El Niño–Southern Oscillation–Driven Rainfall Variability and Delayed Density Dependence Cause Rodent Outbreaks in Western South America: Linking Demography and Population Dynamics

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abstract: It is well known that some rodent populations display dramatic density fluctuations in semiarid regions of western South America after the unusual rainfall levels associated with El Niño–southern oscillation (ENSO) disturbances. These correlated phenomena have led some ecologists to believe that rodent outbreaks are determined solely by density-independent factors (e.g., rainfall regime). However, demographic studies have detected strong delayed density-dependent effects in one of the most irruptive rodent species, the leaf-eared mouse *Phyllotis darwini*. We tested the effects of rainfall and delayed density-dependent factors by constructing a structured model based on demographic data estimated from a capture-mark-recapture study of this species in Chile. A model including both rainfall and delayed density-dependent effects predicts the observed population dynamics rather accurately over a 10-yr period. Interestingly, small changes in model parameters result in large changes in model dynamics, which strongly suggests that local variations in demographic features are important in explaining the asynchronous pattern in outbreak occurrences. These findings suggest that inextricably intertwined endogenous and exogenous forces cause rodent outbreaks in western South America. The former are characterized by delayed nonlinear feedbacks, whereas the latter are characterized by the positive effects of the El Niño phases and the negative effects of the La Niña phases of the ENSO disturbance.

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A central theme in population ecology is to understand the spatiotemporal dynamics of populations. Because the dynamics of natural populations are a mixture of deterministic and stochastic forces, the chief aim is to determine both the density-dependent structure and the density-independent factors that affect demographic processes (Royama 1992). The relative importance of density dependence and density independence in determining population dynamics has been a key issue long debated by ecologists (Nicholson 1933; Andrewartha and Birch 1954). However, a synthesis seems to have arisen, merging theoretical and empirical approaches (Royama 1992; Sharov 1992; Turchin 1995; Stenseth et al. 1996*a*; Leirs et al. 1997). Indeed, a full understanding of the numerical fluctuations in animal populations can only be reached by connecting population dynamic patterns with underlying demographic processes (Leirs et al. 1997).

The dramatic fluctuations displayed by some small mammal populations have fascinated ecologists for a long time (Elton 1924; Elton and Nicholson 1942; Moran 1953). A clear example is the increasing attention and research aimed at understanding the multiannual cyclic dynamics exhibited by some boreal microtine populations (Hansson and Henttonen 1988; Stenseth and Ims 1993; Norrdahl 1995). While some authors have emphasized the role of empirically based biological mechanisms (Krebs and Myers 1974; Ostfeld et al. 1993), others have focused on more theoretical approaches (Akçakaya 1992; Hanski et al. 1993; Bjørnstad et al. 1995; Turchin 1995; Stenseth et al. 1996*b*). Although mechanistic explanations provide explicit biological causes, phenomenological approaches (e.g., time-series models) have the advantage of highlighting the general structure of population dynamics (Berryman 1991; Turchin 1995). Recently, the combination of theoretical

and empirical approaches using empirically based models (Stenseth et al. 1996*b*; Turchin and Hanski 1997; Turchin and Ostfeld 1997) has made exciting inroads into population ecology. In particular, the integration of demography and population dynamics through use of statistical models applied to capture-mark-recapture (CMR) data for developing structured-population dynamics models represents one of the most promising tools for working toward an understanding of rodent fluctuations (Leirs et al. 1997).

In contrast to the many studies on northern rodents, few studies have been conducted on population dynamics of Neotropical small mammals (see O'Connell 1986), in spite of several species showing dramatic fluctuations in their numbers (Rodriguez 1993). For instance, ecologists have long been aware that some rodent populations undergo outbreaks in semiarid regions (Pearson 1975; Péfaur et al. 1979; Fuentes and Campusano 1985; Meserve and Le Boulengé 1987; Jiménez et al. 1992; Jaksic et al. 1996) and in temperate rainforests (Philippi 1879; Hershkovitz 1962; Murúa and González 1985; Murúa et al. 1986) of western South America. Further, Fuentes and Campusano (1985), Jiménez et al. (1992), Meserve et al. (1995), and Jaksic et al. (1997) have shown that irruptions in semiarid Chile are correlated with years of unusually high rainfall and increased primary production related to the occurrence of El Niño–southern oscillation (ENSO) disturbances. Consequently, it is widely believed that density-dependent factors do not affect these population systems and that density-independent factors are the drivers (i.e., rainfall regimes; Meserve and Le Boulengé 1987). Nevertheless, the ultimate causes of rodent outbreaks and their relationships with large-scale global disturbances such as ENSO are as of yet poorly understood (Lima and Jaksic 1999*a*). Moreover, Lima and Jaksic (1998*b*) detected delayed density-dependent effects from time-series analyses in one of the most irruptive rodents involved in the outbreaks (*Phyllotis darwini*). The same authors reported both delayed density-dependent and density-independent (rainfall) effects on reproductive parameters of that rodent species (Lima and Jaksic 1998*a*). Thus, these recent results suggest that rodent outbreaks in semiarid western South America may be the result of density-dependent and density-independent factors operating together.

The aim of this article is to develop a population dynamic model based on empirical information on demography for an irruptive rodent species, the leaf-eared mouse, *P. darwini*. First, we describe the demographic data. Second, we apply statistical models to investigate time-specific variation, density-dependent effects, and rainfall effects on survival probabilities. Third, we incorporate the demographic information in a stage-structured population dynamic model (Tuljapurkar and Caswell 1997) and explore

the resulting dynamic behaviors. Fourth, we compare the model predictions with the observed data. Finally, we discuss the main implications of our results for understanding rodent outbreaks in semiarid western South America.

Demographic Data

Study Area

The study site was Las Chinchillas National Reserve, at Aucó (31°30′S, 71°06′W), 300 km north of Santiago. Located in the coastal ranges, the reserve has a rugged topography with numerous ridges dissected by deep ravines and with few flat areas. Elevation ranges from 400 to 1,700 m. The climate is semiarid, with scarce rainfall concentrated in the winter months. Mean annual precipitation is 175 mm but with high interannual variability (Jaksic et al. 1996). The vegetation is a thorn scrub, but the species composition depends on solar exposure (Jiménez et al. 1992). Slopes that face to the north (equatorial) receive higher solar radiation and have sandy soils with scattered gravel patches and rock outcrops. Because of the xeric character of these slopes, grasses are scarce (mainly *Nassela* sp. and *Stipa* sp.) but cacti (*Trichocereus* sp., *Tephrocactus ovatus*), bromeliads (*Puya berteroniana*), and sclerophyllous shrubs (*Bahia ambrosioides*, *Cordia decandra*, *Bridgesia incisaefolia*, *Flourensia thurifera*) are abundant. In contrast, slopes that face to the south (polar) receive less solar radiation and thus are more mesic; soils appear to contain more organic matter, grasses are more abundant, there are no cacti or bromeliads, and a different assemblage of shrubs is present (*Adesmia* sp., *Porlieria chilensis*, *Colliguaya odorifera*, *Proustia* sp.). Thus, differences in species composition, physiognomy, and cover of the vegetation between solar exposures are the major features that determine spatial structure (xeric vs. mesic habitats).

