



Interspecific competition and demography of small mammals in linear habitats

VANESA N. SERAFINI; M. DANIELA GÓMEZ[✉] & JOSÉ W. PRIOTTO

Grupo de Investigaciones en Ecología Poblacional y Comportamental (GIEPCO), Instituto de Ciencias de la Tierra, Biodiversidad y Sustentabilidad Ambiental-Consejo Nacional de Investigaciones Científicas y Técnicas (ICBIA-CONICET), Universidad Nacional de Río Cuarto (UNRC).

ABSTRACT. Interspecific competition may influence demographic parameters and affect population sizes of competing species. In this study, we evaluated the effect of *Akodon azarae* abundance on demographic parameters of other assemblage species through capture-mark-recapture data (CMR). In addition, we assessed the effects of time fluctuation, anthropogenic disturbances (burning), climate (rainfall and temperature) and endogenous variables (sex and abundance) on those parameters. The study was carried out in a railway bank in central Argentina through monthly CMR surveys from November 2011 to May 2014. We estimated species abundance using Pradel's closed population models throughout a robust design. We modeled recapture and survival probabilities by Cormack Jolly Seber models and seniority probabilities and population growth rates by Pradel's models. *Akodon azarae* abundance showed an inverse pattern to *Mus musculus* and *Calomys musculinus* abundance. Population numbers of *A. azarae* declined after fire, whereas *M. musculus* and *C. musculinus* increased their numbers and became the most abundant species. *Akodon azarae* abundance did not affect any demographic parameters of the other species. Instead, time fluctuations, sex and temperature explained those parameters. Even though burning changed species population numbers for a short period of time, it did not affect demographic parameters of any species. Although *A. azarae* is considered a dominant species, we did not find evidence that its abundance affects the demography of other small mammal species. Railway banks would offer shelter and food for all species during the year, allowing them to avoid competition for available resources. However, anthropogenic disturbances can produce changes in the composition of small mammal assemblage since they affect habitat quality and allow invasive species such as the *Mus musculus* to establish.

[Keywords: abundance, anthropogenic disturbances, capture-mark-recapture models, recruitment probabilities, survival probabilities, *Akodon azarae*, house mouse]

RESUMEN. Competencia interespecífica y demografía de pequeños mamíferos en hábitats lineales. La competencia interespecífica puede influir en los parámetros demográficos y afectar el tamaño poblacional de las especies competidoras. En el presente estudio evaluamos el efecto de la abundancia poblacional de *Akodon azarae* sobre los parámetros demográficos de otras especies del ensamble mediante datos de captura-marcado-recaptura (CMR). Además, evaluamos los efectos de la variación temporal, las perturbaciones antropogénicas (quemadas), el clima (precipitaciones y temperaturas) y variables endógenas (sexo y abundancia) sobre dichos parámetros. El estudio fue realizado en un terraplén de ferrocarril en el centro de la Argentina, a través de muestreos mensuales de CMR desde noviembre de 2011 hasta mayo de 2014. Estimamos la abundancia usando modelos de Pradel con diseño robusto para poblaciones cerradas. Modelamos las probabilidades de recaptura y sobrevivencia mediante modelos de Cormack Jolly Seber y las probabilidades de permanencia y tasas de crecimiento poblacional mediante modelos de Pradel. La abundancia de *A. azarae* disminuyó después de la quema, mientras que las abundancias de *M. musculus* y *C. musculinus* aumentaron hasta convertirse en las especies más abundantes. La abundancia de *A. azarae* no afectó ningún parámetro demográfico de las demás especies del ensamble. Dichos parámetros fueron explicados por la variación temporal, sexo o temperatura. Si bien la quema modificó los números poblacionales durante un período de tiempo corto, no afectó ningún parámetro poblacional. Aunque *A. azarae* es considerada una especie dominante, no encontramos evidencia de que su abundancia afecte la demografía de las demás especies. Los terraplenes de ferrocarril ofrecerían refugio y alimento a todas las especies durante el año, lo que permitiría evitar la competencia por los recursos disponibles. Sin embargo, las perturbaciones antropogénicas pueden producir cambios en la composición del ensamble permitiendo que especies invasoras como el ratón doméstico se establezcan.

[Palabras clave: abundancia, disturbios antrópicos, modelos CMR, probabilidad de reclutamiento, probabilidad de sobrevivencia, tasa de crecimiento, *Akodon azarae*, ratón doméstico]

INTRODUCTION

Populations inhabiting spatially heterogeneous landscapes are influenced by multiple environmental factors that vary over space and time (Tuljapurkar 1990; Post et al. 1997). Intrinsic and extrinsic factors may influence different demographic parameters of animal populations (e.g., survival, reproduction, and recruitment) in different directions and magnitudes (Oli and Dobson 2003; Chen et al. 2014). Competition and predation are considered among the most important biotic processes influencing species distribution and abundance (Huitu et al. 2004). Additionally, the effects of weather on vital rates are also important to elucidate the ecological and demographic mechanisms underlying the dynamics of populations in fluctuating environments (Coulson et al. 2000; Oli and Dobson 2001; Ozgul et al. 2004).

The effect of competition on populations depends on interacting species, the strength of the interactions, and the availability of resources (Paine 1966; Bowers and Dooley 1991). Changes in abundance of dominant species (numerically and competitively) may have strong effects on community structure and species diversity (Valone and Brown 1995; Brady and Slade 2001). Competitive interaction effects may be either direct, through interactions between dominant species and other community members (interference competition), or indirect, by changing the interactions among them (Brady and Slade 2001; Sozio and Mortelliti 2016). Interspecific competition may influence demographic parameters, such as individual growth, fecundity and/or survival (Begon et al. 1996), and therefore affect population sizes of competitive species.

Evaluating interspecific competition through field studies can be difficult (Hoeck 1989). Several studies have showed that the removal of dominant species may lead to an increase in the abundance and affect the competitive relationships of subordinate species (Paine 1966; Busch et al. 2005; Brunner et al. 2013). To be able to make strong inferences about interspecific competition effects on populations, it is important to evaluate demographic parameters through capture-mark-recapture (CMR) methods (Sozio and Mortelliti 2016). These methods consider the variation in recapture probabilities and provide unbiased estimates of demographic parameters (Priotto et al. 2010; Gómez et al. 2016). Another essential element to consider in the evaluation of interspecific

competition is the use of less biased probabilistic models of abundance estimations (Otis et al. 1978; Graipel et al. 2014; Gómez et al. 2016). Closed population designs provide more robust estimators and reduce bias (Otis et al. 1978; Graipel et al. 2014).

Among species groups that coexist in agricultural landscapes, small mammals are crucial due to their contribution to well-structured food webs (Salamolard et al. 2000; Butet and Leroux 2001; Li and Wo 2007; Arlettaz et al. 2010). Additionally, they consume and disperse plant material (Kollmann and Bassin 2001; Kollmann and Buschor 2002; Baraibar et al. 2009; Fischer et al. 2011) and mycorrhizal fungi (Schickmann et al. 2012), and consume and control invertebrates (Gliwicz and Taylor 2002). In central Argentina, particularly in the southwest of Córdoba province, the small mammal assemblage is mainly represented by the Cricetidae rodents *Calomys musculinus*, *C. venustus*, *C. laucha*, *Akodon azarae*, *A. dolores*, *Oxymycterus rufus* and *Oligoryzomys flavescens*. In addition, the house mouse, *Mus musculus* is also found (Simone et al. 2010; Martínez et al. 2014; Gómez et al. 2015, 2016).

