Demography and population dynamics of the mouse opossum (*Thylamys elegans*) in semi-arid Chile: seasonality, feedback structure and climate

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Here we present, to the authors' knowledge for the very first time for a small marsupial, a thorough analysis of the demography and population dynamics of the mouse opossum (*Thylamys elegans*) in western South America. We test the relative importance of feedback structure and climatic factors (rainfall and the Southern Oscillation Index) in explaining the temporal variation in the demography of the mouse opossum. The demographic information was incorporated into a stage-structured population dynamics model and the model's predictions were compared with observed patterns. The mouse opossum's capture rates showed seasonal (within-year) and between-year variability, with individuals having higher capture rates during late summer and autumn and lower capture rates during winter and spring. There was also a strong between-year effect on capture probabilities. The reproductive (the fraction of reproductively active individuals) and recruitment rates showed a clear seasonal and a between-year pattern of variation with the peak of reproductive activity occurring during winter and early spring. In addition, the fraction of reproductive individuals was positively related to annual rainfall, while population density and annual rainfall positively influenced the recruitment rate. The survival rates were negatively related to annual rainfall. The average finite population growth rate during the study period was estimated to be 1.011 ± 0.0019 from capture–recapture estimates. While the annual growth rate estimated from the seasonal linear matrix models was 1.026, the subadult and adult survival and maturation rates represent between 54% (winter) and 81% (summer) of the impact on the annual growth rate.

Keywords: El Niño; structured models; small marsupials; demography; temporal variation; Chile

1. INTRODUCTION

The relative importance of endogenous and exogenous factors in population regulation has long troubled ecologists (Nicholson 1933; Andrewartha & Birch 1954). The feedback structure of natural populations has broad implications for understanding population dynamics and the structure of the food web (Stenseth *et al.* 1997, 1998a; Berryman 1999). Because population fluctuations are the result of demographic processes (mortality, recruitment, emigration and immigration), understanding the variation in these processes is a starting point in demographic studies (Julliard *et al.* 1999). Temporal variability in demographic rates is the result of different factors operating on different time-scales, such as within-year variability (seasonality) and between-year variability. Consequently, we need to estimate the intra- and inter-annual variation in demographic rates and identify the underlying causes of this temporal variation (Leirs *et al.* 1997; Stenseth *et al.* 1998b, 1999; Yoccoz *et al.* 1998; Lima *et al.* 1999a). Recent developments using both capture–mark–recapture and matrix population dynamics models (Leirs *et al.* 1997; Yoccoz *et al.* 1998; Lima *et al.* 1999a; Nichols *et al.* 2000; Coulson *et al.* 2001) have provided links between demographic mechanisms and population dynamics.

Population outbreaks of small mammals in western South America are correlated with years of unusually high rainfall and increased primary production, which are related to the occurrence of El Niño events (Pearson 1975; Péfaur *et al.* 1979; Fuentes & Campusano 1985; Jiménez *et al.* 1992; Meserve *et al.* 1995; Jaksic *et al.* 1997; Lima *et al.* 1999b). However, while some small mammal species seem to show dramatic population fluctuations (e.g. the highly irruptive species *Phyllotis darwini* and *Akodon olivaceus*) (Jiménez *et al.* 1992; Meserve *et al.* 1996; Jaksic *et al.* 1997; Lima & Jaksic 1998a; Lima *et al.* 1999b), others seem to exhibit more stable dynamics (e.g. the rodents *Abrothrix longipilis* and *Abrocoma bennetti* and the didelphid *Thylamys elegans*) (Meserve *et al.* 1995).

In this study, we analyse the demography and population dynamics of the mouse opossum (*T. elegans*), which is a poorly studied species, just like most other South American marsupials. We evaluate the seasonal and between-year variation in (i) survival rates, (ii) recruitment rates, (iii) maturation rates, and (iv) the fraction of reproductive individuals, and we test the relative importance of endogenous and exogenous factors (rainfall and the Southern Oscillation Index (SOI), which gauges El Niño) in explaining the between-year variation observed in the demographic rates studied. Finally, we incorporate the demographic information in a stage-structured population dynamics model (Leslie 1945; Usher 1969; Tuljapurkar & Caswell 1997; Caswell 2001; Coulson *et al.* 2001) and explore the resulting population dynamics.

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2. DATA AND THE STUDY SITE

(a) *The species*

The mouse opossum (*T. elegans*, Waterhouse 1839) is a didelphid marsupial that is widely distributed in western South America from Peru to central Chile (Palma 1997). In Chile, this species inhabits semi-arid and Mediterranean-type ecosystems (Meserve & Le Boulengé 1987) (figure 1). These ecosystems are characterized by a strong seasonal pattern of rainfall with most of the annual precipitation (90%) occurring during winter (from May to August) (Jaksic *et al.* 1997; Lima *et al.* 1999b). This species is an insectivorous marsupial with an average adult weight of ca. 30 g. The reproductive pattern of the mouse opossum is poorly known, but seem to be markedly seasonal, starting in mid- or late winter and lasting until November or December (Meserve & Le Boulengé 1987). As with other small South American marsupials, the females produce one to two litters with an average size of between 11 and 13 offspring (as judged by the number of functional nipples) (Mann 1978; Palma 1997).

