Effect of environmental factors on the abundance variations of two native rodents in agricultural systems of Buenos Aires, Argentina

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Abstract Our aim was to assess the effect of environmental factors on short temporal abundance variations of the two most abundant native rodents of agricultural agroecosystems, Akodon azarae and Calomys laucha. We conducted a 3-year longitudinal sampling of rodents, and recorded meteorological data such as temperature and precipitation, predation rate by Leopardus geoffroyi, Tyto furcata and Athene cunicularia, vegetation cover and height, characteristics of cropfields and their borders. The effect of these factors on rodent abundance was evaluated through generalized linear mixed models. Abundance variations of both rodent species were explained by characteristics of both cropfields and their borders. At the studied temporal scale, meteorological variables did not have a direct effect on abundance variations, but probably influenced through vegetation characteristics and were expressed in seasonal variations. For A. azarae there was also an effect of predation by L. geoffroyi (positive) and T. furcata (negative), while predation by A. cunicularia did not contribute to explain abundance variations of any species.

Key words: environment, GLMM, populations, predation, rodents.

INTRODUCTION

The causes of numerical fluctuations are one of the main questions in population ecology, just like the factors underlying multiannual population cycles and outbreaks (Jaksic 2001; Lima et al. 2001). It was suggested that discrepancies in outbreaks topology among different species, as lemmings and voles, are related to different trophic interactions, with interactions with food resulting in more irregular outbreaks than interactions with predators. Other hypotheses propose that different dynamics may result from different sensitivities to climatic factors that may cause irregular fluctuations (Ims et al. 2011). There are many studies that describe population dynamics of rodents for the Northern hemisphere (e.g. Hansen et al. 1999; Hanski et al. 2001; Krebs 2013) but little is known about the Neotropical region. Most of these latter studies have focused on multi-year population dynamics of rodents of arid and semiarid regions of Chile (Lima & Jaksic 1998; Lima et al. 1999) and central Argentina (Andreo et al. 2009a,b). These multi-year fluctuations were associated to both direct and indirect (through the abundance of resources) effects of climatic factors, which in temperate areas are also responsible of the seasonal variation in abundance (Jaksic 2001; Jaksic & Lima 2003). Associated to the large temporal scale of these studies there was also a coarse grained spatial scale, which did not take in account spatial heterogeneity, as is caused by intensive agricultural activities. Processes associated to the patterns of abundance variation at small temporal and spatial scales may increase their importance in anthropic systems subject to frequent perturbations, and probably differ from those associated to larger scales.

In rural ecosystems, rodent dynamics are not only affected by natural variables, such as climatic variations, but are also influenced by land use. In terrestrial ecosystems, a great proportion of land is actually devoted to agriculture (Paruelo et al. 2005) which has caused major changes in landscapes, with a loss, deterioration and fragmentation of habitats for wildlife (Singleton et al. 2003; Massawe & Makundi 2011). Ecological compensation areas as wildflower strips have been widely promoted to decrease the negative effects of farming on wildlife. Since these areas were also shown to contain large numbers of
small mammals, there is concern about negative effects from dispersal of pest species into adjacent cropfields (Briner et al. 2005). Most small mammal research in agrarian landscapes focused on crop damage and rodent control, while little is known about the short-term impact of farming practices on population dynamics and demography (Jacob 2003). Besides the effect of agriculture at large scales (landscapes and ecosystems), at smaller scales populations are affected by the type of crops, level of human disturbance and the area covered by crops and other (Vitta et al. 2003). In contrast to rural areas of Australia, in Pampas systems commensal species are rare in cropfields and their edges, probably because of competition with native species (Busch et al. 2005; Miño et al. 2007; Fraschina et al. 2017). Also, in comparison to common voles in Europe, rodent species in these agroecosystems do not reach pest densities, and probably have less effect on crops because their diet is composed by a great proportion of insects, as well as seeds and other parts of plants (Ellis et al. 1997).

Although there are many studies about the population ecology of these species in the Pampean region, the effect on their abundance of weather, vegetation, land use and predation were not previously assessed simultaneously.

In this work we want to assess the effect of weather factors, vegetation structure, predation and agrarian labours on two small rodents, *A. azarae* and *C. laucha*, abundance variations at small temporal (3 years, seasonal) and spatial scales in a Pampean agroecosystem (Buenos Aires province, Argentina).

The hypotheses being tested were:

1. The abundance of both species is affected by temperature and precipitation variations.
2. Border plant cover and height affects *A. azarae* abundance in borders.
3. The abundance of *C. laucha* is affected by both border characteristics as well as by the type and stage of crops.
4. The effect of predation by the *Leopardus geoffroyi* and *Tyto furcata* on rodent abundance is higher than the effect of *Athene cunicularia*, because the latter is a generalist and opportunistic predator of rodents while the forermers are specialists. Moreover, it can be expected a positive association between predation rate by *A. cunicularia* and rodent abundance.

**METHODS**

**Study area**

Field work was conducted in agroecosystems of Exaltación de la Cruz Department (34°19'0"S and 59°14'0"W), Buenos Aires province, Argentina. The study area is located in the
Rolling Pampas, an ecoregion that includes part of Buenos Aires, Córdoba and Santa Fe provinces, within banks of La Plata and Paraná rivers at northeast, Salado river at southwest and Matanza river at southeast. This region presents a highly rolling topography in comparison with other neighbour areas, forming an exoreic drain system (Bilenca & Minarro 2004). The climate is sub-humid temperate, with a mean annual temperature of 16°C and an annual precipitation of approximately 1000 mm. Originally, the area was covered by grasslands, with a vegetation structure that corresponded to a prairie in humid years and pseudosteppe or steppe during dry years (Soriano et al. 1991). The vegetation was represented by tall perennial grasses, as *Nassella* spp. [(Trin.) E. Desv.] and *Piptochaetium* spp. (J. Presl.). Nowadays 90% of the land is devoted to crops as soybean, wheat, corn and sunflower (Viglizzo et al. 2001; Paruelo et al. 2005), so the landscape is a matrix of cropfields (covering more than 95% of the area) with grassland corridors along their edges (borders) and small woodlots with a mixture of exotic and native tree species (Fraschina et al. 2012). Changes in plant phenology and in the stage of development of crops cause seasonal qualitative and quantitative variations in resources, both in cropfields and borders. The borders have abundant vegetation cover throughout the year, while cropfield cover varies from low levels after ploughing and sowing to high cover when crops are mature (Busch et al. 1997; Hodara & Busch 2006).

According to previous studies (Bellocq 1987, 1988, 1998; Bellocq & Kravetz 1994; Guidobono et al. 2016) the most frequent rodent predators are the *L. geoffroyi*, *T. furcata* and *A. cunicularia*. Jaksic and Meserve (1993), Korfanta et al. (2005) and Pereira et al. (2006), found that these predators are resident and in consequence may exert an effect on their prey all along the year. Another potential rodent predator, *Lycalopex gymnocercus*, is an omnivorous and opportunistic predator that consumes mainly fruits (Schalk & Morales 2012), and in lower proportions arthropods, mammals, birds, reptiles and amphibians (Lucherini & Luengos Vidal 2008; Varela et al. 2008; Schalk & Morales 2012).

**Study design**

We conducted a longitudinal sampling in three cropfields and their borders. All sites were neighbouring to other crop or livestock fields. Implanted crops in summer were soybean and maize, while during winter in most cases fields were without plant cover, except in one occasion in which wheat was planted.

