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ORIGINAL ARTICLE

Population dynamics of two rodent species in agro-ecosystems of central Argentina: intra-specific competition, land-use, and climate effects

Verónica Andreo · Mauricio Lima ·
Cecilia Provensal · José Priotto · Jaime Polop

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Abstract Understanding the role of feedback structure (endogenous processes) and exogenous (climatic and environmental) factors in shaping the dynamics of natural populations is a central challenge within the field of population ecology. We attempted to explain the numerical fluctuations of two sympatric rodent species in agro-ecosystems of central Argentina using Royama's theoretical framework for analyzing the dynamics of populations influenced by exogenous climatic forces. We found that both rodent species show a first-order negative feedback structure, suggesting that these populations are regulated by intra-specific competition (limited by food, space, or enemy-free space). In *Akodon azarae* endogenous structure seems to be very strongly influenced by human land-use represented by annual minimum normalized difference vegetation index (NDVI), with spring and summer rainfall having little influence upon carrying capacity. *Calomys venustus'* population dynamics, on the other hand, seem to be more affected by local climate, also with spring and summer rainfall influencing the carrying capacity of the environment, but combined with spring mean temperature.

Keywords Density regulation · Exogenous effects · Feedback structure · Population dynamics models

Introduction

The wide spectrum of population dynamics observed in small mammal fluctuations has intrigued ecologists for a long time (Elton 1924). Most studies focusing of rodent dynamics in the Northern Hemisphere have emphasized the role of endogenous processes as the most important factors driving numerical oscillations (Ostfeld et al. 1993; Hörnfeldt 1994; Stenseth et al. 1996). In contrast, most studies of rodent dynamics from the Southern Hemisphere have emphasized the role of exogenous (climate) factors in driving the observed fluctuations (Pearson 1975; Jaksic and Lima 2003). Recently, ecologists have begun to understand how both feedback structures and exogenous factors interact in shaping the dynamics of small mammal populations (Leirs et al. 1997; Lima et al. 1999, 2001, 2002a, b, 2006, 2008, Murúa et al. 2003a, b).

Rodent populations from agro-ecosystems in central Argentina exhibit important inter-annual fluctuations in density (Crespo 1966; Crespo et al. 1970) that seem to be driven by factors such as climate, agricultural practices, and the interaction of these with intra and inter-specific competition of rodents (Kravetz and Polop 1983; Castellarini et al. 2002). For example, *Akodon azarae* (Fisher 1829) and *Calomys venustus* (Thomas 1894) are two of the most

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V. Andreo · C. Provensal · J. Priotto · J. Polop
Departamento de Ciencias Naturales,
Universidad Nacional de Río Cuarto,
Agencia Postal No 3, CP 5800 Río Cuarto,
Córdoba, Argentina

M. Lima (✉)
Centro de Estudios Avanzados en Ecología y Biodiversidad
(CASEB), Pontificia Universidad Católica de Chile,
193 Correo 22, Santiago CP 6513677, Chile
e-mail: mlima@bio.puc.cl

J. Priotto
Consejo Nacional de Investigaciones Científicas y Técnicas,
CONICET, Buenos Aires, Argentina

abundant small rodents inhabiting the agro-ecosystems of the Pampean region in Argentina. They are usually found in relatively stable habitats with high vegetation cover including crop field edges, roadsides, and railway banks (borders), and remnant areas of native vegetation (Mills et al. 1991; Priotto and Polop 1997). Although seasonal changes in Argentinean rodent species are quite well studied, there have been no previous attempts to study long-term inter-annual population changes and to deduce the relative importance of endogenous and exogenous processes in shaping the dynamics of small rodents in agro-ecosystems. Therefore the objective of this study was to analyze the effects of endogenous feedback structure and climatic factors on the dynamics of *A. azarae* and *C. venustus* in agro-ecosystems of central Argentina, using simple and appropriate population dynamics models.

Materials and methods

Study site

The study was carried out in the rural area of Chucul (Fig. 1), south-west of Córdoba, Argentina (33°01′34″S; 64°11′21″W). The area is a typical undulating pampean plain (600–900 m a.s.l.). The climate of the region is temperate with an average annual temperature of 23°C in January and 6°C in July. Annual rainfall is high, especially in summer, averaging 800 mm. The natural transitional landscape of woodland (dominated by *Prosopis alba*, *P. nigra*, *P. caldenia*, *Celtis tala*, *Acacia caven* and *Geoffroea decorticans*) and pampean natural grassland (*Stipa* spp.) remains in patches between crop fields. The vegetation has undergone marked alterations as a result of agriculture and cattle farming. Currently, the landscape mainly consists of individual crop fields surrounded by wire fences with borders dominated by weed species. The study was conducted on a railway bank with an average width of 50 m. The low train frequencies (<10 per year) allow the development of natural pastures and weeds interspersed with bushes. Despite the influence of nearby crop fields, the vegetation bears some resemblance to native vegetation. In this barely disturbed habitat rodent species such as *A. azarae* and *C. venustus* reach high population densities.