Trapping Procedures

Four subpopulations of *Phyllotis darwini* were monitored through mark-recapture procedures on two opposite-facing slopes in two creeks, 2 km apart. Trapping was performed from October 1987 to January 1992, alternating between creeks on a monthly basis. Four trapping grids were used: two in opposite-facing slopes of El Grillo Creek (26 trapping sessions) and two in El Cobre Creek (26 trapping sessions). From July 1992 to April 1996, live trapping was relaxed to every 3 mo (i.e., in January, April, July, and October), and from April 1996 to February 1998, trapping was done monthly. From 1992 to 1998, trapping was only carried out in the two subpopulations of El Cobre Creek. Each 7 × 7 (stations) trapping grid had stations separated by 15 m, thus covering an area of 105 m ×

105 m (including a boundary strip of 7.5 m), or 1.1 ha. Grids were equipped with one Sherman trap in each station. Trapping sessions occurred every other month in each creek, with traps activated simultaneously on the equatorial- and polar-facing slopes of a given creek during five consecutive nights. All traps were kept permanently in the field and closed when not in use. Traps were baited with rolled oats and checked every morning. Each individual captured was marked with a metal ear tag and the species, body mass, reproductive condition (females were classified as immature, perforated vagina, pregnant, lactating), and sex was determined.

The Species

The species we studied was the leaf-eared mouse *P. darwini* (Meserve and Le Boulengé 1987; Jiménez et al. 1992). This species is a granivorous-folivorous rodent with an average adult weight of about 50 g. It is widely distributed in semiarid Chile (Meserve and Le Boulengé 1987). Breeding of the leaf-eared mouse is markedly seasonal; it starts in October and lasts until January or February (Meserve and Le Boulengé 1987). Females produce two or three litters with an average size of about 5.2 (Fulk 1975; Meserve and Le Boulengé 1987). In the laboratory, females become sexually mature at approximately 2–3 mo of age (Lima et al. 1997).

Capture-Recapture Models

Trapping results were analyzed according to Pollock's "robust design" (Pollock 1982; Nichols and Pollock 1990). We divided the total sampling program into several primary periods, which in turn were divided into several secondary-sampling periods. The time between primary periods (2 mo) was sufficiently long to permit demographic processes to occur (death, birth, and dispersal). The time between secondary sessions (1 d) was sufficiently short to assume that demographic processes were negligible (see Nichols and Pollock 1990). We applied open population models (Lebreton et al. 1992) to data collected during the primary periods to estimate survival and capture probabilities and closed population models (Otis et al. 1978) to data collected during the secondary periods to estimate population size.

We used the program MARK (White 1998) to estimate survival and recapture probabilities. We used the maximum-likelihood method to estimate model parameters. For the primary period data (survival assessment) we estimated probability of survival (ϕ) and of capture (p). For the secondary period (population size assessment) we estimated the probability of first capture (p), the probability of recapture (c), and the population size (N). The pro-

cedure used to select a model to compute these population estimates is explained in detail by Lebreton et al. (1992) for open population models. We used the sine function (White 1998) as a link function in all probabilistic models, except when covariates were included for the open population models, when we used the logit function (Lebreton et al. 1992). Both link functions have the advantage of constraining the estimates of ϕ and p within the interval (0–1) (Lebreton et al. 1992).

The criterion for selecting a model was based on parsimony and biological significance of the variables and factors included therein. To choose a particular model we used the small-sample quasi-likelihood version of Akaike's information criterion (QAIC$_c$; White 1998). To test specific factors between nested models we used likelihood ratio tests (LRT; Lebreton et al. 1992). Population sizes were estimated for juveniles (individuals <35 g) and adults using closed population models. Closed models were used to estimate population size and to test time variation on the probability of first capture ($p(t)$) and the probability of recapture ($c(t)$; White 1998).

Survival processes were modeled to test specific factors, such as time (t) and seasonality (s). To the best model selected we tested the effects of adding the following covariates: density dependence (dd); dd 0 (population size at the moment of the first capture), dd 2 (population size 2 mo before the first capture of the primary sampling period), dd 4 (population size 4 mo before the first capture), dd 6 (population size 6 mo before the first capture), dd 8 (population size 8 mo before the first capture), dd 10 (population size 10 mo before the first capture), and dd 12 (population size 12 mo before the first capture). Also, we tested the effects of rainfall (based on the rainfall during the 3 mo previous to the trapping period). We removed the first year of data (October 1987–September 1988) in order to test the effects of delayed density dependence together with the other factors. We tested the statistical models separately for adults and juveniles. To test these covariates we used an analysis of deviance (ANODEV; White 1998). This analysis provides a means of evaluating the impact of a covariate by comparing the amount of deviance explained by the covariate against the amount of deviance not explained by this covariate (McCullagh and Nelder 1989; Skalski et al. 1993).

During the period of study used to develop the model (October 1988–January 1992), we made 2,406 captures of 590 individual *P. darwini*. The population trajectories in the two creeks are shown in figure 1. During many trapping periods, the numbers of individuals caught at secondary periods were too small for applying closed models. At El Cobre Creek, LRT tests selected a model with constant probability of first capture, and constant recapture probability ($p(.)$ $c(.)$ $N(.)$) during 12 trapping periods,
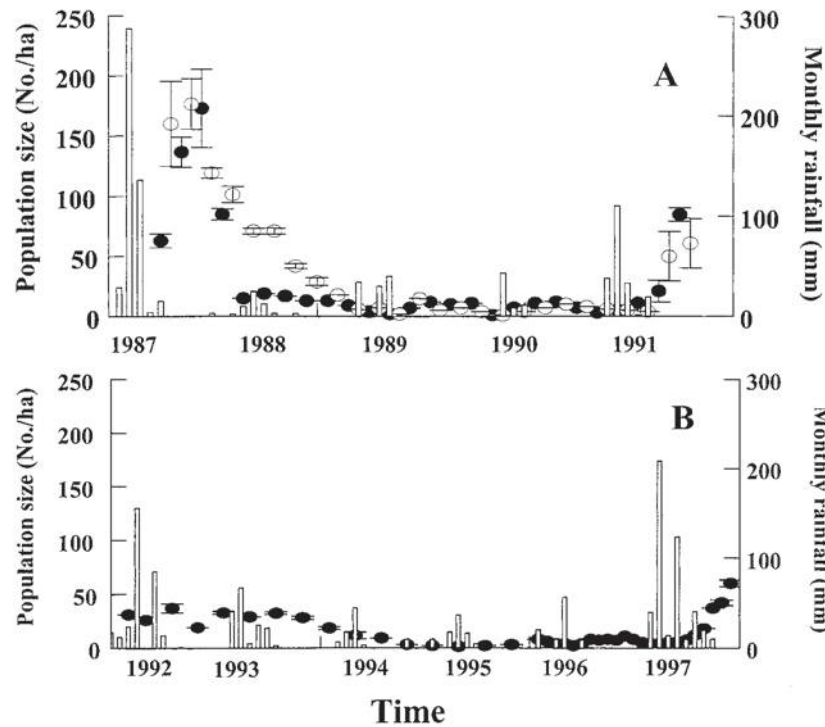
Figure 1: Monthly rainfall (*columns*) and population size (closed model estimates) of *Phyllotis darwini* in Aucó, Chile. *A*, Data used for statistical analyses: El Cobre Creek (*filled circles*) from October 1987 to December 1991 and El Grillo Creek (*open circles*) from November 1987 to January 1992. *B*, Data used for testing the population dynamic model from El Cobre Creek (July 1992 to February 1998). Vertical bars are ±1 SEM.

while a model with time variation in first capture probability ($p(t)$ $c(.)$ $N(.)$), recapture probability ($p(.)$ $c(t)$ $N(.)$), or both ($p(t)$ c(t) $N(.)$) was selected during 13 periods. However, at El Grillo Creek the constant ($p(.)$ $c(.)$) $N(.)$) model was selected during eight trapping periods, while time variation models in first capture and recapture probabilities were selected during two trapping periods.

