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José Priotto · Daniela Gómez · Jaime Polop

A demographic analysis of population responses to the manipulation of adult males in *Calomys venustus* (Rodentia, Sigmodontinae)

Abstract In many species of mammals, adults play an important role in influencing the survival and/or reproduction of juveniles. Adult males could have a negative effect on population density when their absence becomes a limiting factor in female fertilization. We tested the hypotheses that the absence of overwintering males (adult males) reduces the population growth rate through a delay in the onset of reproductive activity of Cohort 1 females in *Calomys venustus* populations. The study was carried out in two control and two experimental enclosures (0.25 ha). Adult males were removed after their offspring were born. Weekly trapping sessions were carried out from spring to autumn. To estimate population growth rates (λ), apparent survival (ϕ) and seniority probability (γ) were estimated using capture–mark-recapture models. Models were constructed with these two parameters and recapture probability (p) constrained to vary as a function of time, enclosure and/or treatment. We derived estimates of population growth rates through the estimates of ϕ and γ. The best models for ϕ and γ did not show a treatment effect. Variability between the four enclosures was greater than between control and experimental enclosures. Enclosures had different growth rates at the beginning of the study but were equaled at the end. Temporal variation in population growth rates was a result of temporal vari-

ation of γ. The two controls showed the highest growth rates earlier in time. The results did not support the hypothesis tested in this study. It seems that the number of overwintering males do not affect the population growth rate.

Keywords Population growth · Seniority · Sigmodontinae · Small mammals · Survival

J. Priotto (✉) · D. Gómez
Departamento de Ciencias Naturales,
Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Universidad Nacional de Río Cuarto,
Agencia Postal No. 3, 5800 Río Cuarto, Córdoba, Argentina
E-mail: jpriotto@exa.unrc.edu.ar
Tel.: +54-358-4676236
Fax: +54-358-4676230

J. Polop
Departamento de Ciencias Naturales,
Universidad Nacional de Río Cuarto,
Agencia Postal No. 3, 5800 Río Cuarto, Córdoba, Argentina

Introduction

Variation in population abundance is a consequence of changes in demographic parameters such as survival, recruitment, and immigration (Lima et al. 2001; Dobson and Oli 2001). These demographic parameters may have different impacts on population dynamics, with some parameters influencing population growth more directly than others (Oli and Dobson 2003).

Demographic parameters can vary with individual characteristics such as age, sex, weight and reproductive condition, and also as a function of biotic and abiotic environmental variables (Lebreton et al. 1992; Eccard et al. 2002; Crespin and Lima 2006). Intra- and inter-specific competition as well as predation can also affect demographic parameters (Gurevitch et al. 1992; Eccard et al. 2002; Crespin and Lima 2006). Regarding intra-specific competition and age structure of a population, adults play an important role influencing the survival and/or reproduction of juvenile individuals in many species of small mammals (Rodd and Boonstra 1988; Wolff 1992; Pusenius and Viitala 1993; Wolff et al. 2002). The presence of adult animals can cause poor survival, sexual maturation inhibition, reproduction delay, or lack of reproduction of juveniles (Rodd and Boonstra 1988; Wolff et al. 2001, 2002). Therefore, slight decreases in juvenile performance (survival and reproduction) caused by the presence of adults can deeply reduce the growth of a population (Lin et al. 2004). Thus, changes in population age structure would determine differences in population abundances.

