

## Population dynamics of rice rats (a Hantavirus reservoir) in southern Chile: feedback structure and non-linear effects of climatic oscillations

Roberto Murúa, Luz A. González and Mauricio Lima

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We studied a fluctuating population of the long-tail rice rat (*Oligoryzomys longicaudatus*), the main Hantavirus vector in southern Chile, and spanning 19 years of monitoring. We determined that a first-order feedback structure and non-linear effects of Antarctic Oscillation Index (AAOI) and Southern Oscillation Index (SOI) explain 96% of the variation in annual per capita population growth rates. One important result of this study is that first-order feedback structure captures the essential features of population dynamics of long-tailed rice rats. This regulatory structure suggests that rice rats are limited by food, space or predators and regulated by intra-specific competition. The first-order dynamics observed in long-tailed rice rats strongly suggests that Hantavirus have no harmful effects on survival or reproductive processes. Besides the non-linear climatic signature in population dynamics, the periodic event of bamboo-flowering and mast seeding strongly influence rice rats population growth rates. Because of this, bamboo flowering may be used as a signal for forecasting long-tail rice rats outbreaks and for implementing information and health policies to avoid human-rodent contacts in specific areas. The observed effects of the two large-scale climatic indexes that influence climatic variability along southern Pacific Ocean, the AAOI and the SOI, emphasizes the role of considering non-linear feedback structures and climatic forces for understanding small rodent population dynamics. Because long-tailed rice rats represent the major Hantavirus reservoir in southern Chile and Argentina, we need to gain an in-depth understanding of the structure and functioning of these small rodent populations in face of the potential consequences of global change and climatic fluctuations.

R. Murúa and L. A. González, Instituto de Ecología y Evolución, Facultad de Ciencias, Univ. Austral de Chile, Casilla 567, Valdivia, Chile. – M. Lima, Center for Advanced Studies in Ecology and Biodiversity, Pontificia Univ. Católica de Chile, Casilla 114-D, Santiago CP 6513677, Chile (mlima@genes.bio.puc.cl).

Deducing the feedback structure has been a central task in population dynamics since Nicholson (1933), in particular, determining the order and the non-linearity in the feedback component of population dynamics (Royama 1992, Turchin 1995, Berryman 1999). On the other hand, the importance of the exogenous factors in population dynamics has been emphasized since Andrewartha and Birch (1954). Nevertheless, nowadays the central point in population ecology is to understand

the joining effects of the regulatory structure and the exogenous (climatic and stochastic) influences (Royama 1992, Berryman 1999, Lima et al. 1999, 2001a, b, 2002a, b, c, Stenseth 1999, Bjørnstad and Grenfell 2001). In fact, recently there is a growing interest for studying the effects of large-scale global climatic indexes on population dynamics and this issue has attracted the attention of population ecologists (reviewed by Stenseth et al. 2002a).

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Historical records have long existed about rodent outbreaks in southern temperate forests of Chile (Hershkovitz 1962). Indeed, since 1552 there have been anecdotal records of rodent outbreaks around the southern town of Valdivia, in association with masting bamboo *Chusquea* spp. (Philippi 1879, Hershkovitz 1962, Murúa et al. 1986, 1996, Gallardo and Mercado 1999, Jaksic and Lima 2003). In particular, long-tailed rice rat (*Oligoryzomys longicaudatus*) populations have been reported as experiencing the most dramatic outbreaks (Hershkovitz 1962, Murúa et al. 1986, 1996, Gallardo and Mercado 1999, González et al. 2000). The putative chain of effects is the increased food availability brought by bamboo blooming and the subsequent dramatic increase in population density ("ratada" sensu Hershkovitz 1962, Gallardo and Mercado 1999). The population peaks are often so high that massive invasion of mice occur into homes and other human-inhabited areas (Pavletic et al. 1998, Toro et al. 1998). Long-tailed rice rats are the main Hantavirus (Andes strain) reservoir (Lopez et al. 1996, Levis et al. 1997, Schmaljohn and Hjelle 1997, Murúa 1998, 1999, Toro et al. 1998, Cantoni et al. 2001). Its dramatic outbreaks are an important source of public health concern due to the increased risks of human infection (Schrag and Wiener 1995, Murúa et al. 2002). For instance, during the period 1993–2001 Hantavirus infected 180 people in southern Chile with 44.7% mortality (<http://epi.minsal.cl/index.htm>). Consequently, understanding the ecological factors driving numerical fluctuations in reservoir rodent populations represents a fundamental step toward implementing management policies for outbreak forecasting and control (Mills 1999).