Small mammal data

We used mark–recapture data from small-mammal live-trapping conducted on four consecutive nights each month from January 1990 to June 2007 in a 6 × 10 grid (0.30 ha). Stations in the grid were separated by 10 m. One Sherman-type live trap baited with a mixture of peanut butter and cow fat was placed in each station. Small mammals captured were marked with a distinct numerical code, consisting of little cuts of the ears, and standard data on species, sex, reproductive condition, length, and weight were also recorded. Population abundance was estimated from the minimum number of animals known to be alive (MNKA). In this study we used peak annual MNKA obtained after the reproductive season of each year.

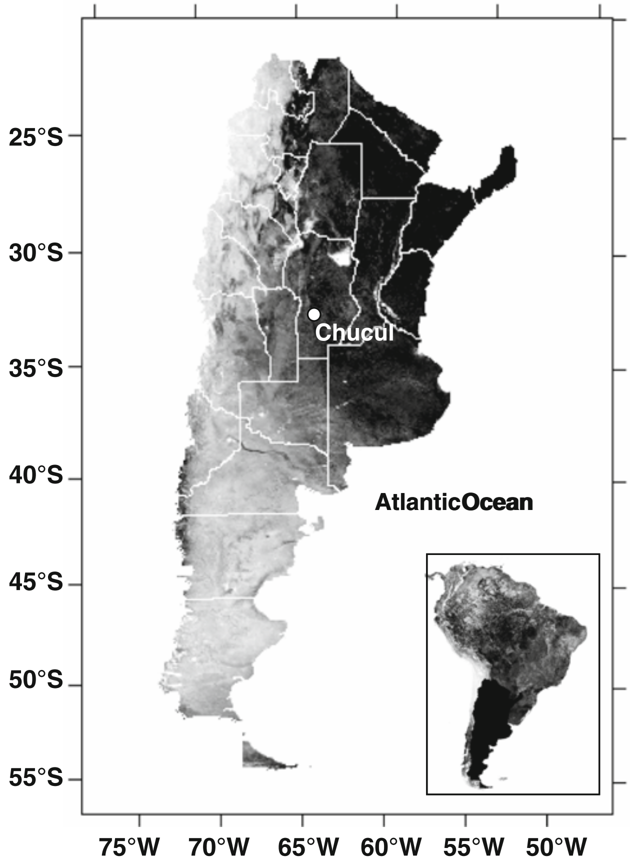

Fig. 1 Map of Argentina showing the location of Chucul rural area (Córdoba province)

Mouse life history

Both species are omnivorous, but *A. azarae* (25–30 g) consumes higher proportions of arthropods whereas *C. venustus* (55 g) eats higher proportions of leaves and seeds (Bilenca et al. 1992; Castellarini et al. 1998). Populations of both species show a strong seasonal variation in abundance, with a minimum in spring and peaks in autumn (*C. venustus*) or late autumn–early winter (*A. azarae*) followed by a dramatic fall (Mills et al. 1991; Castellarini and Polop 2002). Reproduction is also seasonal; the breeding season may last from September–October to April–June (Mills et al. 1992; Polop et al. 2005).

Climatic and NDVI data

Data series of monthly temperature (minimum, median, and maximum) and rainfall were provided by the agro-meteorological laboratory from Río Cuarto National University (Argentina). We used seasonal estimates of these variables for the analyses performed in this study.

Normalized difference vegetation index (NDVI) is a measure of the presence and condition of green vegetation and is calculated as a normalized ratio of the red and near infrared bands (Lillesand and Kiefer 1994). NDVI values range from -1 to 1, with bare soil having values near 0, and high values indicating increasing green biomass and photosynthetic activity. NDVI data series for this study was obtained from the global inventory modeling and mapping studies (GIMMS) AVHRR 8 km, bimonthly (1981–2006) data set, available at http://glcf.umiacs.umd.edu/data/gimms/ (Tucker et al. 2005).