In most rodent species, females are generally assumed to have a greater impact on inhibiting juvenile performance than males, due to the fact that females typically compete for exclusive offspring-rearing space (Bond and Wolff 1999; Wolff and Macdonald 2004). Thus, many studies analyze the effect of adult female removal on demographic parameters of juveniles (Saitoh 1981; Rodd and Boonstra 1988; Pusenius and Viitala 1993). However, in studies on the role of males in population dynamics developed in different taxa it is recognized that the presence and behavior of males may also have an important role in population processes (Rankin and Kokko 2007). There are several ways in which male removal may have positive or negative effects on population densities. Positive effects may be observed when male harassment produces additional female mortality as well as when males have a larger influence on resource availability than females (Reale et al. 1996; Rankin and Kokko 2007); whereas negative effects may be observed in species with male parental care or when a lack of males is a limiting factor in female fertilization (Bessa-Gomes et al. 2004; Wright 2006; Rankin and Kokko 2007). In relation to the latter, some studies found a lower proportion of breeding females as a result of a lower male capacity to inseminate them when the adult sex ratio was severely skewed (Ginsberg and Milner-Gulland 1994; Solberg et al. 2002).

Calomys venustus (big field mouse) is one of the most abundant species in small-rodent communities in agrarian ecosystems of southern Córdoba province (Argentina). This species inhabits natural pastures, and linear and less disturbed border habitats, including crop-field edges, railway banks, and roadsides (Kravetz and Polop 1983; Polop and Sabattini 1993; Priotto and Polop 1997). *C. venustus* females reach sexual maturity at around 40 days of age. Meanwhile, males are matured after 60 days of age (Polop et al. 2005). Females do not share their home range with other females (territorial sex), while males share it with both sexes. This suggests a promiscuous-polygynous social mating system for this species. In addition, the lack of differences in home range sizes between sexes (300 m^2 in average) is inconsistent with this type of mating system (Priotto et al. 2002). Density varies seasonally from minimum in spring (September–October) to maximum in autumn (May–June). Populations are characterized by annual turnover, at the onset of breeding period (spring) the overwintering animals produce the first cohort of the year (C1). During the summer, C1 and surviving overwintering cohort produce the second cohort (C2). In late summer, when the overwintering and C1 cohorts have disappeared, females of C2 produce the third cohort (C3). These last two cohorts (C2 and C3) become the overwintering cohort in the following breeding period (Priotto and Polop 2003; Polop et al. 2005). The proportions of C2 and C3 in the overwintering cohort depend on the density phase of population (Provensal and Polop 2008). The number of individuals of the overwintering cohort would depend on the quality of individuals and the environmental conditions associated with winter (frosts and low vegetation cover) (Priotto 2000; Provensal and Polop 2008).

At the beginning of the breeding period, C1 females mate only with overwintering males because C1 males become reproductively mature 20 days later than C1 females (Priotto et al. 2006). Overwintering males typically decline in number more rapidly than females (Provensal 2001; Priotto and Polop 2003) as it was observed in other rodent species (Krebs and Boonstra 1978; Redfield et al. 1978; Beacham 1980). Thus, the number of overwintering males would be a limiting factor to the onset of C1 female reproductive activity. A low number of overwintering males could produce a delay in the beginning of C1 reproduction. This would cause a minor number of recruited individuals during the reproductive period and therefore a decrease in population growth rates.

Taking into account that differences in population structure at the beginning of the breeding period may produce changes in population growth rates we tested the hypothesis that the absence of overwintering males (hereafter adult males) reduces the seasonal population growth rate (from spring to autumn). This is due to the fact that a delay in the onset of reproductive activity of C1 females could produce a minor number of recruited individuals during the reproductive period. This hypothesis was assessed trough the manipulation of adult males in enclosed populations of *C. venustus*.

In order to estimate population growth rates, apparent survival and recruitment probabilities were estimated using capture–mark-recapture models (CMR). The most recent developments in CMR analysis provide powerful and flexible tools for estimating and modeling survival probabilities and other demographic parameters (Crespin et al. 2002; Ozgul et al. 2004; Crespin and Lima 2006). We tested the effects of adult males on the observed variation in survival probabilities of C1 individuals. We estimated and modeled recruitment and realized population growth rate using a Pradel's reverse-time CMR model. We examined the impact of adult male absence in these parameters and investigated the relative contribution of survival and recruitment to realized population growth rate.