**Rodent samplings**

Rodent populations were sampled at three sites including cropfields and their borders at 45 days intervals for 3 years (November 2008–December 2011). The studied sites were selected in order to ensure the continuity of the study and were separated by more than 200 m to ensure independence among them because rodents infrequently travel this distance (Leon et al. 2007; Kittel 2009). At each site, three lines of 25 Sherman live traps (8 × 9 × 23 cm) were placed, one along the borders and two parallel lines within cropfields, perpendicular to the first and the last border trap respectively (Figure 1). The distance between traps in each line was 10 m. The distance between the first trap in the cropfield and the trap-line in the border was 20 m (Figure 1). Traps were baited with a mix of peanut butter, bovine fat and rolled oats and were checked every morning for three consecutive days. Each captured animal was

![Fig. 1. Rodent sampling design. Three lines of 25 Sherman traps were placed in each one of the three sampling sites. One line was placed along the border and two in parallel lines in the cropfield. Distance between traps in each line was 10 m. doi:10.1111/aec.12650 © 2018 Ecological Society of Australia](image-url)
identified to species and sex. Reproductive status, corporal length, body weight, trap location and date of capture were recorded for all individuals. Rodents were given an individual mark by ear tags. Finally, they were released at the site of capture.

**Precipitation and temperature records**

Meteorological data were recorded placing temperature and humidity dataloggers at each cropfield (HOBO; Hepta Instruments) and from databases published online – with prior permission of the publishers (www.tutiempo.net/BuenosAires/). We calculated the accumulated precipitation and the daily mean minimum and maximum temperatures for the 45 days period before each sampling.

**Cover, height and type of vegetation in the two habitat types**

The green and total plant cover (%), crop height and border plant height were recorded at each site. The type and stage of crops, when present, were also recorded.

**Predation rates**

Sampling of *L. geoffroyi* scats and owl pellets was carried out simultaneously with rodent samplings. Search of *L. geoffroyi* latrines and scats was conducted within woodlots near the trapping sites of rodents. Scats were assigned to *L. geoffroyi* by size and form, since there are no other wild felids with similar weight and aspect in northern Buenos Aires province (for more details, see Guidobono et al. 2016). *A. cunicularia* pellets were collected from burrows, or searching close to perches or individuals. Pellets of *T. furcata* were found under trees in woodlots. Additionally, pellets were collected in refuges such as water tanks and attics of houses. To ensure the origin of pellets, they were collected in sites where individuals were observed.

The number of rodent preys per pellet or scat was determined from the number of jaws and teeth found in them. We could not differentiate *C. laucha* and *C. musculus* remains, but we considered them that mainly corresponded to *C. laucha*, because *C. musculus* was rarely captured along the study (for methodological details see Guidobono et al. 2016).

**Data analysis**

In order to analyse the effect of environmental factors on rodent abundance generalized linear mixed models (GLMM), using the package lme4 (Bates et al. 2017), with binomial error structure, a log-link function and the Laplace approximation method were used (Bolker et al. 2009; Zuur et al. 2009; Crawley 2012). The ‘MuMin’ package (Bartoń 2017) was used in order to adjust models containing all possible combination of the explanatory variables, including some interactions (Candidate models). The number of parameters included in each candidate model was limited by the number of cases used for each model (Burnham & Anderson 2002). Null models for each rodent species were also constructed. In order to avoid redundancies, we estimated collinearity between main effects by means of the variance inflation factor (VIF) customized to mixed models (Schweinberger 2014). According to Zuur et al. (2010), VIF < 3 indicate absence of collinearity. For variables that showed VIF values >3, we conducted pairwise correlations using the package stats (R Core Team and Contributors Worldwide 2017) in order to find the correlated variables. A combination of site–month–year as a random effect was used in order to correct over-dispersion when the dispersion factor was larger than 1.5 (Harrison 2015). We applied an information-theoretic approach to selection of models and estimators (Burnham & Anderson 2002). Akaike’s information criterion with correction for small sample size (AICc) was used to rank candidate models (Burnham & Anderson 2002). The best model had the smallest value of AICc (Burnham & Anderson 2002). We also computed \( w_i \) as the weight of evidence in favour of model \( i \) being the best model in the candidate set (Akaike’s weights). We also considered all other models with AICc values smaller than those of the null model (Symonds & Moussalli 2011), and with a \( \Delta \text{AICc} \) lower than 2 in relation to the best model (Richards 2005) to be supported by the data. Selected models were averaged to obtain a final model using the model averaging function (Symonds & Moussalli 2011; Bartoń 2017; R Core Team and Contributors Worldwide 2017). The magnitude of the effect of explanatory variables on rodent abundance variations was assessed through their relative importance value (the sum of weights of the models where the variable is included) and through the limits of the confidence intervals of the estimator (a variable contributes to explain abundance variations when the confidence interval of the estimator does not include the zero). In order to determine the difference between levels of categorical explanatory variables post-hoc tests were conducted using the multcomp package (Hothorn et al. 2017). The interaction of two continuous explanatory variables was explored with a simple slopes analysis using the jtools package (Long 2018). Finally, following Midgley et al. (2003), the performance of each candidate model was assessed through the ‘explained deviance (ED)’, estimated as: \( 1 – (\text{residual deviance/null deviance}) \). Models were adjusted using overall rodent abundance, abundance in borders and abundance in cropfields, separately. All analyses were carried out using the R statistical software (R Development Core Team 2017).

The abundance of each species at each site was estimated by the Trap Success: Number of individuals captured/(number of traps × number of nights). We estimated an overall Trap Success for both cropfields and borders (TS\(_{\text{EB}}\)) and a Trap Success for borders (TS\(_{\text{EB}}\)) and cropfields (TS\(_{\text{EB}}\)) separately.

Taking in account that we could not estimate predator abundances, as a proxy of predation rate, we estimated the mean number of rodents found per pellet or scat for each predator (total number of rodents found divided by the number of pellets or scats), rodent species, and sampling period. In consequence, we assumed that main variations in predation rate were related to individual consumption rather than to variations in predator numbers.

Explanatory variables for both species were: year as a three-level fixed factor (2009, 2010 and 2011), season as a four-level fixed factor (spring, summer, autumn and winter),
accumulated precipitation, daily mean minimum temperature, daily mean maximum temperature, L. geoffroyi predation rate, T. furcata predation rate, A. cunicularia predation rate, cropfield use as a six-level fixed factor (corn, weeds, implanted pasture, soybean, bare soil and wheat), stage of crops as a four-level fixed factor (initial, intermediate, mature and stubble), total and green plant cover of cropfield, total and green plant cover of borders, crop height and border plant height. We also included as explanatory variables, for A. azarae: C. laucha TSo, TSb, and TSc, and for C. laucha: A. azarae TSo, TSb, and TSc. All main effects were calculated considering a 45-day period before the sampling in which the response variable was recorded. We also considered delayed effects, relating the response variable to environmental factors evaluated between 45 and 90 days (delay 1) and between 90 and 135 days (delay 2) before the corresponding rodent sampling.

RESULTS

Rodent samplings

A total of 511 individuals were captured with a trapping effort of 16 200 Sherman trap-nights. Captured rodents included native sigmodontines: A. azarae (n = 333), C. laucha (n = 109), O. flavescens (n = 30), C. musculinus (n = 27) and O. rufus (n = 7), one caviid: C. aperea (n = 2) and two species of introduced murines: R. norvegicus (n = 2) and M. musculus (n = 1). In border habitats all rodent species described were trapped, A. azarae was the most frequently trapped species, representing 77% of the captures, C. laucha and O. flavescens represented 7% of the captures each, while C. musculinus represented 6% of the captures. O. rufus represented only the 2% of captures and M. musculus, R. norvegicus and C. aperea, combined, represented the remaining 2% of the captures. In cropfields only four rodent species were captured, C. laucha was the most frequent species, representing 75% of the captures, A. azarae represented 18% of the captures (being trapped in trap stations near borders), C. musculinus resented 5% of the captures and O. flavescens represented the remaining 2% of the captures.

