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We describe changes in abundance of two rodent species over a 12-year period and assess the relationship between population abundance, climate, and agricultural practices in southern Córdoba Province, Argentina. We estimated abundance from trapping edges of agricultural areas, railway rights of way, and roadsides. Variables considered were: normalized difference vegetation index (NDVI), surface temperature, minimum and maximum temperature, rainfall, and cultivated areas of different crops. Species abundances varied over time; those of *Akodon dolores* declined, whereas those of *A. azarae* increased. Climatic and environmental changes may have had differential influences on species abundances. Autumn abundance of *A. dolores* was positively related to spring rainfall and area of harvested sorghum, and negatively related to NDVI. *Akodon azarae* abundance was negatively correlated with winter minimum temperature, spring rainfall, and sorghum harvested area, but positively associated with NDVI. On the other hand, both species were negatively correlated with each other. We suggest that environmental conditions may have changed the competition outcome for *Akodon* spp., and thus, had direct, differential effect on species abundances.

Keywords: agroecosystem; rodent abundance; weather; crops; agricultural practices; Argentina

Introduction

Rodent populations exhibit important fluctuations over time as well as spatially (Henttonen et al. 1985; Taitt & Krebs 1985; Mills et al. 1991; Stenseth 1999). A number of factors including climate, plant productivity, food availability, vegetative cover, predation, and competition may cause complex changes in relative abundance as well as assemblage composition (Flowerdew 1987; Oli & Dobson 2001; Alain et al. 2006; Gillespie et al. 2008). Exogenous factors such as climate and environment affect individual life histories, and thus both abundance and distribution of species (Stenseth et al. 2003). Many studies have shown the importance of global climatic variables in determining the dynamics of small mammal population (Leirs et al. 1997; Lewellen & Vessey 1998; Dickman et al. 1999; Ernest et al. 2000; Lima et al. 2001; Stenseth et al. 2002; Zhang et al. 2003; Letnic et al. 2005). Many authors suggest that more unfavorable climatic conditions for rodents, as cold and wet winters, increase the direct mortality by exposure, and assume that hot and dry summers would cause a decrease in food and habitat quality (Mills et al. 1991, 1992; Castellarini et al. 2002). Additionally, land management is another factor which markedly affects community composition and population density in many rodents (Hansson 1999; Millán de la Peña et al. 2003; Zhang et al. 2003; Bilenca et al. 2007). Agricultural practices (sowing, weeding and harvesting) are associated with an abrupt environmental variation that reduces the system offering (cover and food), producing direct rodent mortality. The effects that rise from changes in agricultural practices and sowed surfaces combined with extreme climatic conditions could promote a greater destroyed habitat, individual emigration and exposure of small rodents to predation (Crespo 1966; Crespo et al. 1970; de Villafañe et al. 1977; Kravetz 1978; Kravetz & Polop 1983; de Villafañe et al. 1988; Mills et al. 1991; Bonaventura et al. 1992; Bilenca 1993).

In the last 20 years, important changes in crop and agricultural practices have occurred in Argentina (Viglizzo et al. 2001; Paruelo et al. 2005). These transformations were the result of the increase of sown-cultivated surfaces in general and the increase of sown-cultivated surfaces of some type of crops to the detriment of others. Moreover, since the 1990s the direct sowing crop system has been applied and extended in replacement of traditional farming (Bilenca et al. 2007), with the soybean crop producing the greatest modifications in the agricultural and cattle farming practices in the region (Paruelo et al.

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2005). These changes have modified the quantity and quality of resources for native fauna both temporally and spatially, thus influencing the relationship between animals and their habitats (Crespo 1966; Kravetz & Polop 1983; Mills et al. 1991; Ellis et al. 1998; Busch et al. 2005; Bilenca et al. 2007).