Unfortunately, much of the information on population dynamics of long-tailed rice rats is anecdotal, or at best short-spanned, and thus there are no adequate databases for analysing its numerical fluctuations. Thus, the main objective of this study is to analyse the effects of endogenous feedback (density-dependent) mechanisms and climatic influences on population dynamics of the long-tailed rice rat (*Oligoryzomys longicaudatus*), the major Hantavirus vector and reservoir in southern areas of Chile and Argentina. In this paper, we analyse for the first time the feedback structure and climatic effects, being represented by two global climatic indexes which influence the climatic variability in the southern hemisphere, the Southern Oscillation Index (SOI) and the Antarctic Oscillation Index (AAOI), on population fluctuations of long-tailed rice rats in southern Chile during a 19 yr period.

## Materials and methods

### The study site

The study site is located in Bosque Experimental San

Martín, 72 km north from Valdivia city, Chile (39° 38' S; 73° 7' W; Fig. 1a). The area experiences mild wet winters and shorts dry summers. Annual precipitation in the vicinity of the study area ranges from 1003 to 2854 mm (mean 2051 mm). Temperatures range from a monthly mean of 7.3°C in winter to 17.5°C in summer. The area is characterised as a Valdivian temperate rain forest, dominated by evergreen trees and dense understorey vegetation, epiphytes and lianas (Murúa et al. 1986, González and Donoso 1999).

### The data

The data presented here are based on a long-term monitoring study of small mammals spanning September 1979 to August 1998 at San Martín (Biological Station) Experimental Preserve (Fig. 1b). Small mammals were live-trapped monthly. The study site contained a 12 × 12 live-trapping grid with stations located at 10 m from each other (this covering 1.2 ha). One Sherman live-traps protected by wooden shelters and baited with rolled oats were located at each station (total traps = 144). Each trapping period consisted of 11 days during 1979 and 4 of days from 1980 onward; upon initial capture each individual was marked and weighed to the nearest 0.5 g using a Pesola scale, and classified as adult, subadult or juvenile according to body mass and sexual maturity. Gender, reproductive status and species were recorded for each capture (Murúa et al. 1986).

The data on population dynamics are derived from censuses conducted at the end of the reproductive period of small mammals (May–July), where population densities are at their yearly maximum in the temperate rain forest ecosystem (Murúa et al. 1986), consequently we used the data from May–July 1980 to May–July 1998. The density of the population was expressed as the minimum number known alive (MNKA, Krebs 1966), based on capture-mark-recapture techniques.

### Exogenous variables (climate)

We used three climatic variables to represent environmental conditions. In particular, we use two large-scale global climatic indexes that represent some of the climatic variability across the southern Pacific Ocean. These indexes are; the Southern Oscillation Index (SOI) and the Antarctic Oscillation Index (AAOI). In addition we used local yearly and seasonal rainfall in neighbouring Valdivia town (Fig. 1c). SOI is one of the indices used to gauge the occurrence and strength of the El Niño Southern Oscillation (ENSO), and compares meteorological conditions in two tropical areas of the Pacific Ocean. SOI is calculated as the difference be-