(b) *Study area and trapping design*

The study site, Las Chinchillas National Reserve at Aucó (31°30' S, 71°06' W), is located 300 km north of Santiago (figure 1). Situated in the coastal ranges, the reserve has a rugged topography with numerous ridges dissected by deep ravines and with some flat areas. The site's elevation ranges from 400 to 1700 m and the climate is semi-arid, with scarce rainfall concentrated in the winter months. The site's mean annual precipitation is 175 mm, but with extensive interannual variability (Jaksic *et al.* 1996) ranging from 10 to 520 mm annually.

The vegetation is a thorn scrub with the species composition depending on solar exposure (Jiménez *et al.* 1992). Slopes facing to the north (equatorial) receive higher solar radiation and, thus, are more xeric. In contrast, slopes facing to the south (polar) receive less solar radiation and, thus, are more mesic.

Mouse opossums were monitored through capture–mark–recapture methods on two opposite-facing slopes of each of two creeks that are 2 km apart. Trapping was performed regularly from October 1987 to January 1992 alternating between the creeks on a monthly basis. Four trapping grids were used: two on opposite-facing slopes of El Grillo creek (26 primary trapping sessions) and two on opposite-facing slopes of El Cobre creek (26 primary trapping sessions). There was a single trapping bout in May 1992, but only in the two grids of El Cobre creek. From July 1992 to April 1996, live trapping was conducted in El Cobre creek every three months (January, April, July and October) and from May 1996 to June 2000 trapping was conducted monthly in El Cobre creek.

Each 7 × 7 trapping grid had 49 stations separated by 15 m. The grids were equipped with one Sherman trap at each station, with the traps activated simultaneously on the xeric and mesic slopes of a given creek over five consecutive nights (secondary trapping sessions). All traps were permanently kept in the field and were closed when not in use. The traps were baited with rolled oats and checked every morning. Each individual captured was marked with a metal ear tag and their body mass, reproductive condition (females were classified as immature,

pregnant or lactating), sex and species determined. In addition to the didelphid *T. elegans* three other small mammals were frequently captured, namely the cricetid rodents *A. olivaceus*, *P. darwini* and *Oligoryzomys longicaudatus*.

(c) *Climatic data*

We used two climatic variables for representing the environmental conditions: the SOI and the accumulated yearly rainfall. The SOI is one of the indices used for representing the occurrence and strength of the El Niño Southern Oscillation (ENSO) and compares meteorological conditions in two tropical areas of the Pacific Ocean. The SOI is calculated as the difference between the monthly-standardized atmospheric pressure between Tahiti (French Territory) and Darwin (Australia). Periods characterized by large negative index values correspond to El Niño events (wherein warm tropical waters intrude into the western coasts of the Americas), whereas periods characterized by large positive index values correspond to La Niña events (when the cold Humboldt and California currents strongly influence the American coastline). We used the yearly averaged SOI index in our analyses. The values of this index over the last century are available at Internet web site <http://www.dnr.qld.gov.au/longpdk/longpdk.htm>.

Annual precipitation data were obtained from the meteorological station of La Serena (29° 90' S, 71° 20' W at 50 m elevation during the period 1900–1999), which is located in the Elqui River basin (figure 1). Data from this location (which provides the longest climatic time-series for that region) are also assumed to adequately represent the meteorological conditions in northern semi-arid Chile.

3. ESTIMATING DEMOGRAPHIC PARAMETERS

Our basic data consist of capture–recapture histories that were obtained on the basis of 93 primary occasions. The age category of each individual (subadult or adult) was determined according to the body size recorded when the individual was first caught, with individuals of less than 20 g being classified as subadults (Meserve & Le Boulengé 1987) and individuals of less than 10 g being considered as juveniles. These individuals are non-trappable because they are lactating and are in the nests. Survival rates were estimated for juveniles and adults (females and males) together, in order to increase the sample sizes. We obtained 594 captures corresponding to 297 individuals. The minimum number of individuals known alive was used as an index of population density. However, because *T. elegans* is able to enter torpor, the estimates of the capture rates may cause some biases in population density estimates using the minimum number of individuals known alive procedure. Survival (ϕ), recruitment ($1 - \gamma$), maturation (ψ) and recapture (p) rates were modelled by using the capture–mark–recapture statistical modelling approach (Lebreton *et al.* 1992), applying the program MARK (White & Burnham 1999). The recruitment rate was estimated by the method developed by Pradel (1996) by 'reading' the capture histories backward (reverse-time capture–recapture methods). This makes it possible to estimate the probability that an individual caught at time $t + 1$ was present in the population at time t . These probabilities are called

Figure 1. (a) Map of semi-arid Chile and the study area at Las Chinchillas National Reserve. (b) The monthly population fluctuation in the size of the minimum number of individuals known alive estimates for the mouse opossum *T. elegans* at Las Chinchillas National Reserve from 1987 to 1999. The data from spring 1987 to summer 1992 are from the El Cobre and El Grillo creeks, whereas the data from autumn 1992 are from El Cobre creek only.

seniority probabilities (γ) (Pradel 1996) and represent the resident fraction of the population. Seniority probabilities can be used for estimating other related demographic parameters, such as a direct estimation of the population growth rate (λ) and elasticities (see § 5f) (see also Nichols *et al.* 2000). Estimates were obtained through the maximum-likelihood method assuming a multinomial distribution of the capture histories. We constrained the estimates so as to be constant within four seasons for each year (i.e. assuming no within-season variation).

