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Demographic dynamics of *Akodon azarae* (Cricetidae: Sigmodontinae) in linear habitats of agricultural landscapes of central Argentina

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Linear habitats are capable of providing essential resources for small mammals within agroecosystems. We analyzed demographic parameters of *Akodon azarae* in a linear habitat of central Argentina. We used capture-mark-recapture models to determine temporal variations in survival, recruitment and population growth rate. The effects of temperature, rainfall and vegetation cover as well as of population abundances on the mentioned parameters were assessed in a 10-year study. Survival and growth rate showed seasonal variation, which was greater than the interannual variability observed. Temperature affected only recruitment. Linear habitats would provide resources for long term survival and reproduction of *A. azarae*.

Keywords: CMR; population growth rate; recruitment; survival; temporal variation

Introduction

One of the most important threats to the persistence of animal populations is landscape modification by humans, through loss, degradation and subdivision of habitats (Foley et al. 2005; Fischer & Lindenmayer 2007). These fragmentation processes may lead to population declines and thus make species more susceptible to extinction as a result of stochastic events (Lindenmayer & Fischer 2006). Agricultural landscapes in particular are given frequently as examples of habitat modification. In highly altered landscapes such as agricultural systems, linear habitats such as road verges, hedgerows, riparian strips and railway banks become important contributors to biodiversity conservation (Gelling et al. 2007; Sabino-Marques & Mira 2011; Sullivan et al. 2012). These linear structures may not only be habitat corridors contributing to landscape connectivity, but also create key habitats since they provide food and other essential resources for survival and reproduction of many species (Gomez & Anthony 1998; Gelling et al. 2007; Sullivan et al. 2012).

In Central Argentina, agricultural systems consist of monocultures of a few crops with a network of roadsides, fence lines, railways and other border habitats that keep remnant native flora and a lot of introduced weeds (Ellis et al. 1997; Busch et al. 2000). These habitats serve as shelter for small mammals and may be interconnected to form corridors throughout cropland habitats (Ellis et al. 1997). In addition,

these linear habitats maintain high plant cover throughout the year and may allow the continuity of ecological processes in heavily altered environments. They often comprise suitable habitats for small mammals and they may be critical to the conservation of these species (Sommaro et al. 2010; Gomez et al. 2011; Coda et al. 2014).

Considering the relevance of the linear habitats for the persistence of small mammal populations, the understanding of the mechanism underlying their dynamics would be a key focus for the management of non-crop linear habitats in agricultural landscapes. Fluctuations in population numbers contain two components: seasonal variation and interannual variation. Both are consequences of changes in demographic parameters such as survival and recruitment (Lima et al. 2001; Ozgul et al. 2007; Grande et al. 2009). A thorough understanding of population dynamics requires a detailed understanding of variation in demographic parameters and in the factors that cause such variation (Ozgul et al. 2007). The use of the capture-mark-recapture (CMR) statistical modeling to obtain estimates of demographic parameters provides an ideal link between demographic mechanisms and population dynamics (Lima et al. 2003). These demographic parameters may have different impact on population dynamics, with some parameters influencing population growth more directly than others (Oli & Dobson 2003). Therefore, identification and estimation of life history parameters that

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influence the population growth rates are crucial to the understanding of changes in population size. Demographic parameters can vary with individual characteristics such as sex, weight and reproductive condition. Changes in the population are generally thought of as a function of exogenous and endogenous factors. The former includes density independent factors as climatic variables whereas the latter includes population level characteristics (Lima et al. 2001; Ozgul et al. 2007).