The results of applying statistical models to adults (individuals captured as adults the first time) showed the importance of time variation in survival and capture rates (see table 1). The goodness-of-fit test yielded no evidence of lack of fit ($\chi^2 = 12.01$, df = 25, $P = .98$) for the full-time variation model. When compared with the constant survival model, the full-time variation model in survival rates was significantly better (likelihood ratio $\chi^2 = 36.62$, df = 18, $P = .01$). Although the full-time model was significantly different compared with a reduced model including seasonal-time variation ($\chi^2 = 23.48$, df = 13, $P = .04$), the latter was more parsimonious (see table 1, AIC$_c$). The seasonal time-specific survival model assumes a constant survival rate for each month between years, but different survival rates among months within a year. It is important to note that elsewhere we (Lima and Jaksic 1999*c*) documented strong seasonal effects on survival

rates. The ecological model including seasonality and delayed density dependence of 8 mo in survival rates was the most parsimonious according to the AIC$_c$ values, but models including delayed density dependence of 4 and 6 mo were also significant (table 1). In fact, we found a significant negative delayed density dependence of 8 mo (ANODEV, $F = 20.68$, df = 1, 3, $P = .019$), 4 mo (ANODEV, $F = 19.66$, df = 1, 3, $P = .021$), and 6 mo (ANODEV, $F = 16.88$, df = 1, 3, $P = .026$) in seasonal survival rates. In contrast, we found marginal effects of 10-mo lag (ANODEV, $F = 10.28$, df = 1, 3, $P = .049$), and nonsignificant effects of direct density dependence (ANODEV, $F = 0.99$, df = 1, 3, $P = .39$), and delayed density effects of 2 mo (ANODEV, $F = 1.39$, df = 1, 3, $P = .32$) and 12 mo (ANODEV, $F = 3.18$, df = 1, 3, $P = .17$). In the same vein, rainfall during the previous 3 mo did not show any significant effects on adult survival rates (ANODEV, $F = 0.33$, df = 1, 30, $P = .60$). In sum, we conclude that seasonality and delayed density dependence around 6 mo influence adult survival in the leaf-eared mouse.

Juvenile data (individuals <35 g without external signs of reproductive activity when captured the first time; see Meserve and Le Boulengé 1987) were treated as a different

Table 1: Statistical models for adult survival probabilities

Model	AIC$_c$	Number of parameters	Deviance
{ϕ(seas. + dd 8 mo)p(.)}	548.29	8	92.02
{ϕ(seas. + dd 4 mo)p(.)}	548.37	8	92.10
{ϕ(seas. + dd 6 mo)p(.)}	548.63	8	92.36
{ϕ(seas. + dd 10 mo)p(.)}	549.69	8	93.43
{ϕ(seas. + dd 12 mo)p(.)}	553.36	8	93.68
{ϕ(seas. + dd 2 mo)p(.)}	556.15	8	99.88
{ϕ (seas. + dd 0 mo)p(.)}	557.13	8	100.86
{ϕ(seas.) p(.)}	558.56	7	104.38
{ϕ(seas. + di)p(.)}	559.23	8	102.96
{ϕ(.)p(.)}	561.44	2	117.52
{ϕ(t)p(.)}	563.06	20	80.90
{ϕ(t)p(t)}	582.88	38	58.57

Note: The statistical models tested are denoted according to each model-specific variation in survival (ϕ) and capture (p) probabilities; t denotes full time-specific variation; (seas.) denotes seasonal time-specific variation; (.) denotes no time-specific variation (a single value estimated for all time periods); (dd 0 mo) denotes direct density-dependent effects on survival rates; (dd 2–12 mo) denotes delayed density-dependent effects on survival rates at different lags; (di) denotes density-independent (rainfall) effects on survival rates. AIC is the estimated Akaike's information criterion: lower values indicate more parsimonious models.

group and analyzed alone. We estimated juvenile survival rate only from the 2 mo following initial capture as a juvenile because the matrix model assumes that juveniles mature within a 2-mo period (see "The Stage-Structured Population Model"). In addition, the goodness-of-fit test yielded no evidence of lack of fit ($\chi^2 = 12.14$, df = 10, $P = .28$) for the full-time variation model results of the statistical models applied to juvenile CMR data. The seasonal model was the most parsimonious (AIC$_c$; see table 2). The likelihood ratio tests showed that full-time variation model on juvenile survival (likelihood ratio $\chi^2 = 9.84$, df = 14, $P = .77$) was not significant in relation to the seasonal variation model. Also, the full temporal variation model in recapture rates was not significant compared with a constant model (likelihood ratio $\chi^2 = 14.49$, df = 12, $P = .27$).

Elsewhere, we (Lima and Jaksic 1998*a*) determined that the annual accumulated precipitation level and the population size the previous year determined the fraction of reproductive females during the breeding season in *P. darwini*. However, the number of offspring produced by a reproductive female was negatively correlated with population size the previous year (Lima and Jaksic 1998*a*). In sum, two ecological factors (delayed density dependence and rainfall) seem to influence both reproduction and survival in *P. darwini*.

The Stage-Structured Population Model

A time-dependent projection matrix is the starting point of our research on the population dynamics of *Phyllotis darwini*. The transition matrix considers two stage classes (juvenile and adult females) and a time interval of 2 mo (same as the trapping bouts during 1987–1992). Therefore, six time steps represent a year. The basic assumption of this model is that juveniles become adult within a time step (2 mo), which is reasonable according to growth patterns reported by Lima

Table 2: Statistical models for juvenile survival probabilities

Model	QAIC$_c$	Number of parameters	Deviance
{ϕ(seas.)p(.)}	300.41	7	285.93
{ϕ(.)p(.)}	310.55	2	306.49
{ϕ(.)p(t)}	321.85	14	292.00
{ϕ(t)p(.)}	322.28	21	276.09
{ϕ(t)p(t)}	393.24	47	276.09

Note: The statistical models tested are denoted according to each model-specific variation in survival (ϕ) and capture (p) probabilities; t denotes full time-specific variation; (.) denotes no time-specific variation (a single value estimated for all time periods); (seas.) denotes seasonal variation (only within-year variation). QAIC$_c$ is the quasi-likelihood version of Akaike's information criterion.

et al. (1997). However, because there is a strong seasonal structure in the survival and reproductive rates, the matrix model incorporates this intraannual time structure in the demographic parameters. The basic matrix structure can be expressed as

$$\begin{bmatrix} 0 & B(t) \\ S_J(t) & S_A(t) \end{bmatrix},$$ (1)

where $B(t)$ is the bimonthly net reproductive rate per adult female. A seasonal indicator that characterizes the seasonality of the breeding period composes this rate. The value of $B(t)$ is lower during three time periods of the year (corresponding to the months of May, July, and September) and higher during the remaining three time steps (November, January, and March; see Meserve and Le Boulengé 1987; Jaksic et al. 1997). The seasonal indicator is representative of the fraction of currently reproductive females and is multiplied by the female litter size to express the net reproductive rate per adult female. The variable $S_J(t)$ is the seasonal (within-year variation) survival rate of juveniles estimated by the seasonal model in table 2. Lastly, $S_A(t)$ is the seasonal adult survival (see table 1).