Reproductive rates were estimated for each month for adult males and females together as the fraction of reproductively active individuals (females perforated, pregnant or lactating and males with external scrotal testes). We estimated the seasonal and between-year pattern of variation in the fraction of reproductive individuals using a generalized linear model (GLM) (S-PLUS 2000) with a binomial error structure and logit link function (McCullagh & Nelder 1989; Venables & Ripley 1997). In order to determine whether the external variables explained a significant part of the between-year variation, we calculated the fraction of reproductive adult individuals for each trapping session of the breeding period (October–January). We evaluated the appropriateness of including the external covariables (density, annual rainfall and SOI) using Akaike's information criterion (AIC) ($AIC = -2(\log\text{-likelihood}) + 2p$, where p is the number of parameters). Nested models for survival and recruitment were compared by means of the likelihood ratio test (LRT) (Lebreton *et al.* 1992).

In order to parameterize the matrix model we needed to estimate maturation rates as the probability of a subadult at time t being an adult at time $t + 1$. We used multi-state models (Hestbeck *et al.* 1991; Nichols *et al.* 1992; Brownie *et al.* 1993) for estimating the maturation rates. We applied a statistical multistrata model for estimating the transition rate between subadults and adults. We modelled the subadult and adult survival rates for the general model with the best model selected from the previous survival analysis.

We tested the following external quantitative variables for all capture–mark–recapture models (i.e. the survival, recruitment, maturation and reproductive rates): (i) population sizes during summer (in order to evaluate the presence of direct density dependence), (ii) annual accumulated rainfall, and (iii) the annual SOI.

4. POPULATION MODELS

(a) A seasonal stage-structured matrix model

We used a simple linear, time-invariant matrix model with monthly time-steps (Caswell 2001). Only the female fraction of the population is modelled. The basic stage-structured matrix model is given as

$$\mathbf{M} = \begin{bmatrix} 0 & 0 & S_{ad} \times R_{ad} \\ S_{ad} & S_{sub} \times (1 - M_{sub}) & 0 \\ 0 & S_{sub} \times M_{sub} & S_{ad} \end{bmatrix}, \quad (1)$$

where R_{ad} (=percent of reproductive individuals) $\times$ (0.5 $\times$ litter size) represents the monthly reproductive rate per adult female, the sex ratio is assumed to be 0.5, the litter size is assumed to be 11, an offspring's survival

from a newly born to a subadult is assumed to be related to the survival of their mother (S_{ad}) (see Yoccoz *et al.* 1998), S_{sub} represents the monthly survival rate of subadults and M_{sub} represents the monthly maturation rate from subadult to adult. Finally, the monthly adult survival rate is given by S_{ad} .

In order to account for the seasonal variation in demography (if documented in the demographic modelling) we used different matrix models for each season (each lasting for 3 months), where $\mathbf{M}_{sp}$ is used for spring; $\mathbf{M}_{su}$ is used for summer, $\mathbf{M}_{au}$ is used for autumn and $\mathbf{M}_{wi}$ is used for winter. Following Yoccoz *et al.* (1998) the annual matrix model is from early spring of one year to early spring of the following year and may be given as

$$\mathbf{M}_y = \mathbf{M}_{wi}^3 \times \mathbf{M}_{au}^3 \times \mathbf{M}_{su}^3 \times \mathbf{M}_{sp}^3, \quad (2)$$

where each of the right-hand side matrix models is given as equation (1), but with seasonally dependent parameter estimates.

(b) Sensitivity and elasticity

Sensitivity coefficients (s_{ij}) are defined by absolute changes, whereas elasticity coefficients (e_{ij}) are defined by relative changes. Both coefficients can be evaluated on the basis of the right and left eigenvectors and the dominant eigenvalue (population growth rate) of the matrix (Caswell 1978, 2001). However, since small mammals are strongly affected by seasonal changes in the environment (Kalela 1957; Schaffer & Tamarin 1973; Krebs & Myers 1974), we evaluate the sensitivities (absolute and relative) of the annual population growth rate to changes in each demographic rate at each season during the year (see Caswell & Trevisan 1994; Yoccoz *et al.* 1998).