Akodon azarae, a small rodent (adult average weight 25 g), is one of the most abundant rodent species in agricultural systems of the center-south of Córdoba province, Argentina (Gomez et al. 2011; Polop et al. 2012). Its abundance has been increasing in the last 20 years, replacing another species of the same genus, *A. dolores* (Polop et al. 2012). *Akodon azarae* is found in a variety of slightly disturbed habitats with high grass cover, including natural pastures and linear habitats as road borders and railway banks (Hodara et al. 2000; Busch et al. 2001). This species is an opportunistic omnivore (Suárez & Bonaventura 2001) and shows continuous activity, being mainly active during daytime and crepuscular hours (Priotto & Polop 1997). Populations turn over annually, and individual lifespan is of about 12 months (Zuleta et al. 1988; Hodara et al. 2000). The reproductive period of this species begins in spring (mid-September) and finishes in autumn (May).

Seasonal changes in population abundances of *A. azarae* in linear habitats (railway banks) seem to be mainly explained by rainfall and vegetation whereas interannual fluctuations seem to be described mainly by a negative first order feedback structure, suggesting that this species could be regulated by intra specific competition (Andreo et al. 2009a, 2009b). It has also been detected that exogenous factors play a secondary role in its dynamics: the collapse in the abundances of this species seems to be related to reductions in vegetation cover caused by human land use (Andreo et al. 2009a). Although seasonal and interannual changes in population abundance of this species have already been studied in the same study area, little is known about the effects of environmental variables on the basic demographic processes responsible for those abundance patterns. Moreover, the studies on population fluctuations have been developed considering equal capture probabilities of individuals (non-probabilistic estimations); conversely, CMR methods take account for variation in capture probabilities and provide unbiased estimates of demographic parameters. Therefore, it would be essential to estimate population sizes using less biased probabilistic models (Graipel et al. 2014) that allow the understanding of demographic processes that produce

fluctuations in *A. azarae* populations. In this sense, the aim of the present study was to analyze temporal variation of demographic parameters and their impact on population dynamics of *A. azarae* in a linear habitat within the agroecosystems of central Argentina. We applied CMR models to a set of data, collected over 10 years (1990–1999), to determine the variations in survival, recruitment and population growth rate within each year and between the years of the study. We also assessed the effects of endogenous (population abundance) and exogenous (temperature, rainfall and vegetation cover) factors on the observed variation within each component.

Materials and methods

Study site

The study was carried out in a railway bank (33°01′34″ S; 64°11′21″W), with an average width of 50 m, located in an agroecosystem near to Chucul locality in the southwest of Córdoba province, Argentina. The climate of the region is temperate with an average temperature of 23°C in summer and 6°C in winter and annual rainfall of 800 mm. The region belongs to the Espinal ecoregion (Burkart et al. 1999); however, its physiognomy has undergone a marked transformation due to intensive agriculture and livestock practices. The landscape was a heterogeneous mosaic with a few isolated fragments of natural habitats. It consisted of many pasture and cultivated fields and a network of linear habitats developed along the crop field margins, road sides, river sides, fencerows and railways. These linear habitats supported a mixed vegetation, dominated by native herbaceous species together with introduced weedy and invasive plants. Currently, the landscape has similar characteristics but the cultivated fields have undergone some changes; the area of harvested sorghum has decreased and the area of harvested soybean has strongly increased (Polop et al. 2012).

Data analyses

We used CMR data, collected from April 1990 to August 1999, of small mammals caught through live trapping. Monthly trapping sessions were conducted for five consecutive days in a 6 x 10 grid of live traps, similar to Sherman live traps. Traps were individually placed every 10 m and they were baited with a mixture of peanut butter and suet. Trapped animals were identified and marked with ear tags. Sex, reproductive state (males: scrotal or abdominal testicles, females: perforated or imperforated vagina, pregnancy evidence, visible nipples or not), length and weight were recorded. Population abundances were

estimated using methods applied for closed populations. The estimations were obtained using the program CAPTURE (White et al. 1982) incorporated as an independent module into the program MARK (White & Burnham 1999). We compared the abundance values obtained in this study using CMR models with those obtained by Andreo et al. (2009a, 2009b) using a relative density index (RDI = total captures/trap-nights × 100) and minimun number known alive (MNKA).

