variable in any season (Appendix 1). In maize fields, green plant cover was the only positive predictor for the presence of *A. azarae* in summer, while in late autumn (stubble maize fields) its presence was positively associated to *Stellaria media* (chickweed, annual dicot) (Appendix 1). In spring and winter, we did not conduct the microhabitat analysis in field habitats because there were not sufficient captures.

The area under the ROC curves (AUC) varied between 0.525 (in winter) and 0.655 (in spring), indicating

poor discrimination capacity between the proportion of presences of *A. azarae* correctly predicted and absences incorrectly predicted in edge habitats. However, the ROC plot had an AUC = 0.78, providing a reasonable discrimination ability for the chosen habitat model in maize fields in summer.

The presence of *C. laucha* in edge habitats in spring was negatively associated to green plant cover, while in winter, its presence was predicted by *Baccharis pingraea* (perennial dicot) (Appendix 1). In summer and late autumn, we did not evaluate microhabitat use for this species in edge habitats because of the low number of captures (Appendix 1).

In maize fields, *C. laucha* presence was predicted by *Tagetes minuta* (wild marigold, annual dicot) in spring, while in summer total plant cover and senescent maize plants contributed negatively to the presence of this species (Appendix 1). In late autumn, the presence of *C. laucha* within stubble maize fields was positively associated to *Cynodon dactylon* (Bermuda grass, perennial monocot) and *Sida rhombifolia* (Arrowleaf sida), while *Carduus acanthoides* (plumeless thistle, annual dicot) was the only negative predictor (Appendix 1). In winter, *Coronopus didymus* (annual dicot weed) and green plant cover were negatively associated to the presence of *C. laucha* within arable maize fields (Appendix 1).

Microhabitat models for *C. laucha* in maize field habitats showed poor discrimination ability because AUC ranged between 0.596 (in late autumn) and 0.686 (in spring). However, the area under the ROC curve for the model in edges in winter had a reasonable discrimination capacity, with an AUC = 0.754.

Discussion

Akodon azarae and *Calomys laucha* showed different patterns of habitat use, reflecting both spatial and temporal variations in agrarian landscapes composed by cultivated areas with maize and their weedy adjacent edges. *A. azarae* used mainly the field margins, but it showed an increased use of maize fields when the crop reached maturity in summer. However, *C. laucha* used maize fields in a higher proportion than edges habitat in all periods, independently of the crop stage, of the agricultural practices related to maize cycle, and population variations. This pattern of macrohabitat use is in agreement with previous studies, and the differences were attributed to distinct diets, space to shelter as well as interspecific competition by both exploitation and interference (Bilenca and Kravetz 1998; Hodara et al. 2000; Busch et al. 2001).

According to the pattern of microhabitat use, the association of different vegetation variables with the presence of rodents was very different and variable by species depending on the moments of the year. Considering the results from logistic regression models, we did not detect any vegetation predictor of *A. azarae*

abundance within edge habitat. However, the distribution of *A. azarae* is closely associated to vegetation cover in agrarian landscapes (Ellis et al. 1998; Hodara and Busch 2006). In spite of the specific composition and phenological stage of weed plant communities of edges change through time, this habitat type is structurally stable and highly homogeneous by its dense plant cover, without discriminating by plant species. Two possible explanations would permit the understanding of the lack of discrimination ability of *A. azarae* at the trap site level in edges. When the system cropfield-edge is highly contrasting, *A. azarae* selects at larger scale (macrohabitat), and the pattern of habitat use is determined by the ability to relocate the home range seasonally (Morris 1987a), or probably they respond to a spatial gradient from burrows than to differences in microhabitat structure within edges (Bowers 1995). When we analyzed the spatial distribution of *A. azarae* within maize fields, its presence was associated to those sites with high green plant cover in summer, while this species selected particular sites with the presence of the dicot weed *Stellaria media* within stubble fields in late autumn. An increased use of maize fields before and after crop harvesting (summer and autumn, respectively) and of sites with high availability of green plant material during breeding season was associated to the high consumption of invertebrates by reproductive females as a source of proteins. Bilenca and Kravetz (1998) concluded that green cover and insects are specific resources that satisfy nutrient and energetic requirements for reproduction of *A. azarae* females.