Methods

Experimental setup and field procedures

The study was performed in four 0.25 ha (40 m × 62.5 m) outdoor enclosures on Espinal Reservation in the National University of Río Cuarto Campus, Argentina (33°07′S, 64°14′W). The study area comprised a natural pasture interspersed with brush and weed species, similar to *C. venustus* natural habitats. The four enclosures had similar habitat conditions (floristic composition and vegetation cover). For a detailed description of the study area and enclosure construction, see Priotto and Polop (2003) and Priotto et al. (2004).

Enclosures were successful in limiting the entry of competing herbivores and terrestrial predators. Although the natural pasture within each enclosure had a high vegetative cover of about 95% throughout the year, each enclosure was supplied with 15 uniformly distributed artificial shelters (400 × 200 mm) built with bricks. Cotton and chaff were placed in each shelter. Six shelters in each enclosure were enclosed by a concrete circle of 1 m diameter and 0.7 m high. Each one was covered with iron mesh and was called a nest. On the inner margin of each enclosure, a 1-m-wide grass strip was devegetated with herbicide.

The study was carried out between September 1997 and May 1998. Study populations were settled in the enclosures in September and October and the experimental demographic samples were taken from November to May. To assemble the study populations, individuals were captured at the end of a warm winter (annual minimum temperature −1°C) from an area located 30 km away from the enclosures. These individuals came from a population in a density decline year (Provensal and Polop 2008). In September, 12 individuals (six adult males and six adult females) were mated in each enclosure, one pair by nest. The initial population in each enclosure at the end of October was made up by the six pairs and their first litters (C1 individuals). All individuals were marked with a numerical code in their ears. Sex and birth dates of offspring were recorded for the first litters. Treatments were assigned randomly to each enclosure; in two enclosures (Experimental I and II) adult males were removed after first litters were born. The other two enclosures served as controls (Control I and II). Nests were opened and individuals dispersed into each enclosure after the offspring of the first litter had been weaned. Initial population abundances were 41 and 42 individuals in control enclosures and 29 and 31 individuals in experimental enclosures.

Each enclosure had a grid of 6 × 10 traps placed at 6-m intervals and 32 additional traps were placed in the devegetated edge. One Sherman live-trap was placed at each station and baited with a mixture of peanut butter and cow fat. Traps were checked each morning, and for each captured individual sex and body measurements (weight and length of body and tail) were recorded. All new individuals were marked with numbered eartags and released at their site of capture. Trapping sessions were carried out from November to May. The trapping regime used Pollock's robust design (Pollock et al. 1990), which involved two levels of trapping intensity. There were ten weekly primary capture sessions, each with three daily secondary capture sessions. The time between secondary periods was short enough to assume the population as demographically closed. The time between primary periods was long enough to consider the population as demographically open with regard to the estimation of population rates. The time intervals between primary trapping sessions were unevenly spaced and so all survival estimates were standardized to 7 days. In order to detect animals that were not able to settle in the habitat area of the plot, animals that were trapped two consecutive times in the devegetated edge within a secondary trapping session were removed from the population since we assumed that they were not able to settle within the enclosures. During the study, only one animal was removed because it did not settle in the habitat area of the plot, therefore all studied animals were able to settle in the plot.

Analytical procedures

We estimate the population growth rate (λ) with associated variance:

$$\lambda_t = \frac{\phi_t}{\gamma_{t+1}} \text{ (Pradel 1996)};$$

$$\text{var}(\lambda_t) = \lambda_t^2 \left[\frac{\text{var}(\phi_t)}{\phi_t^2} + \frac{\text{var}(\gamma_{(t+1)})}{\gamma_{(t+1)}^2} - \frac{2\text{cov}(\phi_t, \gamma_{(t+1)})}{\phi_t \gamma_{(t+1)}} \right],$$

Delta method (Powell 2007);

where ϕ is apparent survival and γ is seniority probability.

