

# Population dynamics of a South American rodent: seasonal structure interacting with climate, density dependence and predator effects

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Understanding the role of interactions between intrinsic feedback loops and external climatic forces is one of the central challenges within the field of population ecology. For rodent dynamics, the seasonal structure of the environment necessitates changes between two stages: reproductive and non-reproductive. Nevertheless, the interactions between seasonality, climate, density dependence and predators have been generally ignored. We demonstrate that direct climate effects, the nonlinear effect of predators and the nonlinear first-order feedback embedded in a seasonal structure are key elements underlying the large and irregular fluctuations in population numbers exhibited by a small rodent in a semi-arid region of central Chile. We found that factors influencing population growth rates clearly differ between breeding and non-breeding seasons. In addition, we detected nonlinear density dependencies as well as nonlinear and differential effects of generalist and specialist predators. Recent climatic changes may account for dramatic perturbations of the rodent's population dynamics. Changes in the predator guild induced by climate are likely to result, through the food web, in a large impact on small rodent demography and population dynamics. Assuming such interactions to be typical of ecological systems, we conclude that appropriate predictions of the ecological consequences of climate change will depend on having an in-depth understanding of the community–weather system.

**Keywords:** demographic seasonal structure; climate; rodents; nonlinear predator response; El Niño Southern Oscillation; semi-arid Chile

## 1. INTRODUCTION

Although it is widely recognized that endogenous (direct and delayed density-dependent structure) and exogenous factors jointly influence natural populations (Nicholson 1933; Andrewartha & Birch 1954; Turchin 1995; Berryman 1999), we have only a rather fragmentary understanding of how intrinsic feedback loops and climate factors interact (but see Grenfell *et al.* 1998; Lima *et al.* 1999; Coulson *et al.* 2001). It is known, for instance, that large-scale global climatic fluctuations, such as the North Atlantic Oscillation and the El Niño Southern Oscillation (ENSO), influence local weather and population dynamics (Forchhammer *et al.* 1998; Lima *et al.* 1999; Post & Stenseth 1999; Holmgren *et al.* 2001; Jaksic 2001; Ottersen *et al.* 2001; Stenseth *et al.* 2002a). For example, strong effects of the ENSO have been demonstrated in semi-arid and Mediterranean ecosystems of western South America (Jaksic 2001). In semi-arid Chile, as in other arid and semi-arid regions (Brown *et al.* 1997), unusually high rainfall associated with the ENSO affects primary productivity, small rodent population dynamics and predator guilds (Jaksic *et al.* 1997).

Rodent dynamics is also known to be influenced by the seasonal structure of the environment (Åström *et al.* 1996; Stenseth 1999). Seasonality for rodent populations implies dynamic changes between two stages: the reproductive season (summer in northern rodents, rainy season in semi-

arid rodents) and the non-reproductive season (winter in northern rodents, drought season in semi-arid rodents). In addition, seasonal environments may have two important consequences for small-rodent dynamics: first, a change in the maximum per capita population growth rates, and, second, a change in the strength of density dependencies between seasons (Stenseth *et al.* 1998, 2002b,c; Hansen *et al.* 1999; Merritt *et al.* 2001).

By focusing on the interactions between seasonality, climate and predator guilds in semi-arid Chile, we provide, through this perspective, new insights into the interactions between climate and the biotic community for understanding leaf-eared mouse (*Phyllotis darwini*) population dynamics. We achieve this through statistical capture–mark–recapture (CMR) modelling of long-term data on the leaf-eared mouse, and demonstrate a varying seasonal structure given by nonlinear intrinsic, climatic and predator effects on the population dynamics of the rodent studied.

## 2. MATERIAL AND METHODS

### (a) Data

Our study site, Las Chinchillas National Reserve at Aucó (31°30' S, 71°06' W), is located in the semi-arid region of central Chile (figure 1). CMR data on leaf-eared mouse density (figure 2a) were obtained, together with occurrence data on five species of predators (figure 2b–f). The leaf-eared mouse is a granivorous–folivorous rodent with an average adult weight of 50 g, widely distributed in semi-arid Chile (Meserve & Le Boulengé 1987). Breeding in the leaf-eared mouse is markedly

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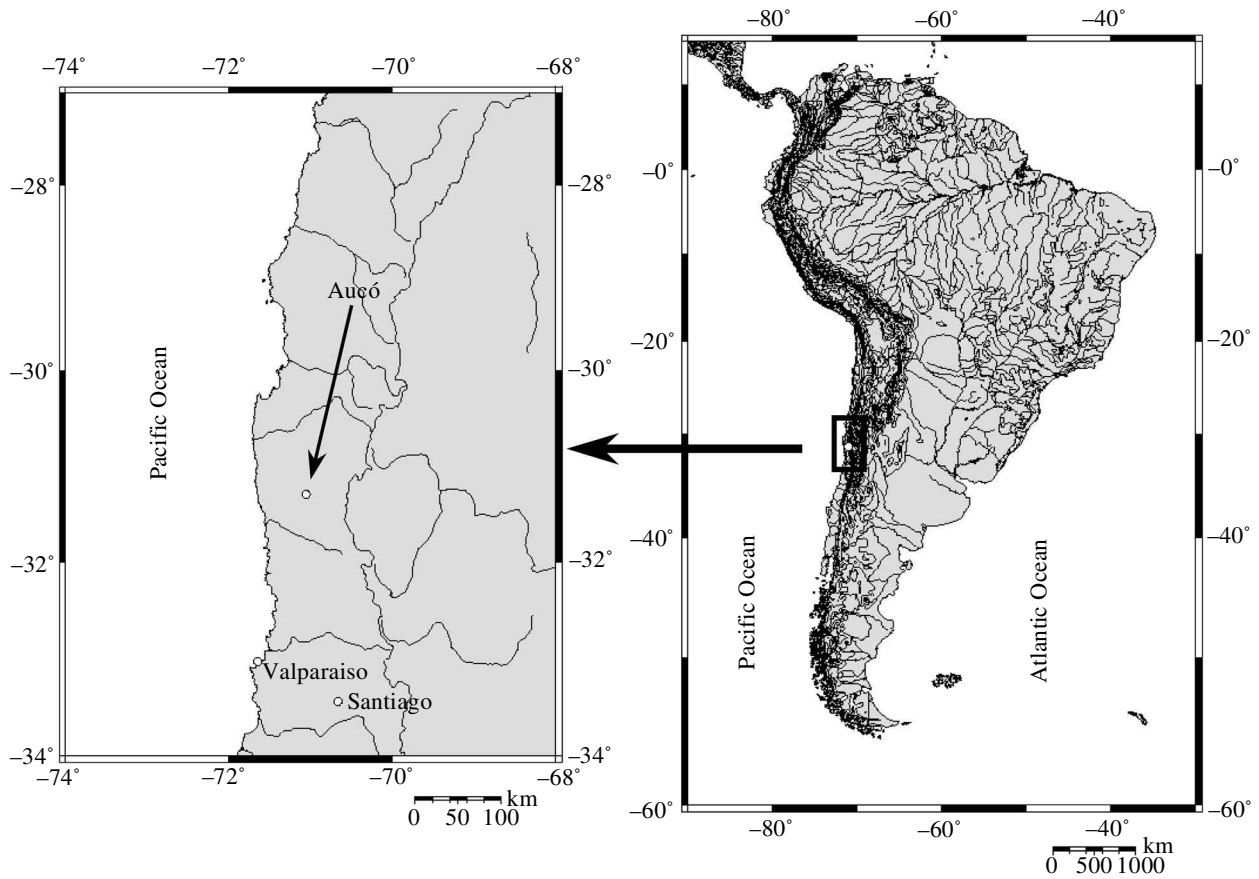