Diagnosis

Population dynamics are the result of the combined effects of feedback structure (ecological interactions within and between populations), limiting factors (food limitation by plants, or predator limitation through competition for enemy-free space), climatic influences (rainfall), and stochastic forces. To understand how these factors may determine rodent population fluctuations, we modeled both system-intrinsic processes (both within the population and between various trophic levels) and exogenous influences as a general model based in the *R*-function (Berryman 1999). The *R*-function represents the realized per-capita population growth rates that reflect the processes of individual survival and reproduction (Berryman 1999). Defining $R_t = \log(N_t) - \log(N_{t-1})$, we can express the *R*-function as (sensu Berryman 1999):

$$R_t = f(N_{t-1}, N_{t-2}, \ldots, N_{t-d}, \varepsilon_t) \tag{1}$$

This model represents the basic feedback structure and integrates the stochastic and climatic forces that drive population dynamics in nature. Our first step was to estimate the order of the dynamic process (Royama 1977), i.e., how many time lags (N_{t-i}) should be included in the model for representation of the feedback structure. To estimate the order of the process we used the partial rate correlation ($PRCF_i$) between R_t and $\ln(N_{t-i}) = X_{t-i}$, after the effects of shorter lags were removed. We wrote Eq. 1 in logarithms to calculate the partial correlations.

$$R_t = \ln\left(\frac{N_t}{N_{t-1}}\right) = A + B_1 \cdot X_{t-1} + B_2 \cdot X_{t-2} + \varepsilon_t \tag{2}$$

where R_t, the realized per-capita rate of change, is calculated from the data. We used the Population Analysis System, Single-Species Time-Series Analysis, to calculate $PRCF_{t-d}$ (PAS can be downloaded from http://classes.entom.wsu.edu/pas/). For statistical convenience we assumed a log–linear relationship between R_t and lagged population density (Royama 1977).

Models of population dynamics

We used the non-linear logistic population model of discrete time proposed by Royama (1992), derived from the logistic equation of Ricker (1954). This model represents a randomly distributed population competing for a common resource which is consistent with scramble competition (Johst et al. 2008).

$$R_t = b - \exp^{(a \cdot X_{t-1} + C)} \tag{3}$$

where R_t is the realized logarithmic per-capita population growth rate, b is a positive constant representing the maximum finite reproductive rate, X_{t-1} is the logarithmic population density in $t-1$, C is a constant representing competition and resource depletion, and a indicates the effect of interference on each individual as density increases (Royama 1992); $a > 1$ indicates that interference intensifies with density and $a < 1$ indicates habituation to interference. Therefore, density in each time period is obtained:

$$X_t = X_{t-1} + b - \exp^{(a \cdot X_{t-1} + C)} \tag{4}$$

To model the effects of climate on the endogenous feedback structure of rodent populations we added extra terms to Eq. 3 representing vertical and/or lateral effects. Thus, the equation becomes:

$$R_t = b - \exp^{(a \cdot X_{t-1} + C + d \cdot \text{climate})} + e \cdot \text{climate} \tag{5}$$

where, d and e are the coefficients that account for lateral and vertical effects of climate, respectively.

We fitted Eq. 5 using the *nls* library in the program R by means of non-linear regression analyses. After models were fitted to the data, we calculated the Akaike information criterion corrected for small-sample bias (AIC_c), differences in AIC_c (Δ_i), likelihood, Akaike weights (w_i), evidence ratios (w_i/w_j), and log (likelihood) for each model (Burnham and Anderson 2004). Models with the lowest AIC_c values were selected to draw inferences and run deterministic predictions. We used total trajectory and one-step-ahead deterministic predictions to simulate the dynamic behavior of the fitted models and correlations between observed and predicted values of population abundance to assess the performance of each of them.

Results

Population dynamics of the two rodent species studied here showed irregular numerical fluctuations (Fig. 2a, b), with years of high abundance and a sudden decrease during the period 1992–1997 for *A. azarae* (Fig. 2b). The maximum abundance of *A. azarae* was observed in 1991 and that of *C. venustus* (Fig. 2a) in 2004. In addition, the PRCF strongly suggested first-order dynamics for both species (Fig. 2c, d), which was also evident from the observed *R*-functions (Fig. 2e, f). For *C. venustus*, however, a second lag also seemed to contribute in some measure to the determination of *R* (Fig. 2c). The time series plot of *A. azarae* (Fig. 2b) seems to exhibit a discontinuity (a shift in dynamics) between 1992 and 1997, which is even more evident from *R*-function (Fig. 2f). This plot seems to show two *R*-functions, one at high population abundance and the other at low population abundance, suggesting a strong vertical perturbation effect.

Population dynamics models fitted for *C. venustus* and *A. azarae,* values of estimated parameters, coefficient of determination (R^2), AIC$_c$, ΔAIC$_c$, likelihood, Akaike weights (w_i), evidence ratios (w_i/w_j) and log (likelihood) for each model are shown in Tables 1 and 2, respectively. The maximum finite reproductive rate was fixed at 1.7 (the maximum observed *R* in the series) for *C. venustus* in order to obtain convergence of the models, but this was not necessary for *A. azarae*.