We used the program MARK (White and Burnham 1999) to estimate apparent survival (ϕ) and recapture (p) probabilities (see Table 1 for explanation and notation of the models run). We followed the approach by Lebreton et al. (1992) to carry out an analysis of survival from capture–recapture data. First, to assess the goodness-of-fit of the CJS model we used the program U-CARE (Choquet et al. 2003). Second, several models were constructed with these two parameters constrained to vary as a function of time (t), enclosure (e), and treatment (tr). Models were ranked according to Akaike's information criterion, corrected for small sample size (AIC_c), a relative measure of fit, i.e., the balance between the number of parameters and the fit of the model (Burnham and Anderson 1998). Model comparison was based on the differences in AIC_c values (ΔAIC_c), so when ΔAIC_c values were greater than two units, the model with the lowest AIC_c could be considered a statistically better description of the process that generated the data. We started by modeling survival and

Table 1 Explanation and notation of effects for describing apparent survival (ϕ), recapture rate (p) and seniority (γ)

Notation	Biological significance
1: (.)	Constant apparent parameter (1 value)
2: (t)	Parameter different among trapping sessions (10 values)
3: (e)	Parameter different among the four enclosures (4 values)
4: ($e \times t$)	Parameter different among each enclosure and trapping session (40 values)
5: ($e + t$)	As 3, with additive time effect (14 values)
6: (tr)	Parameter different across treatment (2 values)
7: (tr × t)	As 6, with combined time effect (20 values)
8: (tr + t)	As 6, with additive time effect (12 values)

recapture probabilities as a function of time and enclosure (a set of 25 candidate models). The best models were selected and included in the analysis of treatment effect to test if these two parameters were best modeled by treatment or enclosure.

Seniority probability (γ) could be considered as survival probabilities that extend backward in time (Williams et al. 2002). It was estimated by a method developed by Pradel (1996). Analyzing the encounter history going backwards in time, it is possible to estimate γ, which is defined as the probability that if an individual is alive and in the population at time t then it certainly was alive and in the population at time $t - 1$ (Pradel 1996). Seniority was constrained according to time, enclosure (e), and/or treatment (tr, Table 1). 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).

Results

The capture data of each enclosure are summarized in Table 2 as 'reduced m-arrays' (Burnham et al. 1987; Bell et al. 2003). Each row of the m-array represents first recaptures for a given release cohort. Re-released recaptures are added to the release totals in the next row, so that multiple recaptures are pooled with first recaptures from a new release cohort.

Survival analysis

The goodness-of-fit test showed that the general model ($\phi_{(e \times t)}$, $p_{(e \times t)}$) fitted the data satisfactorily ($\chi^2_{48} = 44.1916$; $P = 0.6296$). The best approximating model for describing survival probabilities did not show treatment effect (Table 3; Tables 4 and 5 in Electronic Supplementary Material). Apparent survival showed enclosure effects being the variability between the four enclosures greater than between control and experimental ones (Table 3; Tables 4 and 5 in Electronic Supplementary Material). Although the experimental II enclosure had a higher survival probability (0.9201), the experimental I had similar survival probability (0.8635) than both control enclosures (0.8723 and 0.8618).

Recruitment analysis

We used the most parsimonious model identified for survival and recapture and tested for enclosure, treatment, and/or time variations in seniority. The best approximating model for describing seniority did not show treatment effect either (Table 3; Table 6 in Electronic Supplementary Material). The estimation of seniority indicated a combined effect between enclosure

and time. In spite of these differences among enclosures some particularities could be observed between control and experimental enclosures. Thus, the recruitment probabilities showed an earlier peak (late spring) in control enclosures, whereas in experimental enclosures were higher in summer (Fig. 1a, b).