We have been studying rodent assemblages in the rural area of Chucul, Río Cuarto Department (Córdoba, Argentina) since 1984, and eight rodent species (*Calomys musculinus*, *C. laucha*, *C. venustus*, *Akodon azarae*, *A. dolores*, *Oligoryzomys flavescens*, *Oxymycterus rufus* and *Mus musculus*) have been registered (Kravetz & Polop 1983). In these assemblages, *A. dolores* was the most abundant akodontine rodent in native pasture and edge habitats (Kravetz & Polop 1983; Polop et al. 1985), indicating that it was a long-term inhabitant of the area. On the other hand, *A. azarae* only became numerous (Andreo, Lima, et al. 2009; Andreo, Provensal, et al. 2009) when local populations of *A. dolores* declined. *Akodon azarae* is found in linear and relatively stable habitats with high vegetation cover, such as field and road borders, railway banks and remnant areas of native vegetation (Zuleta et al. 1988; Mills et al. 1991; Busch & Kravetz 1992; Andreo, Lima, et al. 2009; Andreo, Provensal, et al. 2009). Studies about feeding habits (Martinez et al. 1990) have shown that *A. dolores* has a generalist food strategy during winter, eating a wide range of arthropods, seeds and leaves. Castellarini et al. (2003) characterized this species as mainly carnivorous both in borders and in cultivated fields. *Akodon azarae* feeds mainly on insects but also on plant material and seeds (Bilenca & Kravetz 1998; Ellis et al. 1998). Populations of both *Akodon* species show seasonal fluctuations, with a minimal densities in spring and maximal densities in late autumn–early winter, followed by a dramatic decline (Piantanida 1981; Zuleta et al. 1988; Mills et al. 1991; Busch & Kravetz 1992). Reproduction is also seasonal: the breeding season begins in spring and lasts until autumn (Piantanida 1981; Zuleta et al. 1988; Mills et al. 1992).

The relationship between population fluctuations, climate and environmental variables has seldom been quantified here. Studies of *C. venustus* and *A. azarae* population dynamics in the study area (Castellarini & Polop 2002; Castellarini et al. 2002; Andreo, Lima, et al. 2009) propose that NDVI and rainfalls would affect some fluctuations of small rodent population abundance at seasonal and inter-annual level. On the other hand, they suggest that some populations are regulated by competition (limited by food, space or space free of enemies), and others would be more affected by local climate parameters such as rainfall and temperature that affect the environment carrying capacity. Although biology and ecology of these

akodontine species is quite well studied, there are no previous attempts to study the effects of climate and environment on the long-term changes in these species in order to explain the observed decline in abundance of one species (*A. dolores*) and the increase of the other one (*A. azarae*) in the time period previous to the analyses performed by Andreo, Lima, et al. (2009). In this study we describe the variation in abundance of *A. dolores* and *A. azarae* populations over a 12-year period, and explore the effects of changes in climate and agricultural practices in southern Córdoba Province, Argentina.

Materials and methods

Study area

The study area (50 km^2) was in the rural zone of Chucul, Department of Río Cuarto, Córdoba Province, Argentina (33°01′34″ S; 64°11′21″ W). For a description of the study area, see Castellarini et al. (2002).

Assessing Akodon *abundance*

To determine changes in abundance of rodents, we used data from trapping carried out in autumn over a 12-year period (1984–1995) on crop field edges, railway embankments and roadsides. We used 2–8 trap-lines with 20 trapping stations located at 5-m intervals for four consecutive nights each in April, May and June. The location of these trap-lines varied in each month and the distance among them was greater than 200 m. One live trap or one snap trap was placed at alternate trap stations. The bait was a mixture of peanut butter and cow fat. All animals caught were removed.

Trap success was used as an estimate of relative density: RDI = (captures/(number of trap nights)) × 100. The mean autumn RDI value of each year was used for the analyses, since it is the period when species reach their highest abundances. We assumed that a relative measure represents population peaks and troughs, and provides good estimates of the relative population changes (Debrot 1981; Saucy 1984), allowing us to show annual abundance fluctuations.

Obtaining environmental variables

We used several climatic and environmental variables including: normalized difference vegetation index (NDVI), land surface temperature (LST), absolute minimum and maximum temperature, rainfall, and sown area of corn, soybeans, and sorghum. NDVI is positively related to the level of photosynthetic activity, green leaf biomass, fraction of green

vegetation cover and annual net primary productivity (Tucker et al. 2005). NDVI and LST were obtained using summer images from a meteorological satellite of the National Oceanic and Atmospheric Administration/Advanced Very High Resolution Radiometer (NOAA/AVHRR) with a spatial resolution of 8×8 km. The study area surface approximately reaches 50 km^2. The information was processed using the software ENVI 3.6.

