

# Population dynamics of two sympatric rodents in a variable environment: rainfall, resource availability, and predation

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**Abstract.** Precipitation plays an important role in the dynamics of species found in arid and semiarid environments. However, population fluctuations generally are driven by a combination of multiple factors whose relative contribution may vary through time and among species. We monitored fluctuations of species in three trophic levels for >17 years at a semiarid community in north-central Chile. The region is strongly affected by the El Niño Southern Oscillation, resulting in high variation in rainfall that triggers dramatic changes in food resource availability, with strong effects on upper trophic levels. We focused our analyses on the role played by endogenous and exogenous (climatic) factors on the dynamics of two important rodent species in the community, *Octodon degus* and *Phyllotis darwini*. We documented population fluctuations of several orders of magnitude in response to wet and dry episodes of different strength and duration. *P. darwini* reached similar maximum densities, regardless of the duration of high-rainfall events, whereas *O. degus* showed additive effects of multiple wet years. Time series diagnostic tools revealed oscillations with a 5-year periodicity in rainfall, which may be the cause of the same periodicity and a weak second-order signal observed in the rodent dynamics. However, the dynamics of both rodent species were dominated by strong first-order processes, suggesting an important role of direct density dependence. Intraspecific competition, expressed as the ratio of rodent density/rainfall (or food resources) explained more than two-thirds of the variation in the population rate of change, whereas less than one-third was explained by lagged rainfall (or food resources). We detected no significant effects of predation. Our results contribute to a growing number of examples of dynamics governed by the combined effect of density dependence and climatic forcing. They also reveal strong bottom-up regulation that may be common in other arid environments.

**Key words:** bottom-up regulation; density dependence; El Niño; ENSO; north-central Chile; *Octodon degus*; *Phyllotis darwini*; population dynamics; predator–prey interactions; semiarid habitat; sympatric rodent species; time series.

## INTRODUCTION

Understanding the causes underlying population fluctuations has challenged ecologists for decades. This reflects the need to understand and predict population changes and apply this knowledge to conservation and management, as well as a desire to reach a consensus on the principal drivers of ecological dynamics (e.g., Bjørnstad and Grenfell 2001). The historical debate over the relative roles of endogenous (e.g., competition, predation) and exogenous (e.g., climate, disturbance) factors in population dynamics (Nicholson 1933, An-

drewartha and Birch 1954) appears to have been resolved in a general agreement that both types of forces influence population fluctuations (Turchin 2003).

Endogenous factors are density dependent; they cause changes in a dynamic variable (e.g., the per capita growth rate) and are affected in turn by those changes. In contrast, exogenous factors are density independent and may influence the per capita growth rate, but are not affected in turn by those changes. Among exogenous factors, much attention in the last decade has been directed at the role of climatic forcing (reviewed by Stenseth et al. 2002). The dynamics of many animal species are influenced by climatic variations mediated by large-scale changes in atmospheric/oceanic conditions such as the North Atlantic Oscillation (NAO) (e.g., Post and Stenseth 1999, Forchhammer et al. 2002, Lekve et al. 2003, Vucetich and Peterson 2004, Anders and Post 2006, Berryman and Lima 2006, Sæther et al. 2006,

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Saldaña et al. 2007, Rouyer et al. 2008), the Arctic Oscillation (e.g., Aanes et al. 2002, Chan et al. 2005, Ambrose et al. 2006), and the El Niño Southern Oscillation (ENSO) (e.g., Sillett et al. 2000, Lima et al. 2002a, b, 2006, Letnic et al. 2005, Peña et al. 2005, Anders and Post 2006, Leaper et al. 2006). Increasing awareness of climate change has generated new interest in this subject due to anticipated effects of global warming on species dynamics and ecosystem function (e.g., Sæther et al. 2000, Aanes et al. 2002, Schmitz et al. 2003, Ims and Fuglei 2005). To better understand and predict changes due to global warming, we need to clarify the role played by climate on species dynamics and disentangle its interactions with endogenous factors (Stenseth et al. 2002).

Toward this end, we analyzed a long-term ecological data set on two small-mammal species from a semiarid site in north-central Chile (Meserve et al. 2003). This region is strongly affected by ENSO events, resulting in high variation in rainfall, which triggers dramatic changes in resource availability, with consequential effects on higher trophic levels (Jaksic et al. 1997, Jaksic 2001, Lima et al. 2002b, Meserve et al. 2003, Holmgren et al. 2006). Rainfall-induced changes in resources have major influences on the dynamics of small mammals in the thorn scrub of semiarid Chile (Lima and Jaksic 1998, Lima et al. 2001b, 2002b, 2006). More specifically, rainfall, together with negative feedback of population density, can explain the pronounced population fluctuations of *Abrothrix olivaceus* and *Phyllotis darwini* in this area (Lima et al. 2006). The life histories of these species are characterized by short life spans and rapid reproduction; thus, they are able to respond quickly to changes in precipitation (Meserve et al. 2003, Lima et al. 2006). Herein, we conduct a comparative analysis of the dynamics of *P. darwini* and a longer-lived, more slowly reproducing species, *Octodon degus*, also a dominant species in semiarid Chile (Meserve et al. 2003). Because it has a lower reproductive rate than *P. darwini* and exhibits delayed demographic responses to precipitation (Previtali 2006), we expect *O. degus* to respond more slowly to changes in resources than does *P. darwini*, and consequently to have a lower maximum population rate of change. Additionally, these two species differ in other aspects of their biology; *P. darwini* is a granivorous-herbivorous and nocturnal species, and lacks a clear social structure, whereas *O. degus* is an herbivorous, diurnal, and highly social species (Meserve 1981, Meserve et al. 2003). By being diurnal, *O. degus*, encounters primarily generalist predators such as foxes, seasonally active predators such as reptiles, and an array of raptors that are variably seasonal in their residence patterns; in contrast, *P. darwini* is an important prey of the more specialist owls. Therefore, we expect a stronger effect of predator-induced mortality on *P. darwini* than on *O. degus*, which for the former species could translate into second-order dynamics driven by predator-prey interactions. Additionally, predators may influence

population dynamics of prey by altering prey behavior in response to predator risk (Kotler and Holt 1989). Competition for enemy-free space may be stronger in *P. darwini* than in *O. degus* because social behavior in the latter has been demonstrated to reduce predation risk (Ebensperger and Wallem 2002).