Survival (Φ), capture (p) and seniority (γ) probabilities as well as population growth rates (λ) were estimated and modeled following CMR methods (Lebreton et al. 1992) and Pradel's reverse models (Pradel 1996) through the MARK program. A total number of 674 individuals (341 females and 333 males), obtained in 2456 captures, were used in the analyses. The program U-CARE (Choquet et al. 2003) was used to assess the goodness of fit of the models. We started by modeling Φ and p probabilities using Cormack Jolly Seber (CJS) models. Several models, including no time variation (.), monthly variation (m), season variation (s), between year variation (y) and full time variation (t) were tested. The effect of the gender (sex) was also evaluated, considering both combined and additive contribution of this factor to time survival and capture probabilities. Models were ranked according to Akaike's information criterion, corrected for small sample size (AICc). This provides a relative measure of fit, i.e. the balance between the number of parameters and the fit of the model (Burnham & Anderson 1998). Model comparison was based on the differences in AICc values (ΔAICc); so, when ΔAICc values were greater than two units, the model with the lowest AICc could be considered a statistically better description of the process that generated the data.

The most parsimonious models identified in the preceding analyses were selected to examine the influence of monthly population abundance and environmental factors on survival and recapture probabilities. Environmental factors included monthly normalized difference vegetation index (NDVI), monthly temperature and rainfall. Data series of climatic variables were provided by the agrometeorological laboratory of Universidad Nacional de Río Cuarto. NDVI data series for this study were obtained from the global inventory modeling and mapping studies AVHRR 8 km (Andreo et al. 2009b). The grid was partially and completely burnt in September 1991 and September 1995, respectively. The effect of this anthropogenic disturbance was also tested. The effect of each covariate on a parameter was evaluated by comparing the difference in AICc between models with and without the covariate; ΔAICc > 2 was taken as an evidence of support for the relationship between the parameter and the covariate.

The 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 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 – γ) of population growth rate (Nichols et al. 2000). We modeled seniority probabilities using Pradel's reverse time CMR model (Pradel 1996), using the best models for capture probabilities and following the same steps used to survival analyses.

Population growth rate (λ) was modeled using the Pradel survival and lambda model, using the best models for survival and capture probabilities. To minimize the number of parameters to be estimated in λ analyses, we only analyzed the effect of each explanatory factor without combined or additive contributions to population growth rates. We estimated the relative contribution of survival and recruitment to λ (Nichols et al. 2000). The seniority probability (γ) and its complement (1 – γ) can be interpreted as the relative contributions of survival and recruitment to the realized population growth (Nichols et al. 2000; Ozgul et al. 2007). Seniority values greater than 0.5 would indicate a greater relative influence of survival on the realized population growth rate with respect to the influence exerted by recruitment (Ozgul et al. 2007).

Results

Population abundances

Throughout the study seven native rodent species were captured in the trapping grid: *Akodon azarae* (45.78% of the registered captures), *A. dolores* (0.29%), *Calomys venustus* (34.54%), *C. musculinus* (8.85%), *C. laucha* (0.65%), *Oxymycterus rufus* (1.85%) and *Oligoryzomys flavescens* (4.71%). We also captured three exotic species: *Mus musculus* (3.02%), *Rattus norvegicus* (0.05%) and *R. rattus* (0.26%).

Population abundances of *A. azarae* showed irregular fluctuations; we registered high abundance values during some years, while during others these values were clearly lower (Figure 1). Population numbers showed a marked drop during the years 1992–1993 and 1996–1997, after fires (Figure 1).