Our analyses indicated that population abundance of the previous year explained 49 and 47% of the variation in per-capita growth rates of *C. venustus* (Table 1) and *A. azarae* (Table 2), respectively. All models show a nonlinear ($a \neq 1$) negative first-order feedback structure (i.e., *R* is a nonlinear decreasing function of population abundance in a previous time), but in *C. venustus,* $a < 1$ and in *A. azarae*, $a > 1$. Exogenous effects improved the explained variance of the first-order feedback models by an average of 10% for both species, ranging from 1 to 22% and from 0 to 31% for *C. venustus* and *A. azarae*, respectively (Tables 1 and 2; Tables A1 and A2 in the electronic supplementary material, ESM). If we remove the points (corresponding to the abundances of 1992, 1993, 1995, and 1996) from the *R*-function (see gray dots in Fig. 2f), model fits improved substantially. The dynamics of *A. azarae* seemed to be mainly affected by

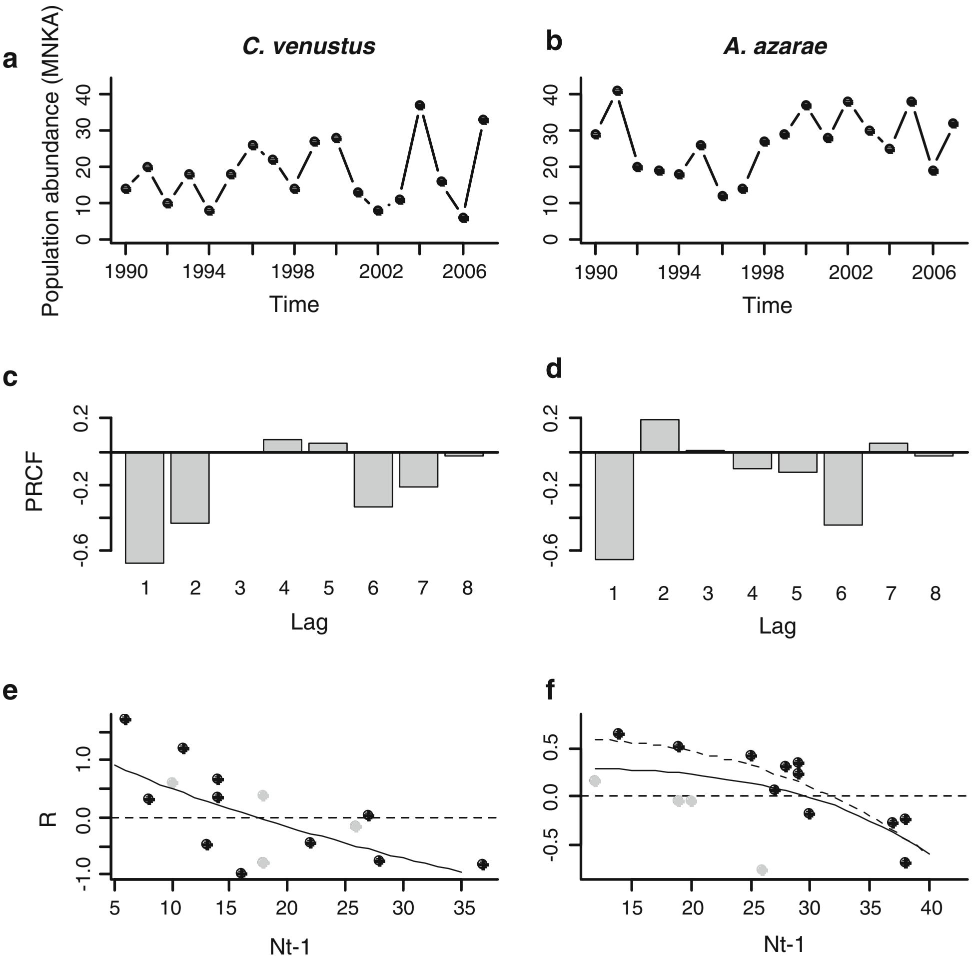

Fig. 2 Peak annual abundance (*MNKA*), partial rate correlation function (*PRCF*), and relationship between the logarithmic annual per-capita rate of change ($R_t = \ln N_t - \ln N_{t-1}$) and population abundance (N_{t-1}) expressed as MNKA (*R*-function) for *C. venustus* (**a**, **c**, **e**) and *A. azarae* (**b**, **d**, **f**) during 1990–2007. *Grey points* are those we removed from the *A. azarae* *R*-function to fit models. *Curves* are the non-linear Ricker logistic model (equivalent to Eq. 3) fitted to the data (*continuous line*) using the complete series (*dashed lines*) removing grey points from the *A. azarae* series