(c) Models including endogenous and exogenous factors

The matrix models may be expressed as nonlinear, density-dependent and time-variant dynamic models by including the found functional relationships of seasonality, feedback structure (density dependence) and climate, i.e.

$$\mathbf{M}_{(s,n,c)} = \begin{bmatrix} 0 & 0 & S_{ad}(s,n,c) \times R_{ad}(s,n,c) \\ S_{ad}(s,n,c) & S_{sub}(s,n,c) \times (1 - M_{sub}(s,n,c)) & 0 \\ 0 & S_{sub}(s,n,c) \times M_{sub}(s,n,c) & S_{ad}(s,n,c) \end{bmatrix}, \quad (3)$$

where s , n and c represent the seasonal, endogenous and climatic effects on demographic rates, respectively. All demographic models (survival, maturation and the fraction of reproductive individuals) have the same logistic structure, i.e.

$$\theta(s, n, c) = \frac{1}{1 + e^{-[\beta_s + \beta_1 \times N_t + \beta_2 \times C_t]}}, \quad (4)$$

where $\theta(s, n, c)$ represents a demographic rate (e.g. adult survival, maturation, or the fraction of reproductive females), β_s represents the seasonal indicator of the demographic parameter ($s \rightarrow wi = \text{winter}$, $sp = \text{spring}$, $su = \text{summer}$ and $au = \text{autumn}$ or s is a constant when the

Figure 2. Seasonal variation patterns of the four demographic parameters of the mouse opossum in central Chile, i.e. the fraction of reproductive individuals (open circles and solid line), recruitment rates (open squares and dashed line), adult survival rates (filled circles and dotted line) and maturation rates (filled squares and dot-dashed line), according to the different statistical models. Vertical bars are $1 \pm \text{s.e.}$

parameter did not show seasonal variation), β_1 represents the negative feedback effect and β_2 is the climatic effect.

5. RESULTS

The estimates of population density are given in figure 1.

(a) Capture rates

The goodness of fit of the general model revealed that it is adequate ($\chi^2_{41} = 14.41$ and $p = 1.00$) and that the general model (ϕ_{time} and p_{time}) fitted the data satisfactorily. The model with full-time variation in the capture rates fitted the data significantly better than the model with constant capture rates (LRT of p_{time} versus p , $\chi^2_{91} = 147.78$ and $p = 0.0001$). Constraining the full-time variability on the capture rates to be seasonal and between year provides the best description of the temporal variability in the capture rates with fewer parameters (LRT of p_{time} versus $p_{\text{season} + \text{year}}$, $\chi^2_{75} = 83.86$ and $p = 0.229$). The seasonal pattern of variation in the capture rates suggests that individuals of *T. elegans* have lower capture rates during winter and spring, higher capture rates during summer and peak capture rates in autumn.

(b) Survival rates (ϕ)

There was no significant full-time (monthly and yearly) variation when compared with the constant model (LRT of $\phi_{\text{time}} p_{\text{time}}$ versus ϕp_{time} , $\chi^2_{91} = 86.65$ and $p = 0.614$). However, we did detect a marginal seasonal variation in the survival rates (LRT of $\phi p_{\text{season} + \text{year}}$ versus $\phi_{\text{season}} p_{\text{season} + \text{year}}$, $\chi^2_3 = 7.73$ and $p = 0.052$), but there was no significant between-year variation (LRT of $\phi_{\text{season} + \text{year}} p_{\text{season} + \text{year}}$ versus $\phi_{\text{season}} p_{\text{season} + \text{year}}$, $\chi^2_{13} = 5.44$ and $p = 0.96$). The seasonal pattern of survival

Table 1. The statistical models tested denoted according to each model-specific variation in the survival (ϕ) and capture (p) probabilities.

(time denotes the full time-specific variation, season denotes the seasonal time-specific variation, year denotes the between-year variation and a full point denotes no time-specific variation, which is a single value estimated for all time-periods. AIC_c is the estimated Akaike's information criterion: models with lower values and marked with an asterisk indicate more parsimonious models.)

model	AIC_c	number of estimable parameters	deviance
$\{\phi_{\text{rainfall}} p_{\text{season} + \text{year}}\}$	664.36*	19*	297.43*
$\{\phi_{\text{season}} p_{\text{season} + \text{year}}\}$	666.71	21	295.16
$\{\phi p_{\text{season} + \text{year}}\}$	667.81	18	302.89
$\{\phi_{\text{year}} p_{\text{season} + \text{year}}\}$	686.06	30	293.97
$\{\phi_{\text{season} + \text{year}} p_{\text{season} + \text{year}}\}$	691.22	34	289.68
$\{\phi p\}$	698.00	2	366.81
$\{\phi p_{\text{time}}\}$	787.87	93	219.03
$\{\phi_{\text{time}} p\}$	794.57	93	225.73
$\{\phi_{\text{time}} p_{\text{time}}\}$	1132.84	184	132.39

Table 2. The statistical models tested denoted according to each model-specific variation in the seniority (γ) (recruitment rate = $1 - \gamma$) and capture (p) probabilities.