Demographic parameters

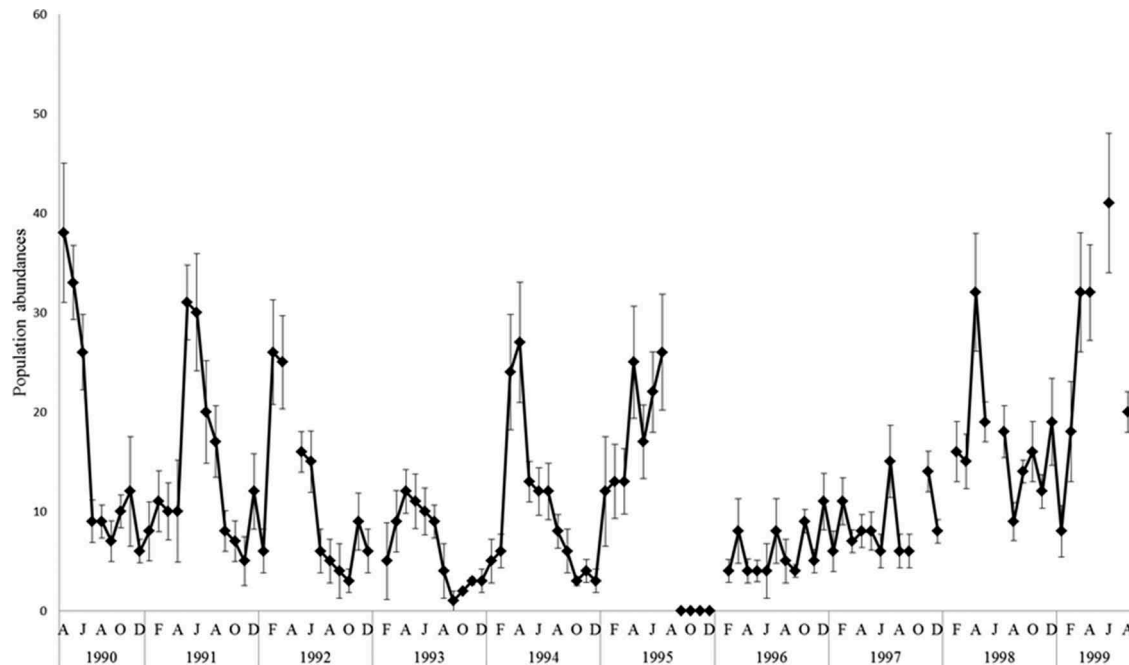According to the GOF test, the global model that included sex and time dependent survival and

Figure 1. Monthly population abundances of *Akodon azarae* estimated by capture-mark-recapture in a railway located in an agroecosystem near Chucul locality, Córdoba province, Argentina; from April 1990 to August 1999.

recapture probabilities (Φ (sex*t), p (sex*t)), provided no evidence of lack of fit (X^2_{221} = 109.630, p > 0.99), but indicated under dispersion of data (^c = 0.49). The most parsimonious model indicated an effect of the sex and month on survival probabilities and an effect of sex and temperature on recapture probabilities ((Φ (sex + month), p (sex + temperature)), Table 1. Both sexes showed a similar survival pattern; however, males had slightly higher survival than females. The lowest survival values were registered early during the non-reproductive

period (July) and at the beginning of the reproductive one (October) in both sexes (Figure 2a). Recapture probabilities varied with temperature and sex. Lower values were registered with higher temperatures and females were more recaptured than males.

The best model to describe variation in seniority probabilities showed an additive effect between sex and temperature (γ (sex + temperature), p (sex + temperature)), Table 1. Thus, when we analyzed recruitment (1 – γ), the number of recruited

Table 1. Statistical best models denoted according to each model-specific variation in the probabilities of survival (ϕ), seniority (γ), population growth rate (λ) and recapture (p).

Demographic parameter	Best models	AIC_c[a]	$\Delta_i AIC_c$[b]	AIC_c weights	K[c]
Survival	$\left\{ \phi_{(sex+month)}, p_{(sex+temp)} \right\}.$ $\left\{ \phi_{(sex+montht)}, p_{(sex+month)} \right\}$	**2090.3444** 2093.9827	**0.0000** 3.6383	**0.4233** 0.0686	**16** 26
Seniority	$\left\{ \gamma_{(sex+temp)}, p_{(sex+temp)} \right\}$ $\left\{ \gamma_{(sex+month)}, p_{(sex+month)} \right\}$	**2265.2983** 2267.8111	**0.0000** 2.5128	**0.76403** 0.21750	**6** 25
Population growth rate	$\left\{ \phi_{(sex+month)}, p_{(sex+temp)}, \lambda_{(month)} \right\}$	**7778.6653**	**0.0000**	**0.95697**	**28**