Table 1 Best population dynamics models fitted to time series for *C. venustus* (1990–2007)

	Models for *Calomys venustus*	Estimated parameters					R^2	AIC$_c$	ΔAIC$_c$	Likelihood	w_i	w_i/w_j	Log (likelihood)	k
		a	b	c	d	f								
A	$R_t = b - \exp(a \times Cv_{t-1} + c) + d \times medianspr$	0.11	1.7	1.80**	0.337		0.63	33.543	0.000	1.000	0.189	1.000	−13.608	4
B	$R_t = b - \exp(a \times Cv_{t-1} + c + d \times sumRain) + f \times medianspr$	0.11	1.7	1.90**	−0.0003	0.34	0.71	33.565	0.021	0.989	0.187	1.011	−9.060	5
C	$R_t = b - \exp(a \times Cv_{t-1} + c) + d \times sumRain$	0.46**	1.7	−0.36	0.0027		0.61	34.503	0.960	0.619	0.117	1.616	−11.587	4
D	$R_t = b - \exp(a \times Cv_{t-1} + c)$	0.63**	1.7	−1.28*			0.49	35.506	1.963	0.375	0.071	2.668	−13.833	3
E	$Rt = b - \exp(a \times Cv_{t-1} + c + d \times (sprRain + sumRain) + f \times medianspr)$	0.09	1.7	2.11**	−0.00019	0.40*	0.71	35.585	2.041	0.360	0.068	2.775	−10.063	5
F	$Rt = b - \exp(a \times Cv_{t-1} + c) + d \times (sprRain + sumRain)$	0.41*	1.7	−0.13	0.0016		0.58	35.703	2.160	0.340	0.064	2.945	−12.186	4
G	$R_t = b - \exp(a \times Cv_{t-1} + c + d \times NDVIminanual) + f \times medianspr$	0.11	1.7	2.01**	−0.352	0.369	0.65	36.681	3.138	0.208	0.039	4.801	−10.613	5
H	$R_t = b - \exp(a \times Cv_{t-1} + c + d \times sumRain)$	0.68**	1.7	−1.03	−0.0012		0.56	36.793	3.250	0.197	0.037	5.078	−12.732	4

a, non-linearity coefficient; *b*, maximum finite reproductive rate; *c*, equilibrium point; *d* and *f*, coefficients for different effects; R^2, coefficient of determination; AIC$_c$, Akaike information criterion corrected for small sample bias; ΔAIC$_c$, differences in AIC$_c$; likelihood, $\exp(-\Delta\text{AIC}_c/2)$; w_i, Akaike weights; w_i/w_j, evidence ratios; *k*, number of estimated parameters; $R_t = \ln(N_t) - \ln(N_{t-1})$, realized logarithmic per-capita population growth rate; Cv_{t-1}, logarithmic abundance of *C. venustus* in $t - 1$; *sum*, summer; *spr*, spring; *median*, mean temperature; *NDVIminannual*, annual minimum NDVI

** $P < 0.01$, * $P < 0.05$, $P < 0.1$

its abundance (model A.2, $R^2 = 0.87$, $\Delta\text{AIC}_c = 0$; Table 2), although spring rainfall (acting both in an additive and/or non-additive manner) and summer and spring rainfall together also seemed to affect *A. azarae*'s population dynamics ($\Delta\text{AIC}_c < 2$, Table 2; Table A3 in ESM).

The best model for *C. venustus*, according to AIC$_c$ values, is the one including spring mean temperature as an additive positive effect (model A). However, we could not discriminate it from the next four models ($\Delta\text{AIC}_c \le 2$, Table 1) which indicated that summer rainfall alone (model C) and summer and spring rainfall together also seemed to be positively involved in the dynamics of *C. venustus*. On the other hand, model B, which explained 71% of the variability in *R*, combines a lateral effect of summer rainfall with a vertical effect of spring mean temperature. However, simulations of model E, which included lateral effects of summer and spring rainfall and spring mean temperature seemed to better predict the observed fluctuations of the *C. venustus* population than the simulations of model B (correlations between observed and predicted values of density were 0.70 and 0.66 for total trajectory predictions and 0.56 and 0.62 for one-step-ahead predictions for model E and B, respectively, Fig. 3a, b).