Figure 1. The study site in central Chile and location of the study site, Las Chinchillas National Reserve at Aucó (31°30' S, 71°06' W), which is located 300 km north of Santiago city.

seasonal, starting in July–August and lasting until December or January (Meserve & Le Boulengé 1987). Females produce two or three litters with an average size of five pups (Meserve & Le Boulengé 1987). The barn owl (*Tyto alba*) is a specialized feeder on leaf-eared mice, the Magellanic owl (*Bubo magellanicus*) prefers larger mammal prey, and the burrowing owl (*Speotyto cunicularia*), Austral pygmy owl (*Glaucidium nanum*) and culpeo fox (*Pseudalopex culpaeus*) are generalist predators. Pellets and faeces of these five predators were used as indices of their respective abundances in the field. We used spring (September–November) estimates of leaf-eared mouse density and predator numbers as indicators of rodent and predator densities during the breeding season, and autumn (February–March) estimates as indicators of rodent and predator abundances during the non-breeding season. In addition, climate variability was estimated from the annual precipitation pattern (figure 2g). The rodent data consist of capture–recapture histories obtained from 106 primary trapping sessions between October 1987 and July 2001, during which extensive numerical fluctuations were observed. We obtained a total of 2420 captures, corresponding to 1210 females.

**(b) Statistical analysis**

Survival ( $\phi$ ), residency ( $\gamma$ ) probabilities and the population growth rate ( $\lambda$ ) of females were modelled by using the CMR-statistical modelling approach (Lebreton *et al.* 1992), applying the program MARK (White & Burnham 1999). Estimates were obtained by the maximum-likelihood method, assuming a multinomial distribution of capture histories. We tested different models to describe the temporal variation in these three demographic parameters (see electronic Appendix A available on The Royal Society’s Publications Web site).

We used the following approach to model seasonal structure:

$$N_t^{\text{nonbr}} = N_{t-1}^{\text{br}} \times \lambda^{\text{br}}(N_{t-1}^{\text{br}}, P_{t-1}^{\text{br}}, C_{t-1})$$

$$N_t^{\text{br}} = N_{t-1}^{\text{nonbr}} \times \lambda^{\text{nonbr}}(N_{t-1}^{\text{nonbr}}, P_{t-1}^{\text{nonbr}}, C_{t-1}), \tag{2.1}$$

where  $N^{\text{nonbr}}$  and  $N^{\text{br}}$  are the rodent population densities at the beginning of the non-breeding and breeding seasons, respectively,  $P^{\text{nonbr}}$  and  $P^{\text{br}}$  are the indices of predator abundance during the non-breeding and breeding seasons, respectively,  $C$  is the climate proxy, and  $\lambda^{\text{nonbr}}$  and  $\lambda^{\text{br}}$  are the monthly average finite population growth rates during the respective seasons. CMR statistical modelling procedures can be used to estimate  $\lambda^{\text{nonbr}}$  and  $\lambda^{\text{br}}$  independently of population size (Nichols *et al.* 2000). Consequently, model 1 can be rewritten in terms of the estimated seasonal growth rates, given that  $N_t^{\text{nonbr}}/N_{t-1}^{\text{br}} = \lambda^{\text{br}}$  and  $N_t^{\text{br}}/N_{t-1}^{\text{nonbr}} = \lambda^{\text{nonbr}}$ :

$$\lambda^{\text{br}} = \exp[f_1(N_{t-1}^{\text{br}}) + f_2(P_{t-1}^{\text{br}}) + f_3(C_{t-1})]$$

$$\lambda^{\text{nonbr}} = \exp[g_1(N_{t-1}^{\text{nonbr}}) + g_2(P_{t-1}^{\text{nonbr}}) + g_3(C_{t-1})], \tag{2.2}$$

where  $f_i$  and  $g_i$  are unknown functions representing the seasonal effects of rodent density, predator abundance and climate state on population growth rates. By using per capita growth rates, defining the seasonal  $R$ -functions (Turchin 1995; Berryman 1999) as  $R^{\text{br}} = \log(N_t^{\text{nonbr}}/N_{t-1}^{\text{br}}) = \log(\lambda^{\text{br}})$  and  $R^{\text{nonbr}} = \log(N_t^{\text{br}}/N_{t-1}^{\text{nonbr}}) = \log(\lambda^{\text{nonbr}})$  and taking natural logarithms of both sides of equation (2.2) we obtain:

$$R_t^{\text{br}} = f_1(N_{t-1}^{\text{br}}) + f_2(P_{t-1}^{\text{br}}) + f_3(C_{t-1})$$

$$R_t^{\text{nonbr}} = g_1(N_{t-1}^{\text{nonbr}}) + g_2(P_{t-1}^{\text{nonbr}}) + g_3(C_{t-1}). \tag{2.3}$$