Effect of environmental factors on rodent abundance

Akodon azarae

For this species, we only adjusted models using TSo and TSb because numbers in cropfields were not enough to adjust models. After the GLMM analysis, the best model had a ΔAIC value with respect to the null model of 256.25, while other six models had ΔAIC < 2 with respect to the best model. According to the average model, variables with the highest relative importance values (1.00) were cropfield plant height, green plant cover in borders with delay 1, border plant height with delay 2 and season. Cropfield height had a positive effect on overall A. azarae abundance, while green plant cover had a negative effect. Confidence intervals of the last variable included zero values, and in consequence its effect is not important. The effect of the border plant height with delay 2 on A. azarae abundance showed an interaction with the season (relative importance value = 0.91), with a highest positive effect on A. azarae abundance in summer, suggesting that high vegetation in borders in spring favours an increase in abundance in summer. Predation rate of T. furcata with delay 2 (in the previous season) had a negative effect on A. azarae abundance, but with a lower relative importance (0.75) and with zero values included in its confidence interval. Relative importance of the other variables were low (Table 1).

For the abundance of A. azarae in borders were included 13 models with ΔAIC < 2 with respect to the best model. The average model showed the importance of the cropfield height with delay 2 and the interaction between border height with delay 2 and the season (relative importance = 1), as for the overall abundance of A. azarae. The other variables showed relative importance values <0.7 (Table 2).

Calomys laucha

For this species we adjusted models for the overall abundance (TSo), abundance in cropfields (TSb) and in borders (TSb). For TSo, 14 models with ΔAIC < 2 with respect to the best model were included. According to the average model, the season was the best variable to explain C. laucha abundance variations, with the highest abundance in summer (relative importance = 1.00, Table 3). The effect of predation rate by L. geoffroyi (positive) and T. furcata (negative) showed relative importance values of 0.49 and 0.63, but the confidence intervals included the zero. Interactions of variables also showed low relative importance values, although confidence intervals of the interaction between L. geoffroyi and T. furcata predation rates did not include zero (Table 3).

For C. laucha abundance in fields eight models were selected. According to the average model, the season was again the best variable to explain abundance variations, showing the highest abundance in summer (relative importance = 1, Table 4). Green plant cover in borders had a negative effect on C. laucha abundance in fields (relative importance = 0.86), suggesting that individuals of this species move between habitats according to their relative conditions. Predation rate by T. furcata had a relative
Table 1. Candidates and average models for Akodon azarae overall abundance variations (TSo)

| Candidate models | 1 | 2 | 3 | 4 | 5 | 6 | 7 | Average model |
|------------------|---|---|---|---|---|---|---|---------------|
| Estimator        | SE | Estimator | SE | Estimator | SE | Estimator | SE | Estimator | SE | RVI | Estimator | SE |
| Intercept        | 3.24 | 0.54 | -2.07 | 0.86 | -3.32 | 0.56 | -1.82 | 0.88 | -2.28 | 0.87 | -3.09 | 0.54 | -2.25 | 0.59 | -2.64 | 0.91 |
| Bh.2             | 0.61 | 0.39 | -0.66 | 0.82 | 0.55 | 0.40 | -0.85 | 0.81 | -0.58 | 0.84 | 0.53 | 0.39 | -0.55 | 0.53 | 1.00 | -0.07 | 0.88 |
| Ch.1             | 0.81 | 0.24 | 0.76 | 0.24 | 0.84 | 0.25 | 0.67 | 0.24 | 0.80 | 0.25 | 0.74 | 0.25 | 0.62 | 0.25 | 1.00 | 0.76 | 0.25 |
| gb.B1            | -1.07 | 0.42 | -2.67 | 1.03 | -0.96 | 0.43 | -2.86 | 1.02 | -2.37 | 1.04 | -1.14 | 0.42 | -2.60 | 0.86 | 1.00 | -1.88 | 1.10 |
| Spring           | -0.79 | 0.61 | -0.90 | 0.62 | -0.97 | 0.62 | -0.70 | 0.62 | -1.08 | 0.62 | -0.62 | 0.61 | -1.39 | 0.32 | 1.00 | -0.90 | 0.63 |
| Summer           | -3.02 | 0.69 | -3.13 | 0.68 | -2.96 | 0.70 | -2.98 | 0.66 | -3.05 | 0.69 | -2.87 | 0.68 | -1.71 | 0.30 | 1.00 | -2.91 | 0.74 |
| Winter           | -0.27 | 0.70 | -0.95 | 0.79 | -0.43 | 0.72 | -1.03 | 0.77 | -1.03 | 0.81 | -0.30 | 0.69 | -0.97 | 0.30 | 1.00 | -0.67 | 0.78 |
| TfP.1            | -0.55 | 0.29 | -0.59 | 0.28 | -1.70 | 0.85 | -1.51 | 0.86 | -0.86 | 0.36 | 0.75 | -0.91 | 0.62 | 0.24 | 0.96 | 1.66 | 1.10 |
| Bh.2 x           | -1.35 | 1.07 | -1.54 | 1.11 | -1.33 | 1.09 | -1.66 | 1.10 | -2.28 | 0.87 | -1.43 | 1.05 | 0.91 | -1.46 | 1.10 |
| Spring           | 1.57 | 0.62 | 1.66 | 0.61 | 1.38 | 0.63 | 1.53 | 0.60 | -0.58 | 0.84 | 1.44 | 0.61 | 0.91 | 1.53 | 0.62 | 1.24 | 0.57 | 0.97 | 1.24 | 0.57 |
| Summer           | -0.77 | 0.56 | -0.05 | 0.69 | -0.70 | 0.58 | -0.01 | 0.67 | 0.80 | 0.25 | -0.78 | 0.55 | 0.91 | -0.42 | 0.72 | 0.22 | 0.92 | 0.71 |
| Bh.2 x Tg.B1     | 1.83 | 1.06 | 1.95 | 1.04 | 1.62 | 1.08 | 1.95 | 0.86 | 0.52 | 1.83 | 1.03 | 0.91 | 0.22 | 0.92 | 0.71 | 1.24 | 0.57 | 0.97 | 1.24 | 0.57 |
| Bh.2 x Tg.P.1    | 0.98 | 0.70 | 0.86 | 0.72 | 0.22 | 0.92 | 0.71 | 1.24 | 0.57 | 0.97 | 1.24 | 0.57 | 0.91 | 0.22 | 0.92 | 0.71 |
| Ch.1 x Tg.P.1    | 0.90 | 0.89 | 0.90 | 0.89 | 0.89 | 0.89 | 0.89 | 0.57 | 0.89 | 0.89 | 0.89 | 0.89 | 0.89 | 0.89 | 0.89 | 0.89 | 0.89 | 0.89 |
| Log-Likelihood   | -173.72 | -172.24 | -175.67 | -171.26 | -174.54 | -173.01 | -176.20 | 1.24 | 0.57 | 0.97 | 1.24 | 0.57 |
| AICc             | 379.72 | 379.85 | 380.62 | 381.10 | 381.35 | 381.39 | 381.68 | 0.90 | 0.13 | 0.90 | 1.38 | 1.63 | 1.67 | 1.96 |
| AAIcc            | 0.23 | 0.22 | 0.15 | 0.12 | 0.10 | 0.10 | 0.10 | 0.08 | 0.23 | 0.22 | 0.15 | 0.12 | 0.10 | 0.10 | 0.08 | 0.23 | 0.22 | 0.15 | 0.12 | 0.10 | 0.10 | 0.08 |

Explanatory variables were: border plant height with delay 2 (Bh.2), crop height with delay 1 (Ch.1), green plant cover of borders with delay 1 (gb.B1), Tyto furcata predation rate with delay 2 (TfP.2), season (spring, summer and winter, autumn was the reference level). Table entries state the corresponding statistics: Estimators of the association with the explanatory variable, standard error of the estimator (SE), relative variable importance (RVI), explained deviance (ED), the maximized log-likelihood, Akaike’s information criterion corrected for small sample size (AICc), difference between the AICc of the best model and the AICc of model (ΔAICc) and Akaike’s weights (wᵢ). Estimator values in Bold implies an important explanatory variable (the CI 95% of the estimator excluded zero).

Null model AICc = 635.97.

Number of estimable parameters in the global model: 19.