Dynamics of *A. azarae* seemed to be mainly affected by its abundance and the vertical effects of annual minimum NDVI (model A.1, $R^2 = 0.76$, $\Delta\text{AIC}_c = 0$), although summer and spring rainfall together also seemed to have an effect in *A. azarae*'s population dynamics (model B.1, $\Delta\text{AIC}_c > 2$, Table 2). When simulating the dynamics of model A.1 and B.1, both of them seem to capture the structure of the observed dynamics effectively (correlations between observed and predicted values of density were: 0.73 and 0.76 for total trajectory predictions, and 0.80 and 0.82 for one-step-ahead predictions for models A.1 and B.1, respectively (Fig. 3c, d). These models including the NDVI were able to simulate the collapse observed during the period 1992–1997.

Discussion

The population dynamics of both rodent species studied here showed irregular numerical fluctuations which seem to be described by a negative first-order feedback structure, suggesting that both species are regulated by intra-specific competition. However, endogenous structure seems to be stronger in *A. azarae* than in *C. venustus* population dynamics. Mechanisms such as territoriality, aggressive behavior, social and spatial organization observed in some small mammal species, may regulate population dynamics operating as density-dependent factors on maturation and recruitment (Stenseth et al. 1996; Prévot-Julliard et al.

Table 2 Best population dynamics models fitted to *A. azarae* time series (1990–2007)

	Estimated parameters					R^2	AIC_c	ΔAIC_c	Likelihood	w_i	w_i/w_j	Log (likelihood)	k
	a	b	c	d	f								
Models for *Akodon azarae* (complete series)													
A.1 $R_t = b - \exp(a \times Aa_{t-1} + c) + d \times NDVIminanual$	2.377	−1.5827*	−8.6174	6.7**		0.76	10.535	0	1	0.646	1	2.46	5
B.1 $R_t = b - \exp(a \times Aa_{t-1} + c + d \times (sprRain + sumRain)) + f \times NDVIminanual$	1.702	−1.3565*	−5.4979	−0.0009	6.3833**	0.78	13.97	3.435	0.18	0.116	5.57	3.215	6
C.1 $R_t = b - \exp(a \times Aa_{t-1} + c + d \times NDVIminanual)$	1.107	0.934	−1.7532	−6.2628		0.69	14.537	4.001	0.135	0.087	7.394	0.459	5
D.1 $R_t = b - \exp(a \times Aa_{t-1} + c + d \times (sprRain + sumRain) + f \times NDVIminanual)$	0.393	2.2411	0.654	−0.0005	−2.5964	0.76	15.07	4.535	0.104	0.067	9.655	2.665	6
E.1 $R_t = b - \exp(a \times Aa_{t-1} + c + d \times sprRain) + f \times NDVIminanual$	2.387	−1.5405*	−8.5781	−0.0003	6.5527**	0.76	15.389	4.853	0.088	0.057	11.321	2.506	6
F.1 $R_t = b - \exp(a \times Aa_{t-1} + c)$	3.609	0.3079	−13.42			0.47	19.844	9.308	0.01	0.006	105.016	−4.255	4
Models for *Akodon azarae* (4 points removed)													
A.2 $R_t = b - \exp(a \times Aa_{t-1} + c)$	2.98*	0.63**	−10.77*			0.87	1.63	0	1	0.273	1	5.68643	4
B.2 $R_t = b - \exp(a \times Aa_{t-1} + c + d \times sprRain)$	3.05**	0.62**	−10.64*	−0.0013		0.91	2.411	0.7814	0.6765734	0.185	1.478	8.082232	5
C.2 $R_t = b - \exp(a \times Aa_{t-1} + c) + d \times sprRain$	3.64*	0.21	−13.28*	0.000988		0.91	2.611	0.9814	0.612189	0.167	1.6335	7.982075	5
D.2 $R_t = b - \exp(a \times Aa_{t-1} + c + d \times (sprRain + sumRain))$	2.96*	0.61**	−9.93*	−0.0013		0.9	3.311	1.6814	0.4314023	0.118	2.318	7.632407	5
E.2 $R_t = b - \exp(a \times Aa_{t-1}) + c + d \times (sprRain + sumRain)$	3.50*	0.054	−12.83*	0.0007		0.9	3.711	2.0814	0.3532023	0.096	2.8312	7.430642	5
F.2 $R_t = b - \exp(a \times Aa_{t-1} + c) + d \times medianspr$	3.42*	2.09	−12.40*	−0.076		0.88	5.691	4.0614	0.1312417	0.036	7.6195	6.442932	5

a, non-linearity coefficient; *b*, maximum finite reproductive rate; *c*, equilibrium point; *d* and *f*, coefficients for different effects; R^2, coefficient of determination; AIC_c, Akaike information criterion corrected for small sample bias; ΔAIC_c, differences in AIC_c; likelihood, $\exp(-\Delta AIC_c/2)$; w_i, Akaike weights; w_i/w_j, evidence ratios; *k*, number of estimated parameters; $R_t = \ln(N_t) - \ln(N_{t-1})$, realized logarithmic per-capita population growth rate; Aa_{t-1}, logarithmic abundance of *A. azarae* in $t - 1$; *sum*, summer; *spr* spring; *median*, mean temperature; *NDVIminannual*, annual minimum NDVI