[a]Measure of each model fit.
[b]Models are ordered by ΔAIC$_c$, only models with ΔAIC$_c$ ≤ 4.
[c]Number of estimable parameters. (+) symbol means additive effects. The most parsimonious models are highlighted in bold.
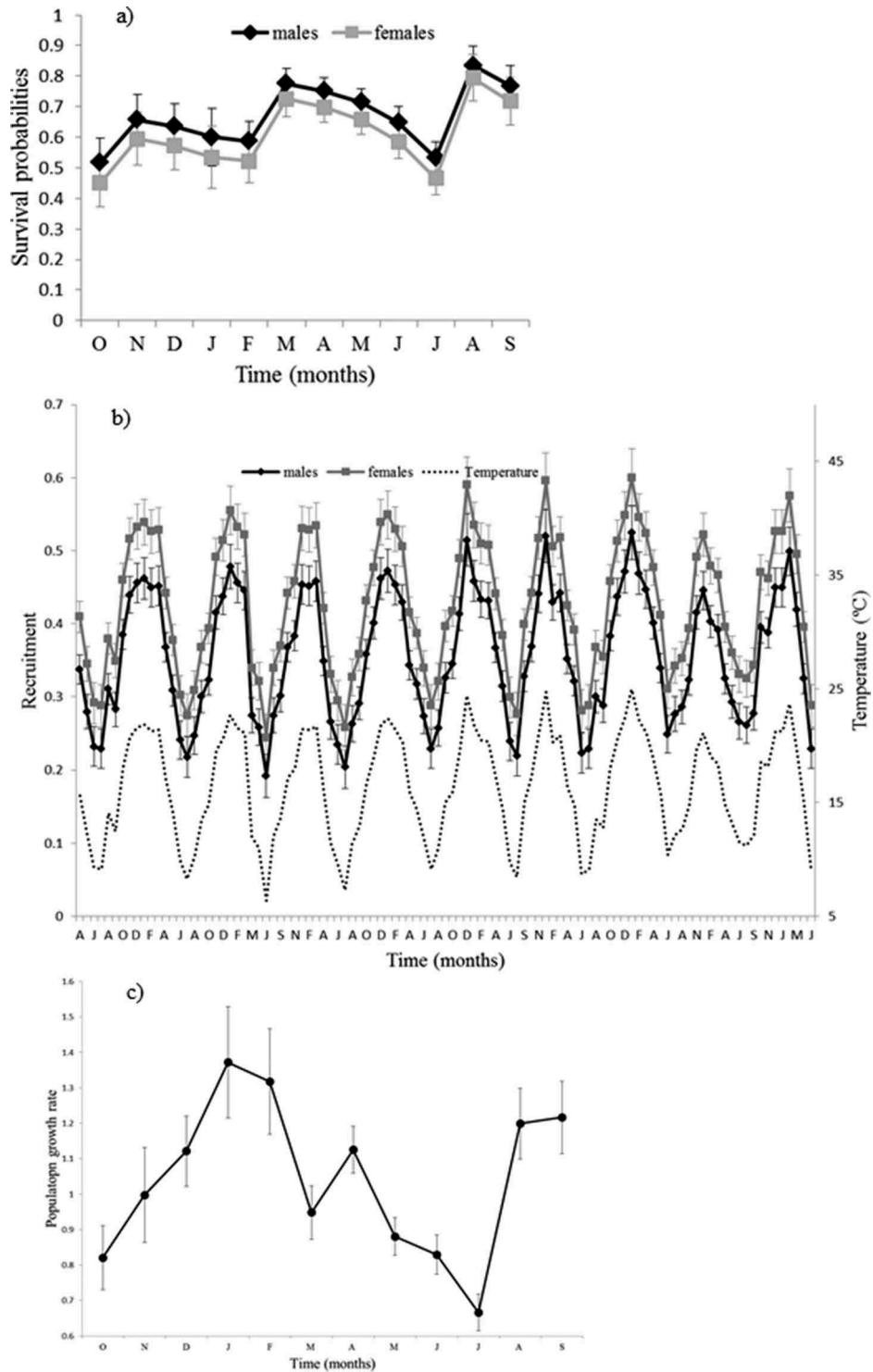
Figure 2. Demographic parameters of *Akodon azarae*. a, Survival probabilities estimated with the model {ϕ (sex + month), p (sex + temp)}; b, recruitment probabilities estimated with the model {γ (sex + temp), p(sex + temp)}; c, population growth rates estimated according to the statistical model {ϕ (sex + temp), p (sex + temp), λ (month)}.