Data series of absolute minimum and maximum temperature and rainfall were obtained from the Agrometeorology Laboratory of Río Cuarto National University (RCNU), Argentina. Spring (October–December) and summer (January–March) rainfall were obtained by adding totals for those months. Also, we determined annual rainfall for each year and compared it with averages from a 25-year series (1974–2001) for the region (Agrometeorology Laboratory, RCNU). Absolute winter minimum temperature was obtained from averaging the lowest absolute values of July–September, and summer maximum temperature from averaging the highest temperatures of January–March. Both variables were compared with the values in the 25-year series. The preceding variables (NDVI, LST, rainfall and temperature) were obtained for periods prior to autumn population estimates, as mentioned above, assuming that there might be lagged effects on rodent populations.

Annual values of harvested areas for different crops in Río Cuarto Department were provided by the Secretary of Agriculture, Cattle and Renewable Resources, Córdoba Province; one annual value of each crop was utilized for the analyses.

Data analyses

To assess the relationship between rodent abundances and climatic and environmental variables, multiple regression analyses were applied to each species. Manual backward stepwise method was used to select variables. Variance inflation factors (VIFs) were computed to evaluate colinearity among the independent variables. Variables with VIF lower than 10 (or that yielded an average VIF of 5) were retained. We tested model residuals for normality, homogeneity of variance and autocorrelation. After models were fitted to the data, we calculated the Akaike information criterion (AIC). The models with the lowest AIC values were selected to draw inferences. We also performed simple pairwise correlations among the variables of the selected model.

We simulated the behavior of the fitted models using total trajectory simulations. We also estimated correlations between observed and predicted values of population abundance to assess the performance of

each of them. We transformed abundance values to natural logarithm to achieve normality. All statistical analyses were performed with R Version 2.8.1 (R Development Core Team 2008).

Results

Akodon *abundance*

During the studied period, 235 *A. azarae* and 155 *A. dolores* individuals were captured. Generally, abundance of *A. dolores* decreased from 1984 to 1992, and only one individual was captured during the last four years of the study. On the other hand, the abundance of *A. azarae* varied inversely, reaching very high levels in 1991, declining to a few individuals in 1992, and then recovering to previous levels (Figure 1).

Environmental variables

With respect to climatic and environmental variables, we identified two distinct periods (1984–1988 and 1991–1995), separated by two unusual years (1989 and 1990). Winter minimum and summer maximum temperatures were on average higher in the 1984–1988 period than in the 1991–1995 period. In contrast, NDVI values were lower in the first period than in the second. During the unusual years, summers were very hot and dry. Maximum temperatures (35.3°C) were higher than the mean (34.1°C $\pm$ 1.0°C), and rainfall in spring and summer 1989 was only 50% (182 mm) and 37% (122 mm), respectively, of the mean seasonal values (Figure 2). The lowest annual rainfall values during the 25-year series (1974–2001) were recorded in 1989 and 1990. Green vegetation cover (NDVI) also showed its lowest values in 1989 and 1990 summers (0.50 and 0.51 respectively) compared with the mean value of the study period (0.6 $\pm$ 0.06).

The area of harvested sorghum has decreased markedly from 1984 to 1995 and that of corn abruptly declined in 1988 and 1989, but recovered somewhat afterwards. The area of harvested soybean has strongly increased since about 1988 (Figure 3).