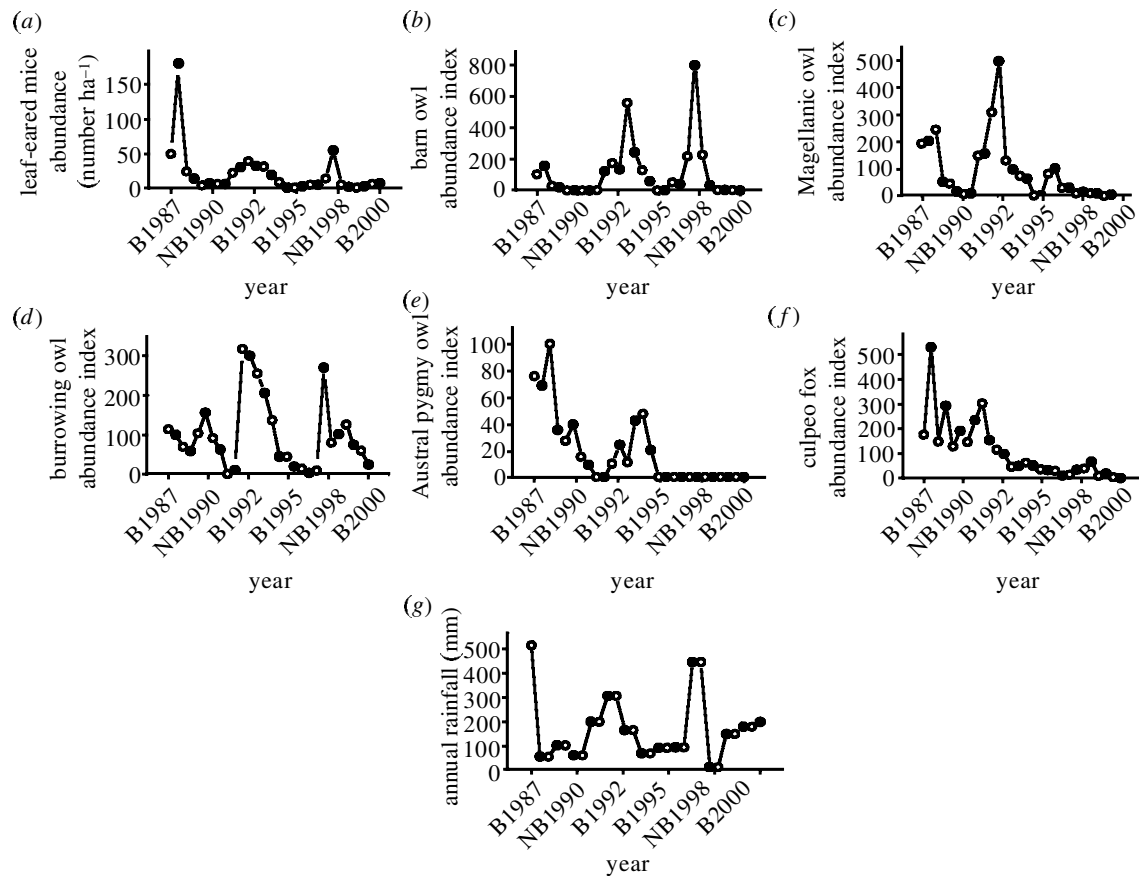


Figure 2. (a) Population dynamics of the leaf-eared mouse (*Phyllotis darwini*). (b) Time-series of the abundance index of (b) the barn owl (*Tyto alba*), (c) the Magellanic owl (*Bubo magellanicus*), (d) the burrowing owl (*Speotyto cunicularia*), (e) the Austral pygmy owl (*Glaucidium nanum*) and (f) the culpeo fox (*Pseudalopex culpaeus*). (g) Time-series of the annual accumulated rainfall in mm. B, breeding seasons (open circles) and NB, non-breeding seasons (filled circles).

We estimated the unknown functions  $f_i$  and  $g_i$  using rodent density, predators (generalists and specialists) and climate as covariables in a non-parametric regression approach. The per capita population growth rate was modelled using a non-parametric regression in order to identify possible nonlinearities. We used generalized additive models (GAM; Hastie & Tibshirani (1990); see Stenseth *et al.* (1997) and Bjørnstad *et al.* (1998) for ecological examples). The complexity of the curve (the number of degrees of freedom) was between one and three, and the number of terms ( $f_i$  and  $g_i$ ) was tested by the Schwarz's Bayesian criterion (SBC) (S-PLUS 2000). The SBC is obtained as the  $-2 \times \log\text{-likelihood} + \text{npar} \times \log(\text{nobs})$ , where  $\text{npar}$  represents the number of parameters and  $\text{nobs}$  the number of observations in the fitted model. In consequence, we can use this statistical modelling approach to select climatic influences and the model structure. In addition, we tested whether Lotka–Volterra approaches (such as equation (2.3)) or logistic-based models (Berryman 1999, 2001) best represented the structure of the models. We tested the effects of population density, climate (rainfall), specialist predators (barn owl and Magellanic owl) and generalist predators (Austral pygmy owl, burrowing owl and culpeo fox) on the population dynamics of the leaf-eared mouse.

### 3. RESULTS

The best demographic models for population growth rate ( $\lambda$ ) and survival ( $\phi$ ) and residency probabilities ( $\gamma$ )

were those incorporating seasonality—by dividing the year into breeding (July–January) and non-breeding (February–June) seasons—and between-year variability (supplementary table 1 in electronic appendix A). The three demographic parameters showed strong temporal variation (figure 3). In particular, a shift was observed in the demographic and population dynamical structure from a period of high survival rates and low population growth-rate variation (1987–1994), to a period of low survival rate and high population growth-rate variability thereafter (figure 3*a,c*).