individuals increased during the months with higher temperatures and there were more recruited females (Figure 2b).

The most parsimonious model identified for population growth rates (λ) indicated a pattern of monthly variation (Table 1). The population growth

rate showed the lowest values during the non-reproductive period (June–July) while the highest ones were obtained in the middle of reproductive period (January–February) (Figure 2c). We also investigated whether the relative contribution of survival and recruitment to λ varied over time. Monthly estimates of γ ranged from 0.52 to 0.77 for males and from 0.44 to 0.71 for females (minimum and maximum values correspond to January and July, respectively, for both sexes). Thus, the contribution of survival was higher than that the effect of recruitment during all months of study ($γ > 0.05$), except in January when the peak of recruitment was registered.

Discussion

Temporal variations in demographic rates constitute a common phenomenon within animal populations and may alter population dynamics of small mammals (Lima et al. 2001, 2003; Ozgul et al. 2007). General patterns of demographic parameters within small mammal populations of Argentina have been described (Mills et al. 1992; Priotto & Polop 2003; Gomez et al. 2007; Polop & Suárez 2010); however, they have not been deduced from CMR statistical analyses. Large temporal data sources are required to obtain reliable information on the effects of temporal variations in demographic rates. In this sense, the present study provided adequate data for a rigorous examination of temporal patterns in the demography and population size of *A. azarae* using CMR models.

There are several factors that can determine inaccuracies and biases of abundance estimations using non-probabilistic estimations, with the probability of capturing individuals being the most important one (Graipel et al. 2014). Thus, probabilistic estimations have been considered more appropriate than the use of abundance indexes (Nichols 1986; Graipel et al. 2014). Results on the comparison between the abundance values of this study and those obtained by Andreo et al. (2009b) showed that in spite of a high degree of concordance among estimations, the MNKA method generally underestimated population sizes in relation to CMR models, as it was reported for other *Akodon* species (Pacheco et al. 2013). On the other hand, RDI showed population trends but did not provide a real estimate of the number of animals and can only be used for comparative analyses of the same species. Thus, considering that in the area of study there were enough data to apply probabilistic methods, population size estimates obtained through closed population estimations would be considered more robust and they are preferable.

Demographic parameters showed strong temporal variability. Both survival and population growth rate appeared to show greater variation within a year (monthly) than between years. In addition, we found that exogenous factors, such as temperature, were operating on recruitment. Although the effects of anthropogenic disturbances, such as burnings, may decrease abundance peaks during the subsequent years, their effects on demographic parameters were tempered by their low frequency. Endogenous (e.g. abundance) and exogenous (e.g. NDVI) factors would affect interannual dynamics of A. azarae (Andreo et al. 2009a) but would not have effects on demographic parameters. These complementary findings suggest that the integration of demographic analyses using robust data series and simple population dynamics models is crucial to achieve a complete understanding of the dynamics of natural populations.