Our goal was to test the generality of the strong and complex role of climatic effects on these two species as well as to better understand the underlying mechanisms. We compared the two species utilizing exploratory analyses of species densities with time series statistical tools. To explain dynamical features observed over 17 years in these species, we investigated the relative influence of density, rainfall, food, and predator abundance on per capita rates of population change. This enabled us to draw inferences on the roles played by intraspecific competition for food or enemy-free space on population dynamics of these species, and interpret these in the context of changing climatic conditions.

## METHODS

### Study site

Our study was conducted in Fray Jorge Forest National Park (71°40' W, 30°38' S) in coastal northern Chile. The climate is arid mediterranean (López-Cortés and López 2004) with cool, wet winters and warm, dry summers. During 1989–2005, annual rainfall averaged  $141.22 \pm 108.75$  mm (mean  $\pm$  1 SD; data from an on-site meteorological station), with strong interannual variability due to El Niño Southern Oscillation events (Fig. 1a).

Small-mammal sampling grids were located in a valley with relatively homogeneous thorn scrub vegetation, consisting of spiny drought-deciduous and evergreen shrubs, and a highly variable and seasonal herbaceous cover on a predominantly sandy substrate. The most abundant herbaceous plants in this area are *Plantago hispidula*, *Moscharia pinnatifida*, and *Schizanthus litoralis* (Gutiérrez et al. 2004).

### Small-mammal densities

We used data from monthly live-trapping of small mammals from March 1989 through January 2006 on four 0.56-ha plots. Trapping sessions were four consecutive nights (and three intervening days) using  $5 \times 5$  trapping grids (15-m station intervals), with two Sherman-type live traps (9 cm high  $\times$  11 cm wide  $\times$  30 cm long; Sherman Traps, Tallahassee, Florida, USA) per station; traps were baited with rolled oats and checked in the morning and afternoon. Captured individuals were marked with uniquely numbered ear tags and we recorded sex, reproductive condition, and body mass before releasing them. We calculated density as the mean minimum number known alive (MNKA) per ha assuming a 7.5-m buffer around trapping grids. To summarize changes in density caused by mortality and

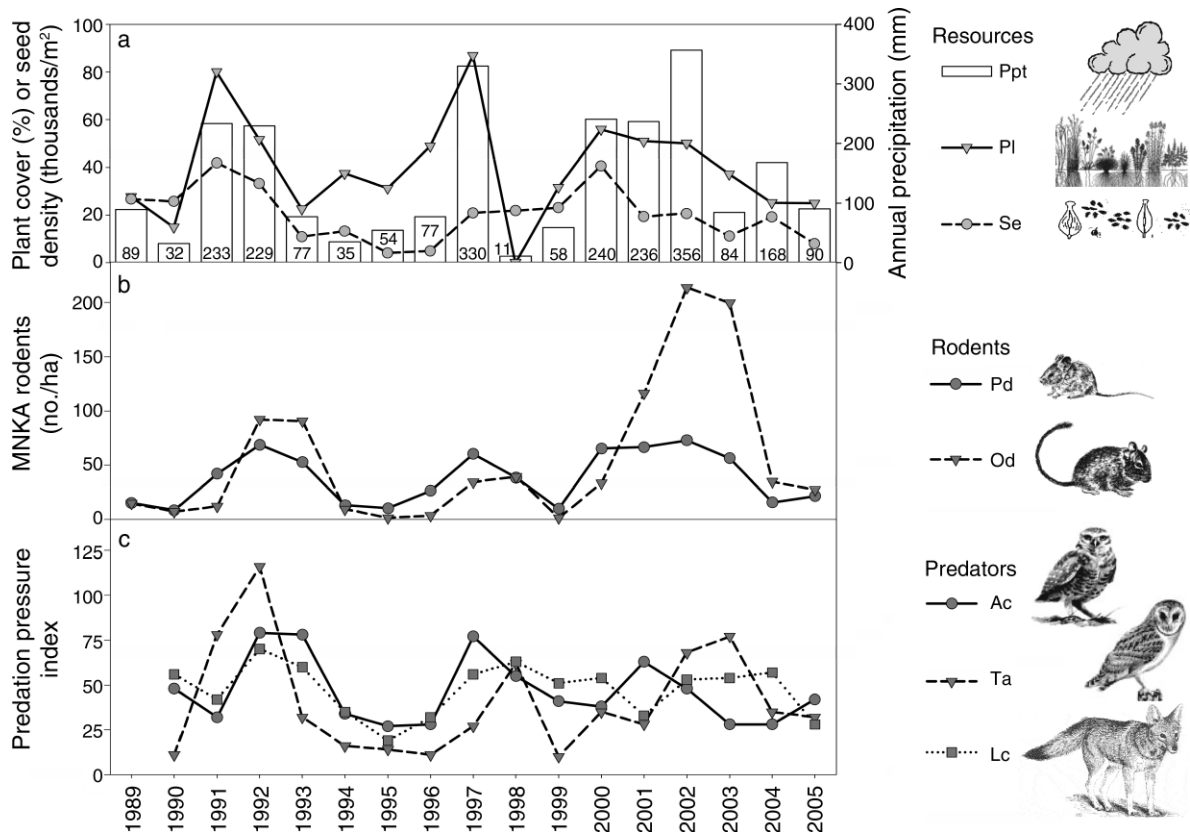


FIG. 1. Time series of three trophic levels: (a) resources, including total annual rainfall (Ppt, values in histogram bars) and annual peaks for percentage of ephemeral plant cover (Pl) and seed density (Se); (b) rodents, showing minimum number known alive (MNKA/ha) for individuals of *Phyllotis darwini* (Pd) and *Octodon degus* (Od); and (c) predators, including the annual peak of the number of pellets collected from Burrowing Owl (*Athene cunicularia*, Ac) and Barn Owl (*Tyto alba*, Ta), and the number of scent stations visited by culpeo foxes (*Lycalopex culpaeus*, Lc) during monthly censuses.

recruitment, we used the maximum density recorded between October and May.