Rodent abundances and environmental variables

Autumn abundance of *A. dolores* was significantly correlated to climatic and environmental variables (adjusted $R^2 = 0.84$, $F = 20.75$, d.f. = 3 and 8, $p = 0.0004$). It was positively related to spring rainfall and area of harvested sorghum, and negatively related to NDVI (Table 1, Figure 2). The distribution of model residuals was normal ($W = 0.92$; $p = 0.30$), variances were homogeneous (Bartlett's K-squared = 0.02, df = 1, $p = 0.89$) and there was no autocorrelation ($D - W = 2.08$, $p = 0.84$). On the other hand,
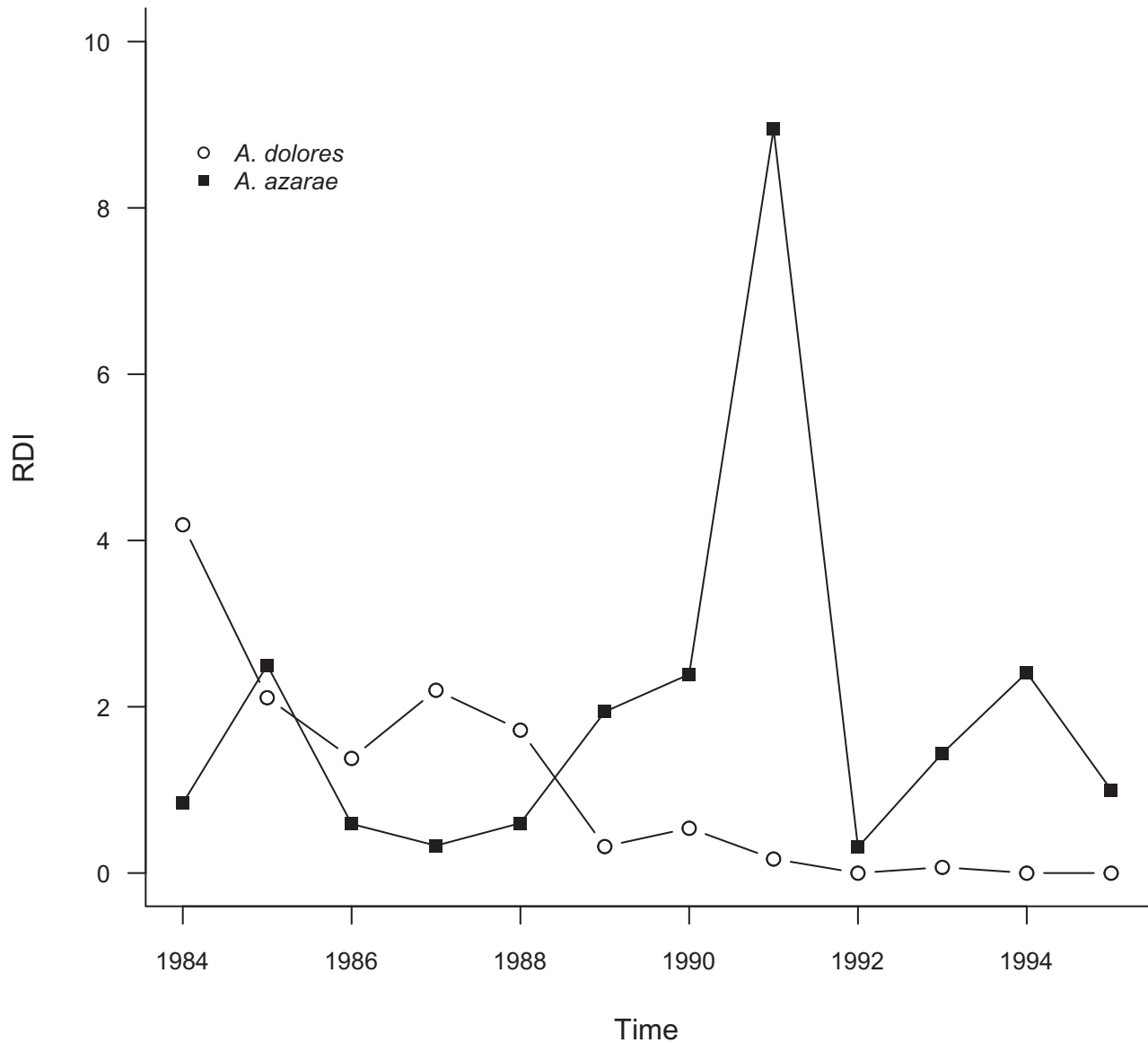
Figure 1. Annual variation of mean autumn relative density (RDI) of *Akodon dolores* and *A. azarae* captured in edge habitats of Chucul (Córdoba, Argentina). Period 1984–1995.