(time denotes the full time-specific variation, season denotes the seasonal time-specific variation, year denotes the between-year variation and a full point denotes no time-specific variation, which is a single value estimated for all time-periods. The covariates are as follows: DD, population density; rainfall, annual rainfall effects. AIC_c is the estimated Akaike's information criterion: models with lower values and marked with an asterisk indicate more parsimonious models.)

model	AIC_c	number of estimable parameters	deviance
$\{\gamma_{\text{season} + \text{DD} + \text{rainfall}} p_{\text{season} + \text{year}}\}$	620.88*	23*	244.88*
$\{\gamma_{\text{season} + \text{year}} p_{\text{season} + \text{year}}\}$	625.45	34	223.98
$\{\gamma_{\text{season}} p_{\text{season} + \text{year}}\}$	626.11	21	254.58
$\{\gamma_{\text{year}} p_{\text{season} + \text{year}}\}$	626.37	30	234.33
$\{\gamma p\}$	695.34	2	364.15
$\{\gamma p_{\text{time}}\}$	712.72	93	144.58
$\{\gamma_{\text{time}} p\}$	742.24	93	174.10
$\{\gamma_{\text{time}} p_{\text{time}}\}$	1063.43	184	68.36

variation showed lower estimates during spring and summer (0.592) (s.e. = 0.0245) and higher estimates during autumn and winter (0.730) (s.e. = 0.0256) (figure 2). A model with negative effects of the annual rainfall was the most parsimonious for the survival rates (table 1).

(c) Recruitment rates ($1 - \gamma$)

As expected, the recruitment rates showed strong temporal variability (table 2). Similarly to the adult survival rates, we reduced the full-time variation model to simpler models that adequately represented the time

Table 3. Statistical models of the fraction of reproductive individuals with a binomial error structure and logit link function.

(Seasonal denotes the seasonal time-specific variation (in this model we used only two seasons, i.e. the breeding season, which is winter and spring and the non-breeding season, which is summer and autumn) and year denotes the between-year variation. The external covariates are as follows: DD, population density effects; rainfall, annual rainfall effects; SOI, effects of the SOI. AIC_c is the estimated Akaike's information criterion: models with lower values and marked with an asterisk indicate more parsimonious models.)

model	AIC	number of parameters
season	121.70*	2*
year	217.13	12
season + year	217.68	14
external covariates		
season + rainfall	112.83*	3*
season + DD	114.79	3
season + DD + rainfall	114.53	4
season + DD + SOI	115.79	4
season + rainfall + SOI	116.25	4
season + DD + rainfall + SOI	118.14	5
season + SOI	118.95	3

variation in the recruitment rates. These reduced models showed seasonal and between-year variation in the recruitment rates. There was significant between-year variability in addition to seasonal effects (LRT of $\gamma_{\text{season} + \text{year}}$ versus γ_{season} , $\chi^2_{13} = 30.60$ and $p = 0.004$). We also found significant seasonal variability in the recruitment rates (LRT of $\gamma_{\text{season} + \text{year}}$ versus γ_{year} , $\chi^2_4 = 10.35$ and $p = 0.035$). The recruitment rates are higher during spring, lower during summer and intermediate during winter and autumn (figure 2). The model including seasonality and positive effects of population density and rainfall was the best according to AIC criterion (table 2).

(d) Fraction of reproductive adults (*R*)

The best model for describing the temporal variation in the fraction of reproductively active individuals included seasonal and between-year variation (table 3). The seasonal pattern of reproduction showed an increase in the fraction of reproductive individuals by early winter to spring and a decrease during summer and early autumn. This pattern is consistent with the seasonal variation in the recruitment rates (figure 2). When the additional effects of extrinsic variables were analysed, we found that the best model included seasonality and the positive effects of annual rainfall (table 3). Altogether, the annual rainfall explains 42% of the between-year variability in the fraction of reproducing individuals.

(e) Maturation rates (ψ)

There was no significant between-year variability in addition to seasonal effects in the maturation rates (LRT of $\psi_{\text{season} + \text{year}}$ versus ψ_{season} , $\chi^2_{12} = 13.09$ and $p = 0.36$). We found significant seasonal variability in the maturation rates (LRT of $\psi_{\text{season} + \text{year}}$ versus ψ_{year} , $\chi^2_4 = 14.82$ and $p = 0.005$) (table 4). We showed in figure 2 that the maturation rates were very high during winters, intermediate in

spring and very low in summer and autumn. The best model according to the AIC_c criterion was one that included seasonal variation, negative effects of population density and positive rainfall effects, but a model with only seasonal variation was also very similar (table 4).