#### Predation

To investigate the influence of predation on the dynamics of *P. darwini* and *O. degus*, we used indirect measures of the abundance of their principal predators, owls and foxes, respectively. Snakes (*Philodryas*) and lizards (mainly *Callopistes palluma*) also are predators of *O. degus*. However, we did not consider them in the analysis because we assumed that their impact is probably negligible due to their lower energetic requirements relative to those of foxes (Jaksic 1997). Starting in September 1990, we made monthly collections of owl pellets on permanent routes that included known owl roosts, perches, and burrows in a  $\sim 5$  km<sup>2</sup> area of the park enclosing the small-mammal trapping grids. We distinguished among pellets produced by Burrowing Owls (*Athene cunicularia*) and Barn Owls (*Tyto alba*), which are the two principal predators of *P. darwini* (Silva et al. 1995, Jaksic et al. 1997). We did not consider a third owl species present in the community, the Magellanic Horned Owl (*Bubo magellanicus*), because it relies heavily on *Abrocoma bennetti* as its main prey

(Jaksic et al. 1997). As an index of the predation pressure on *P. darwini*, we used the annual peak number of pellets (i.e., the greatest number of pellets collected in any sampling period) of *A. cunicularia* and *T. alba*, defining the year as extending from September through August.

We also collected data on the activity of culpeo foxes (*Lycalopex culpaeus*), the main predators of *O. degus* (Jaksic et al. 1993, 1997). We used three olfactory lines dispersed among the small-mammal trapping plots and covering an area of  $\sim 0.5$  km<sup>2</sup>. Each line consisted of 21 scent stations spaced  $\sim 100$  m apart and consisting of smoothed sand cleared of vegetation (1 m diameter) with a cotton-swabbed stick soaked in a predator lure (Bobcat #1 lure; Cronk's Outdoor Supplies, Wiscasset, Maine, USA) placed in the middle. The three lines were operated at least two days each month. Fox activity was estimated as the number of scent stations visited (e.g., scratch marks, lure stick removed) during the first two days of olfactory line surveys. For this study, as an index of the predation pressure on *O. degus*, we used the annual peak of fox activity recorded between September and August.

### Food resource availability

Ephemeral plant cover has been sampled monthly during the growing season since 1989 using the point-intercept method, with sampling points at 5-cm intervals on 10 1.5-m segments randomly located along four permanent transects/trapping grid (Gutiérrez et al. 1997). For this analysis we only considered the peak ephemeral cover estimate for the growing season, generally occurring during September–October. Every four months we collected 20 soil samples per trapping grid using a 35.4-cm<sup>2</sup> collecting tube (3 cm diameter × 5 cm depth; for more details, see Gutiérrez and Meserve 2003). We computed seed densities as the mean number of seeds/m<sup>2</sup> and used the peak for each year, which generally occurs in December (Gutiérrez and Meserve 2003). For the granivorous-herbivorous *P. darwini*, food availability was represented by seed density, ephemeral plant cover, or their combination, whereas for the herbivorous *O. degus* we considered only ephemeral plant cover. Additionally, rainfall was used as a proxy for food due to its strong correlation with availability of food resources (Gutiérrez et al. 2004).

### Analyses

We calculated the realized per capita population growth rate ( $R_t$ ) as

$$R_t = \log_e(N_t) - \log_e(N_{t-1}) \quad (1)$$

where  $N_t$  is the population density of *O. degus* or *P. darwini* at time  $t$ .

We used time series analysis to investigate patterns in the changes of rodent densities through time and in the relationship between  $R_t$  and lagged densities. This involved the use of diagnostic statistical tools that provided a quantitative description of the observed population trajectory and revealed aspects of the series, such as stationarity and the order of the dynamics (Appendix). For example, we investigated the presence of oscillatory dynamics in the time series for rodents and for rainfall and determined their periodicity using the autocorrelation function (ACF). A similar signal in both series would be indicative of rainfall being a strong driver of rodent dynamics.

We investigated the effects of potential ecological predictor variables on  $R_t$  by building a set of candidate multiple regression models of the form  $R_t = f(N_{t-1}, N_{t-2}, F_t, F_{t-1}, P_{t-1}, \dots, \varepsilon_t)$ ; where  $F_t$  and  $F_{t-1}$  represented current and lagged availability of food resources,  $P_{t-1}$  the effects of predation pressure,  $\varepsilon_t$  is an error (noise) term, and  $f$  is the functional form of the relationship between the population rate of change and the predictor variables. We fitted only models with linear relationships, given the rather small sample size (17 data points) relative to the high number of predictor variables (Burnham and Anderson 2002). We also constructed models that included nonadditive effects of the main factors expressed as the consumer/resource or demand/supply ratio

(Berryman 1999). These interactions depicted either intraspecific competition for food as the ratio of  $N_{t-1}/F_t$  or density-dependent predation pressure as the ratio of  $P_{t-1}/N_{t-1}$ . In all models, variables were first log-transformed.