Realized population growth rate

To estimate realized population growth rate for each enclosure, we used four survival values since there was not temporal variation in survival estimations and the estimations of seniority for each enclosure and time interval. Enclosures had different growth rates at the beginning of the study but were equaled at the end (Fig. 2a, b). Temporal variation in growth rates was a result of temporal variation of seniority. The population growth rates of two control enclosures showed highest variations earlier in time (spring) with higher values in control I, whereas those of experimental enclosures showed variations at the end of spring and the beginning of summer (Fig. 2a, b). The average population growth rates from spring to autumn were 1.10 and 0.98 in control enclosures and 0.99 and 1.03 in experimental ones. Final population abundances (autumn) were 45 and 41 individuals in control and 29 and 32 individuals in experimental enclosures.

Power analysis

To test the statistical power of the treatment effect analysis, we determined the distribution of ϕ and γ through β distributions obtained from the number of individuals in the control and experimental enclosures. Afterwards, the distributions were determined using the quadruple number of replicates. Random samplings of β distributions (for ϕ and γ) were simulated to determine the resultant distribution of λ for both number of replicates. The distributions of ϕ, γ and λ for both number of replicates were overlapped to determine statistical power. Results from power calculations are shown in Fig. 3a, b. To find differences in survival probabilities between control and experimental enclosures a quadruple number of replicates would increase the statistical power from 30 to 70%. On the other hand, the statistical power of seniority probabilities and realized population growth rates would not improve.

Discussion

In our study, the results did not support the hypothesis that the absence of adult males (experimental enclosures) reduces population growth rates. Although an earlier onset of reproductive activity of C1 females in the presence of adult males (control enclosures) produced a

Table 2 *Calomys venustus* mark–recapture data of each enclosure represented in reduced *m*-array format

Release occasion	New releases	Observed recaptures recapture occasion									Total recaptures
		2	3	4	5	6	7	8	9	10	
Enclosure I											
1	7	5	0	1	0	0	0	0	0	0	6
2	10		4	3	1	0	0	0	0	0	8
3	5			5	0	0	0	0	0	0	5
4	17				13	0	0	0	0	0	13
5	23					11	1	0	0	1	13
6	17						5	0	0	0	5
7	25							8	2	0	10
8	15								7	1	8
9	33									16	16
Enclosure II											
1	13	10	0	1	0	0	0	0	0	0	11
2	13		3	7	0	0	0	0	0	0	10
3	3			2	0	0	0	0	0	0	2
4	13				9	1	0	0	0	0	10
5	9					5	1	0	0	0	6
6	17						6	0	0	0	6
7	17							5	1	0	6
8	9								4	0	4
9	10									5	5
Enclosure III											
1	10	7	1	0	0	0	0	0	0	0	8
2	12		4	4	1	0	0	0	0	0	9
3	5			5	0	0	0	0	0	0	5
4	10				10	0	0	0	0	0	10
5	11					7	0	0	0	0	7
6	11						5	0	0	0	5
7	24							6	1	0	7
8	23								7	4	11
9	33									12	12
Enclosure IV											
1	12	10	1	0	0	0	0	0	0	0	11
2	15		12	0	0	0	0	0	0	0	12
3	16			16	0	0	0	0	0	0	16
4	16				15	0	0	0	0	0	15
5	14					11	0	0	0	0	11
6	10						6	0	0	0	6
7	40							16	5	3	24
8	32								22	4	26
9	52									26	26

Table 3 Statistical best models are denoted according to each model-specific variation in the probabilities of survival (ϕ), seniority (γ) and capture (p)

Model	Best model	AIC_c[a]	$\Delta_i AIC_c$[b]	K[c]	Deviance
Survival model	$\left\{\phi_{(e)}, p_{(e+t)}\right\}$	9993.2637	−3.8092	16	268.4533
Recruitment model	$\left\{\phi_{(e)}, p_{(e+t)}, \gamma_{(e \times t)}\right\}$	2379.5918	−17.9050	43	273.8740

See, for details, Tables 4, 5, and 6 in Electronic Supplementary Material available on Ecological Research Web site
[a] Measure of each model fit
[b] Difference in AIC_c with next-best model
[c] Number of estimable parameters

greater number of recruited individuals at the beginning of the summer, the population growth rates at the end of the study were similar between the control and experimental enclosures.