The small mammal assemblage has been widely studied in the past and several studies have provided empirical evidence of competitive dominance of *A. azarae* over the other rodent species. In food addition experiments, *A. azarae* was the only species that increased its abundance (Cittadino et al. 1994), and in behavioral studies this species showed competitive dominance over *C. laucha* and *O. flavescens* when resources were limited (Cueto et al. 1995; Courtalon et al. 2003). Moreover, Busch et al. (2005) performed a removal study of *A. azarae* where *M. musculus* populations were favored, increasing their abundance, and showed higher pregnancy and lactation rates in removal borders. Furthermore, studies carried out in Australia and New Zealand showed that *M. musculus* is registered in high numbers in agricultural fields with few or no competitors (Singleton 1989; Ylönen et al. 2002; Pocock et al. 2005; Singleton et al. 2005). However, in Europe and North America, the house mouse has not been successful in agriculture fields, possibly because it would not be a good competitor with native rodent species like *Apodemus sylvaticus* and *Microtus* spp. (Berry and Tricker 1969; Tattersall et al. 1997). A study carried out in an urban area of Argentina showed that the abundance and reproductive activity of the house mouse were

higher in those habitats where native species were rare or absent (Gómez et al. 2008).

Although several studies of interspecific competition in the small mammal assemblage in Argentina have been carried out (Cittadino et al. 1994; Cueto et al. 1995; Courtalon et al. 2003; Busch et al. 2005), none of them were performed through the estimation of demographic parameters with CMR models. Therefore, the aim of this work was to evaluate the effect of interspecific competition between *A. azarae* and the other assemblage species using a demographic approach with CMR data. We hypothesize that, if there is competition between species, changes in the abundance of the dominant species modify the demographic parameters of the less competitive species in the assemblage. Therefore, we predicted that changes in *Akodon azarae* abundance will affect demographic parameters of the less competitive species.

MATERIALS AND METHODS

Study area

We carried out this study on a railway bank in the rural area of Chucul, in the southwest of Córdoba province, Argentina (64°11' W - 33°01' S). In this area, the weather is temperate with an annual average temperature of 23 °C and annual rainfall of 700-800 mm. Although the area belongs to the Espinal ecoregion (Burkart et al. 1999), native vegetation has undergone marked alterations as a result of agriculture and cattle farming. At present, the landscape mainly consists of a heterogeneous matrix of crop fields surrounded by different types of linear habitats including crop field margins, roadsides, riversides, fencerows and railways. All these linear habitat types support mixed vegetation dominated by native herbaceous species together with introduced weedy and invasive plants. Moreover, they have a homogeneous plant cover of about 85% throughout the year and a high availability of seeds in the soil (Priotto et al. 2002).

Data collection

We analyzed the degree of competitive interference between species using small mammal data collected as part of demographic studies of the assemblage species. We live-trapped small mammals in a 6x15 grid using traps similar to Sherman live-traps covering the entire width of the railway bank (60 m).

We placed traps every 10 m and baited them with a mixture of peanut butter and cow fat. We checked traps daily in the morning. We carried out monthly surveys through CMR methods from November 2011 to May 2014 during three consecutive nights per month, with the exception of five months due to logistical reasons (September 2012, June, August, September and October 2013, and January 2014). In July 2013, the grid was completely burned. We also modeled the effect of this anthropogenic disturbance on the demographic parameter estimations. We identified trapped animals and marked each individual with ear tags. We also recorded weight, length, sex and reproductive state (males: scrotal or abdominal testicles, females: perforated or non-perforated vagina, pregnancy evidence, visible nipples or not).

Data analyses

We developed all statistical analyses with RMark library (Laake 2013) in R program (R Core Team 2016). We estimated and analyzed abundances of the most commonly captured species: *A. azarae*, *C. musculus*, *C. venustus* and *M. musculus*. Abundance of each species was estimated using methods for closed populations through a robust design with a full heterogeneity estimator, by which the data are organized into primary and secondary sample occasions. In this study, primary occasions refer to the periods between months and the secondary occasions to the periods within each month (corresponding to the three sampling nights). Abundance is estimated in the secondary occasions, assuming that the period is short enough to consider migration and birth rate/mortality negligible (Cooch and White 2019). This model provides robust estimates of abundance for each period as derived parameters (Gómez et al. 2016).

We evaluated interspecific competition including *A. azarae* abundance as a predictor of demographic parameters of the target species. To compare the effect of competition with the effect of other variables, we constructed and compared several models: no time variation (.), monthly variation (m), season variation (s) and full-time variation (t). We also assessed the effects of endogenous (sex and population abundance) and exogenous (temperature, rainfall and anthropogenic disturbance) factors, including both combined and additive contributions (Appendix). The null model was also included. All co-variables were standardized to have zero mean and a variance

equal to one to help convergence (White and Burnham 1999). Data series of climatic variables were provided by the Universidad Nacional de Río Cuarto agrometeorological laboratory.

Models were ranked according to Akaike's information criterion, corrected for small sample size (AICc) (White and Burnham 1999). Model comparison was based on the differences in AICc values (ΔAICc), and models with ΔAICc values lower than two units were taken as an evidence of support for the relationship between the parameter and the covariate. Model average was performed to estimate demographic parameters when there was more than one model with the same explanatory power (e.g., ΔAICc lower than two units or similar weights). First, we modeled recapture probabilities (p), since they contribute less to biological interpretation (Crespin and Lima 2006), with full time variation in apparent survival (Φ) (Appendix). Second, using the most parsimonious model selected for recapture probabilities, we modeled apparent survival in relation to time variation and the co-variables mentioned above (Appendix). We used Cormack Jolly Seber (CJS) models for the estimations of both recapture and survival probabilities.

Finally, we modeled seniority probabilities (γ) and population growth rates (λ) through Pradel's reverse models (Pradel 1996), using the best models for recapture and apparent survival probabilities (Appendix). Seniority probabilities (γ) can be considered as survival probabilities that extend backward in time (Williams et al. 2002). They were estimated by the method developed by Pradel (1996). If an individual is alive and in the population at time t , γ is defined as the probability that it was alive and in the population at time $t-1$ (Pradel 1996). Seniority probabilities are used to estimate other related demographic parameters, such as the recruitment component ($1-\gamma$) of population growth rate (Nichols et al. 2000). Population growth rate (λ) was modeled using the Pradel survival and lambda model. To minimize the number of parameters to be estimated in these analyses, we only incorporated the effect of each explanatory factor without combined contributions in the models.

We used U-CARE program (Choquet et al. 2003) to assess the goodness of fit of the models. We estimated variance inflation factors, i.e., median \hat{c} using the most complex model

with the time-sex interaction on both apparent survival (Φ) and recapture probabilities (p) (White and Burnham 1999).