We ran the set of candidate models and obtained maximum likelihood estimates for the coefficients using S-PLUS (2002). Model selection was based on Akaike's information criterion adjusted for small sample size ( $AIC_c$ ). We interpreted only models in which the difference between the  $AIC_c$  with the most parsimonious model ( $\Delta AIC_c$ ) was  $<10$  and considered a model with  $\Delta AIC_c < 2$  as equally informative as the best model (Burnham and Anderson 2002). We also calculated the Akaike weights ( $w_i$ ) to obtain a measure of the relative support for each model in the candidate set (Burnham and Anderson 2002). To assess how much of the variation in the population rate of change was explained by each covariate in the model, we calculated their contribution to the model's coefficient of multiple determination (Sokal and Rohlf 1981; see Vucetich and Peterson [2004] for an ecological example).

## RESULTS

### Food resources

During the study period, we had four high-rainfall events (1991–1992, 1997, 2000–2002, and 2004) that differed both in duration (2, 1, 3, and 1 years, respectively) and magnitude (229–233 mm, 330 mm, 236–356 mm, and 168 mm, respectively; Fig. 1a). Most of these high-rainfall events were associated with an El Niño event. Rainfall had oscillatory dynamics with a 5-year periodicity apparent in the ACF of the series (Appendix). In response to each of the high-rainfall events, ephemeral cover increased (up to 87% cover in 1997) and then declined, even during extended (multiple-year) high-rainfall events (e.g., 1992, 2001; Fig. 1a). Seed densities did not track precipitation as closely, suggesting important feedbacks between ephemeral growth and seed banks. For instance, seed bank density reached very low levels after a prolonged drought from 1993 to 1996, and then experienced a fourfold increase in response to plant growth in 1997; however, this peak density only approximated mean density over the entire study period ( $20.25 \pm 11.20$ , mean  $\pm$  SD) possibly due to depletion of the seed bank. We also observed a decline in seed density after the first year of multiyear high-rainfall events, particularly in 1992 and 2001–2002 (Fig. 1a).

### Small mammals

Both rodent species exhibited strong numerical responses to high-rainfall events. However, the timing, duration, and magnitude of those changes differed markedly. For instance, *O. degus* showed cumulative effects of multiple-year rainfall events. With a single wet year (i.e., 1997), population density increased to almost 40 individuals/ha in the following year; on the other



TABLE 1. Multiple regression models of the population rate of change ( $R_t$ ) of the rodents *Phyllotis darwini* (Pd, models 1–16) and *Octodon degus* (Od, models 17–29).

No.	Model	$r^2$	$K$	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	$w_i$
1	$R_t = \text{Pd}_{t-1} + \text{Ppt}_t$	0.64	4	38.10	15.86	0.00
2	$R_t = \text{Pd}_{t-1} + \text{Ppt}_t + \text{Ppt}_{t-1}$	0.83	5	31.04	8.81	0.01
3	$R_t = \text{Pd}_{t-1} + \text{Pl}_t + \text{Se}_{t-1}$	0.55	5	46.11	23.87	0.00
4	$R_t = \text{Pd}_{t-1} + \text{Ta}_{t-1}$	0.52	4	42.36	20.12	0.00
5	$R_t = \text{Pd}_{t-1} + \text{Ac}_{t-1}$	0.47	4	43.81	21.57	0.00
6	$R_t = \text{Pd}_{t-1} + \text{Ppt}_t + \text{Ta}_{t-1}$	0.68	4	38.48	16.25	0.00
7	$R_t = \text{Pd}_{t-1} + \text{Ppt}_t + \text{Ac}_{t-1}$	0.67	4	38.78	16.55	0.00
8	$R_t = \text{Pd}_{t-1}/\text{Ppt}_t$	0.61	3	35.43	13.19	0.00
9	$R_t = \text{Pd}_{t-1}/\text{Ppt}_t + \text{Ppt}_{t-1}$	0.69	4	35.61	13.37	0.00
10	$R_t = \text{Pd}_{t-1}/\text{Ppt}_t + (\text{Ta}_{t-1} + \text{Ac}_{t-1})/\text{Pd}_{t-1}$	0.63	4	38.66	16.42	0.00
11	$R_t = \text{Pd}_{t-1} + (\text{Pl}_t + \text{Se}_t)$	0.62	4	38.78	16.54	0.00
12	$R_t = \text{Pd}_{t-1} + (\text{Pl}_t + \text{Se}_t) + (\text{Pl}_{t-1} + \text{Se}_{t-1})$	0.88	5	26.37	4.13	0.11
13	$R_t = \text{Pd}_{t-1}/(\text{Pl}_t + \text{Se}_t)$	0.62	3	35.10	12.87	0.00
14	<b><math>R_t = \text{Pd}_{t-1}/(\text{Pl}_t + \text{Se}_t) + (\text{Pl}_{t-1} + \text{Se}_{t-1})</math></b>	<b>0.87</b>	<b>4</b>	<b>22.24</b>	<b>0.00</b>	<b>0.87</b>
15	$R_t = \text{Pd}_{t-1} + (\text{Pl}_t + \text{Se}_t) + (\text{Ta}_{t-1} + \text{Ac}_{t-1})$	0.63	5	43.25	21.02	0.00
16	$R_t = \text{Pd}_{t-1}/(\text{Pl}_t + \text{Se}_t) + (\text{Ta}_{t-1} + \text{Ac}_{t-1})/\text{Pd}_{t-1}$	0.63	4	38.58	16.35	0.00
17	$R_t = \text{Od}_{t-1} + \text{Ppt}_t$	0.50	4	61.04	31.31	0.00
18	$R_t = \text{Od}_{t-1} + \text{Pl}_t$	0.32	4	65.60	35.87	0.00
19	$R_t = \text{Od}_{t-1} + \text{Ppt}_t + \text{Ppt}_{t-1}$	0.94	5	34.80	5.07	0.07
20	$R_t = \text{Od}_{t-1} + \text{Pl}_t + \text{Pl}_{t-1}$	0.69	5	58.51	28.77	0.00
21	$R_t = \text{Od}_{t-1} + \text{Lc}_{t-1}$	0.32	4	65.73	36.00	0.00
22	$R_t = \text{Od}_{t-1} + \text{Ppt}_t + \text{Lc}_{t-1}$	0.50	5	65.66	35.92	0.00
23	$R_t = \text{Od}_{t-1} + \text{Pl}_t + \text{Lc}_{t-1}$	0.32	5	70.26	40.53	0.00
24	$R_t = \text{Od}_{t-1}/\text{Ppt}_t$	0.49	3	57.63	27.90	0.00
25	$R_t = \text{Od}_{t-1}/\text{Pl}_t$	0.29	3	62.50	32.76	0.00
26	<b><math>R_t = \text{Od}_{t-1}/\text{Ppt}_t + \text{Ppt}_{t-1}</math></b>	<b>0.94</b>	<b>4</b>	<b>29.73</b>	<b>0.00</b>	<b>0.93</b>
27	$R_t = \text{Od}_{t-1}/\text{Pl}_t + \text{Pl}_{t-1}$	0.68	4	54.13	24.40	0.00
28	$R_t = \text{Od}_{t-1}/\text{Ppt}_t + \text{Lc}_{t-1}/\text{Od}_{t-1}$	0.50	4	61.06	31.33	0.00
29	$R_t = \text{Od}_{t-1}/\text{Pl}_t + \text{Lc}_{t-1}/\text{Od}_{t-1}$	0.32	4	65.74	36.01	0.00