The best model for female population growth rate during the breeding season has nonlinear density dependence (figure 4*a*), positive linear rainfall effects (figure 4*b*) and nonlinear and non-monotonic effects of the ratio of total abundance of predators to leaf-eared mouse density (figure 4*c*; table 1). The model explains 97% of the variation in breeding-season population growth rates. The best model for female population growth rate during the non-breeding season has a nonlinear negative effect of the density ratio of barn owls to leaf-eared mice (figure 5*a*), a nonlinear positive effect of rainfall (figure 5*b*), a nonlinear and non-monotonic effect of burrowing owl density (figure 5*d*) and a nonlinear negative effect of the culpeo fox to leaf-eared mouse density ratio (figure 5*c*; table 1). The model explains 98% of the variation in population growth rates during the non-breeding season.

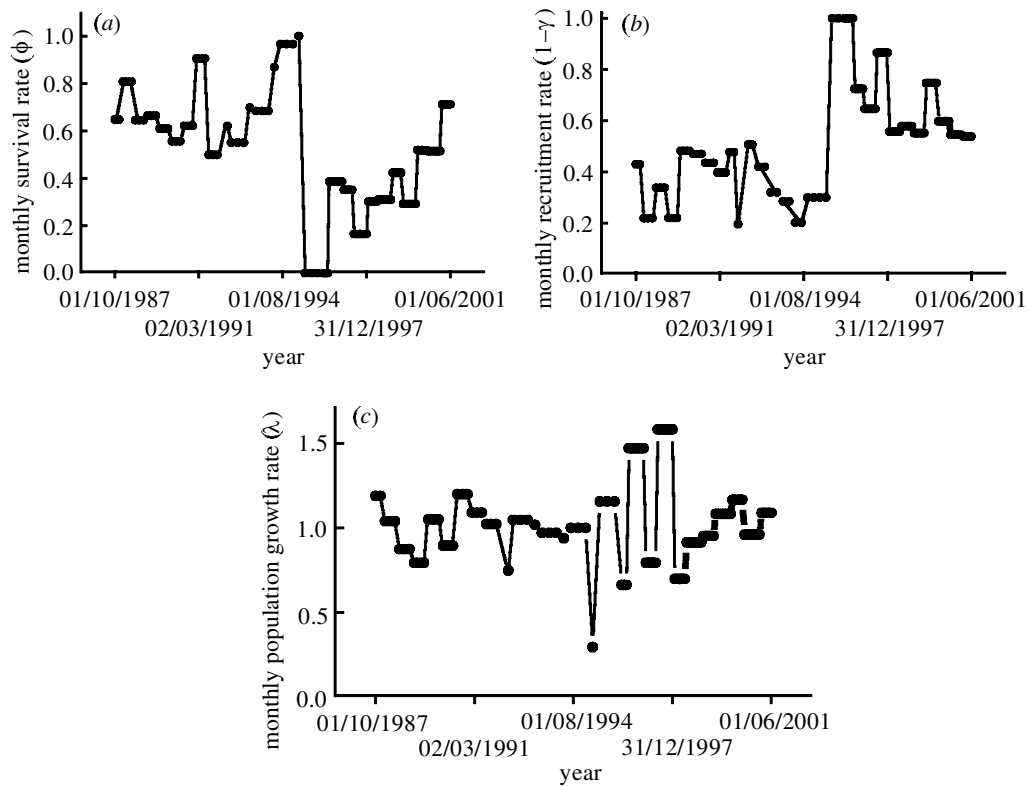


Figure 3. (a) Temporal variability of the survival rate ( $\phi$ ) according to the model  $\{\phi(\text{breeding and non-breeding}) p(\cdot)\}$  using CMR data; note the sudden decline during 1995. (b) Temporal variability of recruitment rate ( $1-\text{residency probability}$ ;  $1-\gamma$ ) according to the model  $\{\gamma(\text{breeding and non-breeding}) p(\cdot)\}$  using the Pradel method and CMR data. (c) Temporal variability of the population growth rate ( $\lambda$ ) according to the model  $\{\phi(\text{breeding and non-breeding}) p(\cdot)\lambda(\text{breeding and non-breeding})\}$  using the Pradel method and CMR data.

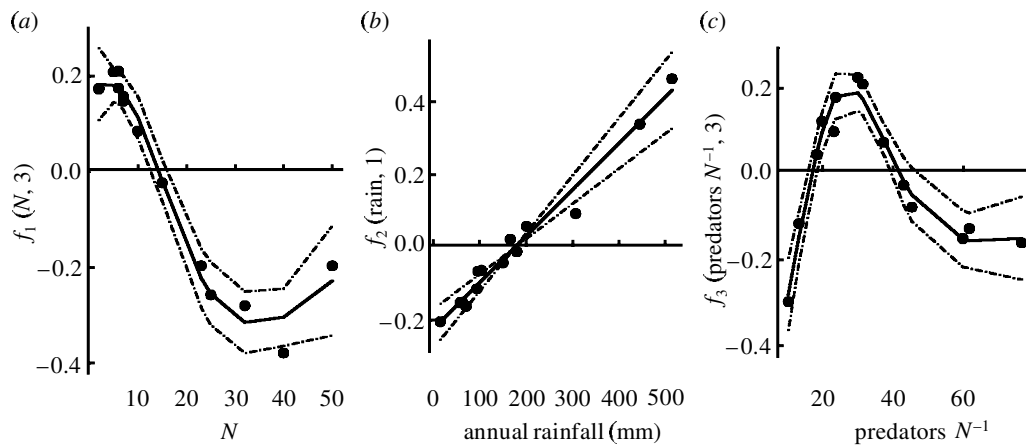


Figure 4. Best GAM model representing the breeding  $R$ -function for leaf-eared mouse dynamics. (a) Partial non-parametric regression line for the population density ( $N_{t-1}$ ). (b) Partial non-parametric regression line for annual rainfall. (c) Partial non-parametric regression line for the ratio of total predator abundance index to leaf-eared mouse abundance. The model was fitted by using natural cubic splines with three degrees of freedom. Dashed lines are 95% confidence intervals;  $R^2 = 0.97$ . The breeding season model is represented by:  $R_t^{\text{br}} = f_1(N; \text{d.f.} = 3) + f_2(\text{rain}; \text{d.f.} = 1) + f_3(\text{predators } N^{-1}; \text{d.f.} = 3)$ .