RESULTS

We captured 771 individuals of seven small mammal species during 6480 trap-nights, 256 *A. azarae* individuals (33.20% of the total registered captures), 117 *C. musculus* (15.18%), 81 *C. venustus* (10.50%) and 317 *M. musculus* (41.12%).

Population abundance

Figure 1 shows abundance estimated through robust design for all species during the sampling period. *Akodon azarae* and *M. musculus* were the most abundant species during the study. Even though *A. azarae* numbers seem to be the opposite of those of *C. musculus* and *M. musculus* at specific times during the study (Figure 1a), no inverse patterns among their abundances were observed (Figure 1b, c, d). Population numbers of *A. azarae* declined after fire whereas *M. musculus* and *C. musculus* increased their numbers, becoming the most abundant species. In the next autumn, *A. azarae* abundance started to increase, reaching values as high as before the fire whereas *M. musculus* and *C. musculus* reached their minimum numbers (Figure 1a).

Demographic parameter estimations

The goodness-of-fit test for the general model CJS $\Phi(\text{sex} \times t) p(\text{sex} \times t)$ did not provide evidence of lack of fit in any of the studied species (*A. azarae* $X^2_{58}=52.20$, $P=0.69$, *C. musculus*: $X^2_{15}=1.24$, $P=1.00$; *C. venustus*: $X^2_4=2.04$, $P=0.73$ and *M. musculus*: $X^2_{41}=19.84$, $P=0.99$). Underdispersion of data was observed in some species (*C. venustus*: $\hat{C}=0.51$, *M. musculus*: $\hat{C}=0.48$).

According to model selection, we did not find evidence that *A. azarae* abundance affects any other species demographic parameters (Table 1, Appendix). Instead, we observed that time fluctuations and extrinsic factors explained variations of demographic parameters. The most parsimonious model for recapture and apparent survival probabilities for *C. musculus* indicated an effect of temperature (Table 1, Figure 2a and 2b). Recapture probabilities were greater during the warmer months. By contrast, survival probabilities were negatively associated with temperature,

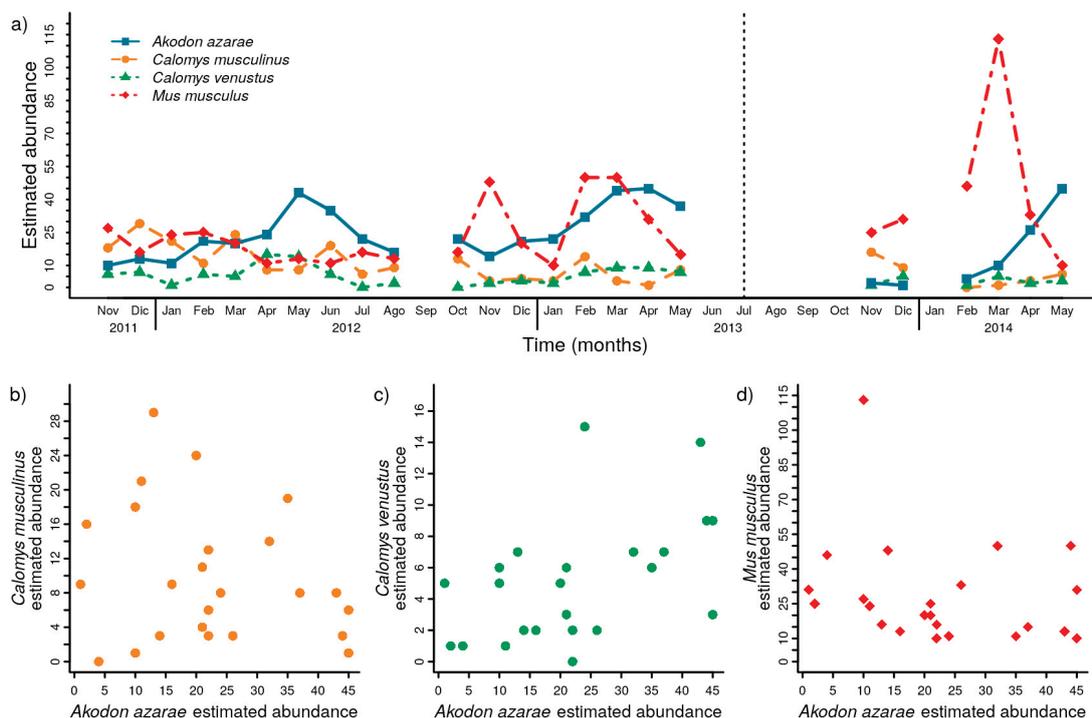


Figure 1. (a) Population abundance of the most captured species during the study. Vertical dotted line (July 2013) indicates the burning event in the grid; relationship between *Akodon azarae* and (b) *Calomys musculus*, (c) *Calomys venustus* and (d) *Mus musculus* abundances.

Figura 1. (a) Abundancia poblacional de las especies más capturadas durante el estudio. Línea punteada vertical (Julio 2013) indica el evento de quema del área de la grilla. Relaciones entre las abundancias de *Akodon azarae* y (b) *Calomys musculus*, (c) *Calomys venustus* y (d) *Mus musculus*.

Table 1. Null and statistical best models ($\Delta AIC_c < 2$) are denoted according to each model-specific variation in the probabilities of survival (Φ), seniority (γ) and recapture (p) probabilities, and population growth rates (λ) for *C. musculus*, *C. venustus* and *M. musculus*. K: number of parameters. T^o: temperature, t: time, f: fire, r: rain, seas: season, (.): null.

Tabla 1. Modelo nulo y mejores modelos ($\Delta AIC_c < 2$), especificando su variación para las probabilidades de sobrevivencia (Φ), permanencia (γ) y recaptura (p), y tasa de crecimiento poblacional (λ) para *C. musculus*, *C. venustus* and *M. musculus*. K: número de parámetros. T^o: temperatura, t: tiempo, f: fuego, r: lluvia, seas: estación, (.): nulo.