Notes: The coefficient of multiple determination is  $r^2$ ; the number of parameters including the intercept and the error term is  $K$ ; Akaike's information criterion corrected for small sample size is AIC<sub>c</sub>; differences in AIC<sub>c</sub> with the most parsimonious model are  $\Delta$ AIC<sub>c</sub>, and Akaike weights are  $w_i$ . Pd<sub>*t-1*</sub> and Od<sub>*t-1*</sub> are population density at time  $t - 1$  of *P. darwini* and *O. degus*, respectively; Ppt<sub>*t-k*</sub> is total annual rainfall; Pl<sub>*t-k*</sub> is ephemeral plant cover; Se<sub>*t-k*</sub> is seed density; Ta<sub>*t-1*</sub> is predation by *Tyto alba*; Ac<sub>*t-1*</sub> is predation by *Athene cunicularia*; Lc<sub>*t-1*</sub> is predation by *Lycalopex culpaeus*. The most parsimonious model for each rodent species is in boldface type.

hand, a two-year rainy event resulted in densities of 90 individuals/ha (1992–1993), and a three-year event resulted in more than 200 individuals/ha in 2002 (Fig. 1b). In contrast, densities of *P. darwini* reached similar maxima of ~65 individuals/ha regardless of the duration of rainfall events (Fig. 1b). Additionally, numbers of *P. darwini* started to decline in the first year of low productivity, whereas *O. degus* exhibited a one-year lag in their response to reduced resource availability. Another noticeable difference between the two species was in the rate of population change. Maximum rates of increase and decrease estimated for *O. degus* were 3.22 and -3.38, respectively, whereas those for *P. darwini* were 1.89 and -1.40. For *degus*, these rates of change resulted in an almost 30-fold change in density over a year, whereas those of *P. darwini* equate to a six- and fourfold increase and decrease, respectively.

The plot of small-mammal density through time showed a slight indication of a linearly increasing trend in the mean population density of both species and an increasing variance for *O. degus* (Fig. 1b). However, these indications of non-stationarity disappeared after log-transformation. Time series diagnostic tools also suggested stationarity and revealed the presence of oscillations with a periodicity of 5 years (Appendix).

With respect to the order of the dynamics, the different time series diagnostic tools suggested that the dynamics of both species are regulated primarily by first-order internal processes, but with indications of a minor role of a second-order process (Appendix).

#### Predators

The three indices of predation pressure included in this analysis showed marked temporal fluctuations coinciding with changes in small-mammal densities. Although peak estimates of all three predator species occurred during the high-rainfall events, there were noticeable differences among them (Fig. 1c). Interestingly, culpeo fox and Burrowing Owl numbers decreased following a prolonged decline in rodent density (i.e., 1994–1996; Fig. 1c), but remained high in 1999; in contrast, Barn Owl activity decreased on both occasions (Fig. 1c). The indexes for all three species were low in 2005, coinciding with low prey density.

#### Multiple regression models

For *P. darwini*, all models that included the effect of predation had  $\Delta$ AIC<sub>c</sub> > 10 (Table 1); in addition, the terms accounting for predation were not significant. Thus, predation does not contribute significantly to