** $P < 0.01$, * $P < 0.05$, $P < 0.1$

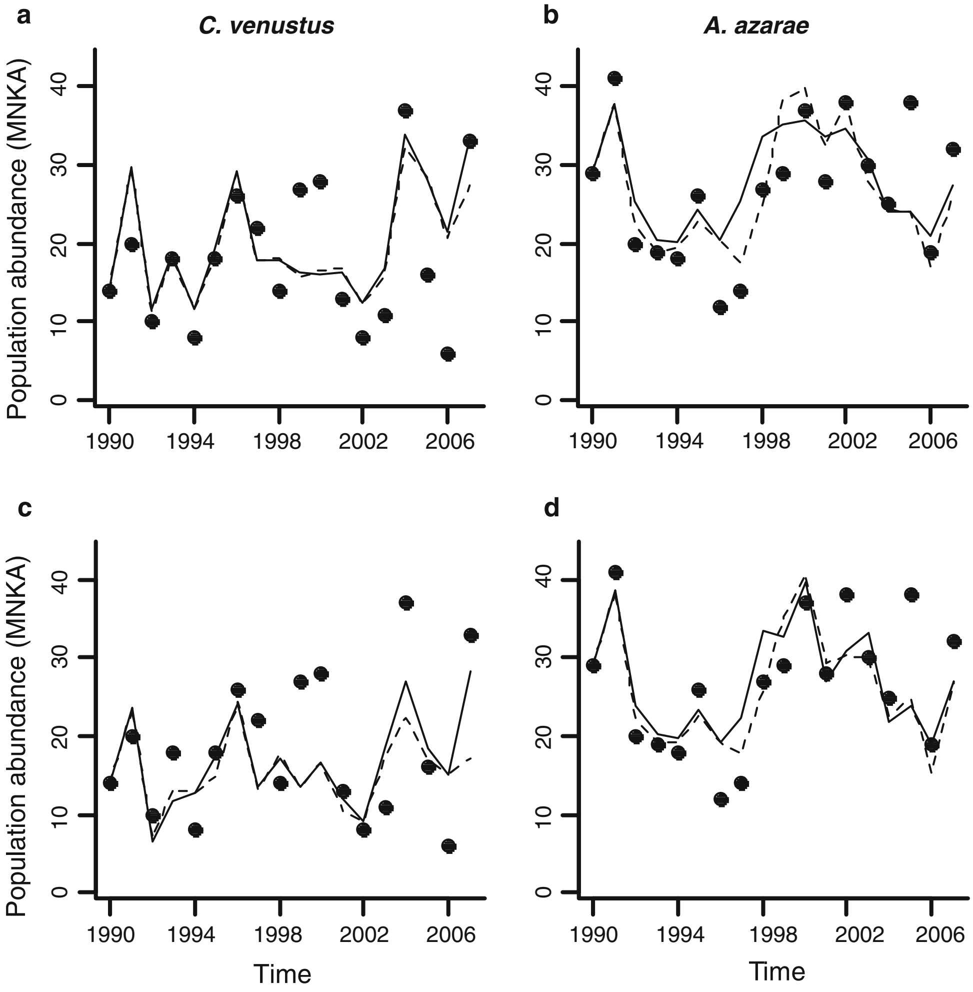

Fig. 3 Comparisons between observed rodent abundances (*points*) and deterministic predictions (*lines*) for the best models for *C. venustus* and *A. azarae*. Runs began with an initial population abundance (MNKA) of 14 individuals for *C. venustus* and 29 for *A. azarae* (*continuous line*). Total trajectory and (*dashed lines*) one-step-ahead prediction. **a** Model B and **c** Model E for *C. venustus*. **b** Model A.1 and **d** Model B.1 for *A. azarae*

1999; Lima et al. 2001, 2002b). In *C. venustus*, climate effects seem to be related to requirements for reproduction in the breeding season (rain and warm temperatures), probably reflecting vegetation growth and ripening, which offer cover and food. Meanwhile, in *A. azarae* climate seems to play a secondary role and the main exogenous perturbation seems to be driven by human land-use, as apparent from the vertical effect of annual minimum NDVI.