The interaction between T. furcata and L. Geoffroyi predation rates had a low value of relative importance, but confidence intervals did not include the zero (Table 4). This interaction, although with low relative importance, was included in both TSo and TSc C. laucha models. According to the simple slope analysis, predation rate of T. furcata has a negative effect on C. laucha overall abundance when L. Geoffroyi predation rates are lower than the mean (Table 5). This analysis was conducted, as an example, for the best model (model 1) of overall abundance, because estimators and standard errors were similar in other models where this interaction appeared.

To describe the changes in abundance of C. laucha in borders (TSo), eight models were selected. According to the average model, only the cropfield plant height with delay 2 had a high relative importance (0.92) on C. laucha abundance in borders with a positive effect. The effect of season had a low value of relative importance (0.18), but according to the confidence intervals, in winter and spring the abundances were lower than in autumn (Table 6).

**DISCUSSION**

Small mammals are strongly affected by environmental conditions at different temporal and spatial scales. In agrarian systems periodic changes in habitat conditions due to farming practices affect the availability of food and cover (Jacob 2003) at both small temporal and spatial scales. The effect of environmental conditions may differ among species in a community (Lima et al. 2002). According to our expectations, in our study the effect of environmental factors differed between the two rodent species, but, contrary to our hypotheses, A. azarae abundance was influenced not only by border characteristics but also by cropfield features. We did not detect a direct effect of meteorological variables, but they probably influenced indirectly through the vegetation and its effect was also expressed in the effect of seasons on C. laucha.
Table 2. Candidate models for *Akodon azarae* abundance variation in borders (TSb).

| Candidate models | 1     | 2     | 3     | 4     | 5     | 6     | 7     |
|------------------|-------|-------|-------|-------|-------|-------|-------|
|                  | Estimator | SE     | Estimator | SE     | Estimator | SE     | Estimator | SE     | Estimator | SE     | Estimator | SE     | Estimator | SE     |
| Intercept        | -2.92   | 0.39   | -2.45   | 0.47   | -1.39   | 0.76   | -3.05   | 0.40   | -1.27   | 0.76   | -3.09   | 0.54   | -2.60   | 0.48   |
| Ch.1             | 0.59    | 0.22   | 0.62    | 0.22   | 0.60    | 0.21   | 0.67    | 0.23   | 0.58    | 0.21   | 0.74    | 0.25   | 0.70    | 0.23   |
| tcC              | -0.52   | 0.27   | -0.54   | 0.27   | -0.54   | 0.26   | -0.57   | 0.26   | N       | N      | N       | N      | N       | N      |
| Spring           | -0.93   | 0.54   | -1.04   | 0.55   | -1.16   | 0.57   | -1.24   | 0.53   | -1.00   | 0.58   | -0.62   | 0.61   | -1.35   | 0.55   |
| Summer           | -2.96   | 0.68   | -3.04   | 0.68   | -3.14   | 0.67   | -3.46   | 0.65   | -3.17   | 0.66   | -2.87   | 0.68   | -3.55   | 0.65   |
| Winter           | 0.24    | 0.58   | -0.04   | 0.60   | -0.68   | 0.69   | -0.18   | 0.56   | -0.63   | 0.69   | -0.30   | 0.69   | -0.47   | 0.60   |
| TfP.2            | 0.17    | 0.74   | 0.86    | 0.72   | 0.56    | 0.74   | 1.27    | 1.12   | 0.91    | 1.00   | -1.34   | 1.13   | -1.43   | 1.05   |
| gcB.1            | 1.06    | 0.98   | -1.11   | 1.03   | -1.27   | 1.12   | -0.91   | 1.00   | -1.34   | 1.13   | -1.43   | 1.05   | -0.95   | 1.06   |
| Bh.2 × tcC       | N       | N      | N       | N      | N       | N      | N       | N      | N       | N      | N       | N      | N       | N      |
| Bh.2 × Spring    | 1.49    | 0.55   | 1.58    | 0.55   | 1.64    | 0.54   | 1.78    | 0.55   | 1.78    | 0.54   | 1.44    | 0.61   | 1.88    | 0.55   |
| Bh.2 × Summer    | -1.02   | 0.47   | -0.95   | 0.47   | -0.27   | 0.60   | -0.77   | 0.47   | -0.25   | 0.59   | -0.78   | 0.55   | -0.69   | 0.48   |
| Bh.2 × TfP.2     | N       | N      | N       | N      | N       | N      | N       | N      | N       | N      | N       | N      | N       | N      |
| Bh.2 × gcB.1     | N       | N      | N       | N      | N       | N      | N       | N      | N       | N      | N       | N      | N       | N      |
| Ch.1 × tcC       | N       | N      | N       | N      | N       | N      | N       | N      | N       | N      | N       | N      | N       | N      |
| Bh.2 × Spring    | -1.10   | 0.98   | -1.15   | 1.14   | -1.45   | 1.12   | -1.36   | 1.15   | -1.20   | 1.15   | -0.94   | 1.00   | -1.14   | 1.07   |
| Bh.2 × Summer    | 1.58    | 0.55   | 1.93    | 0.54   | 1.65    | 0.53   | 1.96    | 0.55   | 2.07    | 0.55   | 1.87    | 0.55   | 1.72    | 0.57   |
| Bh.2 × Winter    | -1.05   | 0.47   | -0.04   | 0.61   | -0.19   | 0.57   | 0.08    | 0.61   | -0.003  | 0.60   | -0.80   | 0.47   | -0.60   | 0.65   |
| Bh.2 × TfP.2     | 0.97    | 0.62   | 0.06    | 0.06   | 0.05    | 0.05   | 0.05    | 0.05   | N       | N      | N       | N      | N       | N      |
| ED               | 0.80    | 0.81   | 0.80    | 0.81   | 0.81    | 0.81   | 0.81    | 0.82   | 0.82    | 0.82   | 0.82    | 0.82   | 0.82    | 0.82   |
| Log-likelihood   | -144.72 | -143.45 | -141.97 | -146.49 | -140.46 | -142.20 | -145.32 | N       | N       | N       | N       | N       | N       | N       |
| AICc             | 318.81  | 319.17  | 319.32  | 319.39  | 319.49  | 319.78  | 319.93  | N       | N       | N       | N       | N       | N       | N       |
| ΔAICc            | 0.00    | 0.36    | 0.51    | 0.58    | 0.68    | 0.97    | 1.12    | 0.09    | 0.08    | 0.07    | 0.08    | 0.07    | 0.08    | 0.07    |
| wi               | 0.13    | 0.11    | 0.10    | 0.10    | 0.10    | 0.09    | 0.08    | N       | N       | N       | N       | N       | N       | N       |

Explanatory variables were: border plant height with delay 2 (Bh.2), crop height with delay 1 (Ch.1), total cover of crop-fields (tcC), green plant cover of borders with delay 1 (gcB.1), *Tyto furcata* predation rate with delay 2 (TfP.2), season (spring, summer and winter, autumn was the reference level). Table entries state the corresponding statistics: Estimators of the association with the explanatory variable, standard error of the estimator (SE), relative variable importance (RVI), explained deviance (ED), the maximized log-likelihood, Akaike’s information criterion corrected for small sample size (ΔAICc), difference between the AICc of the best model and the AICc of model, (ΔAICc) and Akaike’s weights (wi). Estimator values in **Bold** implies an important explanatory variable (the CI 95% of the estimator excluded zero).

Null model AICc = 510.23.

Number of estimable parameters in the global model: 16.