Species	Demographic parameter	Best Models	K	AIC _c ^a	ΔAIC_c ^b	AIC _c weight ^c	Deviance
<i>Calomys musculus</i>	Survival	$\Phi(T^o) p(T^o)$	4	179.521	0.000	0.377	86.760
		$\Phi(.) p(T^o)$	3	185.284	5.76	0.021	94.652
	Seniority	$\Phi(T^o) p(T^o) \gamma(t)$	27	837.413	0.000	0.845	73.712
		$\Phi(T^o) p(T^o) \gamma(.)$	5	854.061	16.647	2.03 ⁴	148.026
	Growth rate	$\Phi(T^o) p(T^o) \lambda(t)$	27	833.190	0.000	0.957	69.489
		$\Phi(T^o) p(T^o) \lambda(.)$	5	852.281	19.02	0.000	146.246
<i>Calomys venustus</i>	Survival	$\Phi(f) p(\text{sex})$	4	114.645	0.000	0.149	72.777
		$\Phi(\text{sex}+f) p(\text{sex})$	5	115.251	0.606	0.111	71.127
		$\Phi(\text{sex}+T^o) p(\text{sex})$	5	115.565	0.920	0.095	71.441
		$\Phi(.) p(\text{sex})$	3	115.897	1.252	0.080	76.230
		$\Phi(\text{sex}) p(\text{sex})$	4	116.120	1.482	0.071	74.260
		$\Phi(\text{sex}+a.cv) p(\text{sex})$	5	116.274	1.629	0.066	72.149
		$\Phi(T^o) p(\text{sex})$	5	116.332	1.688	0.064	74.465
	Seniority	$\Phi(a.cv) p(\text{sex})$	5	116.444	1.799	0.060	74.576
		$\Phi(.) p(\text{sex}) \gamma(\text{seas})$	7	566.043	0.000	0.912	124.759
		$\Phi(.) p(\text{sex}) \gamma(.)$	5	587.667	21.624	1.81 ⁵	153.289
	Growth rate	$\Phi(.) p(\text{sex}) \lambda(\text{seas})$	7	566.043	0.000	0.884	124.759
		$\Phi(.) p(\text{sex}) \lambda(.)$	4	584.667	21.624	1.74 ⁵	153.289
	<i>Mus musculus</i>	Survival	$\Phi(\text{sex}+t) p(\text{sex})$	26	531.700	0.000	0.709
$\Phi(\text{sex}+t) p(.)$			3	563.329	31.662	1.00 ⁷	304.278
Seniority		$\Phi(\text{sex}+t) p(T^o) \gamma(f)$	28	2272.310	0.000	0.344	315.199
		$\Phi(\text{sex}+t) p(T^o) \gamma(r)$	28	2273.049	0.739	0.238	315.938
		$\Phi(\text{sex}+t) p(T^o) \gamma(.)$	27	2274.113	1.803	0.140	319.351
Growth rate		$\Phi(\text{sex}+t) p(\text{sex}) \lambda(t)$	48	2285.604	0.000	0.999	275.664
		$\Phi(\text{sex}+t) p(\text{sex}) \lambda(.)$	27	2391.588	105.984	0	436.826

^aAkaike's information criterion, corrected for small sample size. ^bDifferences in AIC_c (Akaike's information criterion) values. ^cWeight of Model.

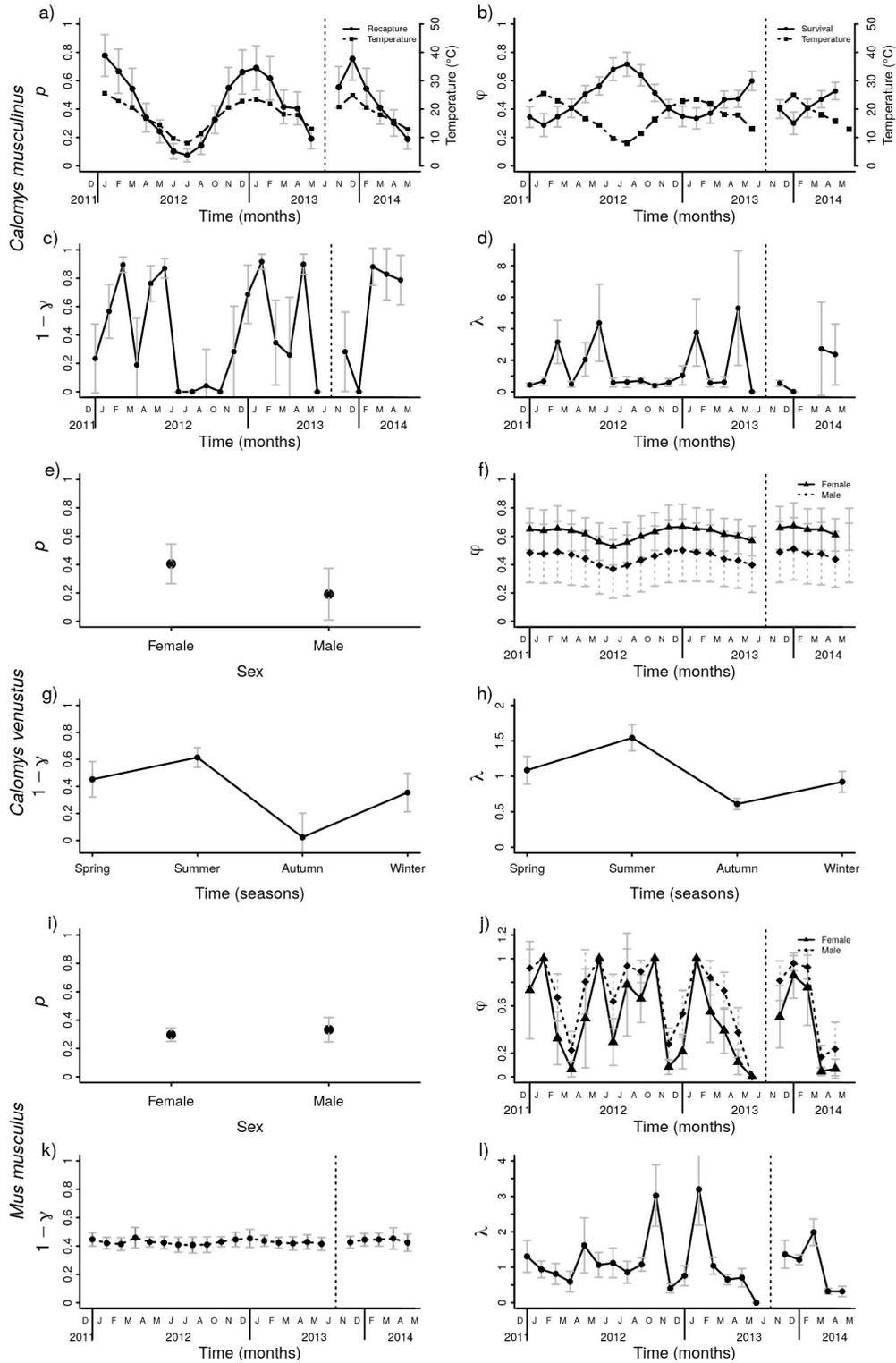


Figure 2. Population parameters (recapture probability (p), apparent survival (φ), recruitment (1-γ) and population growth rate [λ]) of *Calomys musculus* (a, b, c, d), *C. venustus* (e, f, g, h) and *Mus musculus* (i, j, k, l). Vertical dotted line (July 2013) indicates the burning event in the grid.