**4. DISCUSSION**

We have demonstrated that population growth rates exhibit a clear seasonal structure; i.e. factors influencing population growth rates clearly differ between breeding and non-breeding seasons. In addition, we detected non-linear density dependencies as well as nonlinear and differential effects of generalist and specialist predators. The seasonal structure and the factors influencing population growth rates were able to capture the observed temporal

variation in these rates, including their structural variation over time.

During the breeding season, the positive effects of climate (rainfall), through its effects on primary production in semi-arid Chile, have a strong influence on rodent population dynamics. There is a clear seasonality in climatic effects, with winter (May–August) rainfall levels determining plant growth and seed production, which, in turn, influence recruitment during the breeding season. The negative effects of rodent density during the breeding

Table 1. Best population dynamic models for each season. Incorporation of all variables produces a large number of possible models. (We present only the statistically optimal models, chosen by SBC (S-PLUS 2000). SBC is obtained as  $-2 \times \log\text{-likelihood} + n_{\text{par}} \times \log(n_{\text{obs}})$ , where  $n_{\text{par}}$  represents the number of parameters and  $n_{\text{obs}}$  the number of observations in the fitted model. Model parameters were estimated by regression analysis in S-PLUS (2000). Most parsimonious models according to the Bayesian information criterion (BIC) criterion ( $\Delta\text{BIC} > 2$  is considered significant) are chosen and denoted in bold.  $p$ , probability;  $R^2$ , coefficient of determination; BIC, BIC criterion value;  $\Delta\text{BIC}$ , difference in SBC from the most parsimonious model. Model notations are: LEM, leaf-eared mouse abundance; rain, annual rainfall; BO, barn owl abundance; BM, Magellanic owl abundance; BuO, burrowing owl abundance; APO, Australian pygmy owl abundance; TP, total predator abundance.)

	$F_{\text{d.f.}}$	$p$	$R^2$	BIC	$\Delta\text{BIC}$
<b>breeding season GAM models</b>					
$R_{\text{t}}^{\text{br}} = f_1(\text{LEM}; \text{d.f.} = 3) + f_2(\text{rain}; \text{d.f.} = 1) + f_3(\text{TP/LEM}; \text{d.f.} = 3)$	<b>26.07 (7,6)</b>	<b>0.0004</b>	<b>0.97</b>	<b>-35.39</b>	<b>0.00</b>
$R_{\text{t}}^{\text{br}} = f_1(\text{LEM}; \text{d.f.} = 3) + f_2(\text{rain}; \text{d.f.} = 1) + f_3(\text{TP}; \text{d.f.} = 3)$	4.17 (6,7)	0.042	0.78	-11.04	24.35
$R_{\text{t}}^{\text{br}} = f_1(\text{LEM/rain}; \text{d.f.} = 3) + f_2(\text{TP}; \text{d.f.} = 3)$	2.50 (6,7)	0.13	0.78	-5.78	29.61
$R_{\text{t}}^{\text{br}} = f_1(\text{LEM}; \text{d.f.} = 2) + f_2(\text{rain}; \text{d.f.} = 1) + f_3(\text{BO}; \text{d.f.} = 3)$	2.49 (6,7)	0.13	0.69	-5.76	29.63
$R_{\text{t}}^{\text{br}} = f_1(\text{LEM/rain}; \text{d.f.} = 3) + f_2(\text{TP/LEM}; \text{d.f.} = 3)$	2.13 (6,7)	0.17	0.65	-4.31	31.08
$R_{\text{t}}^{\text{br}} = f_1(\text{LEM}; \text{d.f.} = 3) + f_2(\text{rain}; \text{d.f.} = 2)$	2.07 (4,9)	0.17	0.48	-4.17	31.22
$R_{\text{t}}^{\text{br}} = f_1(\text{LEM}; \text{d.f.} = 3) + f_2(\text{rain}; \text{d.f.} = 1) + f_3(\text{BO/LEM}; \text{d.f.} = 3)$	1.54 (6,7)	0.29	0.57	-1.54	33.85
$R_{\text{t}}^{\text{br}} = f_1(\text{rain}; \text{d.f.} = 2) + f_2(\text{TP/LEM}; \text{d.f.} = 3)$	0.82 (5,8)	0.57	0.34	1.82	37.21
$R_{\text{t}}^{\text{br}} = f_1(\text{LEM}; \text{d.f.} = 3) + f_2(\text{TP/LEM}; \text{d.f.} = 3)$	0.92 (6,7)	0.53	0.44	2.06	37.45
<b>non-breeding season GAM models</b>					
$R_{\text{t}}^{\text{nonbr}} = g_1(\text{BO/LEM}; \text{d.f.} = 2) + g_2(\text{rain}; \text{d.f.} = 2) + g_3(\text{CF/LEM}; \text{d.f.} = 2) + g_4(\text{BuO}; \text{d.f.} = 2)$	<b>86.81 (8,5)</b>	<b>0.00006</b>	<b>0.98</b>	<b>-33.41</b>	<b>0.00</b>
$R_{\text{t}}^{\text{nonbr}} = g_1(\text{LEM}; \text{d.f.} = 2) + g_2(\text{rain}; \text{d.f.} = 1) + g_3(\text{TP/LEM}; \text{d.f.} = 3)$	8.89 (6,7)	0.0054	0.88	0.33	33.08
$R_{\text{t}}^{\text{nonbr}} = g_1(\text{BO/LEM}; \text{d.f.} = 3) + g_2(\text{BuO}; \text{d.f.} = 3)$	5.63 (6,7)	0.019	0.83	5.81	39.22
$R_{\text{t}}^{\text{nonbr}} = g_1(\text{BO/LEM}; \text{d.f.} = 2)$	5.93 (3,10)	0.014	0.64	8.25	41.66
$R_{\text{t}}^{\text{nonbr}} = g_1(\text{BO/LEM}; \text{d.f.} = 2) + g_2(\text{rain}; \text{d.f.} = 2) + g_3(\text{BuO}; \text{d.f.} = 2)$	3.69 (6,7)	0.55	0.76	10.49	43.90
$R_{\text{t}}^{\text{nonbr}} = g_1(\text{LEM/rain}; \text{d.f.} = 3) + g_2(\text{TP/LEM}; \text{d.f.} = 3)$	2.95 (6,7)	0.09	0.72	12.87	46.28
$R_{\text{t}}^{\text{nonbr}} = g_1(\text{LEM/rain}; \text{d.f.} = 2) + g_2(\text{BO/LEM}; \text{d.f.} = 2) + g_3(\text{BuO}; \text{d.f.} = 2)$	2.27 (6,7)	0.15	0.66	15.34	48.75
$R_{\text{t}}^{\text{nonbr}} = g_1(\text{BO/LEM}; \text{d.f.} = 2) + g_2(\text{CF/LEM}; \text{d.f.} = 2) + g_3(\text{BuO}; \text{d.f.} = 2)$	2.13 (6,7)	0.17	0.65	15.94	49.35
$R_{\text{t}}^{\text{nonbr}} = g_1(\text{BO/LEM}; \text{d.f.} = 2) + g_2(\text{rain}; \text{d.f.} = 2) + g_3(\text{CF/LEM}; \text{d.f.} = 2)$	1.15 (6,7)	0.42	0.50	20.85	54.26