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Table 3. Candidate models for *Calomys laucha* overall abundance variations (TS<sub>i</sub>)

| Candidate models | 1      | 2      | 3      | 4      | 5      | 6      | 7      |
|------------------|--------|--------|--------|--------|--------|--------|--------|
|                  | Estimator | SE   | Estimator | SE   | Estimator | SE   | Estimator | SE   | Estimator | SE   | Estimator | SE   |
| Intercept        | -5.84   | 0.57  | -5.85   | 0.38  | -6.06   | 0.41  | -5.76   | 0.39  | -4.59   | 1.51  | -4.24   | 1.70  | -6.17   | 0.50  |
| Ch.2             | -0.16   | 0.49  |          |       |          |       |          |       |          |       |          |       |          |       |
| Ap               |         |       |          |       |          |       |          |       |          |       |          |       |          |       |
| gbB              |         |       |          |       |          |       |          |       |          |       |          |       |          |       |
| Spring           | -0.26   | 0.63  | -0.82   | 0.58  | -0.90   | 0.59  | -0.70   | 0.57  | -4.03   | 1.99  | -4.05   | 2.10  | -0.72   | 0.56  |
| Summer           | 1.34    | 0.50  | 0.84    | 0.49  | 0.89    | 0.48  | 1.03    | 0.46  | -0.47   | 1.61  | -0.57   | 1.75  | 0.75    | 0.49  |
| Winter           | -1.48   | 0.84  | -1.29   | 0.63  | -1.78   | 0.72  | -1.86   | 0.77  | 1.52    | 2.14  | 3.97    | 2.57  | -1.87   | 0.76  |
| TIP.2            | -3.44   | 1.17  |          |       | -1.66   | 0.84  | -1.31   | 0.70  | -2.95   | 1.04  | -1.60   | 0.81  |          |       |
| LgP.1            | 0.46    | 2.27  | 3.28    | 2.15  | 1.07    | 2.32  | 1.60    | 2.30  |          |       |          |       |          |       |
| Ch.2 × TIP.2     | 5.53    | 2.24  |          |       |          |       | 5.15    | 2.17  |          |       |          |       |          |       |
| LgP.1 × TIP.2    | 12.30   | 4.05  |          |       | 7.57    | 3.44  | 7.70    | 3.35  |          |       |          |       |          |       |
| Ap × Spring      | 28.02   | 14.91 | 30.33   | 15.32 | 13.10   | 10.34 | 12.65   | 13.10 |          |       |          |       |          |       |
| Ap × Summer      | -28.85  | 19.39 | -49.56  | 22.34 |          |       |          |       |          |       |          |       |          |       |
| Ap × Winter      | 1.04    | 0.54  | 0.70    | 0.58  | 0.76    | 1.52  | 0.47    | 1.61  | 1.42    | 0.57  | 1.42    | 0.51  | 0.77    | 0.93  |
| Ch.2 × LgP.1     | 90.43   | 2.10  | 4.05    | 2.10  | 1.73    | 0.85  | 3.39    | 1.66  | 2.52    | 1.34  | 1.53    | 1.45  |          |       |
| ED               |          |       |          |       |          |       | 5.42    | 2.25  | 5.67    | 2.22  | 5.42    | 2.22  |          |       |

Explanatory variables were: crop height with delay 2 (Ch.2), accumulated precipitation (Ap), green plant cover of borders (gbB), *Tyto furcata* predation rate with delay 2 (TIP.2), *Leopardus geoffroyi* predation rate with delay 1 (LgP.1), season (spring, summer and winter, autumn was the reference level). Table entries state the corresponding statistics: Estimators of the association with the explanatory variable, standard error of the estimator (SE), relative variable importance (RVI), explained deviance (ED), the maximized log-likelihood, Akaive’s information criterion corrected for small sample size (AICc), difference between the AICc of the best model and the AICc of model (ΔAICc) and Akaive’s weights (w<sub>i</sub>). Estimator values in **Bold** implies an important explanatory variable (the CI 95% of the estimator excluded zero).

Null model AICc = 298.68.

Number of estimable parameters in the global model: 16.

Explanatory variables were: crop height with delay 2 (Ch.2), accumulated precipitation (Ap), green plant cover of borders (gbB), *Tyto furcata* predation rate with delay 2 (TIP.2), *Leopardus geoffroyi* predation rate with delay 1 (LgP.1), season (spring, summer and winter, autumn was the reference level). Table entries state the corresponding statistics: Estimators of the association with the explanatory variable, standard error of the estimator (SE), relative variable importance (RVI), explained deviance (ED), the maximized log-likelihood, Akaive’s information criterion corrected for small sample size (AICc), difference between the AICc of the best model and the AICc of model (ΔAICc) and Akaive’s weights (w<sub>i</sub>). Estimator values in **Bold** implies an important explanatory variable (the CI 95% of the estimator excluded zero).

Null model AICc = 298.68.

Number of estimable parameters in the global model: 16.

last effect, however, may also be a consequence of changes in crop stages, not only of temperature or precipitation variations through seasons. Green plant cover on borders had a negative effect on *C. laucha* abundance in fields, suggesting that this species changes its habitat distribution depending on relative
Table 4. Candidates and average models for Calomys laucha abundance variations in crop fields (TSc)

|   | 1     | 2     | 3     | 4     | 5     | 6     | 7     | 8     |
|---|-------|-------|-------|-------|-------|-------|-------|-------|
|   | Estimator | SE  | Estimator | SE  | Estimator | SE  | Estimator | SE  | Estimator | SE  | Estimator | SE  | Estimator | SE  |     |
| Intercept | -5.52 | 0.87 | -5.10 | 0.90 | -3.56 | 2.95 | -5.65 | 2.61 | -5.43 | 0.86 | -5.83 | 0.94 | -5.84 | 0.95 | -5.59 | 1.02 |
| Ap | 3.83 | 3.58 | 1.08 | 1.27 | 2.81 | 1.54 | 2.68 | 3.89 | 1.15 | 3.73 | 1.15 | 3.62 | 1.12 | 3.68 | 1.10 | 3.08 | 1.93 |
| gB | -3.89 | 1.79 | -3.79 | 1.72 | -2.79 | 1.65 | -3.53 | 1.80 | -3.99 | 1.80 | -3.72 | 1.71 | 0.86 | -3.62 | 1.79 |
| Spring | -1.49 | 1.18 | 1.84 | 1.14 | -7.14 | 4.91 | -8.55 | 5.12 | 1.68 | 1.19 | 1.29 | 1.19 | 1.51 | 1.17 | 1.74 | 1.13 | 1.00 | -1.25 | 4.65 |
| Winter | -0.44 | 1.01 | -0.69 | 1.14 | 3.84 | 3.80 | 4.91 | 3.58 | -0.18 | 1.03 | -0.78 | 1.09 | -0.35 | 1.00 | -0.74 | 1.12 | 1.00 | 0.94 | 2.80 |
| LgP.1 | -1.16 | 3.50 | 1.10 | 2.84 | 3.28 | 0.12 | 3.56 | 0.34 | 0.04 | 3.82 | 0.26 | 13.57 | 5.78 |
| LgP.1 × TIP.2 | 13.75 | 5.83 | 60.05 | 31.71 | 60.69 | 32.46 | 0.30 | 60.34 | 32.05 |

Explanatory variables were: accumulated precipitation (Ap), green plant cover of borders (gB), Tyto furcata predation rate with delay 2 (TIP.2), Leopardus geoffroyi predation rate with delay 1 (LgP.1), season (spring, summer and winter, autumn was the reference level). Table entries state the corresponding statistics: Estimators of the association with the explanatory variable, standard error of the estimator (SE), relative variable importance in candidate models (RVI), explained deviance (ED), the difference between the AICc of model and the AICc of the best model and the AICc of model, (ΔAICc) and Akaike’s weights (wA). Estimator values in Bold implies an important explanatory variable (the CI 95% of the estimator excluded zero).

Null model AICc = 261.52.

Number of estimable parameters in the global model: 14.

Environmental conditions in both habitats. Our analysis was focused on short temporal effects on rodent abundance, while in a long-term (24 years) study, Fraschina et al. (2012) found a direct effect of temperature and precipitation on A. azarae and C. laucha abundance, highlighting that rodent population dynamics is affected by multiple factors that operate at different spatial and temporal scales. Andreo et al. (2009b) also found lagged effects of precipitation and NDVI (a proxy of vegetation cover) on A. azarae abundance in longitudinal habitats of rural areas of central Argentina.