abundance of *A. azarae* was weakly and negatively correlated to winter minimum temperature (Adjusted $R^2 = 0.26$, $F_{1,10} = 4.81$, $p = 0.052$) (Table 1, Figure 2). Model residuals were normally distributed ($W = 0.92$, $p = 0.32$) with homogeneous variances (Bartlett's K-squared $= 0.74$, df $= 1$, $p = 0.39$) and no autocorrelation ($D – W = 2.30$, $p = 0.68$). Species differed in their correlations with environmental variables included in the models (Appendix 1). *Akodon azarae* abundance was also negatively correlated with spring rainfall and sorghum harvested area, but positively associated with NDVI. Nevertheless, these variables were not included in the model for *A. azarae*. On the other hand, both species were negatively correlated with each other. Model simulations of *A. azarae*

and *A. dolores* seem to capture the observed pattern of population abundance fluctuations with different levels of fit (correlations between observed and predicted values of *A. azarae* and *A. dolores* abundance were 0.57 and 0.94, respectively).

Discussion

The results suggest that rodent abundance is related to climatic variables for one of two species studied here. Extreme climatic conditions (hot, dry summers) and decreased NDVI coincided with the decline of *A. dolores* abundance. The apparent interaction between precipitation and temperature indicates that they must be considered simultaneously in understanding
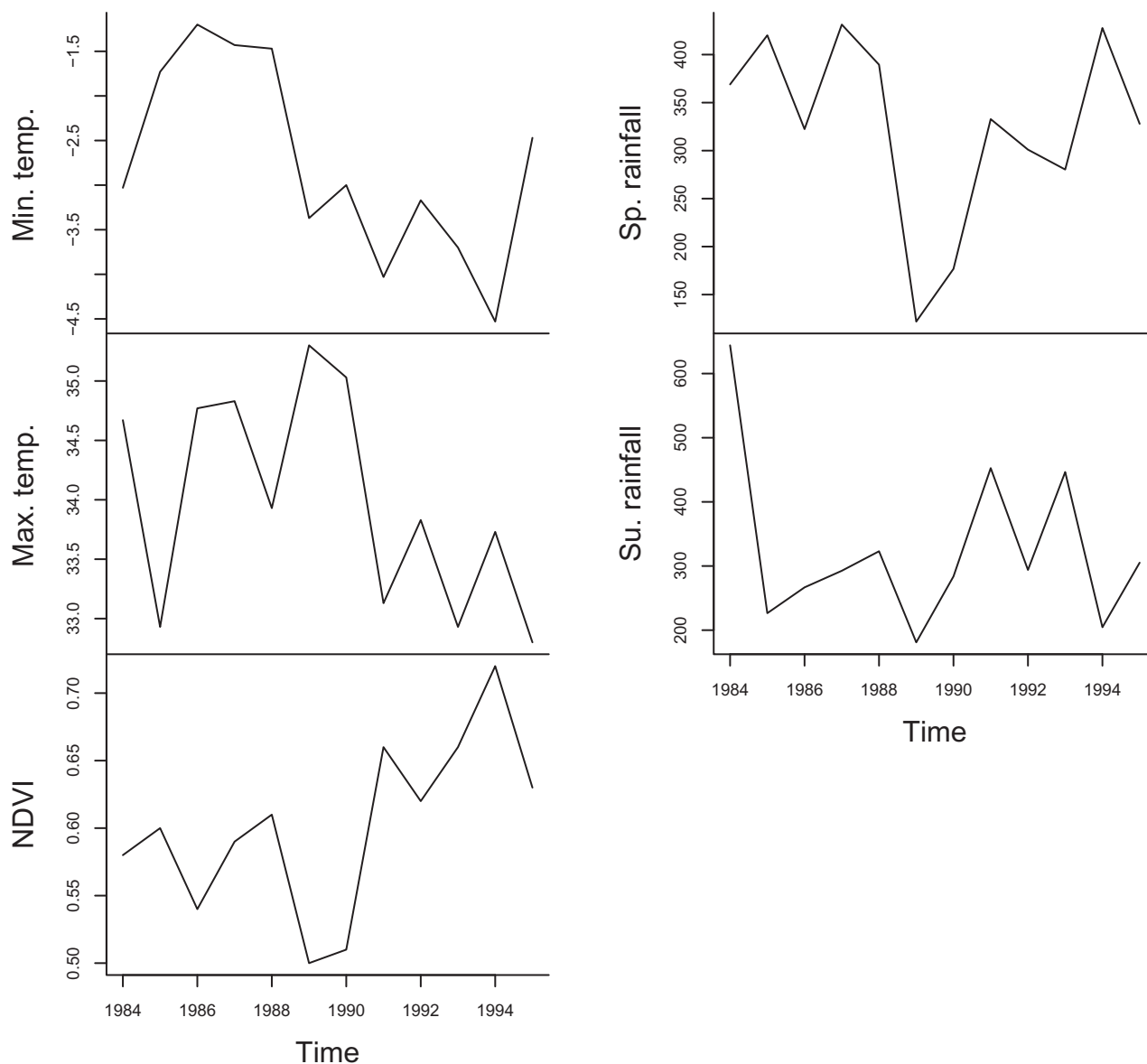
Climatic and environmental variables