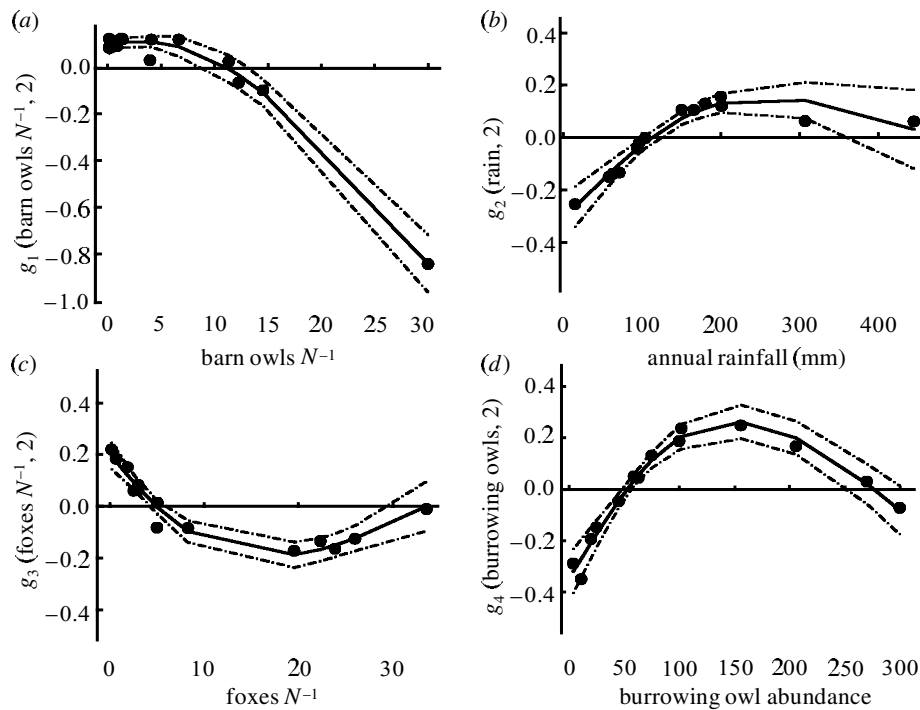


Figure 5. Best GAM model representing the non-breeding  $R$ -function for leaf-eared mouse dynamics. (a) Partial non-parametric regression line for the ratio of the barn owl abundance index to the leaf-eared mouse abundance. (b) Partial non-parametric regression line for annual rainfall effect. (c) Partial non-parametric regression line for the ratio of the culpeo fox abundance index (foxes) to the leaf-eared mouse abundance. (d) Partial non-parametric regression line for the effect of burrowing owl abundance index (burrowing owls). The model was fitted by using natural cubic splines with two degrees of freedom. Dashed lines are 95% confidence intervals;  $R^2=0.98$ . The non-breeding season model is represented by:  $R_t^{\text{nonbr}} = g_1(\text{barn owls } N^{-1}; \text{d.f.} = 2) + g_2(\text{rain}; \text{d.f.} = 2) + g_3(\text{foxes } N^{-1}; \text{d.f.} = 2) + g_4(\text{burrowing owls}; \text{d.f.} = 2)$ .

season are indicative of the classical density-dependent factors, probably related to intraspecific competition for food, territories or social space. In addition, the selected GAM model supports the idea of nonlinear effects of predators during the breeding season. In earlier communications (Lima *et al.* 2001, 2002) we described the negative dynamic influence of barn owls in this system. However, here we specify the seasonal dynamic signature of this interaction at the demographic level. The non-monotonic function (figure 4c) strongly suggests that only when predators are very abundant in relation to rodents are they able to have a negative impact on population growth rates during the breeding season.

However, during the non-breeding season, predators (specialists and generalists) had a clearer effect on leaf-eared mouse population growth rates. In particular, there was a strong negative effect of the abundance ratio of barn owls to leaf-eared mice, and a weaker negative effect of the abundance ratio of culpeo foxes to leaf-eared mice. These two effects suggest that predation may be a very important component of leaf-eared mouse dynamics, and that it has a seasonal structure, operating chiefly during the non-breeding season. In addition, the burrowing owl (a generalist predator) showed a non-monotonic function, suggesting positive effects at low and intermediate densities of rodents, but negative effects when the owls become very abundant. Burrowing owls are mainly insectivores in semi-arid Chile (Jaksic *et al.* 1997); in consequence, the positive effects on leaf-eared mice may be related to the numerical responses of this owl to insect availability, which also tends to increase during rainy years

(Fuentes & Campusano 1985). However, when burrowing owls are very abundant they have a negative impact on rodent dynamics because they also prey upon small rodents. The strong negative effect of the barn owls is not unexpected (Lima *et al.* 2002), but the seasonal structure, the nonlinearity and the logistic relationship (demand–supply ratio; see Berryman (1999)) represent a new and interesting finding, together with the fox effect.