Even though the best models did not differentiate a treatment effect either in survival or seniority probabilities, some results could be biologically meaningful. Apparent survival of four enclosures was relatively high (> 0.8, accord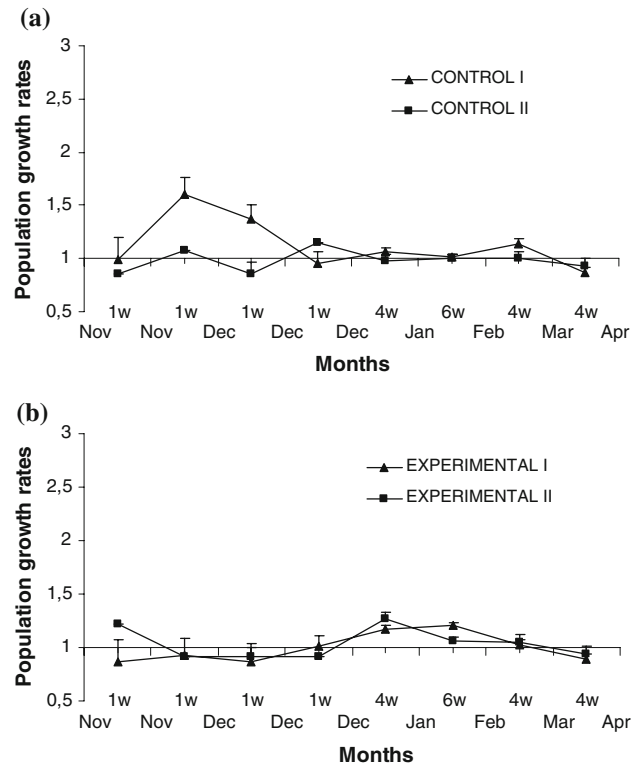ing to Seamans and Gutiérrez 2007) as it was observed in other population enclosure studies (Johannesen and Ims 1996; Johannesen et al. 2003). Control enclosures had lower survival probability than experimental enclosure II. This minor survival of control enclosures could be the result of reproductive activity began 20 days earlier than in experimental ones (Priotto et al. 2006). The earlier beginning in reproduction activity in the presence of adult males would determine the minor survival because of greater physiological or
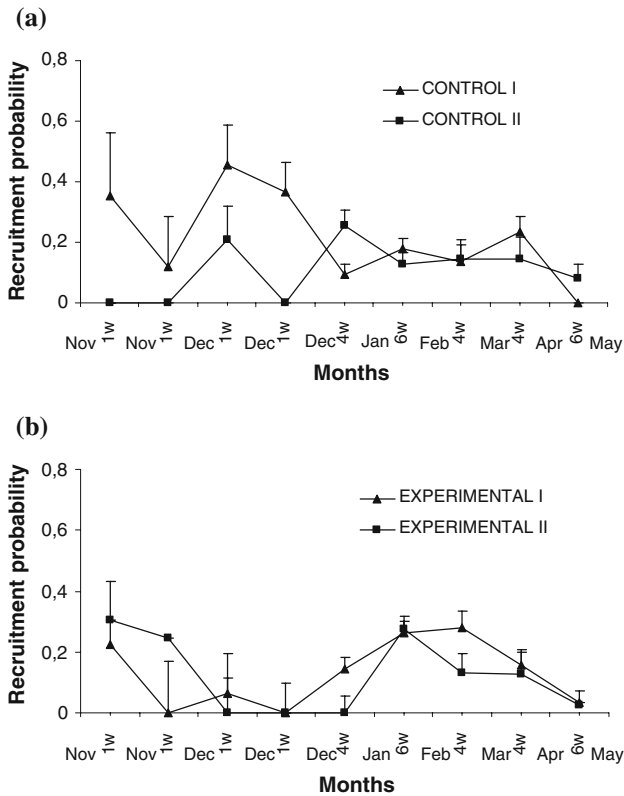
Fig. 1 Recruitment probability $(1 - \gamma)$ of *Calomys venustus* in **a** control and **b** experimental enclosures; *w* week (week interval between sampling occasions), *Nov* November, *Dec* December, *Jan* January, *Feb* February, *Mar* March, *Apr* April and *May* May