(f) Direct estimates of the population growth rates and the contributions of survival and recruitment

The estimates of the population growth rate ranged from 0.66 to 1.52. This range is in agreement with the increases and declines exhibited by the mouse opossum's population dynamics. The average overall population growth rate (λ) was 1.011 ± 0.0019 indicating a slow population growth during the period of the study. The estimates of the seniority probabilities (γ) from the (season + year) variation model (table 2) show that γ varied from 0.0001 to 1.00, thereby indicating a large temporal variation in the relative contribution of adult and subadult survival to population growth. Nevertheless, 72 of the 92 estimates of γ were > 0.5 suggesting a trend of adult and subadult survival being more important than recruitment. Therefore, we can decompose the full-time variation in the relative contributions of subadult and adult survival in the within and between-year variation. For example, adult and subadult survival appear to be more important than recruitment to population growth during summer (94%), autumn (66%) and winter (79%), while spring recruitment represents most of the 45% of the relative changes in population growth (see table A1 in electronic Appendix A of this paper available on The Royal Society's Publications Web site). On the other hand, there was a strong between-year variation in the relative contributions of adult and subadult survival to the population growth rate, which ranged from 0.0001 to 1.00 (see table A2 in electronic Appendix A).

(g) Seasonal matrix models with constant elements

The four seasonal matrices characterizing the annual dynamics are expressed in equation (A1) of electronic Appendix A. The annual asymptotic growth rate of these matrix models was 1.026. The corresponding matrices with the sensitivity coefficients are given in equation (A2) in electronic Appendix A and the matrix with the elasticity coefficients of the seasonal population growth rates are given in equation (A3) in electronic Appendix A.

For example, adult survival had a similar impact on the yearly population growth rate in all seasons (ranging from 0.29 in spring to 0.40 in winter). The elasticities for survival during the first month of life were higher during winter and spring and lower during summer. The maturation rates showed the largest impact on the population growth rates during spring and the lowest impact during autumn. The net reproductive rate per female had a similar impact on the population growth rate during autumn and spring and a higher impact on the yearly population growth rate during winter. Finally, the survival rates of subadults exhibit higher elasticities during summer and autumn and lower elasticities during spring and winter.

(h) Matrix models including feedback structure and climate (rainfall)

We initialized the simulations with 1200 time-steps of constant rainfall assuming average values followed by the

Table 4. The statistical models tested denoted according to each model-specific variation in subadult survival (ϕ_s), adult survival (ϕ_a), maturation (ψ) and capture (p) probabilities.

(season denotes the seasonal time-specific variation, year denotes the between-year variation and a full point denotes no time-specific variation, which is a single value estimated for all time-periods. The external covariates are as follows: DD, direct density-dependent effects; rainfall, annual rainfall effects. AIC_c is the estimated Akaike's information criterion: models with the lower values and marked with an asterisk indicate more parsimonious models.)

model	AIC _c	number of parameters	deviance
$\{\phi_s, \phi_a, p_{\text{season} + \text{year}}, \psi_{\text{season} + \text{year}}, \psi_{\text{season} + \text{DD} + \text{rainfall}}\}$	723.76*	43*	354.29*
$\{\phi_s, \phi_a, p_{\text{season} + \text{year}}, \psi_{\text{season}}\}$	724.30	41	359.06
$\{\phi_s, \phi_a, p_{\text{season} + \text{year}}, \psi_{\text{season} + \text{year}}\}$	741.97	53	345.97
$\{\phi_s, \phi_a, p_{\text{season} + \text{year}}, \psi_{\text{year}}\}$	746.29	49	360.77

Figure 3. (a) A graphical representation of the annual dynamics of mouse opossum in central Chile. (b) Monthly simulation runs with feedback structure and rainfall variability. The size of the population is expressed as the number of females per hectare over a time-period running for 1200 months. The annual rainfall records are from the meteorological station of La Serena during the period 1900–1999. We initialized the model with average population sizes in all simulations and used zero values of rainfall and the SOI during the first 1200 month time-steps.

introduction of proxies for the climatic conditions resulting in a combined density-dependent and density-independent dynamic model. In this model we used a constant monthly subadult survival rate (0.77) and adult survival rate (0.65) as estimated from the capture–mark–recapture models. The assumed negative feedback and positive rainfall effects on the maturation rates were expressed as

$$\psi(s, n, c) = \frac{1}{1 + \exp[-(\beta_s - 0.15 \times n_t + 0.006 \times \text{rainfall})]} \quad (5)$$

where the maturation rates are modelled as seasonally variant with the coefficients $\beta_{\text{winter}} = 1.64$, $\beta_{\text{spring}} = 0.37$,

Figure 4. (a) The frequency distribution of the deviations observed versus the predicted population size of mouse opossum in central Chile. Pearson's correlation coefficient for the predicted versus the observed population sizes was $r=0.54$ with $n=51$ and $p < 0.001$. (b) Model predictions (open circles) and observed seasonal (every three-month period) population sizes of *T. elegans* females (filled circles) at Aucó during the period of October 1987 to June 2000.