The seasonal structure observed in the population dynamics of the leaf-eared mouse poses new and interesting challenges for understanding the factors shaping the observed numerical fluctuations. During the breeding season, population growth rates appear to be limited by food and regulated by intraspecific competition, given that predators seem able to control rodents only when they are very abundant in relation to their prey. By contrast, during the non-breeding season, predation, especially by the barn owl (a specialist predator) and the culpeo fox (a generalist predator), and to a lesser degree food availability, as indexed by rainfall, appear to determine population growth rates. Consequently, the joint effects of climate variability, seasonality and changes in the predator guild (Jaksic *et al.* 1997; Meserve *et al.* 2001) may have profound effects on the population dynamics of the leaf-eared mouse. This is because of the nonlinear effects of both specialist and generalist predators on female population growth rates, and because of the seasonal structure.

The inferred nonlinearities in predation, density dependence and climate effects, together with seasonal structure, may explain some important patterns in the observed data, such as why years with similar rainfall levels have

very different rodent densities. The similarly rainy years of 1987 and 1997, and the similarly dry years of 1989–1990 and 1995–1996, were characterized by very different demographic structures and/or population sizes. The observed seasonal structure may explain the sudden changes in survival rates from periods of relatively high survival to periods of low survival (figure 3a). Interestingly, this change in the temporal demographic structure cannot be simply related to any single external factor. It seems to be a consequence of the effects of climate, together with the nonlinear density dependence and the nonlinear effects of predators, all combined with the seasonality. We believe that the dramatic change in demographic structure observed after 1995 is a combined effect related to the strong link between climate and predator abundance/composition observed in semi-arid Chile (Jaksic *et al.* 1997). For example, the three consecutive years with above-average rainfall between 1991 and 1993 caused an increase in the abundance and diversity of predators in semi-arid Chile (Meserve *et al.* 1995; Jaksic *et al.* 1997), which may be related to the sudden change in leaf-eared mouse demography observed during 1995. As a consequence, changes in the rodent assemblage and in the predator guild (both related to climate) may have profound effects on the demography and population dynamics of the leaf-eared mouse. Basically, this is caused by a large predator to leaf-eared mouse density ratio produced by the arrival of immigrant predators, and the numerical responses of resident barn owls (related to the three consecutive years of high rainfall) may have caused the sudden decrease in mouse survival rates observed after 1994.

These elements pose new challenges for understanding rodent outbreaks in semi-arid Chile. Population dynamics may depend on the environmental history together with present mouse density, weather and predator-guild composition. The results of this study are consistent with recent reports relating nonlinear feedback structures and nonlinear climate effects (Coulson *et al.* 2001; Mysterud *et al.* 2001). We predict that the population dynamics and demography of the leaf-eared mouse will be very different in years with very similar climates (rainfall levels), owing to the combined action of climate and predator-guild composition and abundance. Consequently, we suggest that the interactions between direct and indirect climate effects, nonlinear density dependence and nonlinear predator effects, are the key elements in understanding the population dynamics of this rodent, and perhaps others.

## 5. CONCLUSIONS

We have demonstrated that the essential ingredients in the dynamics of the leaf-eared mouse are as follows.

- (i) A clear seasonal structure of population growth rates caused by different factors operating during the breeding and non-breeding seasons. There is a seasonally specific profile of factors influencing population growth rates.
- (ii) During the breeding season, we detected a first-order feedback structure characterized by a nonlinear negative function of population density for population growth rates; a linear direct effect of rainfall; and a nonlinear and non-monotonic effect of the

total predator abundance to leaf-eared mouse abundance ratio.

- (iii) During the non-breeding season, we found strong nonlinear negative effects of the barn owl abundance to leaf-eared mouse abundance ratio; also, nonlinear negative effects of the culpeo fox to leaf-eared mouse ratio; non-monotonic effects of burrowing owls; and nonlinear positive rainfall effects.

In addition, because the predator guild in semi-arid Chile is strongly influenced by ENSO events, a coupling exists between the leaf-eared mouse, climate and predators. Assuming this to be a general feature of such ecological systems, an important consequence of this interaction is that it will be difficult to predict the ecological effects of climate change in semi-arid Chile. Climate interacts with density dependence through the food-web structure (Forchhammer *et al.* 1998; Lima *et al.* 2002), an interaction that is both indirect (i.e. lagged) and nonlinear (Mysterud *et al.* 2001). Hence, unless we gain an in-depth understanding of the structure and functioning of natural population systems (and communities), the effects of global change and climatic fluctuations will not be easily predicted.

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## REFERENCES

- Andrewartha, H. G. & Birch, L. C. 1954 *The distribution and abundance of animals*. University of Chicago Press.
- Åström, M., Lundberg, P. & Lundberg, S. 1996 Population dynamics with sequential density-dependencies. *Oikos* **75**, 175–181.
- Berryman, A. A. 1999 *Principles of population dynamics and their application*. Cheltenham, UK: Stanley Thornes.
- Berryman, A. A. 2001 Functional web analysis: detecting the structure of population dynamics from multi-species time series. *Basic Appl. Ecol.* **2**, 311–321.
- Bjørnstad, O. N., Begon, M., Stenseth, N. C., Falck, W., Sait, S. & Thompson, D. J. 1998 Population dynamics of the Indian meal moth: demographic stochasticity and delayed regulatory mechanisms. *J. Anim. Ecol.* **67**, 110–126.
- Brown, J. H., Valone, T. J. & Curtin, C. G. 1997 Reorganization of an arid ecosystem in response to recent climate change. *Proc. Natl Acad. Sci. USA* **94**, 9729–9733.
- Coulson, T., Catchpole, E. A., Albon, S. D., Morgan, B. J. T., Pemberton, J. M., Clutton-Brock, T. H., Crawley, M. J. & Grenfell, B. T. 2001 Age, sex, density, winter weather, and population crashes in soay sheep. *Science* **292**, 1528–1531.
- Forchhammer, M. C., Stenseth, N. C., Post, E. & Langvatn, R. 1998 Population dynamics of Norwegian red deer: density-dependence and climatic variation. *Proc. R. Soc. Lond. B* **265**, 341–350. (DOI 10.1098/rspb.1998.0301.)
- Fuentes, E. R. & Campusano, C. 1985 Pest outbreaks and rainfall in the semi-arid region of Chile. *J. Arid Environ.* **8**, 67–72.