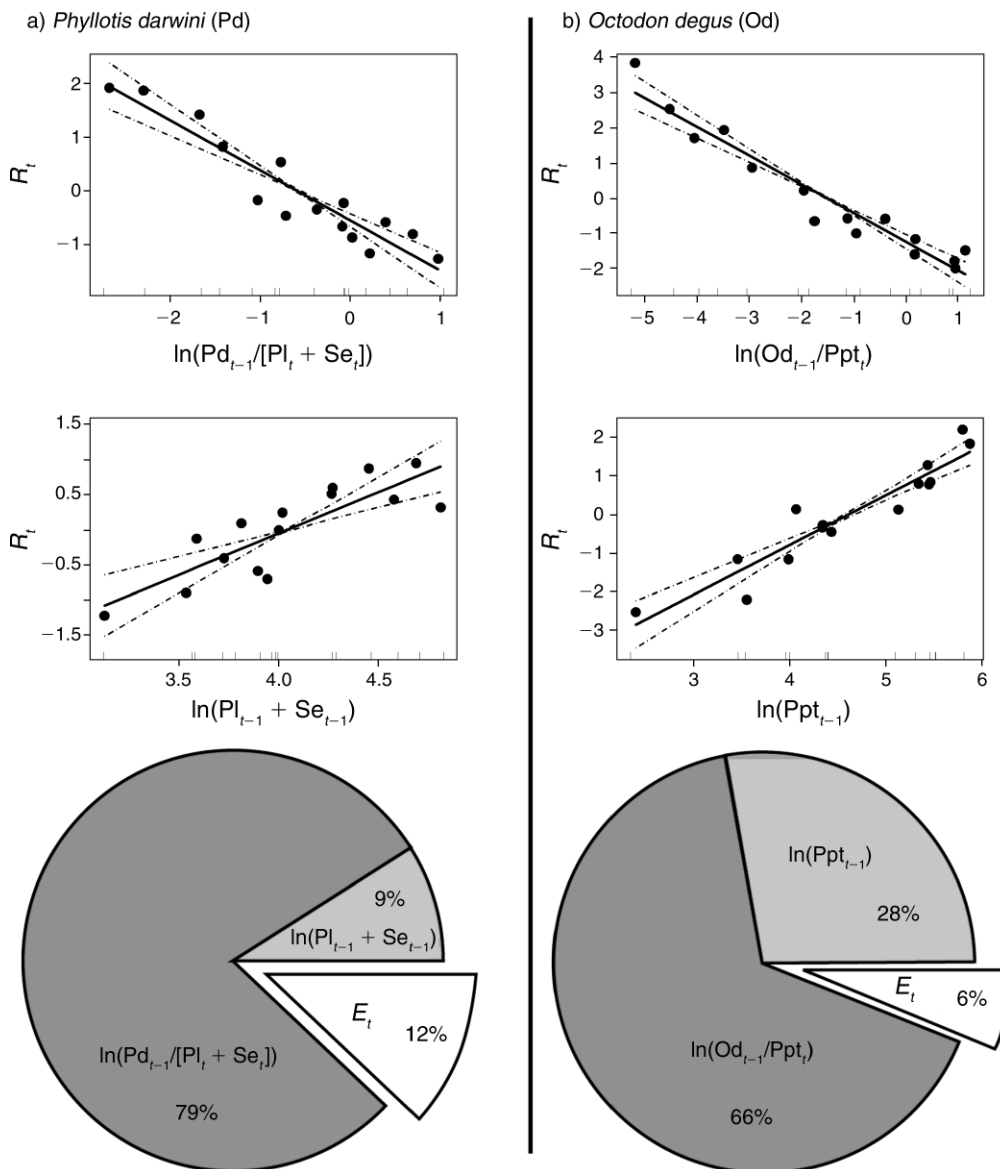


FIG. 2. Effect (partial residual plots; dash-dotted lines show 95% CI) and proportion of the variation in the population rate of change ( $R_t$ ) explained by the ratio of density to current resources (i.e., plants and seeds or precipitation) and by the lagged resources in the most parsimonious models for (a) *Phyllotis darwini* and (b) *Octodon degus*. Partial residual plots show the effect of the predictor in question while adjusting for the other terms in the model. Abbreviations are as in Fig. 1;  $E_t$  is error at time  $t$ .

explaining dynamics of this species. The most parsimonious model for *P. darwini* included a term for the interaction between population density and current food resources (plant cover and seed density combined) and a term accounting for lagged effects of food resources (Model 14, Table 1). This model had an 87% likelihood ( $w_i$ ) of being the best model of the candidate set, given the available data. The second model had considerably less support ( $w_i = 0.11$ ; Model 12 in Table 1), but also included current and lagged effects of plants and seeds combined in addition to the feedback of population density. These two models had high explanatory power, producing the highest  $r^2$  values

of all fitted models. A high percentage of the variation in the population rate of change for *P. darwini* was also explained when population density and lagged rainfall was used as a proxy for food instead of plants and seeds, and more so in an additive form than as a ratio (Model 2 vs. 9 in Table 1). In contrast, when food resources were represented by plants and seeds, the effect was better modeled as a ratio than as an additive term (Model 14 vs. 12 in Table 1). Therefore, *P. darwini* populations grew (i.e.,  $R_t > 0$ ) when the ratio of density to current food resources was small; that is, when population size was small and resources were high (Fig. 2a). On the other hand, populations declined ( $R_t < 0$ ) when density was high

TABLE 2. Maximum likelihood parameter estimates for the most parsimonious models of the population rate of change of *Phyllotis darwini* (Pd) and *Octodon degus* (Od).

Model	Term	Parameter	Value	SE
$R_t = a + b \text{Pd}_{t-1}/(\text{Pl}_t + \text{Se}_t) + c (\text{Pl}_{t-1} + \text{Se}_{t-1}) + E_t$ ( $n = 15$ , $r^2 = 0.88$ , $F = 41.88$ , $P \ll 0.0001$ )	$a$	intercept	-5.227	0.988
	$b$	current food resources	-0.933	0.103
	$c$	lagged food resources	1.172	0.237
	$E_t$	error at time $t$	0.381	
$R_t = a + b \text{Od}_{t-1}/\text{Ppt}_t + c \text{Ppt}_{t-1} + E_t$ ( $n = 15$ , $r^2 = 0.94$ , $F = 90.67$ , $P \ll 0.0001$ )	$a$	intercept	-7.129	0.691
	$b$	current precipitation	-0.817	0.066
	$c$	lagged precipitation	1.295	0.139
	$E_t$	error at time $t$	0.489	

Notes: Notation is as in Table 1. Multiple regression statistics are placed in the row with the parameter explaining most of the variation in  $R_t$ .

and current resources were low, resulting in a large ratio of  $\text{Pd}_{t-1}/(\text{Pl}_t + \text{Se}_t)$ . Additionally,  $R_t$  values were influenced in a linear and positive way by the amount of food available to individuals in the previous year (Fig. 2a). The ratio of population density to current food resources explained most of the variation in  $R_t$  values for *P. darwini* (Table 2, Fig. 2a). The additive lagged effect of food availability in the previous year was also influential, although this explained only 9% of the variation in  $R_t$  (Table 2, Fig. 2a).