Density-Independent Effects on the Demographic Processes

In a previous study, we found a positive linear relationship between the fraction of reproductive females and the annual accumulated rainfall levels (Lima and Jaksic 1998*a*). We incorporated the effects of rainfall on the fraction of reproductive females using a logistic regression model. Thus, the expression for the net reproductive rate per adult female can be formalized as

$$B(t, P) = \frac{1}{1 + e^{-(\beta + \alpha \times P_t)}} \times R,$$ (2)

where β is the smallest fraction of reproductive females (which was observed to be 0), P_t is the annual accumulated rainfall level, and α is the slope of the linear relationship (0.0016; see Lima and Jaksic 1998*a*). The variable R represents the number of females produced by a reproductive female during a time step (litter size). This quantity is estimated at 5.2, which represents half of two sequential litters (Fulk 1975; Meserve and Le Boulengé 1987). Consequently, the basic matrix model can be expressed as a time-dependent and density-independent (represented by the amount of annual rainfall) model:

$$\begin{bmatrix} 0 & B(t, P) \\ S_J(t) & S_A(t) \end{bmatrix}.$$ (3)

We iterate this matrix model using the annual rainfall records from the meteorological stations of Hurtado (30°17′S, 70°41′W, 1,200-m elevation, period 1943–1997) and Pichasca (30°23′S, 70°52′W, 750-m elevation, period 1946–1997), both located in the Limarí River Basin, and Illapel (31°38′S, 71°10′W, 290-m elevation, period 1974–1997), located in the Choapa River Basin. Data from the former two locations are deemed as adequate representations of climatological conditions in northern Chile, largely because they provide the longest time series for that region. Data from the third location, although a short time series, are deemed as representative of local conditions experienced in our primary study site at Aucó, approximately 18 km from the Illapel station. We iterated model (3) using the mean population size of adult and juveniles as initial conditions. The iterated dynamic shows in all cases that a pure density-independent model goes extinct or may increase without limits (fig. 2*A*–*C*).

Density-Dependent Effects on the Demographic Processes

The next step is to include the estimated density-dependent effects on the time-dependent stage-matrix model. In previous studies, we determined the importance of delayed density-dependent effects on population dynamics of *Phyllotis darwini* (Lima and Jaksic 1998*b*, 1999*b*) and on reproductive rates (Lima and Jaksic 1998*a*). Also, we found that statistical models including seasonality and delayed density dependence are the most parsimonious for describing the adult survival rates of *P. darwini*. Consequently, we model the effects of delayed density dependence on these demographic processes.

The effects of delayed density dependence on adult survival rates were modeled using the statistical models estimated from the CMR data. Because the most parsimonious statistical model incorporates the covariate (population size 8 mo before) in simple linear fashion on the seasonal survival structure through a logit link function (see White 1998 for details), we modeled the adult survival rates as a function of time (seasonality) and population size the previous 8 mo (delayed density dependence). This relationship can be expressed as

$$S_A(t, N) = \frac{1}{1 + e^{-[\beta_0(t) + \beta_N \times N_{t-d}]}},$$ (4)

where $S_A(t, N)$ is the adult survival rate expressed as the logit model. The parameter $\beta_0(t)$ is the seasonal coeffi-
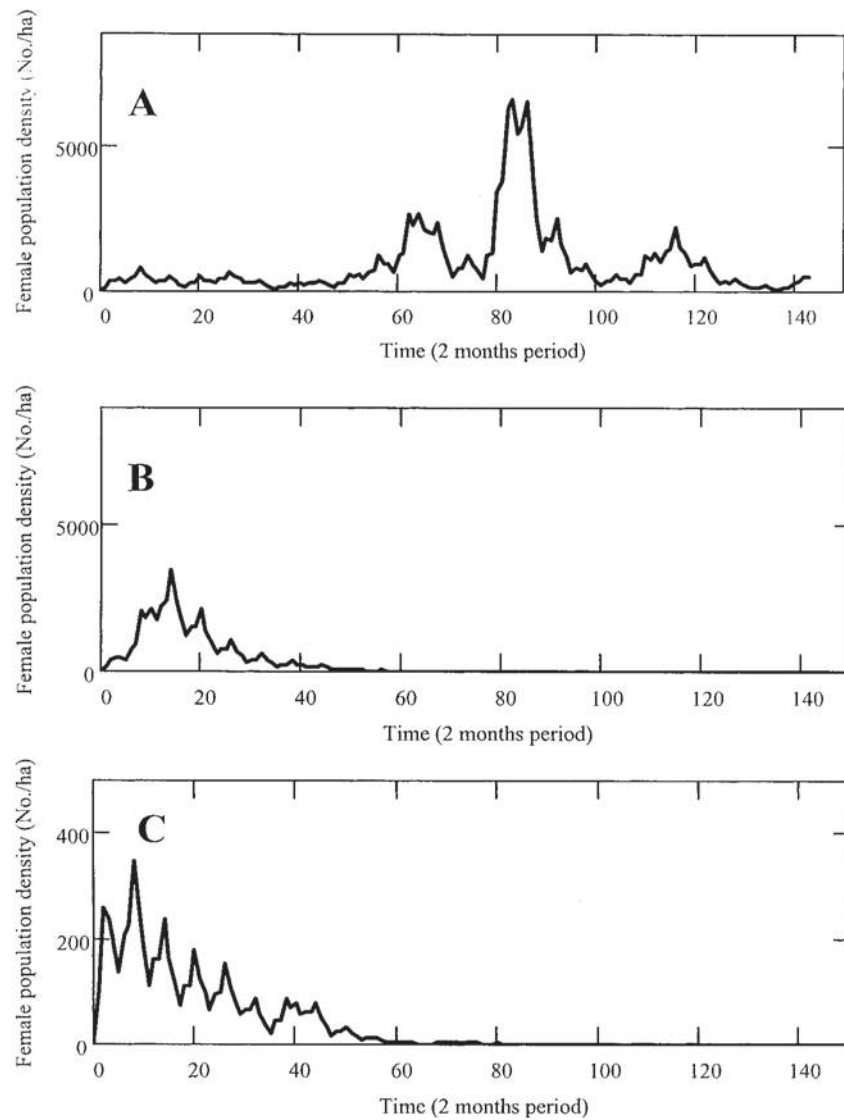
Figure 2: Simulation runs with a pure density-independent model using the annual rainfall records. *A*, Illapel meteorological station (1974–1997); *B*, Hurtado meteorological station (1943–1996); *C*, Pichasca meteorological station (1946–1996).

cients, and β_N is the coefficient of the delayed density-dependent effects estimated by the covariate model. The variable N_{t-d} is the population size the previous year ($t-d$), where $d = 4$ time steps represents an 8-mo delay.