- Grenfell, B. T., Wilson, K., Finkenstädt, B. F., Coulson, T. N., Murray, S., Albon, S. D., Pemberton, J. M., Clutton-Brock, T. H. & Crawley, M. J. 1998 Noise and determinism in synchronised sheep dynamics. *Nature* **394**, 674–677.
- Hansen, T. F., Stenseth, N. C. & Henttonen, H. 1999 Multi-annual vole cycles and population regulation during long winters: an analysis of seasonal density-dependence. *Am. Nat.* **154**, 129–139.
- Hastie, T. & Tibshirani, R. 1990 *Generalized additive models*. London: Chapman & Hall.
- Holmgren, M., Scheffer, M., Ezcurra, E., Gutiérrez, J. R. & Mohren, G. M. J. 2001 El Niño effects on the dynamics of terrestrial ecosystems. *Trends Ecol. Evol.* **16**, 89–94.
- Jaksic, F. M. 2001 Ecological effects of El Niño in terrestrial ecosystems of western South America. *Ecography* **24**, 241–250.
- Jaksic, F. M., Silva, S. I., Meserve, P. L. & Gutiérrez, J. R. 1997 A long-term study of vertebrate predator responses to an El Niño (ENSO) disturbance in western South America. *Oikos* **78**, 341–354.
- Lebreton, J. D., Burnham, K. P., Clobert, J. & Anderson, D. R. 1992 Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* **62**, 67–118.
- Lima, M., Keymer, J. E. & Jaksic, F. M. 1999 ENSO-driven rainfall variability and delayed density dependence cause rodent outbreaks in western South America: linking demography and population dynamics. *Am. Nat.* **153**, 476–491.
- Lima, M., Julliard, R., Stenseth, N. C. & Jaksic, F. M. 2001 Demographic dynamics of a neotropical small rodent (*Phyllotis darwini*): feedback structure, predation and climate. *J. Anim. Ecol.* **70**, 761–775.
- Lima, M., Stenseth, N. C. & Jaksic, F. M. 2002 Food web structure and climate effects on the dynamics of small mammals and owls in semiarid Chile. *Ecol. Lett.* **5**, 273–284.
- Merritt, J. F., Lima, M. & Bozinovic, F. 2001 Seasonal regulation in fluctuating small mammal populations: feedback structure and climate. *Oikos* **94**, 505–514.
- Meserve, P. L. & Le Boulengé, E. 1987 Population dynamics and ecology of small mammals in the northern Chilean semiarid region. *Fieldiana Zool. New Ser.* **39**, 413–431.
- Meserve, P. L. (and 13 others) 1995 Heterogeneous responses of small mammals to an El Niño southern oscillation event in north central semiarid Chile and the importance of the ecological scale. *J. Mammal.* **76**, 580–595.
- Meserve, P. L., Milstead, B. W. & Gutierrez, J. R. 2001 Results of a food addition experiment in a north-central Chile small mammal assemblage: evidence for the role of ‘bottom-up’ factors. *Oikos* **94**, 548–556.
- Mysterud, A., Stenseth, N. C., Yoccoz, N. G., Langvatn, R. & Steinheim, G. 2001 Nonlinear effects of large-scale climatic variability on wild and domestic herbivores. *Nature* **410**, 1096–1099.
- Nichols, J. D., Hines, J. A., Lebreton, J.-D. & Pradel, R. 2000 The relative contributions of demographic components to population growth: a direct estimation approach based on reverse-time capture–recapture. *Ecology* **81**, 3362–3376.
- Nicholson, A. J. 1933 The balance of animal populations. *J. Anim. Ecol.* **2**, 132–178.
- Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P. C. & Stenseth, N. C. 2001 Ecological effects of the North Atlantic Oscillation. *Oecologia* **128**, 1–14.
- Post, E. & Stenseth, N. C. 1999 Climate change, plant phenology and northern ungulates. *Ecology* **80**, 1322–1339.
- S-PLUS 2000 *Guide to statistics*, vol. 1. Seattle, WA: MathSoft, Inc.
- Stenseth, N. C. 1999 Population cycles in voles and lemmings: density-dependence and phase dependence in a stochastic world. *Oikos* **87**, 427–461.
- Stenseth, N. C., Falck, W., Bjørnstad, O. N. & Krebs, C. J. 1997 Population regulation in snowshoe hare and Canadian lynx: asymmetric food web configurations between hare and lynx. *Proc. Natl Acad. Sci. USA* **94**, 5147–5152.
- Stenseth, N. C., Bjørnstad, O. N. & Saitoh, T. 1998 Seasonal forcing on the dynamics of *Clethrionomys rufocanus*: modeling geographical gradients in population dynamics. *Res. Popul. Ecol.* **40**, 85–96.
- Stenseth, N. C., Mysterud, A., Ottersen, G., Hurrell, J. W., Chan, K.-S. & Lima, M. 2002a Ecological effects of climate fluctuations. *Science* **297**, 1292–1296.
- Stenseth, N. C., Viljugrein, H., Saitoh, T., Hansen, T., Kittilsen, M. O., Bølviken, E. & Glöckner, F. 2002b Seasonality, density dependence and population cycles in Hokkaido voles. *Proc. Natl Acad. Sci. USA*. (In the press.)
- Stenseth, N. Chr., Kittilsen, M. O., Hjermmann, D., Viljugrein, H. & Saitoh, T. 2002c Interaction between seasonal density-dependence structures and length of the seasons explain the geographical structure of the dynamics of voles in Hokkaido: an example of seasonal forcing. *Proc. R. Soc. Lond. B* **269**, 1853–1863. (DOI 10.1098.rspb/2002.2099.)
- Turchin, P. 1995 Population regulation: old arguments and a new synthesis. In *Population dynamics: new approaches and synthesis* (ed. N. Capuccino & P. W. Price), pp. 19–40. San Diego, CA: Academic Press.
- White, G. C. & Burnham, K. P. 1999 Program MARK, survival estimation from populations of marked animals. *Bird Study* **46**, 120–138.

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