In *C. laucha*, we detected better vegetation predictors of its presence at microhabitat scale in maize field-edge systems than those obtained for *A. azarae* in both habitat types (Appendix 1). While *C. laucha* rejected to use sites with green plant cover in field edges in spring, it showed differential use with changes in predictor variables depending on the season within maize fields. In spring, *C. laucha* was present in sites with the dicot weed *Tagetes minuta*, which provides good cover near the surface and in height into maize fields when crop cover was scarce because maize plants were recently sowing. Moreover, it was associated with sites covered with monocot and dicot weeds with little cover within stubble fields at the beginning of harsh environmental conditions (late autumn, Appendix 1). All of these sites occupied by *C. laucha* individuals are considered low-quality sites because of increased bare ground, low grassy and forbs cover, and scarce vertical vegetation density. Ellis et al. (1997) detected that *C. laucha* was associated to low-quality microhabitats in arable fields described by similar vegetation variables.

Although both rodent species shared maize fields in summer at the macrohabitat scale, they segregated themselves at scale of trap station within maize fields. This microhabitat segregation was probably related to the allocation of foraging sites and attributed to differences on their diets, being *A. azarae* more insectivorous

and *C. laucha* more granivorous–folivorous (Ellis et al. 1998). Considering that microhabitats are those components of habitat occurring within an individual animal's home range (Morris 1987a), *A. azarae* was present in sites with green plant cover, probably by the features of the plants themselves and by the abundant invertebrate fauna associated with them. Moreover, *C. laucha* would consume fresh and green parts of maize field weeds and maize grains because it requires high amounts of green forage to reproduce (Bilenca et al. 1992; Ellis et al. 1998). The selection or avoidance of some patches over others means they differ in quality and quantity of resources (Morris 1987a). These differences in food consumption suggest coexistence among individuals of both species and avoid interspecific encounters (Rosenzweig 1981).

In early autumn, the effects of maize harvesting largely reduce the vegetation height within fields and force many *A. azarae* individuals to retreat to undisturbed field edges (Cavia et al. 2005) as a response to the increase of predation risk. Experimental and observational evidence suggests that rodents perceive the loss of vegetation cover and habitat structure by harvesting and ploughing actions and respond to predation pressure from avian predators in agrarian systems (Jacob and Hempel 2003; Millán de la Peña et al. 2003). Rodents, as wood mice and meadow voles, under predation pressure altered their foraging behavior (Todd et al. 2000; Macdonald et al. 2000; Moenting and Morris 2006), or reduced their dispersal movements as an indicator of lower habitat quality (Tew and Macdonald 1993; Yletyinen and Norrdahl 2008).

According to the spatial arrangement of habitats, edge habitats are less represented than cropfields in agrarian systems. However, despite their low availability in the landscape, they may be key habitats for different rodent species (Tattersall et al. 2002; Butet et al. 2006). In our study, it happens for *A. azarae* (selector species), while *C. laucha* is competitively excluded from edges towards croplands qualitatively poor by harvesting in autumn and ploughing in winter (Hodara et al. 2000; Busch et al. 2001). However, *C. laucha* seems to be a less sensitive species to the habitat disturbance by agriculture. It would rapidly respond in an adaptive way by colonizing new patches after disturbance and sheltering in modified holes as burrows or under vegetation remains from harvest time where it survives from low temperatures and avian predation risk (Hodara et al. 1997). The spilled cereal grains and planted seeds would provide winter food on arable fields, although the ploughed soil has a bleak appearance.