Fig. 2 Population growth rate (λ) of *Calomys venustus* in **a** control and **b** experimental enclosures; *w* week (week intervals between sampling occasions), *Nov* November, *Dec* December, *Jan* January, *Feb* February, *Mar* March, *Apr* April and *May* May

behavioral demands (in energetic terms), as it was observed in other mammal species (Lindstrom 1999; Lambin and Yoccoz 2001). On the other hand, despite the fact that reproductive activity of experimental I started at the same time as experimental II, the former had similar survival to control enclosures. We were not able to identify whether this lack of differences in survival probabilities would be caused by absence of treatment effect or other external factors. Besides, the low number of replicates reduced our statistical power to find differences in this parameter estimation between control and experimental enclosures (the statistical power increased in 40% considering the quadruple number of replicates). One needs to be cautious that some biologically significant effects might have been missed due to the small sample sizes (Steidl et al. 1997; Lin et al. 2004).

Pradel's model does not differentiate between reproduction and immigration as different sources of recruitment. However, recruitment in our study, developed with enclosed populations, would be almost entirely from reproduction (Priotto 2000). Recruitment probability exhibited temporal and enclosure variations. The temporal variations would be in relation to the annual reproductive pattern observed in this species (Polop et al. 2005). Despite the differences observed among enclosures, it would be important to note that recruitment probabilities peaked earlier in control enclosures (adult male presence) than in experimental ones (Fig. 1). This would be also related to the earlier beginning of the reproductive activity in control enclosures.

As it was formerly established, survival and seniority probabilities did not show treatment effect (adult male absence) when they were tested separately. However, these demographic parameters may account for treatment effect in population growth (Johannesen et al. 2003). Thus, population growth rates were estimated for both controls and both experimental enclosures. Based on our results we found that a delay in the onset of reproductive activity of C1 females at the beginning of the breeding period did not affect growth rates. Enclosures had different growth rates at the beginning of the study but were equaled at the end. Temporal variation in growth rates was a result of temporal variation of seniority probabilities. Both control enclosures showed the highest growth rates earlier in time. Apparent survival did not vary in time, but only in relation to enclosure. In spite of these differences, among enclosure populations, the growth rates became similar and relatively stationary at the end of the study (Fig. 2). This would be due to the fact that seniority probabilities were similar in all enclosures.