Figure 2. Climatic and environmental variables recorded for Chucul, Río Cuarto Department, Córdoba, Argentina in 1984–1995. Min. temp.: winter average minimum temperature; Max. temp.: summer average maximum temperature; NDVI: normalized difference vegetation index (summer average); Sp. rainfall: spring accumulated rainfall (mm); and Su. rainfall: summer accumulated rainfall (mm).

changes in relative abundance. Unfavorable climatic conditions such as cold and wet winters may increase mortality by exposure, while hot, dry summers may cause decreased food and habitat quality (Garsd & Howard 1981, 1982; Mills et al. 1991, 1992; Castellarini et al. 2002; Calisher et al. 2005). The strong decline in *A. dolores* abundance is consistent with concurrent studies of agroecosystems from the same area over a much longer temporal

scale (1984–1999: Castellarini et al. 2002; 1990–2007: Andreo, Lima, et al. 2009) and on a short-term study a few years ago (Simone et al. 2010) in which *A. dolores* has not been captured. In contrast, abundance of *A. azarae* was not related to the environmental variables analyzed.

The harvest area of sorghum decreased, soybean increased, and NDVI values also increased, and *A. dolores* abundance exhibited an inverse relationship
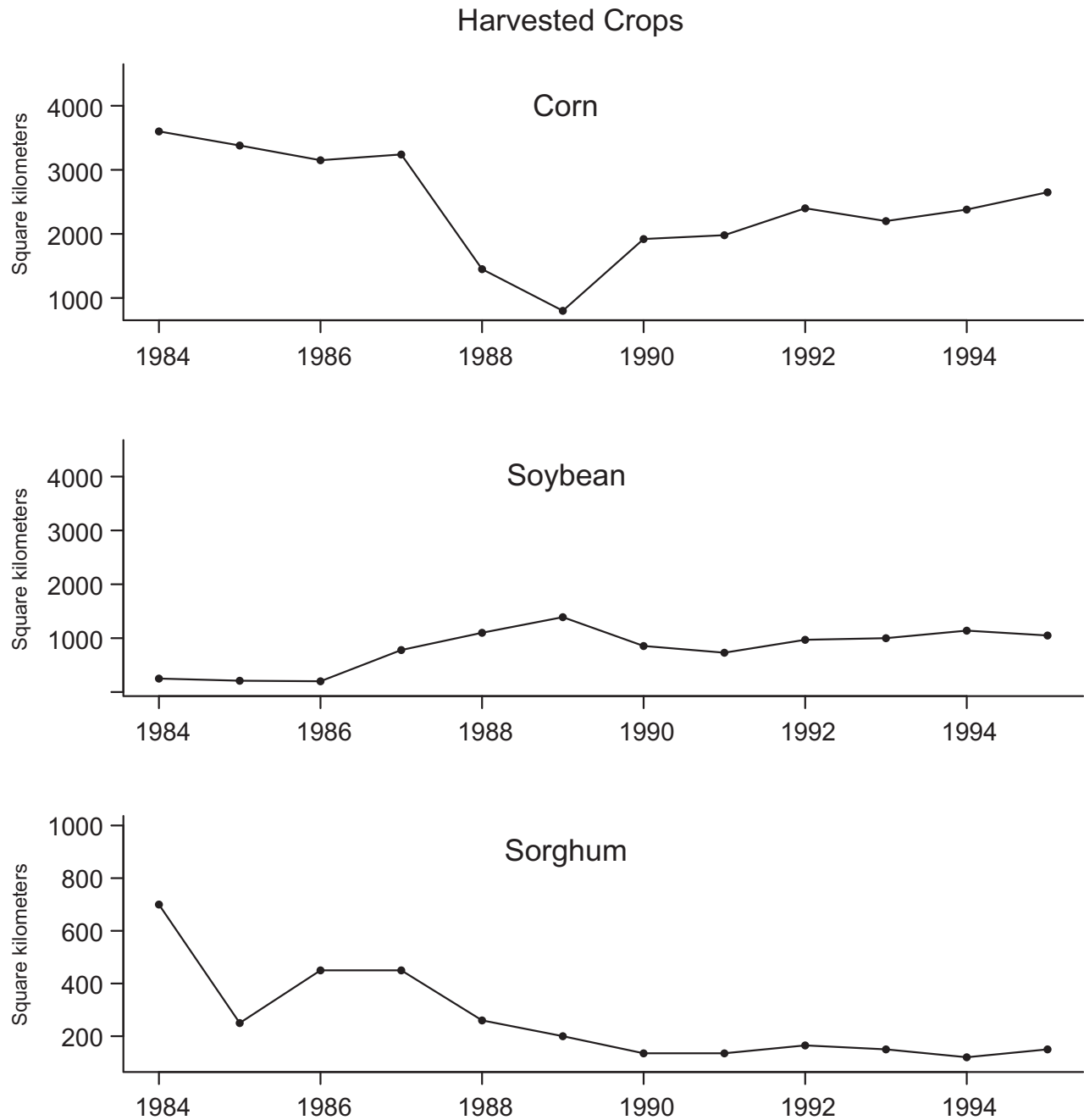
Harvested Crops

Figure 3. Total harvested area (km^2) for three crops in the rural area of Chucul, Río Cuarto Department (Córdoba, Argentina) for the period 1984–1995.