The effects of delayed density dependence on the fraction of reproductive females were modeled using a logistic regression model. Figure 3 shows the relationship between the fraction of reproductive females and population size the previous year. We fitted a logistic regression model ($y = 1/[1 + e^{-(0.61-0.04 \times N_{t-6})}]$, $R^2 = 0.55$, $F = 48.73$, df = 2, 16, $P < .001$).

The number of females produced by a reproductive female was estimated at 5.2, which represents one-half of two sequential litters (Fulk 1975; Meserve and Le Boulengé 1987).

Consequently, the delayed density-dependent effects on the bimonthly net reproductive rate per adult female can be expressed by the following equation:

$$B(t, N) = \frac{1}{1 + e^{-[F(t)-\alpha \times N_{t-6}]}} \times 5.2, \tag{5}$$
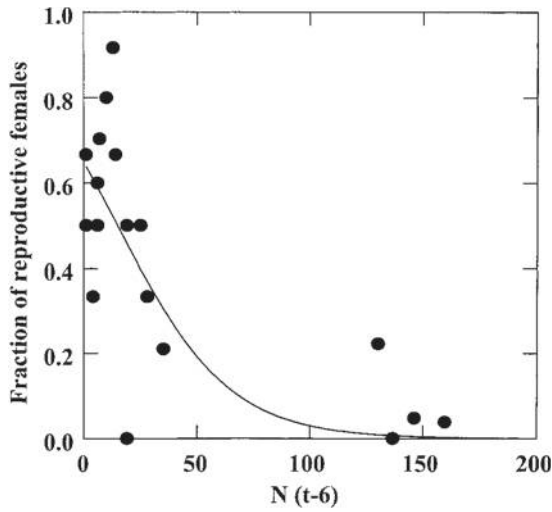
Figure 3: Curve fitted to the relationship between the fraction of reproductive females and the population size the previous year ($y = 1/[1 + e^{-(0.61-0.041 \times N_{t-6})}]$, $R^2 = 0.55$, $F = 48.73$, df = 2, 16, $P < .001$).

where $F(t)$ is the seasonal indicator of the fraction of reproductive females and α is the slope of density dependence on this parameter. The number 5.2 represents the number of females produced by a reproductive female (litter size). The nonlinear density-dependent matrix model can be formalized as

$$\begin{bmatrix} 0 & B(t, N) \\ S_J(t) & S_A(t, N) \end{bmatrix}. \quad (6)$$

Characterization of the Pure Density-Dependent Model Dynamics

We characterized the dynamics of this delayed density-dependent matrix model through their most relevant biological parameters. The stability boundary between equilibrium and nonequilibrium behavior is a basic descriptor of dynamics. We ran the model for each different parameter value during 5,000 time steps, after which the values obtained during the last 500 time steps were plotted, resulting in a bifurcation diagram. A basic feature of our model is seasonality. Thus, a period of six time steps (12 mo) represents a stable point attractor from a multiannual time scale. The bifurcation diagrams for the most relevant biological parameters are shown in figure 4. The stability of population dynamics seems to be governed by three population parameters: the litter size, the maximum frac-

tion of reproductive females, and the juvenile survival rates (fig. 4*A*–*C*).

Higher pregnancy rates, litter size or litter numbers, and juvenile survival rates result in an increase in population oscillations and complexity. The bifurcation diagrams show that increased variability is associated with an increased oscillatory dynamic at an interannual time scale (see fig. 4). We iterated the deterministic skeleton of the model with the fitted parameters during 10,000 time steps, and the first 1,000 were discarded to allow the transients to die out. The result of the model iteration gives rise to both a clear seasonal dynamic and a stable multiannual behavior (fig. 5).

Delayed Density-Dependent and Rainfall Effects on Demographic Processes

The next step to formalize the population system of *Phyllotis darwini* was to incorporate the delayed density-dependent and rainfall effects on the demographic processes. This was done in a straightforward manner, as we used the empirical relationship between the fraction of reproductive females, annual accumulated rainfall, and the population size the previous year. We fitted a nonlogistic regression model where the independent variables were rainfall and population size and the response variable was the fraction of reproductive females (model fitted was fraction of reproductive females = $1/[1 + e^{-(-0.184 - 0.041N_{t-6} + 0.0045P_t)}]$, $R^2 = 0.64$, df = 3, 15, $F = 39.62$, $P < .001$; fig. 6).

Thus, the actual net reproductive rate per adult female (function of delayed density and the annual rainfall) can be represented with the following equation:

$$B(t, N_{t-6}, P) = \frac{1}{1 + e^{-[F(t) + \beta \times N_{t-6} + \alpha \times P_t]}} \times 5.2, \quad (7)$$

where $F(t)$ is the seasonal indicator of the fraction of reproductive females, $-\beta N_{t-6}$ represents the negative effects of population size the previous year, and αP_t represents the positive effects of the annual rainfall on the fraction of reproductive females. Last, we incorporated one-half of two consecutive litters to represent the number of females produced by a reproductive female during a 2-mo period.

The stage-matrix model can be expressed as

$$\begin{bmatrix} 0 & B(t, N_{t-6}, P) \\ S_J(t) & S_A(t, N_{t-4}) \end{bmatrix}, \quad (8)$$