In summary, the pattern of habitat use in *A. azarae* and *C. laucha* was best predicted at the macrohabitat scale (between maize fields and their adjacent weedy margins). This result is consistent with the findings of Morris (1987a), Orrock et al. (2000) and Coppeto et al. (2006), who concluded that microhabitat measurements are less effective predictors of small mammal

presence and abundance than is macrohabitat in other ecosystems. On the other hand, both species showed increased microhabitat selectivity in the “poor habitat” (maize field), which is more likely to have good and poor sites than the edges and individuals can perceive high-quality patches and unsuitable ones. *C. laucha* used proportionally the habitat more available in Pampean agrarian landscapes (cropfields), and it was more influenced by microhabitat characteristics than *A. azarae*, which occupies the better macrohabitat (field edges) but the less represented one in agrarian systems. However, the factors that contribute to the patterns of habitat use are different for both species. *C. laucha* is more affected by interspecific competition with the dominant *A. azarae*, while this latter species appears to largely responses to seasonal agricultural disturbance, which major impact of these activities is to reduce the availability of cover within the maize fields.

According to our results, we consider that rodents may first detect and select macrohabitats, and when they are impoverished and present internal heterogeneity, there is selection at the microhabitat scale of those better sites.

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Appendix

Table 1.

Table 1 List of vegetation variables recorded in each season and the habitat type where each plant species is dominant

Vegetation variable	Habitat	<i>Akodon azarae</i>								<i>Calomys laucha</i>							
		Spring		Summer		Autumn		Winter		Spring		Summer		Autumn		Winter	
		E	M	E	M	E	M	E	M	E	M	E	M	E	M	E	M
Total plant cover		0		0	0	0	0	0	0	0	0	–		0	0	0	0
Green plant cover		0		0	+	0	0	0	0	–	0		0	0	0	0	–
Stratum 1		0		0	0	0	0	0	0	0	0		0	0	0	0	0
Stratum 2		0		0	0	0	0	0	0	0	0		0	0	0	0	0
Stratum 3		0		0	0	0	0	0	0	0	0		0	0	0	0	0
Annual dicot																	
<i>Carduus acanthoides</i>	Edge	0		0	0	0	0	0	0	0	0		0	–	0	0	0
<i>Solidago chilensis</i>	Edge	0		0	0	0	0	0	0	0	0		0	0	0	0	0
<i>Bowlesia incana</i>	Maize field	0		0	0	0	0	0	0	0	0		0	0	0	0	0
<i>Tagetes minuta</i>	Both	0		0	0	0	0	0	0	0	+		0	0	0	0	0
<i>Stellaria media</i>	Maize field	0		0	0	+	0	0	0	0	0		0	0	0	0	0
<i>Coronopus didymus</i>	Maize field	0		0	0	0	0	0	0	0	0		0	0	0	–	0
<i>Matricaria chamomilla</i>	Maize field	0		0	0	0	0	0	0	0	0		0	0	0	0	0
<i>Trifolium repens</i>	Both	0		0	0	0	0	0	0	0	0		0	0	0	0	0
<i>Brassica campestris</i>	Both	0		0	0	0	0	0	0	0	0		0	0	0	0	0
<i>Raphanus sativa</i>	Maize field	0		0	0	0	0	0	0	0	0		0	0	0	0	0
<i>Rumex crispus</i>	Maize field	0		0	0	0	0	0	0	0	0		0	0	0	0	0
Annual monocot																	
<i>Digitaria sanguinalis</i>	Both	0		0	0	0	0	0	0	0	0		0	0	0	0	0
Plants of <i>Zea mays</i>	Maize field	0		0	0	0	0	0	0	0	0		–	0	0	0	0
Perennial dicot																	
<i>Senecio grisebachii</i>	Edge	0		0	0	0	0	0	0	0	0		0	0	0	0	0
<i>Baccharis pingraea</i>	Edge	0		0	0	0	0	0	0	0	0		0	0	+	0	0
<i>Sida rhombifolia</i>	Maize field	0		0	0	0	0	0	0	0	0		0	+	0	0	0
Perennial monocot																	
<i>Stipa</i> sp.	Edge	0		0	0	0	0	0	0	0	0		0	0	0	0	0
<i>Cynodon dactylon</i>	Both	0		0	0	0	0	0	0	0	0		0	+	0	0	0

Results of the associations between vegetation variables and the presence of *Akodon azarae* and *Calomys laucha* from logistic regression analyses in each type of habitat (*E*: edges; *M*: maize fields)

Classification of functional groups was made from Ellis et al. (1997) and Busch et al. (2001) with some modifications according to our data 0, no association; +, positive association; –, negative association

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