Figura 2. Parámetros poblacionales (probabilidad de recaptura (p), sobrevivencia aparente (φ), reclutamiento (1-γ) y tasa de crecimiento poblacional [λ]) de *Calomys musculus* (a, b, c, d), *C. venustus* (e, f, g, h) y *Mus musculus* (i, j, k, l). Línea punteada vertical (julio 2013) indica el evento de quema del área de la grilla.

recording the highest survival probabilities at the lowest temperature values corresponding to austral winter months. Seniority probabilities and population growth rates showed full time variation. Recruitment showed two peaks during the reproductive period and declined abruptly during winter (Figure 2c). Population growth rates showed a similar pattern to recruitment, with values greater than one during the reproductive period (Figure 2d). The most parsimonious model for *C. venustus* recapture probabilities showed differences between sexes, being higher in females than in males (Table 1, Figure 2e). There were eight models (including null model) with similar statistical support for describing *C. venustus* survival probabilities. Most of them included sex as explanatory variable (Table 1). Other explanatory variables included in these best models were temperature, burning event and *C. venustus* abundance. Results of model averaging showed higher survival probabilities in females than in males (Figure 2f). Recruitment probabilities and population growth rates showed seasonal variation with the highest numbers of recruited individuals and population growth rates in summer (Figures 2g and 2h). Finally, the most parsimonious model for *M. musculus* recapture probabilities showed the effect of sex, being slightly higher in males than in females, and for survival probabilities showed a combined effect between sex and time, with higher values in males than in females in almost every month (Table 1, Figures 2i and 2j). There were three models with similar statistical support for describing seniority probabilities (Table 1). Model averaging showed constant recruitment with intermediate values throughout the study period. Population growth rates displayed full time variation without a clear fluctuation pattern (Figures 2k and 2l).

DISCUSSION

Interspecific competition occurs when the abundance of one species has negative effects on the survival and growth rates of other species (Begon et al. 1996; McCallum 2000). Studies carried out to test this kind of interaction in small mammals of Argentina have found that *A. azarae* is the numerically and competitively dominant species in the assemblage (Busch and Kravetz 1992; Cittadino et al. 1994; Cueto et al. 1995; Busch et al. 2005). These studies included removal experiments of the strongest competitor or analyses of the

relationships between the abundance patterns of competitive species. However, the obtained results could lead to misleading conclusions either by a possible increase in the abundance of subordinate species and consequently changes in competitive relationships (Paine 1966; Brunner et al. 2013) or by the non-existence of causality between the observed patterns (Hodara et al. 2000).

Unlike previous works (Cittadino et al. 1994; Cueto et al. 1995; Busch et al. 2005), we evaluated interspecific competition through CMR statistical modeling, which considers the variation in recapture probabilities and provides unbiased estimates of demographic parameters (Priotto et al. 2010; Gómez et al. 2016). We recognize that the present study has some limitations in its design since it was developed in a single grid, but we weighed the time series, which is relevant in this kind of study to obtain reliable information on the effects of temporal variations in demographic parameters (Gómez et al. 2016). Results of our study show that changes in *A. azarae* abundance did not influence the demographic parameters of any species. Thus, we did not find evidence that interspecific competition between *A. azarae* and the target species is occurring. Coexistence of all species could indicate a differentiation in at least one aspect of their niches (Begon et al. 1996). Therefore, the current interspecific relationships may be showing competition in the past (Pritchard and Schluter 2001). In fact, there is evidence that rodents have different activity times in the study area, possibly as a mechanism to avoid competition, e.g., *A. azarae* and *C. venustus* have a partial overlapping on their diets and space use (Bilenca et al. 1992; Polop 1996), but they differ in their respective activity times (Priotto and Polop 1997). Additionally, competition occurs when there are limited resources. So, if the abundance of species never increases to approach the potential carrying capacity of the environment, species do not compete (Huitu et al. 2004). This could be what is happening on this particular study site where resources are not a constraint. Railway banks support a mixed vegetation, dominated by native herbaceous species together with introduced weedy and invasive plants and constitute more stable habitats throughout the year in the agroecosystem, since they are less influenced by the surrounding agricultural activity (Gómez et al. 2016). Thus, interspecific competition for obtaining

resources may not occur in these high-quality habitats.

Despite the stability of railway banks, they are sometimes subject to winter burnings. The burning event assessed in this study produced changes in the relative abundance of species, resulting in an increase in the population numbers of the most generalist species *C. musculinus* and *M. musculus*, which became numerically dominant. The colonization of generalist species was possible because these species are habitat tolerant and opportunistic (Mills et al. 1991; Busch and Kravetz 1992; Busch et al. 1997; Ellis et al. 1998), unlike *A. azarae* and *C. venustus* which are more dependent on vegetation cover (Hodara et al. 2000; Busch et al. 2001; Gómez et al. 2016). Even though species numbers changed after burning, we did not find evidence that this anthropogenic disturbance affects any demographic parameter, which conforms with the results found by Gómez et al. (2016) regarding burning effects on *A. azarae*.

Other endogenous and exogenous explanatory variables seem to explain variations of population demographic parameters. Our models estimated the highest survival probabilities for *C. musculinus* in winter. These results could be a consequence of the increase of minimum and average winter temperatures registered in the study area according to data from the Agrometeorological Laboratory. However, long time series data sources are required to obtain reliable information on the effects of environmental variables on demographic parameters (Gómez et al. 2016).

Obtaining several models with similar statistical support to explain survival of *C. venustus* may be due to the low number of individuals used for parameter estimations. However, some explanatory variables in the best selected models (sex, abundance and temperature) would seem to have an important role in survival probabilities of this species. The highest survival probabilities, number of recruited individuals and peak in population growth rates observed in summer may be related to a higher primary production in that period with sufficient food and shelter availability (Lima and Jaksic 1998; Andreo et al. 2009). Factors that regulate inter-annual dynamics of *C. venustus* (Andreo et al. 2009) seem to be similar to those that affect demographic parameters.

In *M. musculus*, apparent survival showed temporal fluctuation while recruitment showed constant and intermediate values throughout the study. Despite the fact that other studies found that recruitment could be more important than survival in house mouse populations (Berry and Tricker 1969; Lidicker 1976; Berry et al. 1982), survival had the greatest contribution to the population growth in the railway bank (γ was higher than 0.5 during all the study period). These results may differ from other small mammal species, in which survival only contributes to population growth rate in the non-reproductive period (Lima et al. 2003; Gómez et al. 2016). Apparent survival estimated in this study does not distinguish between real mortality and emigration (Nichols et al. 2000; Nichols and Hines 2002; Ozgul et al. 2004, 2007). Thus, lower survival in some periods may suggest higher levels of emigration than mortality. On the other hand, this species has a high reproductive potential (Singleton et al. 2001). House mouse populations in southern Australia can reproduce in any season of the year, but typically breed from spring to autumn (Singleton 1989; Mutze 1991; Twigg and Kay 1994). In Argentine farms, León et al. (2012) did not find seasonal variations in *M. musculus* reproduction, differing from native species. There is also some evidence that food supplies trigger the onset of breeding and the provision of high-quality food can extend the breeding season (Bomford and Redhead 1987). Although Pradel's model does not differentiate between reproduction and immigration as different sources of recruitment, constant recruitment for *M. musculus* would be a consequence of its reproduction, since juveniles and pregnant females were captured year-round. On the other hand, *M. musculus* has increased its representativeness in the railway bank from 3.02% in 1990-1999 (Gómez et al. 2016) to more than 40% during our study period. This change could be a consequence of its above-mentioned demographic characteristics combined with the effects of a major anthropogenic disturbance that occurred in the study area in 2009. This disturbance was the reconstruction of a bridge which produced a reduction of habitat quality and could have negatively affected native species. Thus, this railway bank became more suitable to the generalist and opportunistic *M. musculus*. Although we did not find negative effects of *A. azarae* on *M. musculus* demographic parameters, we observed a spatial segregation of the house mouse in the study area. In the

railway zone next to the bridge, *M. musculus* was numerically dominant (more than 80% of captures).