We documented similar results for *O. degus*. Predation pressure from foxes did not have a significant effect on the population rate of change in any of the models in which this parameter was included. The weight of evidence in support of the best model for *O. degus* was high among the candidate models ( $w_i = 0.93$ ; Table 1). The next model in terms of likelihood (Model 19 in Table 1) had considerably less support ( $w_i = 0.06$ ), but still deserves some consideration ( $\Delta\text{AIC}_c < 6$ ). All other models had virtually no support (Akaike weight  $\approx 0.00$ ,  $\Delta\text{AIC}_c > 10$ ; Table 1). Therefore, variation in  $R_t$  for *O. degus* was best explained by density dependence and by the current and lagged availability of resources, which were better represented by rainfall than by ephemeral plant cover (e.g., Models 26 vs. 27; Table 1). The overwhelming support of the best model indicated that the effects of rainfall-driven changes in resource availability on the population rate of change were better expressed as the ratio of degu density/rainfall, suggesting high intraspecific competition for resources. Positive  $R_t$  values occurred when population size was small and current rainfall was high (low ratio of  $\text{Od}_{t-1}/\text{Ppt}_t$ ), and also when rainfall of the previous year was high (Fig. 2b). Conversely, population declines ( $R_t < 0$ ) were observed when density was high and rainfall in the current or previous year was low (Fig. 2b). The negative effect of the ratio was highly influential and explained 66% of the variation in population change for *O. degus* (Table 2, Fig. 2b). Another 28% was explained by the positive lagged effect of prior rainfall (Fig. 2b).

## DISCUSSION

During 17 years of intensive sampling in semiarid Chile we observed large fluctuations in rodent density associated with rainfall. High-rainfall events triggered large increases of food resources to which populations of *P. darwini* responded by becoming up to six times larger, and those of *O. degus* increased as much as 30-fold in a single year. This increase in degu numbers is surprising, given their low reproductive rate, and can only be explained by immigration from more mesic habitats of the park (e.g., riverine shrublands; Milstead et al. 2007). The duration of this study enabled the detection of different responses of *O. degus* and *P. darwini* to rainfall events that differed in length. *O. degus* showed cumulative increases in population size over consecutive wet years, whereas *P. darwini* always reached a similar maximum population size (Fig. 1). For both species, we detected strong negative effects of intraspecific competition, but the difference in how the species responded to multiple wet years may be due to the different drivers of their dynamics.

The dynamics of these dominant rodent species in the community are driven by changes in food resources, represented by ephemeral plant growth and seeds for *P. darwini*, and rainfall for *O. degus* (Fig. 3). Variation in food availability/rainfall had strong current and lagged effects on rodent dynamics. On the other hand, predation had virtually no detectable effect on either species. This result is not surprising for degus, given the benefits of group living (Ebensperger and Wallem 2002) and temporal variation in numbers of their generalist predators. However, it is surprising that owls, particularly the more specialized Barn Owls, did not have an effect on the dynamics of *P. darwini*. Owls influence the demography of *P. darwini* elsewhere in northern Chile (Lima et al. 2001a). At Fray Jorge, their destabilizing effects could be dampened by switching to insects (i.e., Burrowing Owls), or by being nomadic (i.e., Barn Owls). The presence of Barn Owls in the park declined in response to a decrease in prey availability; conversely, Burrowing Owls remained in the park even when rodent

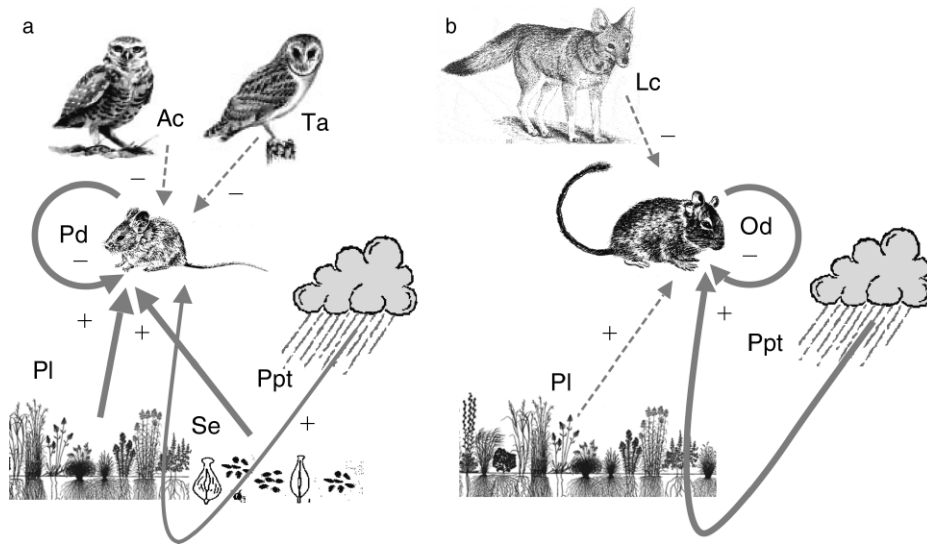


FIG. 3. Conceptual scheme of the interaction and effects of different factors that can influence the dynamics of (a) *Phyllotis darwini* (Pd) and (b) *Octodon degus* (Od). Factors include food resources [ephemeral plants (PI) and seeds (Se)], the predators *Athene cunicularia* (Ac), *Tyto alba* (Ta), and *Lycalopex culpaeus* (Lc), rainfall (Ppt), and feedback from intraspecific competition (circular loops). Dashed lines indicate factors that were hypothesized to play a role but were not found to have a significant effect ( $AIC_c > 10$ ). Solid lines indicate factors that were found to have a significant effect ( $AIC_c < 10$ ), and their thickness symbolizes the strength of the effect.

densities were low for short periods of time (e.g., 1999; Fig. 1). Overall, our results suggest that predation on these rodent species plays only a minor role, in contrast to the strong regulation exerted by energy and food requirements.