where $B(t, N, P)$ is the net bimonthly reproductive rate per adult female, which is a function of the season (t), the annual rainfall level (P), and the delayed density depen-
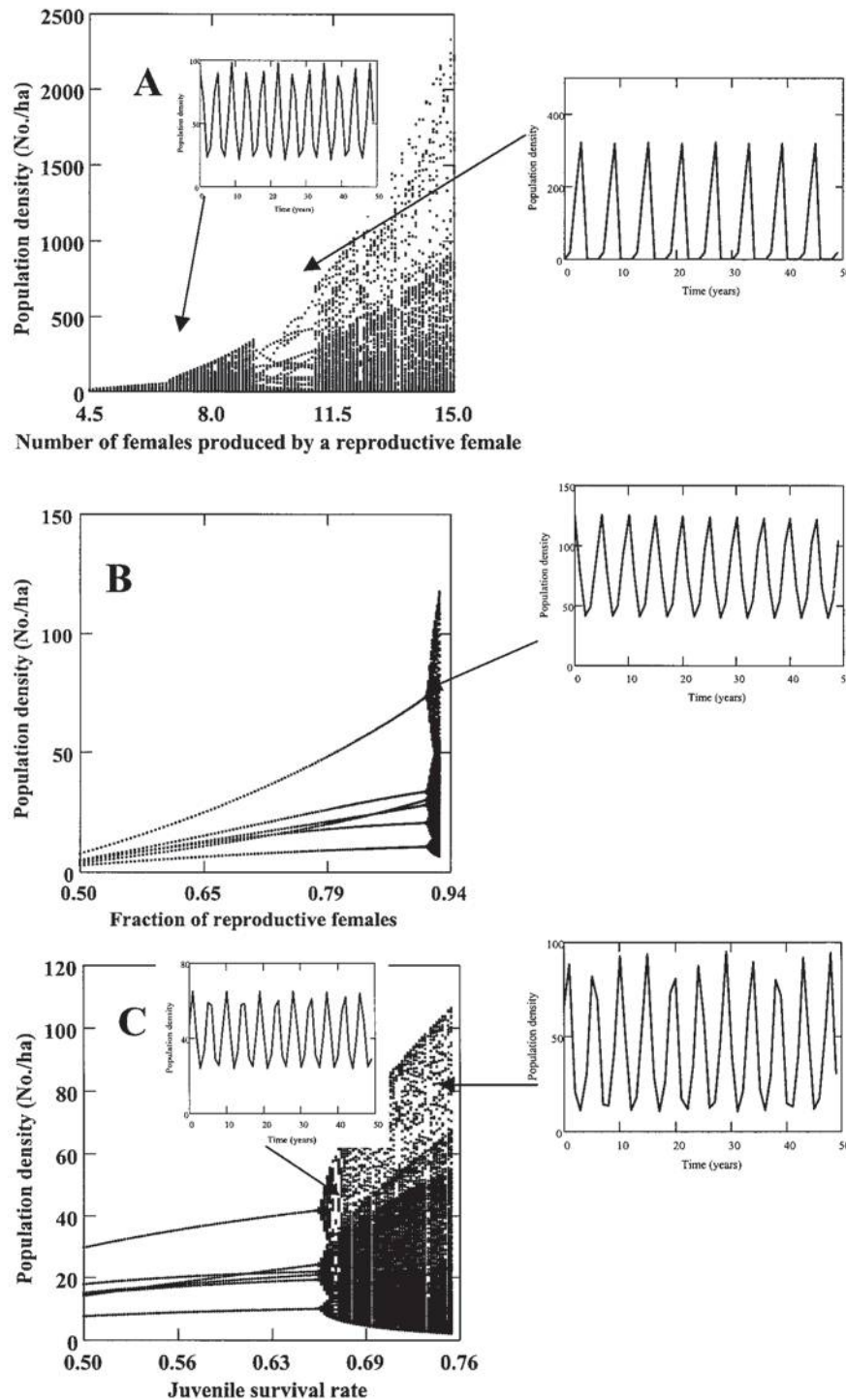
Figure 4: Bifurcation diagrams showing the dynamics of the mathematical model for different values. *A*, Number of females produced per reproductive female (represents litter size and litter number); *B*, the maximum fraction of reproductive females; *C*, the highest juvenile survival rates. Note that the estimated parameter values predict a seasonal dynamics and an interannual equilibrium dynamics. The insets show a sample of the annual dynamics in different regions of the parameter space.
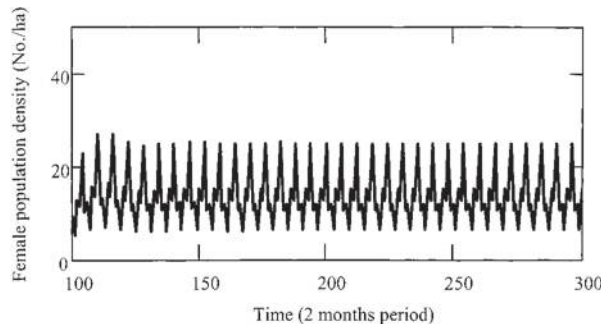
Figure 5: Simulation run with the pure density-dependent model

dence (N_{t-d}; $d = 4$ or 6). The variable S_A is the adult survival rate estimated as the pure density-dependent model (eq. [6]), while the juvenile survival rates, $S_J(t)$, are the seasonal (within-year variation) model estimates.

We simulated the model using the annual records of precipitation from the three meteorological stations (Illapel, Hurtado, and Pichasca). When we used the parameter estimates and precipitation records from 1974 to 1997 from Illapel—which represent the local conditions of our study site—there was a close relation between the "observed" (estimates based on CMR data) and "predicted" population sizes (fig. 7; Pearson's correlation coefficient $r = 0.47$, $N = 27$, $P < .014$, Spearman's correlation coefficient $r = 0.66$). Note that we used the trapping data set from 1993 to 1998 (which was not used to develop the model) to validate the model predictions. Deviations between predictions and observed values are rather symmetric (fig. 7, inset), which indicates that the assumed biological mechanisms are able to produce dynamics consistent with the empirical observations.

Model runs using rainfall data showed population dynamics very similar to those observed. In particular, with the Illapel rainfall data, the model is able to reproduce the dramatic outbreak of 1987–1988, the milder one observed during 1992–1993, and the last increment associated to the El Niño event of 1997 (see Jiménez et al. 1992; Jaksic et al. 1996; Lima et al. 1996; fig. 8*A*). When we used rainfall data from the Pichasca and Hurtado meteorological stations—located approximately 150 km north—the model dynamics did not irrupt during 1987–1988 but showed a dramatic peak during 1983–1984 (fig. 8*B*, *C*). This seems to be the result of an interaction between a slightly different rainfall regime (e.g., during the 1982–1983 ENSO, the increase of annual rainfall levels were more important in Hurtado and Pichasca than in Illapel; fig. 8) and the underlying nonlinear density-dependent dynamics.

Discussion

The results of this study strongly suggest that the interaction between delayed density-dependent factors and rainfall, observed at a demographic level, is the key piece toward understanding population outbreaks of *Phyllotis darwini*—and perhaps other rodent species—in semiarid South America. This interaction between density-dependent and density-independent factors observed both at demographic and population dynamic levels, to our knowledge, has only been detected in the African rodent *Mastomys natalensis* (see Leirs et al. 1997). For a long time it has been widely accepted that rodent outbreaks in western South America are caused only by the increase in rainfall levels during ENSO events (Péfaur et al. 1979; Fuentes and Campusano 1985; Meserve and Le Boulengé 1987; Meserve et al. 1995, 1996; Jaksic et al. 1997). However, the delayed density component detected in the demography and population dynamics of *P. darwini* (Lima and Jaksic 1998*a*, 1998*b*) contradicts the hypothesis of pure rainfall-driven fluctuations. Consequently, the population irruptions of rodents in semiarid South America seem to be more complex than the hypothesized causal chain of ENSO → more rainfall → higher primary productivity → higher rodent density (Jaksic et al. 1997).