According to the survival pattern obtained, lower rates of survival were registered during the non-reproductive period and at the beginning of the reproductive one. Different factors could be responsible for this pattern in *A. azarae*. During the phase of declining abundance (winter), the impoverishment of habitats due to a decrease in green plant cover and food availability would contribute to a high animal mortality. In addition, it has been suggested that high dispersal rates could also contribute to a decrease in the number of individuals during winter (Cittadino et al. 1998). At the beginning of the reproductive season, *A. azarae* populations consist mainly of overwintering individuals, born during the preceding summer and autumn, and which are reproducing for the first time (Zuleta et al. 1988). A high level of mortality of *A. azarae* also occurs at the beginning of the breeding period, due to the death of these overwintering animals (Suárez et al. 2004). When comparing survival between sexes, we observed a lower survival of females; in agreement with Zuleta et al. (1988) who found a higher mortality of females in this species. However, these authors attribute the variability in survival to a differential catchability between sexes and based on our study we cannot attribute this variability to lower capture probabilities, since females were more recaptured than males. This lower survival of females may be due to the fact that reproductive activity implies a greater physiological and behavioral demand (in energetic terms) for females, as it was observed in other mammal species (Crespin et al. 2002).

The negative effect that a lower female survival would have on *A. azarae* populations would be damped by a higher recruitment of females. A higher number of recruited females than males at the beginning and the end of reproductive season has already been reported in this species (Zuleta & Bilenca 1992). These authors suggest that the differential pattern of

recruitment would be in agreement with the predictions based on temporal overproduction of one sex or the other. Parents would have the ability to invest in one sex more than in the other according to differential changes in the life history expectations for both sexes (Trivers & Willard 1973). On the other hand, recruitment probabilities may vary in relation to temperature since more food and green plant cover are available during the months with higher temperatures (December–February); a higher reproductive activity is characteristic of these months. Individuals of *A. azarae* would not have spacing behavior and they could adjust their home ranges together with the increase of density (Ávila et al. 2015). Thus, the newly recruited individuals would not be forced to disperse from their place of birth if resources are enough. Moreover, the size of the litters during the early summer (December–January) is larger than sizes observed the rest of the year (Suárez et al. 2004); this fact would contribute to the higher recruitment observed during the warmer months. The ambient temperature has been suggested as a primary factor affecting the onset of breeding and the number of recruited individuals in bank vole populations (Pucek et al. 1993; Hille & Rödel 2014).

Temporal variation in population growth rates would be the result of temporal variation in recruitment probabilities during the breeding period. On the other hand, variations in survival probabilities had a greater contribution to the population growth in the rest of the months, as observed for other small mammals (Lima et al. 2003). The growth peak observed in autumn, and the subsequent decrease, are in good agreement with the pattern of population abundance observed during the 10 years of the study in linear habitats.

The use of CMR demographic analyses and simple population dynamics models represent two related approaches for the study of rodent populations. The link between demography and population dynamics can be very useful for gaining a full understanding of fluctuations in rodent populations (Lima et al. 2001, 2003; Ozgul et al. 2007). Small mammals contribute to seed dispersal and to the complexity of food webs, influencing the biodiversity of agricultural systems (Carey et al. 1999; Michel et al. 2006; Baraibar et al. 2009). Consequently, this kind of approach is also very useful for the development of conservation and sustainable management strategies for linear habitats that support small mammal populations in these modified landscapes.

It is important to notice that linear habitats are less disturbed than crop fields and may the only portion of the suitable habitat to wildlife in agricultural systems. Furthermore, linear habitats may potentially provide connecting corridors in agricultural landscapes; they can provide food resources, nesting cover and shelter for small mammals, guaranteeing the continuity of ecological processes in altered environments (Gelling et al. 2007; Sabino-Marques & Mira 2011). Railway banks are especially important in intensively farmed regions such as the agricultural system of Córdoba province, due to the fact that they are wider than other linear habitats (40–50 m wide). They also constitute more stable habitats throughout the year since they are less influenced by the surrounding agricultural activity. In conclusion, railway banks would provide potential resources for long term survival and reproduction of *A. azarae*, and their ecological function seems to be crucial for this small mammal species, which inhabit them permanently.

Disclosure statement

No potential conflict of interest was reported by the authors.

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