$\beta_{\text{summer}} = -2.53$ and $\beta_{\text{autumn}} = -3.00$. The fraction of reproductive females was modelled as a logistic function of the seasons and rainfall, i.e.

$$R(s, c) = \frac{1}{1 + \exp[-(\beta_s + 0.012 \times \text{rainfall})]} \quad (6)$$

where the seasonal coefficients were $\beta_{\text{winter}} = -0.50$, $\beta_{\text{spring}} = -0.50$, $\beta_{\text{summer}} = -1.25$ and $\beta_{\text{autumn}} = -1.25$. Using the climatic data of annual rainfall at La Serena station (in 1900–1999, which represent the regional conditions of our study site) results in a fluctuating pattern with some population peaks associated with the rainy years (figure 3). There is a close relation between the 'observed' (estimates based on the capture–mark–recapture data) and 'predicted' population sizes (figure 4)

(Pearson's correlation coefficient $r=0.54$, $n=51$ and $p < 0.001$). The deviations between the predictions and observed values look somewhat symmetrical (figure 4a), which indicates that the assumed biological mechanisms are able to produce dynamics that are consistent with the empirical observations.

(i) *Comparison of the autoregressive structure of the three simulated dynamics*

Comparing the annual observed and predicted dynamics (by sampling the model outputs once every 12 months) demonstrates a very close relationship (figure 5) (Pearson's correlation coefficient $r=0.84$, $n=51$ and $p < 0.001$). Using the capture–mark–recapture statistical models and the Leslie–Usher matrix models, we showed that the simulated annual population dynamics mimic

the observed annual population dynamics to some degree. Previous analysis and time-series modelling showed that a second-order autoregressive model (log-transformed) dominated by first-order feedback describes the mouse opossum's annual population dynamics (Lima & Jaksic 1999). The autoregressive parameters correspond to the area of stability in the parameter space of log autoregressive models (Royama 1992; Bjørnstad *et al.* 1998) (figure 5). Consequently, we may compare the autoregressive structure emerging from the simulated annual dynamics of the matrix population model with the observed density-dependent structure. In this analysis we used the population simulations and sampled the model output once every 12 months in order to give rise to the annual simulated dynamics. The models were run using rainfall data from La Serena for the period 1900–1999. The 100 years of simulated annual dynamics for each model run was split into five series of *ca.* 20 years in order to reproduce short time-series data.

6. DISCUSSION

Our results suggest that the factors observed at the demographic level, such as seasonality, negative first-order feedback and rainfall, are key elements in the population dynamics of the mouse opossum (*T. elegans*). In what follows we focus on three issues: (i) the demographic results, (ii) the linear seasonal matrices and the time-varying pattern (through the different seasons) of the elasticities and sensitivities of the different life-history parameters, and (iii) the consequences of endogenous and exogenous factors for the population dynamics of the mouse opossum.

(a) Demographic analyses

The mouse opossum (*T. elegans*) exhibited an important temporal variability in its capture rates. Seasonal changes in capture rates may reflect changes in resource availability and quality, behaviour, predator densities or environmental variables. In fact, *T. elegans* is characterized by exhibiting an energy-saving behavioural mechanism (torpor) that is used during periods of scarce food availability or high energetic requirements (Rosenmann *et al.* 1980; Sabat *et al.* 1995) and storing energy by means of fat reserves in the tail (Sabat *et al.* 1995). Consequently, its capture rates may be lower during periods of scarce food or low temperatures. In contrast, its capture rates should be higher during favourable periods, thereby reflecting an increase in the activity of individuals. This pattern of activity represents a particular case of temporary emigration as was reported earlier by Kendall *et al.* (1997) for meadow voles (*Microtus pennsylvanicus*) and white-footed mice (*Peromyscus leucopus*). In fact, the higher capture rates observed in late summer and autumn may be caused by an increase in foraging activity in order to achieve the fat reserves needed for surviving during winter and starting the breeding period.

We found a negative feedback effect on the maturation rates of this small marsupial, as has been reported for other small mammal species (Leirs *et al.* 1997; Prévot-Julliard *et al.* 1999). Negative feedback in maturation rates may be associated with competition for food and/or territory (Stenseth *et al.* 1996b). Although spacing beha-

Figure 5. (a) The parameter space for the second-order autoregressive models. The grey circle represents the observed autoregressive estimates, the open circle is the predicted autoregressive estimates using the last 14 years of rainfall and the filled circles are the estimates from five simulated time-series using time-periods of 20 years of rainfall data (1901–1920, 1921–1940, 1941–1960, 1961–1980 and 1980–1999). Pearson's correlation coefficient for the predicted versus the observed annual population densities was $r = 0.84$ with $n = 14$ and $p < 0.001$. (b) Model predictions (open circles and broken line) and observed (filled circles and solid line) annual population sizes of *T. elegans* at Aucó during the period 1987–1999.

viour can lead to negative feedback on maturation rates (Stenseth *et al.* 1996b; Prévot-Julliard *et al.* 1999) there is no information about the social structure of the mouse opossum for testing this hypothesis.

Annual rainfall is positively related to the mouse opossum's recruitment, maturation and reproductive rates. This relationship reflects a direct effect of rainfall on environmental productivity and insect abundance. In fact, in semi-arid Chile high rainfall years are associated with insect outbreaks (Fuentes & Campusano 1985) and, hence, rainfall may be a proxy for insect availability. This positive rainfall effect is consistent with the idea that the dynamics of this species can be determined by food limitation (first-order dynamics). Because of the strong influence of annual rainfall on insect abundance in semi-arid Chile (Fuentes & Campusano 1985), there seems to

be a clear effect of food availability (via rainfall variability) on the reproduction, maturation and recruitment of the mouse opossum.