The abundance of both species was affected by characteristics of cropfields and borders, suggesting that, although each species is more abundant in one habitat (A. azarae in borders and C. laucha in fields), they use both habitats. For example, a mature and tall crop enhances the increase of overall A. azarae abundance that is expressed 45 days later, while border plant height has also a positive effect but only in summer. In Europe, recommendations to farmers for the decrease in Microtus arvalis abundance (which can reach pest levels in crops) is partly based on the effect of plant height on rodent abundance (Jacob et al. 2014).

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habitat characteristics and seasons was also observed for *M. arvalis* in Spain (Rodriguez-Pastor *et al.* 2016).

In European agroecosystems, the spillover from edge habitats of some rodent species, as *M. arvalis*, is considered a threat to crop production. In our system, rodents never achieve pest densities as reported in Europe (>1000 voles per hectare, Jacob *et al.* 2014). In cropfield borders we found a maximum of 50 individuals of *A. azarae* per hectare (Gorosito 2018), and it is rarely captured in fields. *Calomys laucha* has even lower values of abundance both in cropfields and edges. The absence of a spillover of *A. azarae* from field margins to crops is in agreement with the observation for *M. arvalis* in an agrarian landscape in Switzerland (Briner *et al.* 2005).

This is the first report of an effect of predation rate on abundance for the studied species, but this effect was only observed for predation by *T. furcata* and had high relative importance for *A. azarae* but not for *C. laucha*. The effect of *T. furcata* on this latter species was only expressed when *L. geoffroyi* predation rates were lower than the mean and *C. laucha* abundance was probably also low. The differential effect depending on the rodent species is consistent to the hunting habits of this avian predator, which looks for prey mainly along borders (Bellocq & Krajcet 1994), where *A. azarae* is more abundant. A similar effect on rodents living in edges was observed by Figueroa *et al.* (2009) for *Oligoryzomys longicaudatus*, and was related to the sit-and-wait behaviour of *T. furcata* perching in post fences. Contrary to our expectation, predation by *L. geoffroyi* had no effect on *A. azarae* abundance, and for *C. laucha*, its effect was positive and of low relative importance (0.49). Guidobono *et al.* (2016) proposed that *L. geoffroyi* consumes *C. laucha* opportunistically, increasing consumption with higher abundance, and that it prefers to hunt in open areas with low plant cover, as fields in some stages of the crop. Other authors (Bisceglia *et al.* 2008; Pereira 2010) also observed that *L. geoffroyi* shows prey shifts when resources fluctuate temporally. Our results support the prediction that *A. cunicularia* has a lower predation effect than *T. furcata* and *L. geoffroyi*.

In summary, short-term abundance variations of both species were explained by the characteristics of the whole system, and it seems that the existence of alternative habitats which change asynchronously, allows rodent survival in a system that is strongly altered by agrarian labours, but does not produce high increases in abundance and there is no spillover of surplus individuals from margins to crops. Finally, the specialist avian predator *T. furcata* may contribute to prevent *A. azarae* population eruptions.

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### Table 6. Candidates and average models for *Calomys laucha* abundance variations in borders (TSb)

| Candidate models | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | Average model |
|------------------|---|---|---|---|---|---|---|---|---------------|
|                  | Estimator | SE | Estimator | SE | Estimator | SE | Estimator | SE | Estimator | SE | RVI | Estimator | SE |
| Intercept        | -6.42 | 0.42 | -6.55 | 0.58 | -6.31 | 0.49 | -6.49 | 0.49 | -6.40 | 0.50 | -6.45 | 0.67 | -5.42 | 0.55 | -4.83 | 0.37 | -6.20 | 0.66 |
| Ch.2             | 1.41 | 0.42 | 1.39 | 0.42 | 1.19 | 0.46 | 1.45 | 0.45 | 1.40 | 0.44 | 1.41 | 0.42 | 0.77 | 0.45 | 0.92 | 1.32 | 0.47 |
| Ap               | 0.92 | 2.79 | 0.92 | 2.79 | 0.92 | 2.79 | 0.92 | 2.79 | 0.92 | 2.79 | 0.92 | 2.79 | 0.92 | 2.79 | 0.92 | 2.79 |
| gcb              |      |     | 0.05 | 0.86 | 0.10 | 0.55 | 0.10 | 0.55 | 0.10 | 0.55 | 0.10 | 0.55 | 0.10 | 0.55 | 0.10 | 0.55 | 0.10 | 0.55 |
| Spring           |      |     | -1.26 | 0.72 | -1.74 | 0.67 | 0.18 | 1.48 | 0.74 |      |     |      |     |      |     |      |     |      |
| Summer           |      |     | -0.34 | 0.51 | -0.64 | 0.49 | 0.18 | -0.48 | 0.52 |      |     |      |     |      |     |      |     |      |
| Winter           |      |     | -1.55 | 0.86 | -2.15 | 0.78 | 0.18 | -1.83 | 0.88 |      |     |      |     |      |     |      |     |      |
| TIP 1            | -0.45 | 0.85 | 0.18 | 0.65 |      |     |      |     |      |     |      |     |      |     |      |     |      |
| TIP 2            |      |     |      |     |      |     |      |     |      |     |      |     |      |     |      |     |      |
| Ap × Ch.2        | 2.86 | 1.84 |      |     |      |     |      |     |      |     |      |     |      |     |      |     |      |
| Log-likelihood   | -55.53 | -55.47 | -54.28 | -55.49 | -55.53 | -55.53 | -55.53 | -55.12 | -54.49 |      |     |      |     |      |     |      |
| AICc             | 119.70 | 121.90 | 121.91 | 121.93 | 122.01 | 122.01 | 122.01 | 122.12 | 122.31 |      |     |      |     |      |     |      |
| AICc             | 53.12 | 54.28 | 55.33 | 55.49 | 55.53 | 55.53 | 55.53 | 55.53 | 55.53 |      |     |      |     |      |     |      |

Explanatory variables were: crop height with delay 2 (Ch.2), accumulated precipitation (Ap), green plant cover of borders (gcb), Tuco *furcata* predation rate with delay 2 (TIP.2), Leopardus *geoffroyi* predation rate with delay 1, season (spring, summer and winter, autumn was the reference level). Table entries state the corresponding statistics: Estimators of the association with the explanatory variable, standard error of the estimator (SE), relative variable importance in candidate models (RVI), explained deviance (ED), the maximized Log-likelihood, Akaike’s information criterion corrected for small sample size (AICc), difference between the AICc of the best model and the AICc of model, (ΔAICc) and Akaike’s weights (w). Estimator values in **Bold** implies an important explanatory variable (the CI 95% of the estimator excluded zero).

Null model AICc = 261.52.

Number of estimable parameters in the global model: 14.

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work in their properties. We would like to thank Eliana Melignani for the revision of the manuscript. This work was supported by Universidad de Buenos Aires (UBACYT X027) and Consejo Nacional de Investigaciones Científicas y Tecnológicas (PIP 1410) grants.

REFERENCES

Andrade J. F., Poggio S. L., Ermácora M. & Satorre E. H. (2015) Productivity and resource use in intensified cropping systems in the Rolling Pampa, Argentina. *Agron. 67*, 37–51.

Andreo V., Lima M., Provansal C., Priotto J. & Polop J. (2009a) Population dynamics of two rodent species in agro-ecosystems of central Argentina: intra-specific competition, land-use, and climate effects. *Popul. Ecol. 51*, 297–306. https://doi.org/10.1007/s10144-008-0123-3

Andreo V., Provansal C., Scavuzzo M. & Lamfri M. (2009b) Environmental factors and population fluctuations of *Akodon azarae* (Muridae: Sigmodontinae) in central Argentina. *Austral Ecol. 34*, 132–42. https://doi.org/10.1111/j.1442-9993.2008.01889.x

Balsa J. (2001) Las formas de producicion predominantes en la agricultura pampeana al final de la primera expansion agricola (1937). ¿Una via ‘argentina’ de desarrollo del capitalismo en el agro? *Mundo Agrar.* 2, 1–23.