In this study, to consider some methodological aspects would be relevant. Firstly, our study attempts to experimentally test a biologically based hypothesis
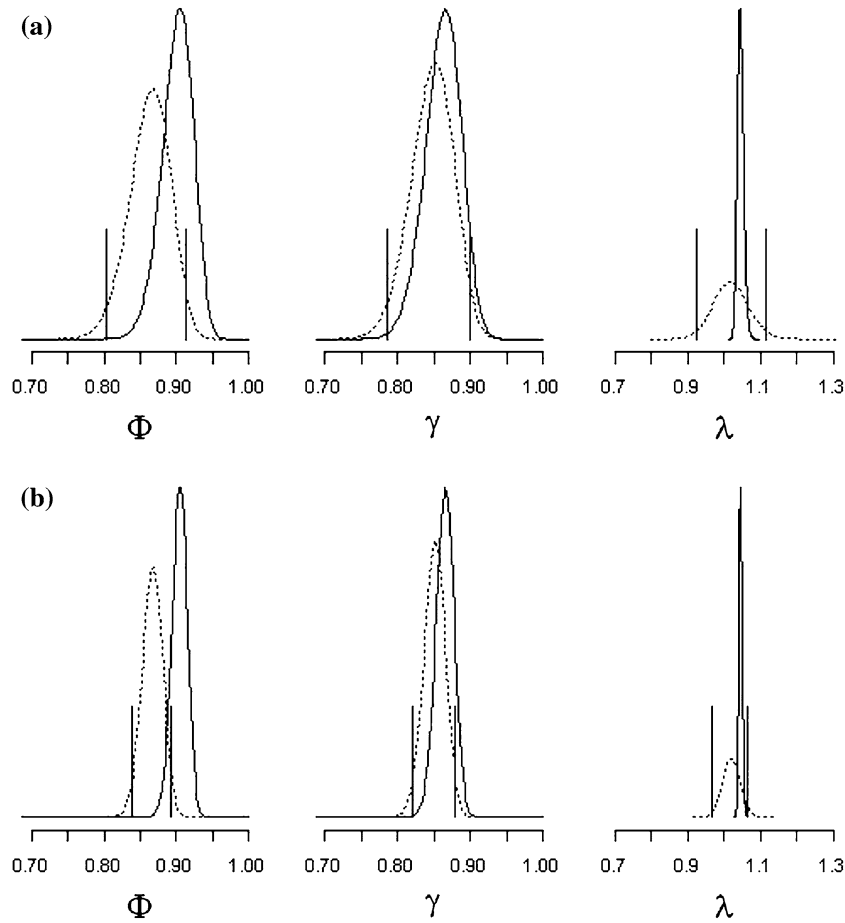
Fig. 3 Statistical power analysis showing the distributions of survival probability (ϕ), seniority probability (γ) and population growth rate (λ). **a** The first situation which considers the number of replicates used in this study. **b** The second situation which considers a quadruple number of replicates

using methods that account for variation in capture probabilities and that provide unbiased estimates of demographic parameters (CMR methods). The advantage of obtaining population growth rates from CMR methods is that it allows exploring population growth trajectory without the problem associated with abundance estimation (Cooch and White 2008) and the estimates could be properly interpreted as the rate of change in the population if the conditions during the study period were maintained indefinitely (Franklin et al. 1996). Secondly, considering that habitat conditions and trapping schedule were similar among enclosures, we did not expect recapture probabilities with an additive effect between enclosure and time. However, this heterogeneity was accounted for in both survival and seniority modeling. Finally, although most demographic studies in mammals involve long-term analysis with annual, seasonal, and/or monthly time scales (Crespin et al. 2002; Pocock et al. 2004; Ozgul et al. 2007), we set up a weekly time scale to experimentally test population changes in a short time interval (7 months). This was possible due to the fact that these rodents have a short life expectancy, multivoltine life cycles, and a clear breeding period (Priotto 2000; Polop et al. 2005).

Considering that juvenile females reach sexual maturity 20 days earlier than juvenile males (Priotto et al. 2006), in the absence of adult males the C1 females would become pregnant just when the C1 males reach sexual maturity. Therefore, the presence of adult males would be a limiting factor for females to start mating. However, the delay in the onset of female reproductive activity, and consequently in the appearance of new individuals in experimental enclosures, would not have a significant effect on the population growth rates at the end of summer and autumn. The positive effect that the earlier peak in recruitment probability would have on growth rate of *C. venustus* population would be damped by lower survival of females that started their reproductive activity earlier. Therefore, a low number of overwintering males at the beginning of the breeding season would not have any significant effect on the population growth rate at the end of it (autumn). However, as our study was conducted with animals from a population in a decline density phase and from a warm winter, it would be important to analyze the effects of different population densities and winter conditions on the number of overwinterings and the population growth rates. This is due to the fact that population

densities at the end of the previous breeding period and the environmental conditions could affect the number of overwinterings at the beginning of the next breeding season in *C. venustus* (Provensal and Polop 2008).

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