with the latter. Concurrently, there was a trend towards changes in crops and agricultural practices that may be related, directly or indirectly, to the shift observed in densities of both akodontine species. The decrease in population density of *A. dolores* appears related to changes in land use patterns and farming practices in agroecosystems of central Argentina (Martínez-Ghersa & Ghersa 2005; Paruelo et al. 2005). New agricultural technologies (no tillage agriculture), planting expansion, increased soybean planting area, and use of more agrochemicals are some of those practices.

Busch et al. (1984) and Maiztegui et al. (1986) suggested that decreased corn and increased soybean plantings would negatively affect densities of *A. azarae*. However, our results do not confirm this, since fluctuations in *A. azarae* abundance do not appear to be clearly related to changes in any one crop.

Table 1. Stepwise regression model for *A. dolores* and *A. azarae* abundances on climatic and environmental variables in Chucul, Río Cuarto Department (Córdoba, Argentina).

Variable	Regression coefficient	SE	*t*-value	*p*
A. dolores				
Spring rainfall	0.00378	0.00126	3.008	0.0169*
NDVI	−5.533	1.900	−2.913	0.0195*
Sorghum harvested (ha)	0.0000148	0.00000562	2.624	0.0305*
Constant	2.275	0.949	2.397	0.0434*
A. azarae				
Winter minimum temperature (average)	−0.296	0.135	−2.194	0.0529*
Constant	0.079	0.949	0.197	0.8478

Rainfall (accumulated); NDVI (normalized difference vegetation index) is the summer average value; sorghum harvested is the annual harvested value. Significant variables ($p < 0.05$) are indicated by *.