Regarding the collapse in *A. azarae*'s fluctuations, we detected some important environmental changes (from 1992 to 1996), mainly related to reductions in plant cover, that may have affected *A. azarae*'s population dynamics but not *C. venustus*'*s* (or at least not in a noticeable manner in the *R*-function). For example, we recorded that both in 1995 and in 1996 the area where the grid was placed or its surroundings were burnt. On the other hand, we detected a regional significant increase in peanut-sown area (Secretaría de Agricultura, Ganadería y Alimentación, Córdoba government: http://www.cba.gov.ar). This regional change in cover was also observed in NDVI minimum values which showed a considerable decrease during the period 1992–1996 (Fig. 4). In fact, several studies have indicated that *A. azarae* shows a strong habitat selection for highly covered and less disturbed habitats such as crop field edges and roadsides (Hodara et al. 2000a; Busch et al. 2001). This marked preference is also evident in microhabitat use, both within borders and in crop fields (Bilenca and Kravetz 1998). J. Priotto (personal communication) has, moreover, observed that captures of *A. azarae* decrease considerably in burnt areas, whereas *Calomys* species are captured normally. Furthermore, considering that *A. azarae* and *C. venustus* have distinct patterns of activity and diet, burning may have different effects on these species, despite their inhabiting the same place (Priotto and Polop 1997; Castellarini and Polop 2002). On the other hand, the regional increase in peanut-sown area and the subsequent reduction in NDVI (mainly in autumn and winter), may have had a substantial effect on *A. azarae*, because when this crop is harvested (autumn) soil is left almost completely bare and *A. azarae* is known to use crop fields during the breeding season (Bilenca and Kravetz 1998).

Fig. 4 Annual minimum NDVI from rural area of Chucul (source: global land cover facility (GLCF), global inventory modeling and mapping studies (GIMMS), normalized difference vegetation index (NDVI) data set)

A first-order negative feedback structure seemed to capture the essential features of *A. azarae* dynamics, suggesting intra-specific competition as the main regulating mechanism. This is consistent with many studies that point out the importance of spacing behavior and intra-specific competition in this rodent. For example, some authors have found that during the breeding season, females of *A. azarae* are strongly territorial and aggressive (Bonaventura et al. 1992; Hodara et al. 2000a; Suárez and Kravetz 2001). Although it seems likely that intra-specific competition may be the regulating factor in *A. azarae*'s population dynamics, it is not clear, however, which is the limiting resource. This rodent species seems to respond positively to both food (Cittadino et al. 1994) and shelter addition (Hodara et al. 2000b). In particular, plant cover seems to be a very important resource for *A. azarae* (Ellis et al. 1997; Hodara et al. 2000a; Busch et al. 2001), mainly for sexually active females, which select microhabitats with a greater amount of green cover and higher densities of insects (Bilenca et al. 1992; Bilenca and Kravetz 1998). Cover also seems to be an important resource for *A. azarae* during winter (non-breeding season), when individuals of both sexes select highly covered areas in borders (Bilenca and Kravetz 1998). Thus, it seems likely that *A. azarae* is limited by areas with high plant cover, which provides refuge from predators and high-quality food (mainly insects).

Population fluctuations of *C. venustus* seemed to be the result of the endogenous feedback structure combined with lateral positive effects of spring and summer rainfall and spring mean temperature. Females of this rodent species show strong territorial behavior (Priotto et al. 2002), which become more pronounced during the breeding season (Priotto and Polop 2003). This is consistent with the lateral effects of the spring–summer rainfall and spring temperature observed in this species. Local weather (rainfall and temperature) seems to be a proxy for the limiting resources of *C. venustus*, probably reflecting an increase in food availability. In fact, *C. venustus* is mainly a folivorous–granivorous small rodent (Castellarini et al. 1998), with higher consumption of leaves in spring and grain in summer. Recent studies of small rodents have showed that the effect of rainfall (or temperature) on primary productivity can be easily incorporated as a lateral perturbation effect (Royama 1992) using simple population models (Lima et al. 2006, 2008). The same approach has been used to predict the dynamics of large mammal populations influenced by climatic variability (Berryman and Lima 2006; Lima and Berryman 2006).

In conclusion, the numerical fluctuations of the two rodent species studied here show first-order feedback structures suggesting that both populations are regulated by intra-specific competition (Johst et al. 2008). However, for the insectivorous rodent *A. azarae*, plant cover and human-induced changes in land-use seem to represent the main exogenous perturbations. On the other hand, the herbivorous rodent *C. venustus* seems to be more affected by rainfall and temperature, probably because of their effects on primary productivity. Our results show that simple, theory-based models, for example those provided by Royama (1992), are also useful in explaining and predicting the dynamics of populations inhabiting highly variable environments such as agro-ecosystems of central Argentina.

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