Our model is able to produce dynamics consistent with the observed population size in magnitude and variability, which suggests that it captures essential population mechanisms. Further, the model skeleton gives rise to strong periodic dynamics at an intraannual scale that are consistent with the seasonal dynamics observed in the data.
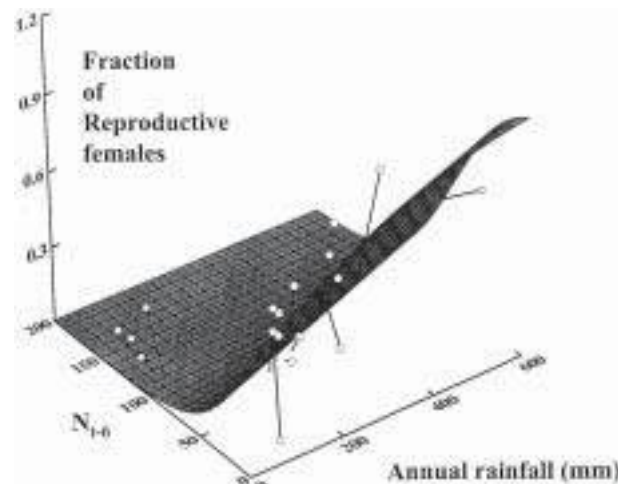

Figure 6: Curve fitted to the relationship between the fraction of reproductive females, the population size the previous year, and the annual rainfall ($y = 1/[1 + e^{-(-0.184 - 0.041 N_{t-6} + 0.0045 Pt)}]$, $R^2 = 0.64$, df $= 3, 15$, $F = 39.62$; $P < .001$).
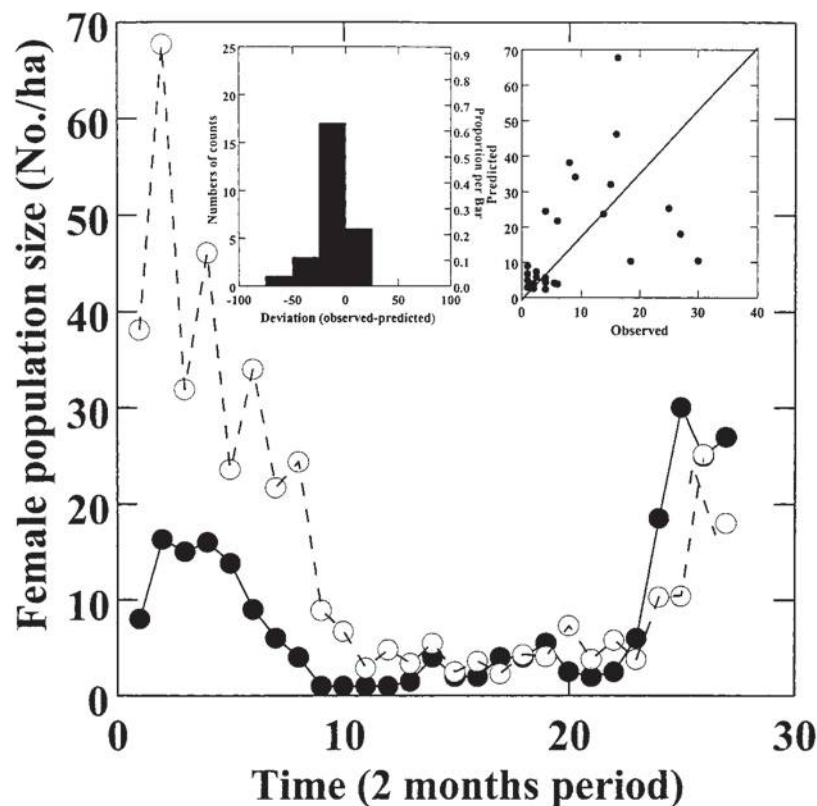
Figure 7: Model predictions (*open circles*) and observed population sizes of *Phyllotis darwini* (*filled circles*) for Aucó from January 1993 to June 1998. The left inset shows the frequency distribution of deviations (observed-predicted population size), while the right inset shows the predicted versus the observed population sizes ($r = 0.47$, $N = 27$, $P < .014$, Spearman's correlation coefficient $r = 0.66$), the diagonal line represents the 1 : 1 ratio.

It is interesting that the model dynamics—without rainfall effects—are characterized by an equilibrium behavior (at an interannual scale) but are able to generate a strong variability in the time-series data when an external perturbation regime (rainfall) is added. This result is consistent with the autoregressive models without noise (skeletons) fitted to the annual time series of *P. darwini*, which revealed the existence of a dampened oscillatory dynamics (Lima and Jaksic 1999*b*). These results emphasize the importance of the interaction between deterministic and stochastic forces in determining population dynamics (see Nisbet and Gurney 1982 for a detailed discussion).

In a different vein, traditionally the attention has been focused on the positive effects of ENSO events on rainfall levels and rodent densities (see Jaksic et al. 1997). However, we emphasize that the severe droughts caused by La Niña events in western South America may play a fundamental role in generating rodent outbreaks, especially when there is an underlying endogenous structure (the skeleton) acting in a delaying manner. Therefore, the population dynamics of *P. darwini* (and perhaps other rodents)

may be characterized by endogenous delayed regulatory mechanisms trapped in a regime of exogenous forces characterized by the positive effects of El Niño and the negative effects of La Niña events. An important point is that the exogenous forces represented by the ENSO disturbances are characterized by a complex oscillatory and aperiodic dynamic (usually between 2 and 10 yr) of variable intensity and that, once established, there is a tendency for the phenomenon to show quasibiennial characteristics (to change from El Niño phase to La Niña or vice versa; see Allen et al. 1996). Therefore, the dramatic population fluctuations under discussion may be the consequences of an exogenous oscillatory force—La Niña and El Niño driving the variability of the rainfall levels—interacting in a complex way with an underlying delayed density-dependent dynamics, here demonstrated in the population system of *P. darwini*.