Although *A. azarae* is proposed as a dominant species (Busch and Kravetz 1992; Cittadino et al. 1994; Cueto et al. 1995; Busch et al. 2005), our results indicate that its abundance did not affect demographic parameters of the other rodent species in the assemblage. As mentioned above, the lack of evidence of this effect could be due to a number of factors, including that we are currently visualizing the ghost of past competition, a differential space and time use by different species or

that other variables have greater effects on demographic parameters than competition. In addition, railway banks could offer shelter and food for all species during the year, allowing them to avoid competition for available resources. Nevertheless, composition of small mammal assemblages can change with anthropogenic disturbances, which affects habitat quality and allows invasive species as the house mouse to establish.

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REFERENCES

- Andreo, V., M. A. Lima, C. Provencal, J. W. Priotto, and J. J. Polop. 2009. Population dynamics of two rodent species in agro-ecosystems of central Argentina: Intra-specific competition, land-use, and climate effects. *Population Ecology* **51**:297-306. <https://doi.org/10.1007/s10144-008-0123-3>.
- Arlettaz, R., M. Krähenbühl, B. Almasi, A. Roulin, and M. Schaub. 2010. Wildflower areas within revitalized agricultural matrices boost small mammal populations but not breeding Barn Owls. *Journal of Ornithology* **151**:553-564. <https://doi.org/10.1007/s10336-009-0485-0>.
- Baraibar, B., P. R. Westerman, E. Carrión, and J. Recasens. 2009. Effects of tillage and irrigation in cereal fields on weed seed removal by seed predators. *Journal of Applied Ecology* **46**:380-387. <https://doi.org/10.1111/j.1365-2664.2009.01614.x>.
- Begon, M., C. R. Townsend, and J. L. Harper. 1996. *Ecology: from individuals to ecosystems*. Blackwell Pub.
- Berry, R. J., A. Cuthbert, and J. Peters. 1982. Colonization by House mice: an experiment. *Journal of Zoology* **198**:329-336.
- Berry, R. J., and B. J. K. Tricker. 1969. Competition and extinction: the mice of Foula, with notes on those of Fair Isle and St Kilda. *Journal of Zoology* **158**:247-265. <https://doi.org/10.1111/j.1469-7998.1982.tb02079.x>.
- Bilenca, D. N., F. O. Kravetz, and G. A. Zuleta. 1992. Food habits of *Akodon azarae* and *Calomys laucha* (cricetidae, rodentia) in agroecosystems of central Argentina. *Mammalia* **56**:371-384. <https://doi.org/10.1515/mamm.1992.56.3.371>.
- Bomford, M., and T. Redhead. 1987. A field experiment to examine the effects of food quality and population density on reproduction of wild house mice. *Oikos* **48**:304. <https://doi.org/10.2307/3565518>.
- Bowers, M. A., and J. L. Dooley. 1991. Landscape composition and the Intensity and outcome of two-species competition. *Oikos* **60**:180. <https://doi.org/10.2307/3544864>.
- Brady, M. J., and N. A. Slade. 2001. Diversity of a grassland rodent community at varying temporal scales: the role of ecologically dominant species. *Journal of Mammalogy* **82**:974-983. [https://doi.org/10.1644/1545-1542\(2001\)082%3C0974:DOAGRC%3E2.0.CO;2](https://doi.org/10.1644/1545-1542(2001)082%3C0974:DOAGRC%3E2.0.CO;2).
- Brunner, J. L., S. S. Duerr, F. Keesing, M. Killilea, H. Vuong, and R. S. Ostfeld. 2013. An experimental test of competition among mice, chipmunks, and squirrels in deciduous forest fragments. *PLoS ONE* **8**(6):e66798. <https://doi.org/10.1371/journal.pone.0066798>.
- Burkart, R., N. Bárbaro, R. O. Sánchez, and D. A. Gómez. 1999. *Eco-regiones de la Argentina*. Administración de Parques Nacionales - Programa de Desarrollo Institucional Ambiental, Buenos Aires, Argentina.
- Busch, M., M. Álvarez, E. A. Cittadino, and F. O. Kravetz. 1997. Habitat selection and interspecific competition in rodents in pampean agroecosystems. *Mammalia* **61**:167-184. <https://doi.org/10.1515/mamm.1997.61.2.167>.
- Busch, M., D. N. Bilenca, E. A. Cittadino, and G. R. Cueto. 2005. Effect of removing a dominant competitor, *Akodon azarae* (Rodentia, Sigmodontinae) on community and population parameters of small rodent species in Central Argentina. *Austral Ecology* **30**:168-178. <https://doi.org/10.1111/j.1442-9993.2004.01434.x>.
- Busch, M., and F. O. Kravetz. 1992. Competitive interactions among rodents (*Akodon azarae*, *Calomys laucha*, *C. musculus* and *Oligoryzomys avescens*) in a two-habitat system. I. Spatial and numerical relationships. *Mammalia* **56**:45-56. <https://doi.org/10.1515/mamm.1992.56.1.45>.
- Busch, M., M. H. Miño, J. R. Dadon, K. Hodara, M. H. Mino, J. R. Dadon, and K. Hodara. 2001. Habitat selection by *Akodon azarae* and *Calomys laucha* (Rodentia, Muridae) in pampean agroecosystems. *Mammalia* **65**:29-48. <https://doi.org/10.1515/mamm.2001.65.1.29>.
- Butet, A., and A. B. A. Leroux. 2001. Effects of agriculture development on vole dynamics and conservation of Montagu's harrier in western French wetlands. *Biological Conservation* **100**:289-295. [https://doi.org/10.1016/S0006-3207\(01\)00033-7](https://doi.org/10.1016/S0006-3207(01)00033-7).
- Chen, L., G. Wang, X. Wan, and W. Liu. 2014. Complex and nonlinear effects of weather and density on the demography of small herbivorous mammals. *Basic and Applied Ecology* **16**:172-179. <https://doi.org/10.1016/j.baae.2014.12.002>.