Andreo, Lima, et al. (2009) reported that abundance of *A. azarae* was twice as high for a longer time series, starting in 1990, than that reported here. They suggested that the population dynamics of this species was mainly affected by density-dependence and influenced by rainfall and NDVI. However, in our model neither rainfall, NDVI values nor the type of crops were significant. The rapid increase of *A. azarae* in 1991 after *A. dolores* disappearance could indicate a competitive release as it was suggested for other species in Australia (*Peromyscus* sp. and *Mus musculus*, Caldwell 1964; *Pseudomys novaehollandiae* and *M. musculus*, Fox & Gullick 1989; *P. gracilicaudatus* and *Rattus luteolus*, Higgs & Fox 1993). Thus, if *A. azarae* was a subordinate species with respect to *A. dolores*, the rapid increase observed might have resulted from the disappearance of *A. dolores*, as other authors have proposed in experimental studies for other species (Fox & Pople 1984; Brown & Munger 1985; Busch et al. 2005). Experiments suggest that one of the first responses to an increase in resource availability is immigration (Gilbert & Krebs 1981; Taitt 1981), and this could explain the greater abundance of *A. azarae* in 1991, a wet year. As dietary overlap between the two *Akodon* species is incomplete (Castellarini et al. 2003), shelter or space may have been the limiting resource for *A. dolores*. Castellarini et al. (2003) characterized *A. dolores* as mainly carnivorous in borders and cultivated fields, whereas *A. azarae* was omnivorous in these habitats. Moreover, *A. azarae* is able to modify its diet according to availability (Bilenca & Kravetz 1998), and shows a positive answer to the addition of new items (Cittadino et al. 1994). In the case of competition and *A. dolores* "replacement" by *A. azarae*, we consider *A. dolores* as a specialist that better exploits a particular type of patch, and *A. azarae* as a generalist. In a non-changing environment we would expect *A. dolores* to be more abundant than *A. azarae* and *A. azarae* to avoid competition by occupying patches with low densities or absence of *A. dolores*. Another type of interaction may occur if competition is very low or infrequent. In that case, generalists would exploit all patches regardless of the density of specialists (Morris 1996). If, for any reason, the environment changes, the generalists will survive better, whereas the other species will decrease in abundance or be excluded from the assemblage. Changes in climate and agricultural practices could, altogether, have produced a below recovery level fall in *A. dolores* abundance, creating an opportunity that was taken by *A. azarae*.

However, Andreo, Lima, et al. (2009) suggested that *A. azarae* abundance is regulated by intra-specific competition, not by inter-specific competition. Nevertheless, *A. dolores* abundance began to decline in 1990, the starting point of the time series analyzed by Andreo, Lima, et al. (2009). Thus, we suppose that regulation mechanisms for *A. azarae* might have been different prior to 1990. Thus, different duration and starting dates of abundance series may indicate that factors crucial for individual persistence might vary seasonally or annually (McMillan et al. 2005; Deitloff et al. 2010).

Our results could also be a consequence of the methodological approach we used, since the removal procedure is an invasive technique that may alter the population structure (Kelt et al. 1994). However, as we varied the location of the trap-lines and maintained a large distance between them, we assume that there is very little or no methodological effect on the results obtained.

We suggest that environmental conditions may have changed the competition outcome for *Akodon* spp., thus exerting a direct, differential effect on species abundances. Time-series analyses of competing natural populations in sympatry within the context of environmental variation may be an important tool for unraveling potential interactions among species.

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Acknowledgments

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Appendix 1

Pearson correlations between mean autumn RDI of *Akodon azarae* and *A. dolores* and environmental and climatic variables included in the regression linear models.

	A. azarae	A. dolores	Winter minimum temperature (average)	Sorghum harvested area (ha)	Spring rainfall	NDVI
A. azarae	1.000					
A. dolores	−0.289	1.000				
Winter minimum temperature (average)	−0.490	0.491	1.000			
Sorghum harvested area (ha)	−0.374	0.910	0.463	1.000		
Spring rainfall	−0.062	0.417	0.280	0.317	1.000	
NDVI	0.272	−0.282	−0.452	−0.325	0.619	1.000

NDVI: normalized difference vegetation index.