We found evidence of important effects of intraspecific competition on the population rate of change, as reflected by the improved fit of models with the interaction between density and resource availability. For both species, rainfall-driven changes in food availability affected population rates of change non-additively, as a demand/supply ratio (Royama 1992, Berryman 1999). The high explanatory power of this form of interaction between rainfall and intraspecific competition was documented previously for *P. darwini* at this site (Lima et al. 2006). We show that the same nonadditive relationship holds when using more direct measurements of food availability, such as seed density and ephemeral plants, instead of total annual precipitation. In contrast, ephemeral plants were not a better predictor of the population rate of change for degus than was rainfall; this may be due to the inclusion of shrub foliage and a more restricted number of ephemeral plants in the diet of *O. degus* (Meserve 1981). An alternative explanation is that rainfall accounts not only for changes in the quantity of plant growth, but also in their quality by altering the composition of local plant assemblages (Gutiérrez et al. 2004). On the other hand, rainfall and food availability may represent different signals for rodents during prolonged wet periods. Seed density and plant cover declined during a second year of high rainfall (e.g., 1992 and 2001; Fig. 1a). The increase in numbers of consumers could be the cause of this

decline. Additionally, plant cover could be reduced due to depletion of soil nutrients (Gutiérrez and Whitford 1987). In any case, additional increases in degu populations during consecutive wet years was better explained by high precipitation recorded in consecutive wet years than by changes in plant cover, whereas the stabilization on the growth of *P. darwini* was better explained by the reduction of food availability and increased competition during those years.

Our results indicate that most of the variation in the population rate of change can be accounted for by direct density-dependent processes, whereas one-third or one-tenth of the variation in the  $R_t$  values of *O. degus* and *P. darwini*, respectively, was explained by delayed effects of resources. Delayed effects of plants on the dynamics of small mammals have also been found elsewhere (e.g., Batzli 1996, Ernest et al. 2000, Turchin and Batzli 2001, Báez et al. 2006). The mechanism may involve delayed regeneration of vegetation after heavy consumption during the peak population phase (Oksanen and Oksanen 1992; but see Klemola et al. 2000) or lethal effects of plants on small mammals caused by toxic secondary compounds produced in response to herbivory (Seldal et al. 1994, Jensen and Doncaster 1999). In our study area, herbivory by small mammals has significant impacts on certain plant species (e.g., *Plantago hispidula*, *Adesmia bedwellii*; J. R. Gutiérrez, unpublished data). However, plants appear to recover rapidly during high rainfall years. We believe that the delayed effects of oscillating resources may be linked to the quasi-periodic El Niño episodes. This lag may be the underlying cause of the apparent second-order processes



in rodent dynamics suggested by some of the diagnostic tools used here (see Appendix).

Time series diagnostic tools should be interpreted with caution (Berryman and Lima 2007). Apparent second-order feedback effects may result from forcing by an autocorrelated exogenous factor (Williams and Liebhold 1995) or by strong nonlinearity of a first-order process (Berryman and Lima 2006). However, spurious second-order dynamics are less likely to be found with relatively high values of the maximum per capita rate of change (Berryman and Turchin 1997). During the period analyzed here, *P. darwini* and *O. degus* showed maximum *R* values of 1.89 and 3.22, respectively, which are within the ranges for other species considered to have sufficiently high *R* values to diminish the probability of encountering this problem (Berryman and Turchin 1997). Nevertheless, the results of time series analysis revealed some patterns suggesting second-order dynamics. We believe that the explanation behind the observed patterns is related to the strong climatic forcing caused by quasi-periodic ENSO in this system. We found a signal for a periodicity of 5 years in the oscillations of rainfall that may be the driver of the same periodicity observed in the rodent dynamics. In addition to the influence of periodicity of rainfall oscillations, Lindström (1999) argued that weather variation can also generate delayed effects due to its influence on the early development of entire cohorts transmitted through maternal effects. Overall, however, our results indicate that the dynamics of these species are dominated by first-order mechanisms, leaving room only for a possible weaker role of second-order processes.

Our study supports the contention that interaction between climate and density-dependent factors may be a widespread phenomenon (Stenseth et al. 2002, 2004), as reported by other authors (e.g., Grenfell et al. 1998, Coulson et al. 2001, Jacobson et al. 2004, Berryman and Lima 2006, 2007, Lima et al. 2006). The relatively simple dynamics of the species studied here, dominated by density dependence and climatic forcing, makes them particularly suitable to further investigation of the relationship between climate and population dynamics. It will be particularly challenging to forecast future population changes due, on the one hand, to limitations of ENSO predictability (Latif et al. 1998) and, on the other, to uncertainty about the effects of global warming on the frequency of El Niño events (Cane 2005).

Moreover, our long-term study overwhelmingly supports the role of strong bottom-up regulation for these rodent species, whereas top-down forces were relatively insignificant (Fig. 3). Further supporting a lack of top-down control in this system, dynamics of small mammals in predator exclusion plots are very similar to those in control plots (Previtali 2006) with weak differences apparent only ephemerally (Meserve et al. 2003). The dominance of bottom-up control may be widespread in arid and semiarid ecosystems; this has been tested for plants (Baéz et al. 2006), and observed in

rodents (Brown and Heske 1990, Ernest et al. 2000, Jaksic 2001, Letnic et al. 2004) and their predators (Jaksic et al. 1997, Letnic et al. 2005). Predicting the effects of global climate change on the nature of ecosystem control and hence on community dynamics remains a major challenge for community ecology.

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## APPENDIX

Time series diagnostic tools (*Ecological Archives* E090-138-A1).