- Choquet, R., R. Anne-Marie, R. Pradel, G. Olivier, and J.-D. Lebreton. 2003. User's Manual for U-CARE, Version 2.0.
- Cittadino, E. A., P. de Carli, M. Busch, and F. O. Kravetz. 1994. Effects of food supplementation on rodents in winter. *Journal of Mammalogy* **75**:446-453. <https://doi.org/10.2307/1382566>.
- Cooch, E., and G. C. White. 2019. Program MARK, a Gentle introduction. 19th edition.
- Coulson, T., E. J. Milner-Gulland, and T. Clutton-Brock. 2000. The relative roles of density and climatic variation on population dynamics and fecundity rates in three contrasting ungulate species. *Proceedings of the Royal Society B* **267**:1771-1779. <https://doi.org/10.1098/rspb.2000.1209>.
- Courtalon, P., A. Dolcemascolo, V. Troiano, M. R. Álvarez, and M. Busch. 2003. Inter and Intraspecific Relationships in *Akodon azarae* and *Calomys laucha* (Rodentia, Sigmodontinae) in Pampean Agroecosystems. *Mastozoología Neotropical* **10**:27-39.
- Crespin, L., and M. A. Lima. 2006. Supervivencia adulta y dinámica poblacional del lauchón orejudo *Phyllotis darwini* en Chile central. *Revista Chilena de Historia Natural* **79**:295-308. <https://doi.org/10.4067/S0716-078X2006000300002>.
- Cueto, G. R., D. N. Bilenca, and F. O. Kravetz. 1995. Interspecific Social Relationships in Three Murid Rodent Species of Central Argentina, after Fasting and Unlimited Food. *Journal of Mammalogy* **76**:811-820. <https://doi.org/10.1163/156853995X00018>.
- Ellis, B. A., J. N. Mills, G. E. Glass, K. T. Mckee, D. A. Enria, and J. E. Childs. 1998. Dietary habits of the common rodents in an agroecosystem in Argentina. *Journal of Mammalogy* **79**:1203-1220. <https://doi.org/10.2307/1383012>.
- Fischer, C., C. Thies, and T. Tschamtké. 2011. Small mammals in agricultural landscapes: Opposing responses to farming practices and landscape complexity. *Biological Conservation* **144**:1130-1136. <https://doi.org/10.1016/j.biocon.2010.12.032>.
- Fraschina, J., V. A. León, and M. Busch. 2012. Long-term variations in rodent abundance in a rural landscape of the Pampas, Argentina. *Ecological Research* **27**:191-202. <https://doi.org/10.1007/s11284-011-0888-2>.
- Gliwicz, J., and J. R. E. Taylor. 2002. Comparing life histories of shrews and rodents. *Acta Theriologica* **47**:185-208. <https://doi.org/10.1007/BF03192487>.
- Gómez, M. D., J. A. Coda, I. Simone, J. J. Martínez, F. Bonatto, A. R. Steinmann, and J. W. Priotto. 2015. Agricultural land-use intensity and its effects on small mammals in the central region of Argentina. *Mammal Research* **60**:415-423. <https://doi.org/10.1007/s13364-015-0245-x>.
- Gómez, M. D., J. W. Priotto, M. C. Provencal, A. R. Steinmann, E. A. Castillo, and J. J. Polop. 2008. A population study of house mice (*Mus musculus*) inhabiting different habitats in an Argentine urban area. *International Biodeterioration and Biodegradation* **62**:270-273. <https://doi.org/10.1016/j.ibiod.2007.08.004>.
- Gómez, M. D., V. N. Serafini, J. A. Coda, and J. W. Priotto. 2016. Demographic dynamics of *Akodon azarae* (Cricetidae: Sigmodontinae) in linear habitats of agricultural landscapes of central Argentina. *Studies on Neotropical Fauna and Environment* **51**:10-18. <https://doi.org/10.1080/01650521.2015.1137167>.
- Graipel, M. E., M. I. M. Hernández, and C. Salvador. 2014. Evaluation of abundance indexes in open population studies: a comparison in populations of small mammals in southern Brazil. *Brazilian Journal of Biology* **74**:553-559. <https://doi.org/10.1590/bjb.2014.0077>.
- Hodara, K., M. Busch, M. J. Kittlein, and F. O. Kravetz. 2000. Density-dependent habitat selection between maize cropfields and their borders in two rodent species (*Akodon azarae* and *Calomys laucha*) of Pampean agroecosystems. *Evolutionary Ecology* **14**:571-593. <https://doi.org/10.1023/A:1010823128530>.
- Hoeck, H. N. 1989. Demography and competition in Hyrax - A 17-year study. *Oecologia* **79**:353-360. <https://doi.org/10.1007/BF00384314>.
- Huitu, O., K. Norrdahl, and E. Korpimäki. 2004. Competition, predation and interspecific synchrony in cyclic small mammal communities. *Ecography* **27**:197-206. <https://doi.org/10.1111/j.0906-7590.2003.03684.x>.
- Kollmann, J., and S. Bassin. 2001. Effects of management on seed predation in wildflower strips in northern Switzerland. *Agriculture, Ecosystems and Environment* **83**:285-296. [https://doi.org/10.1016/S0167-8809\(00\)00202-4](https://doi.org/10.1016/S0167-8809(00)00202-4).
- Kollmann, J., and M. Buschor. 2002. Edge effects on seed predation by rodents in deciduous forests of northern Switzerland. *Plant Ecology* **164**:249-261. <https://doi.org/10.1023/A:1021225728493>.
- Laake, J. L. 2013. RMark: An R Interface for analysis of capture-recapture data with MARK.
- Li, H., and J. Wo. 2007. Landscape pattern analysis: issues and challenges. Pp. 39-61 in J. Wo and R. Hobbs (eds.). *Key Topics in Landscape Ecology*. Cambridge University Press, Cambridge. <https://doi.org/10.1017/CBO9780511618581.004>.
- Lidicker, W. Z. 1976. October. Social behaviour and density regulation in house mice living in large enclosures. *The Journal of Animal Ecology* **45**:677-697. <https://doi.org/10.2307/3575>.
- Lima, M. A., and F. M. Jaksic. 1998. Delayed density-dependent and rainfall effects on reproductive parameters of an irruptive rodent in semiarid Chile. *Acta Theriologica* **43**:225-234. <https://doi.org/10.4098/AT.arch.98-19>.
- Lima, M. A., N. C. Stenseth, H. Leirs, and F. M. Jaksic. 2003. Population dynamics of small mammals in semi-arid regions: a comparative study of demographic variability in two rodent species. *Proceedings Biological Sciences. London Biology* **270**:1997-2007. <https://doi.org/10.1098/rspb.2003.2448>.
- Martínez, J. J., V. Millien, I. Simone, and J. W. Priotto. 2014. Ecological preference between generalist and specialist rodents: Spatial and environmental correlates of phenotypic variation. *Biological Journal of the Linnean Society* **112**:180-203. <https://doi.org/10.1111/bj.12268>.
- McCallum, H. 2000. *Population Parameters: Estimation for Ecological Models*. Wiley-Blackwell, Oxford. <https://doi.org/10.1002/9780470757468>.