The mouse opossum showed a clear seasonal pattern of reproduction, recruitment, survival and maturation. The lagged seasonal pattern of variation in reproductive activity and recruitment suggests the existence of a long period of dependence of juveniles on their mothers, as in other marsupial species. The peak of adult insect density occurs during spring and summer, while the highest availability of larvae occurs in winter, which may explain the high maturation and reproductive rates observed during this season. Insect larvae are rich in energy (fat tissues), while adult insects are rich in protein (Gullan & Cranston 1992). Hence, during winter larvae may provide favourable energetic conditions for reproduction. On the other hand, during spring and summer the availability of protein-rich food may favour the growth and maintenance of the newly recruited mouse opossum.

(b) *Linear seasonal and between-year dynamics*

The dominant eigenvalue of each seasonal matrix model roughly indicates whether there is an increase or a decrease in population size during the seasons. The estimated seasonal matrix models for the within-year (seasonal) dynamics of the mouse opossum are characterized by an increase from winter to spring and from spring to summer and a decrease from summer to autumn and from autumn to winter. The estimated decreasing population growth rate during summer and autumn seems to be a consequence of reduced reproductive activity and recruitment of new individuals. The pattern of seasonal dynamics predicted from the matrix models is somewhat different from the seasonal population growth rates estimated using the Pradel (1996) approach (table A1 in electronic Appendix A). We estimated a decrease from winter to spring and an increase from spring to summer, stationary dynamics from summer to autumn and a decrease between autumn and winter. However, this difference between the estimated and 'predicted' seasonal population growth rates is consistent with the seasonal patterns of reproduction and recruitment. While matrix models incorporate the number of juvenile individuals for the population projection, the direct estimates of the population growth rates are based on trappable individuals (subadults and adults). Thus, the seasonal dynamics estimated with both approaches are uncoupled by approximately one season.

The impact of each demographic rate on the yearly population growth rate during the four different seasons varied seasonally. However, the population growth rate seemed to be primarily affected by the adult survival and maturation rates during all seasons. For instance, adult and subadult survival and maturation represent between 54% (in winter) and 81% (in summer) of the impact on the annual population growth rate. In fact, the lowest availability of insects (both adults and larvae) occurs during late summer and autumn (E. Silva, personal communication), which may represent a bottleneck period during which survival is the most important life-history trait. Indeed, the mouse opossum uses an energy-saving behavioural mechanism (torpor), which is used during periods of scarce food availability (Rosenmann

et al. 1980; Sabat *et al.* 1995). In addition, *T. elegans* stores energy by means of fat reserves in the tail (Sabat *et al.* 1996). Consequently, fat reserves and torpor may confer high survival rates during periods of low food availability. On the other hand, elasticities in part reflect the age structure of the population. At the beginning of the breeding season (winter) most of the individuals are adults, so the adult survival and reproductive parameters then provide most of the relative contribution to the yearly population growth rate. In summer and autumn, there are many subadult individuals. Hence, the relative contribution of the subadult survival and maturation rates increases and the contribution of reproduction decreases over time. In terms of the seasonal contribution to the realized population growth rate using the direct estimation approach (Pradel 1996; Nichols *et al.* 2000), 45% of the seasonal increase in population size from spring to summer is attributable to new recruits entering the population, while the changes in population size during the other seasons are related to survival (between 66 and 94% (see table A1 in electronic Appendix A).

(c) *Endogenous and exogenous dynamics*

Thylamys elegans showed contrasting population dynamics as compared to the irruptive rodent *P. darwini* (Lima *et al.* 1999a), which is probably related to the different feedback structures of the demographics of the two species. The first-order dynamics predicted by the matrix model are consistent with the dynamics of a linear autoregressive model fitted to the annual time-series of *T. elegans* (Lima & Jaksic 1998b, 1999). In this vein, almost all the fluctuations in the population dynamics of this species seem to be caused by the rainfall variability related to the reproduction, maturation and recruitment rates interacting with strong regulatory mechanisms (negative feedback in maturation).

7. CONCLUSIONS

Like other recent studies (Leirs *et al.* 1997; Bjørnstad *et al.* 1998; Stenseth *et al.* 1998b; Lima *et al.* 1999a), we have emphasized that the interaction between negative feedback and environmental disturbances is crucial for understanding the observed dynamics of natural populations. We emphasize that the population dynamics of a small marsupial in semi-arid Chile seem to be the result of strong first-order negative feedback on its maturation rates and of the positive effects of rainfall on its reproduction, recruitment and maturation. These results suggest that the population dynamics of this marsupial are regulated by strong intraspecific competition for food and/or territories and are perturbed by environmental forces that are characterized by ENSO events and interannual rainfall variability. The contribution of this study is that we have, for the first time to the authors' knowledge, determined the feedback structure in a small South American marsupial at demographic and population dynamics levels.

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