One of the main implications of the interaction between the endogenous and exogenous forces is that the occurrence of a rodent outbreak is not totally coupled with increased rainfall. For example, the model simulations
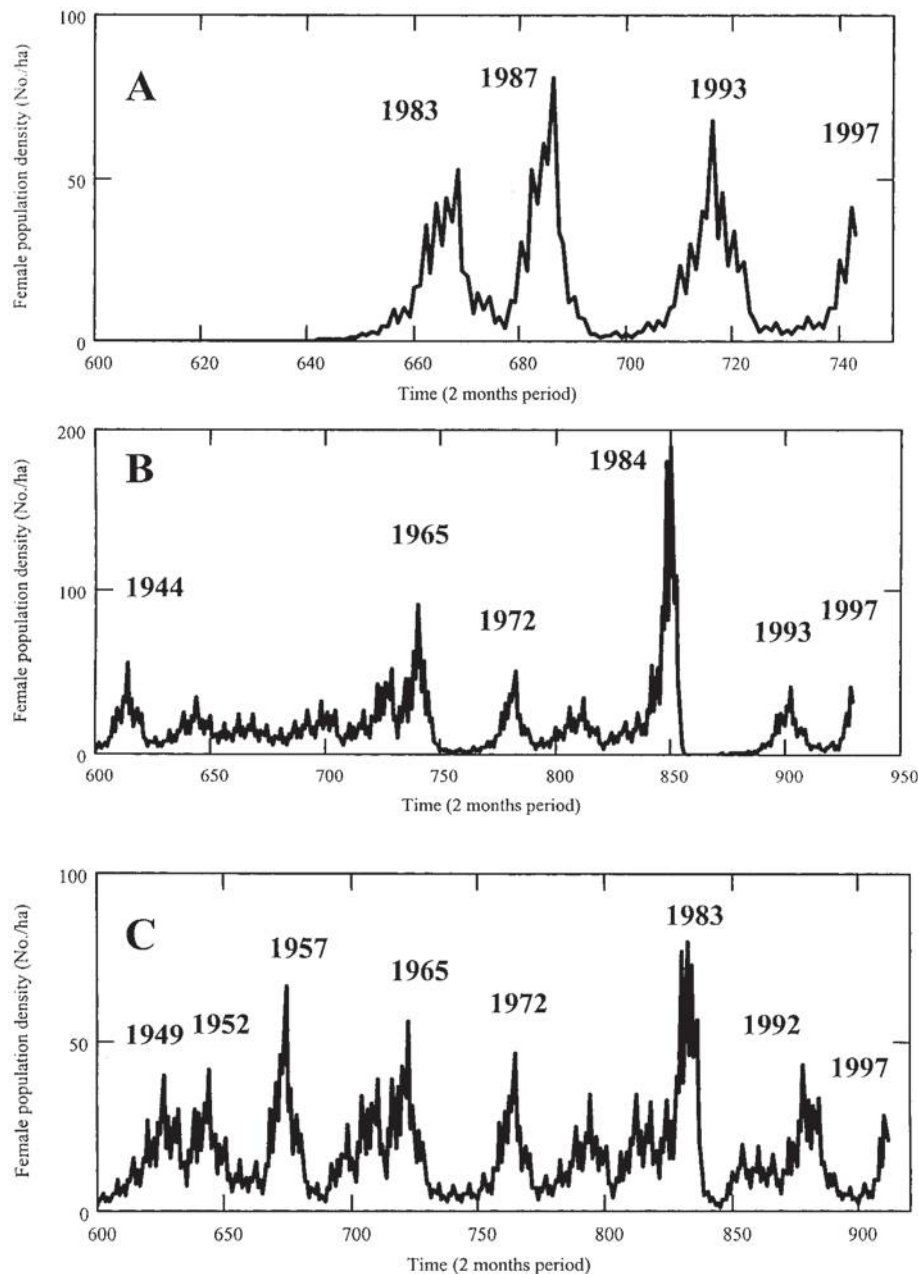
Figure 8: Simulation runs with the delayed density-dependent/density-independent model using the annual rainfall records from the meteorological stations. *A*, Illapel (1974–1997); *B*, Hurtado (1943–1996); and *C*, Pichasca (1946–1996). Note that the same model skeleton gives rise to different population trajectories according to slight differences in rainfall patterns. Numbers are the outbreak years predicted by the model.

when we used the Hurtado and Pichasca rainfall records showed a population irruption occurring during 1984, after a very rainy year (1984), but not during 1987–1988 after a similarly rainy year (fig. 8*B*, *C*). This result is a consequence of the interaction between the delayed regulatory mechanisms and the rainfall variability. In this context, small changes in population parameters or in the

rainfall variability pattern can produce asynchronous outbreaks between rodent populations at a regional level. This model attribute is consistent with the observation that rodent outbreaks are spatially asynchronous even in such a restricted area as semiarid Chile. For instance, rodent populations of the two most irruptive species, *P. darwini* and *Akodon olivaceus*, reached higher densities in the lo-

cality of Fray Jorge (230 individuals/ha approximately) than in Aucó (80 individuals/ha), situated 100 km away, after the ENSO disturbance of 1991–1992 (Meserve et al. 1995, 1996; Jaksic et al. 1996, 1997).

Although we did not conduct a full numerical exploration of the model dynamics, the sensitivity to small parameter changes and to differences in the rainfall pattern suggests the existence of more complex dynamics. Small changes in life-history parameters can explain the empirical observation that the irruptive rodent species are different among local sites. For example, in Fray Jorge, rodent outbreaks are dominated by the species *A. olivaceus* (Meserve et al. 1995, 1996), while in Aucó the most irruptive species is *P. darwini* (Jiménez et al. 1992; Jaksic et al. 1996, 1997; Lima et al. 1996). Therefore, the existence of local variability at the demographic level offers a plausible explanation for this phenomenon. However, the same type of argument in light of a different pattern of variability in the rainfall record may explain why *P. darwini* does not irrupt in central or southern Chile. Thus, our model is able to generate testable predictions; for instance, that higher litter size, pregnancy, and juvenile survival rates lead to more variable and complex population dynamics. In addition, we have identified demographic processes for which good empirical information is lacking about Neotropical rodent species. In sum, we think that further demographic and modeling studies in other irruptive rodent species of western South America are needed for understanding the causes of population outbreaks.

Our model incorporated the effects of delayed density dependence on adult survival and reproductive rates and rainfall effects on reproduction all combined with a seasonal time structure. However, the existence of delayed density-dependent effects on survival and reproduction begs for an experimental test. Two competing hypotheses could explain delayed density dependence: the specialist predation hypothesis (see Hansson and Henttonen 1988; Hanski et al. 1991, 1993; Stenseth et al. 1996*a*, 1996*b*; Turchin and Hanski 1997) and the rodent-plant interaction hypothesis (see Taitt and Krebs 1985; Agrell et al. 1995; Jedrzejewski and Jedrzejewska 1996). In our study site, three resident owls are specialized predators of rodents, the barn owl (*Tyto alba*), the great horned owl (*Bubo virginianus*), and the burrowing owl (*Speotyto cunicularia*; Jaksic et al. 1992, 1993*a*; Castro and Jaksic 1995; Silva et al. 1995). Also, there is abundant evidence that *P. darwini* is the most heavily preyed-upon rodent by these three owl species (Jaksic et al. 1993*b*) and that at least two of the species (barn and burrowing owls) show significant preference for it (Jaksic et al. 1997). In addition, Meserve et al. (1996) demonstrated significant effects of predation on the numbers and survival rates of *P. darwini* in a semiarid locality 100 km north of our study site. The available

evidence also shows that some owls respond numerically to changes in mammalian increases (e.g., the burrowing owl; Silva et al. 1995). In sum, predation is a likely factor determining delayed density dependence in *P. darwini*. Nevertheless, the strong delayed density-dependent effects detected on reproductive parameters (see Lima and Jaksic 1998*a*) also suggest the idea of delayed effects of food quantity or quality. Because *P. darwini* is a folivore-granivore (Meserve and Le Boulengé 1987), high herbage and seed consumption during high-density periods may result in delayed negative effects on plant cover, plant quality, and the seed bank. These speculations also deserve an experimental approach.

We believe that the present study represents a step toward understanding such a complex phenomenon as rodent outbreaks in western South America. Recent studies have emphasized that the interaction between endogenous (deterministic) and exogenous (both stochastic and deterministic) factors is crucial for understanding the dynamics of natural populations (Higgins et al. 1997*a*, 1997*b*; Leirs et al. 1997; Bjørnstad et al. 1998). In the same vein, this study suggests that rodent outbreaks—at least in semiarid Chile—are the result of underlying delayed regulatory mechanisms embedded in a strong oscillatory but aperiodic environment characterized by ENSO-driven rainfall variability.

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