Bartoň K. (2017) Multiverse: Multinomial Mixture Models. *R package version 1.1-1*. CRAN mirror. [Cited 29 January 2018.] Available from URL: http://mirror.cran.r-project.org/CRAN/

Bates D., Maechler M., Bolker B. & Walker J. (2015) Fitting linear mixed-effects models using ‘lme4’. *J. Stat. Soft. 67* (1). Available from URL: http://jstatsoft.org/v67/i01/

Bezerra M. I. (1887) Selección de hábitat de caza y depredación diferencial de *Athene cunicularia* sobre roedores en ecosistemas agrarios. *Rev. Chil. Hist. Nat.* 60, 81–6.

Belloçq M. I. (1898) Dieta de Athene cunicularia (Aves, Strigidae) y sus variaciones estacionales en ecosistemas agrarios de la pampa Argentina. *Physiol. 19*, 17–22.

Belloçq M. I. (1998) Prey selection by breeding and nonbreeding Barn Owls in Argentina. *Auk 115*, 224–9.

Belloçq M. I. & Kravetz F. O. (1994) Feeding strategy and predation of the Barn owl (*Tyto alba*) and the Burrowing owl (*Speotyto cunicularia*) on rodent species, sex and size, in agro ecosystems of central Argentina. *Austral Ecol. 17*, 283–5.

Bellocq M. I. & Kravetz F. O. (1997) Feeding strategy and predation of the Barn owl (*Tyto alba*) and the Burrowing owl (*Speotyto cunicularia*) on rodent species, sex and size, in agro ecosystems of central Argentina. *Austral Ecol. 22*, 533–42.

Bellocq M. I. & Kravetz F. O. (1997) Feeding strategy and predation of the Barn owl (*Tyto alba*) and the Burrowing owl (*Speotyto cunicularia*) on rodent species, sex and size, in agro ecosystems of central Argentina. *Austral Ecol. 22*, 533–42.

Bellocq M. I. & Kravetz F. O. (1997) Feeding strategy and predation of the Barn owl (*Tyto alba*) and the Burrowing owl (*Speotyto cunicularia*) on rodent species, sex and size, in agro ecosystems of central Argentina. *Austral Ecol. 22*, 533–42.

Biogeography 16, 283–5.

Belonga M. I. & Muñoz F. (2004) Identificacion de Areas Valiosas de Pastizal (AVP) en las Pampas y Campos de Argentina, Uruguay y sur de Brasil. Fundación Vida Silvestre, Buenos Aires.

Biseglia S. B. C., Pereira J. A., Teta P. & Quintana R. D. (2008) Food habits of Geoffroy’s cat (*Leopardus Geoffroyi*) in the central Monte desert of Argentina. *J. Arid Eviron. 72*, 1120–6.

Bolker B. M., Brooks M. E., Clark C. J. & Dynamic Mixed Models: a practical guide for ecology and evolution. *Trends Ecol. Evol. 24*, 127–35.

Briner T., Nentwig W. & Airoldi J-P. (2005) Habitat quality of wildflower strips for common voles (*Microtus arvalis*) and its relevance for agriculture. *Agric. Ecosyst. Environ. 105*, 173–9.

Burnham K. P. & Anderson D. R. (2002) Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd edn. Springer, New York.

Busch M., Alvarez M. R., Alejandro C. E. & Kravetz F. O. (1997) Habitat selection and interspecific competition in rodents in pampean agroecosystems. *Mammalia 61*, 167–84.

Busch M., Miño M. H., Dadón J. R. & Hodara K. (2001) Habitat selection by *Akodon azarae* and *Calomys laucha* (Rodentia, Muridae) in pampean agroecosystems. *Mammalia 65*, 167–84.

Busch M., Bilenca D. N., Cittadino E. A. & Cueto G. R. (2005) Effect of removing a dominant competitor, *Akodon azarae* (Rodentia, Sigmodontinae) on community and population parameters of small rodent species in Central Argentina. *Austral Ecol. 30*, 168–78.

Cournalot P. & Busch M. (2010) Community structure and diversity of Sigmodontine rodents (Muridae: Sigmodontinae) inhabiting maize and soybean fields in Pampean agroecosystems, Argentina. *Interciencia 35*, 812–7.

Crawley M. J. (2012) The R Book. John Wiley & Sons Ltd, Chichester.

de la Fuente E. B., Suárez S. A. & Ghera C. M. (2006) Soybean weed community composition and richness between 1995 and 2003 in the Rolling Pampas (Argentina). *Agric. Ecosyst. Environ. 115*, 229–36.

Ellis B. A., Mills J. N., Childs J. E. & et al. (1997) Structure and floristics of habitats associated with five rodent species in an agroecosystem in Central Argentina. *J. Zool. 243*, 437–60. https://doi.org/10.1111/j.1469-7998.1997.tb02794.x

Figueroa R. R. A., Rau J. R., Mayorga S. et al. (2009) Rodent prey of the barn owl *Tyto alba* and short-eared owl *Asio flammeus* during winter in agricultural lands in southern Chile. *Wildlife Biol. 15*, 129–36.

Fraschina J., León V. A. & Busch M. (2012) Long-term variations in rodent abundance in a rural landscape of the Pampas, Argentina. *Ecol. Res. 27*, 191–202. https://doi.org/10.1007/s11284-011-0888-2

Fraschina J., León V. A. & Busch M. (2017) The effect of neighbourhood on rodent communities: an example from Pampean agroecosystems. *Landsc. Res. 42*, 533–42. https://doi.org/10.1080/01426397.2017.1291924

Gehring T. M. & Swihart R. K. (2003) Body size, niche breadth, and ecologically scaled responses to habitat fragmentation: mammalian predators in an agricultural landscape. *Biol. Conserv. 109*, 283–95.

Ghera C. M. & León R. J. (1999) Successional changes in agroecosystems of the Rolling Pampa. In: *Ecosystems of Disturbed Ground* (ed L. R. Walker) pp. 487–502. Elsevier B. V., Amsterdam.

Gorosito I. (2018) Ecología y comportamiento de *Oligoryzonmys flavescens* y *Akodon azarae* en relación con la transmisión de hantavirus (Doctoral Thesis). Universidad de Buenos Aires, Buenos Aires.

Guidobono J. S., Muñoz J., Muschetto E., Teta P. & Busch M. (2016) Food habits of Geoffroy’s cat (*Leopardus Geoffroyi*) in agroecosystem habitats of Buenos Aires, Argentina. *Austral Ecol. 40*, 40–50.

Hansen T. F., Stenseth N. C. & Henttonen H. (1999) Multiannual vole cycles and population regulation during long winters: an analysis of seasonal. *Am. Nat. 154*, 129.

doi:10.1111/aec.12650 © 2018 Ecological Society of Australia
Hanski I., Henttonen H., Korpimäki E., Oksanen L. & Turchin P. (2001) Small-rodent dynamics and predation. *Ecology* 82, 1505–20.

Harrison X. A. (2015) A comparison of observation-level random effect and Beta-Binomial models for modelling overdispersion in Binomial data in ecology and evolution. *PeerJ* 3, e1114. https://doi.org/10.7717/peerj.1114

Hodara K. & Busch M. (2006) Return of preferred habitats (edges) as a function of distance in *Akodon azarae* (Rodentia, Muridae) in cropfield-edge systems of central Argentina. *J. Ethol.* 21, 141–5.

Hothorn T., Bretz F., Westfall P., Heiberger R. M., Schultenmeister A. & Scheibe S. (2017) Simultaneous Inference in General Parametric Models (multcomp package). Universidad Nacional de La Plata, La Plata. CRAN mirror. [Cited 29 January 2018.] Available from URL: http://mirror.fclap.unlp.edu.ar/CRAN/

Ims R. A., Yoccoz N. G. & Killengreen S. T. (2011) Determinants of lemming outbreaks. *Proc. Natl Acad. Sci. USA* 108, 1970–4.

Jacoby J. (2003) Short-term effects of farming practices on populations of common voles. *Agric. Ecosyst. Environ.* 95, 321–5.