- Mills, J. N., B. A. Ellis, K. T. Mckee, J. I. Maiztegui, and J. E. Childs. 1991. Habitat associations and relative densities of rodent populations in cultivated areas of central Argentina. *Journal of Mammalogy* **72**:470-479. <https://doi.org/10.2307/1382129>.
- Mutze, G. 1991. Mouse plagues in South Australia cereal-growing areas III. Changes in mouse abundance during plague and non-plague years, and the role of refugia. *Wildlife Research* **18**:593. <https://doi.org/10.1071/WR9910593>.
- Nichols, J. D., and J. E. Hines. 2002. Approaches for the direct estimation of λ , and demographic contributions to λ , using capture-recapture data. *Journal of Applied Ecology* **29**:539-568. <https://doi.org/10.1080/02664760120108809>
- Nichols, J. D., J. E. Hines, J.D. Lebreton, and R. Pradel. 2000. Estimation of contributions to population Growth: A reverse-time capture-recapture approach. *Ecology* **81**:3362-3376. <https://doi.org/10.2307/177500>. <https://doi.org/10.2307/177500>.
- Oli, M. K., and F. S. Dobson. 2001. Population cycles in small mammals: the α -hypothesis. *Journal of Mammalogy* **82**:573-581. <https://doi.org/10.1093/jmammal/82.2.573>. [https://doi.org/10.1644/1545-1542\(2001\)082%3C0573:PCISMT%3E2.0.CO;2](https://doi.org/10.1644/1545-1542(2001)082%3C0573:PCISMT%3E2.0.CO;2).
- Oli, M. K., and F. S. Dobson. 2003. The relative importance of life-history variables to population growth rate in mammals: Cole's Prediction Revisited. *The American Naturalist* **161**:422-440. <https://doi.org/10.1086/367591>.
- Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical Inference from Capture Data on Closed Animal Populations. *Wildlife Monographs* **62**:6-135.
- Ozgul, A., L. L. Getz, and M. K. Oli. 2004. Demography of fluctuating populations: Temporal and phase-related changes in vital rates of *Microtus ochrogaster*. *Journal of Animal Ecology* **73**:201-215. <https://doi.org/10.1111/j.0021-8790.2004.00797.x>.
- Ozgul, A., M. K. Oli, L. E. Olson, D. T. Blumstein, and K. B. Armitage. 2007. Spatiotemporal variation in reproductive parameters of yellow-bellied marmots. *Oecologia* **154**:95-106. <https://doi.org/10.1007/s00442-007-0817-9>.
- Paine, R. T. 1966. Food Web Complexity and Species Diversity. *The American Naturalist* **100**:65-75.
- Pocock, M. J. O., H. C. Hauffe, and J. B. Searle. 2005. Dispersal in house mice. *Biological Journal of the Linnean Society* **84**:565-583. <https://doi.org/10.1111/j.1095-8312.2005.00455.x>
- Polop, J. J. 1996. Análisis de las respuestas adaptativas del género *Calomys*. Universidad Nacional de Río Cuarto, Córdoba, Argentina.
- Post, E., N. C. Stenseth, R. Langvatn, and J. M. Fromentin. 1997. Global climate change and phenotypic variation among red deer cohorts. *Proceedings. Biological sciences* **264**:1317-24. <https://doi.org/10.1098/rspb.1997.0182>.
- Pradel, R. 1996. Utilization of capture-mark-recapture for estimation of recruitment and population growth rate. *Biometrics* **52**:703-709. <https://doi.org/10.2307/2532908>.
- Priotto, J., D. Gómez, and J. Polop. 2010. A demographic analysis of population responses to the manipulation of adult males in *Calomys venustus* (Rodentia, Sigmodontinae). *Ecological Research* **25**:521-529. <https://doi.org/10.1078/1616-5047-00014>.
- Priotto, J. W., and J. J. Polop. 1997. Space and time use in syntopic populations of *Akodon azarae* and *Calomys venustus* (Rodentia, Muridae). *Mammalian Biology* **62**:30-36.
- Priotto, J. W., A. R. Steinmann, and J. J. Polop. 2002. Factors affecting home range size and overlap in *Calomys venustus* (Muridae: Sigmodontinae) in Argentine agroecosystems. *Mammalian Biology* **67**:97-104. <https://doi.org/10.1078/1616-5047-00014>.
- Pritchard, J. R., and D. Schluter. 2001. Declining interspecific competition during character displacement: Summoning the ghost of competition past. *Evolutionary Ecology Research* **3**:209-220.
- R Core Team. 2016. R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria.
- Salamolard, M., A. Butet, A. Leroux, and V. Bretagnolle. 2000. Responses of an avian predator to variations in prey density at a temperate latitude. *Ecology* **81**:2428-2441. [https://doi.org/10.1890/0012-9658\(2000\)081\[2428:ROAAPT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[2428:ROAAPT]2.0.CO;2).
- Schickmann, S., A. Urban, K. Krätler, U. Nopp-Mayr, and K. Hackländer. 2012. The interrelationship of mycophagous small mammals and ectomycorrhizal fungi in primeval, disturbed and managed Central European mountainous forests. *Oecologia* **170**:395-409. <https://doi.org/10.1007/s00442-012-2303-2>.
- Simone, I., F. Cagnacci, M. C. Provencal, and J. J. Polop. 2010. Environmental determinants of the small mammal assemblage in an agroecosystem of central Argentina: The role of *Calomys musculus*. *Mammalian Biology* **75**:496-509. <https://doi.org/10.1016/j.mambio.2009.12.002>.
- Singleton, G. R. 1989. Population dynamics of an outbreak of house mice (*Mus domesticus*) in the mallee wheatlands of Australia; hypothesis of plague formation. *Journal of Zoology* **219**:495-515. <https://doi.org/10.1111/j.1469-7998.1989.tb02596.x>.
- Singleton, G. R., P. R. Brown, R. P. Pech, J. Jacob, G. J. Mutze, and C. J. Krebs. 2005. One hundred years of eruptions of house mice in Australia - A natural biological curio. *Biological Journal of the Linnean Society* **84**:617-627. <https://doi.org/10.1111/j.1095-8312.2005.00458.x>.
- Singleton, G. R., C. J. Krebs, S. A. Davis, L. Chambers, and P. R. Brown. 2001. Reproductive changes in fluctuating house mouse populations in southeastern Australia. *Proceedings Biological Sciences* **268**:1741-8. <https://doi.org/10.1098/rspb.2001.1638>.
- Sozio, G., and A. Mortelliti. 2016. Empirical evaluation of the strength of interspecific competition in shaping small mammal communities in fragmented landscapes. *Landscape Ecology* **31**:775-789. <https://doi.org/10.1007/s10980-015-0286-1>.

- Tattersall, F., R. Smith, and F. Nowell. 1997. Experimental colonization of contrasting habitats by house mice. *Mammalian Biology* **62**:350-358.
- Tuljapurkar, S. 1990. *Population Dynamics in Variable Environments*. Springer-Verlag, New York, USA. <https://doi.org/10.1007/978-3-642-51652-8>.
- Twigg, L. E., and B. J. Kay. 1994. The Effects of Microhabitat and Weather on House Mouse (*Mus domesticus*) Numbers and the Implications for Management. *The Journal of Applied Ecology* **31**:651. <https://doi.org/10.2307/2404156>.
- Valone, T. J., and J. H. Brown. 1995. Effects of competition, colonization, and extinction on rodent species diversity. *Science (New York, N.Y.)* **267**:880-3. <https://doi.org/10.1126/science.7846530>.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**:120-138. <https://doi.org/10.1080/00063659909477239>.
- Williams, B., J. D. Nichols, and M. J. Conroy. 2002. *Analysis and management of animal populations*. Academic Press, San Diego, California, USA.
- Ylönen, H., J. Jacob, M. J. Davies, and G. R. Singleton. 2002. Predation risk and habitat selection of Australian House Mice *Mus domesticus* during an incipient plague: Desperate behaviour due to food depletion. *Oikos* **99**:284-289. <https://doi.org/10.1034/j.1600-0706.2002.990208.x>.