Jacob J., Manson P., Barfknecht R. & Fredricks T. (2014) Full diversity of the small mammal community of the Neotropical bird community interacting with climatic factors. *Agric. Ecosyst. Environ.* 95, 321–5.

Jaksic F. M. (2001) Ecological effects of El Niño in terrestrial ecosystems of western South America. *Ecography (Cop.)* 24, 241–50.

Jaksic F. M. & Lima M. (2003) Myths and facts on ratadas: bamboo blooms, rainfall peaks and rodent outbreaks in South America. *Austral Ecol.* 28, 237–51. https://doi.org/10.1046/j.1442-9993.2003.01271.x

Jaksic F. M. & Meserve P. L. (1993) The components of density dependence cause rodent outbreaks in western USA. *J. Anim. Ecol.* 62, 75–89.

Jaksic F. M. & Lima M. (2003) Population variability among three small mammal species in the semiarid Neotropics: the role of density-dependent and density-independent factors. *Ecography (Cop.)* 21, 175–80.

Klima M., Keymer J. E. & Jaksic F. M. (1999) El Nino–southern oscillation–driven rainfall variability and delayed density dependence cause rodent outbreaks in western South America: linking demography and population dynamics. *Am. Nat.* 153, 476–91.

Lima M., Juliiard R., Stenseth N. C. H. R. & Jaksic F. M. (2001) Demographic dynamics of a neotropical small rodent *Phyllostis darwini*: feedback structure, predation and climatic factors. *J. Anim. Ecol.* 70, 761–75. https://doi.org/10.1046/j.0021-8790.2001.00536.x

Lima M., Stenseth N. C. & Jaksic F. M. (2002) Population dynamics of a South American rodent: seasonal structure interacting with climate, density dependence and predator effects. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 269, 2579–86.

Long J. A. (2018) Analysis and Presentation of Social Scientific Data (jtools package). Universidad Nacional de La Plata, La Plata. CRAN mirror. [Cited 29 January 2018.] Available from URL: http://mirror.fclap.unlp.edu.ar/CRAN/

Lucherini M. & Luengos Vidal E. M. (2008) *Lycalopex gymnogaster* (Carnivora: Canidae). *Mamm. Species* 820, 1. https://doi.org/10.1644/820.1

Marshall E. J. P., Brown V. K., Boatman N. D., Lutman P. J. W., Squire G. R. & Ward L. K. (2003) The role of weeds in supporting biological diversity within crop fields. *Weed Res.* 43, 77–89. https://doi.org/10.1046/j.1365-3180.2003.00326.x

Massawe A. W. & Makundi R. H. (2011) The type of farming practice may affect the movement and reproduction pattern of rodents in crop fields: a case of study of *Mastomys natalensis*. *J. Biol. Sci.* 11, 22–30.

Midgley G. F., Hannah L., Millar D., Thuiller W. & Booth A. (2003) Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic Region. *Biol. Conserv.* 112, 87–97.

Miño M. H., Cavia R., Gómez Villafañe I. E., Bilanca D. N., Cittadino E. A. & Busch M. (2001) Estructura y diversidad de dos comunidades de pequeños rodéed en agroecosistemas de la provincia de Buenos Aires, Argentina. *Bol. Soc. Conoc. Chilo* 72, 67–75.

Miño M. H., Cavia R., Gómez Villafañe I. E., Bilanca D. N. & Busch M. (2007) Seasonal abundance and distribution among habitats of small rodents on poultry farms. A contribution for their control. *Int. J. Pest Manag.* 53, 311–6. https://doi.org/10.1080/09567870701109549

Paruelo J. M., Guerschman J. P. & Verón S. R. (2005) Expansión agrícola y cambios en el uso del suelo. *Cien. Hoy* 15, 14–23.

Pereira J. A. (2010) Activity pattern of Geoffroy's cats (*Leopardus geoffroii*) during a period of food shortage. *J. Arid Environ.* 74, 1106–9.

Pereira J. A., Fracassi N. G. & Uhart M. M. (2006) Numerical and spatial responses of Geoffroy's cat (*Onctis geoffroii*) to prey decline in Argentina. *J. Mammal.* 87, 1132–9. https://doi.org/10.1644/2005-MAMM-A-333R.2.1

R Core Team & Contributors Worldwide (2017) *The R Stats Package*. Universidad Nacional de La Plata, La Plata. CRAN mirror. [Cited 29 January 2018.] Available from URL: http://mirror.fclap.unlp.edu.ar/CRAN/

R Development Core Team (2017) *R: A Language and Environment for Statistical Computing*. Universidad Nacional de La Plata, La Plata. CRAN mirror. [Cited 29 January 2018.] Available from URL: http://mirror.fclap.unlp.edu.ar/CRAN/

Richards S. A. (2005) Testing ecological theory using the information-theoretic approach: examples and cautionary results. *Ecology* 86, 2805–14. https://doi.org/10.1890/05-0074

Rodríguez-Pastor R., Luque-Larena J. J., Lambin X. & Mougeot F. (2016) ‘Living on the edge’: the role of field margins for common vole (*Microtus arvalis*) populations in recently colonised Mediterranean farmland. *Agric. Ecosyst. Environ.* 231, 206–17. https://doi.org/10.1016/j.agee.2016.06.041

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Schalk C. M. & Morales F. (2012) Predation of a *Rhinella major* (Anura: Bufonidae) by a Pampas Fox (*Lycalopex gymnocercus*) in the Bolivian Gran Chaco. *Herpetol. Notes* 5, 369–70.

Schweinberger M. (2014) Function for Customized Binomial Logistic Regression Results. Unpublished R-skript, Hamburg University, Hamburg.

Singleton G. R., Smythe L., Smith G., Spratt D. M., Aplin K. & Smith A. L. (2003) Rodent diseases in Southeast Asia and Australia: inventory of recent surveys. In: *Rats, Mice and People: Rodent Biology and Management* (eds G. R. Singleton, L. A. Hinds, C. J. Krebs & D. M. Spratt) pp. 477–80. ACIAR, Canberra.

Soriano A., León R. J. C., Sala O. E. et al. (1991) Río de la Plata grasslands. In: *Naturalgrasslands. Introduction and Western Hemisphere* (ed R. T. Coupland) pp. 367–407. Elsevier, Amsterdam.

Symonds M. R. E. & Moussalli A. (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike’s information criterion. *Behav. Ecol. Sociobiol.* 65, 13–21. https://doi.org/10.1007/s00265-010-1037-6

Tew T. E. & Macdonald D. W. (1993) The effects of harvest on arable wood mice *Apodemus sylvaticus*. *Biol. Conserv.* 65, 279–83.

Urcola H. A., de Sarre X. A., Veiga I. Jr, Elverdin J. & Albaladejo C. (2015) Land tenancy, soybean, actors and transformations in the pampas: a district balance. *J. Rural Stud.* 39, 32–40. https://doi.org/10.1016/j.jrurstud.2015.03.001

Varela O., Cormenzana-Méndez A., Krapovickas L. & Bucher E. H. (2008) Seasonal diet of the Pampas fox (*Lycalopex gymnocercus*) in the Chaco dry woodland, northwestern Argentina. *J. Mammal.* 89, 1012–9.

Vigliizzo E. F., Lértora F., Pordomingo A. J., Bernados J. N., Roberto Z. E. & Del Valle H. (2001) Ecological lessons and applications from one century of low external-input farming in the pampas of Argentina. *Agric. Ecosyst. Environ.* 83, 65–81.

Vitta J. I., Tuesca D. & Puricelli E. (2004) Widespread use of glyphosate tolerant soybean and weed community richness in Argentina. *Agric. Ecosyst. Environ.* 103, 621–4.

Zuur A. F., Ieno E. N., Walker N. J., Saveliev A. A. & Smith G. M. (2009) *Mixed Effects Models and Extension in Ecology with R*. Springer Science+Business Media, LLC, New York.

Zuur A. F., Ieno E. N. & Elphick C. S. (2010) A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1, 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x