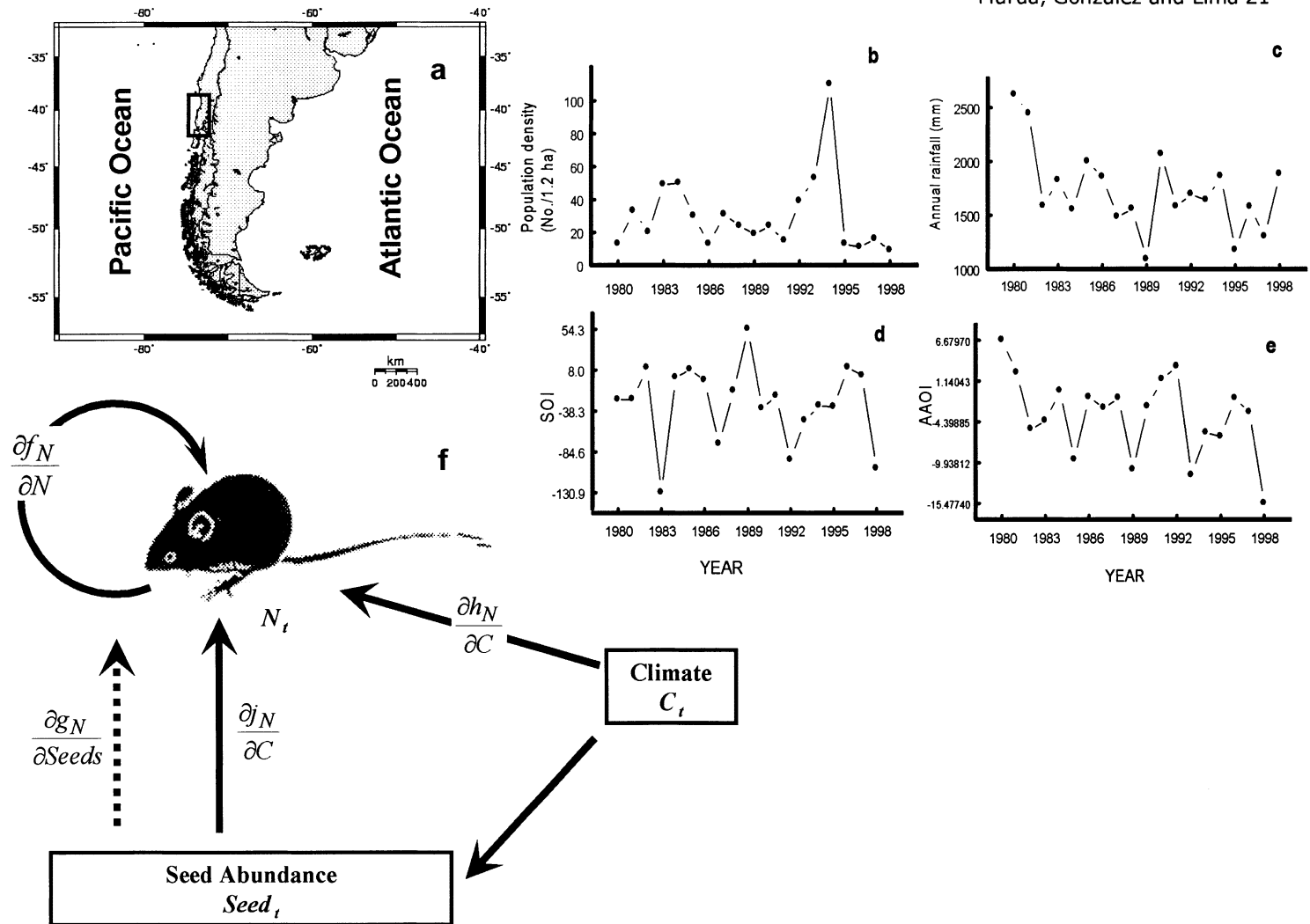


Fig. 1. a) Southern Chile temperate rain forest area, Bosque Experimental San Martín, situated 72 km north of Valdivia city, Chile (39° 38' S; 73° 07' W). b) Annual time series of long-tailed rice rats (*Oligoryzomys longicaudatus*). Population size in the time series is the minimum known alive (MNKA) estimate of individuals per hectare. c) Cumulative annual rainfall (in mm) in Valdivia City for the period 1980–1998. d) Cumulative Southern Oscillation Index (SOI) for the period 1979–1998. e) Cumulative Antarctic Oscillation Index (AAOI) for the period 1979–1998. f) A graphical model illustrating the potential interactions between seeds, rice rats and climate in southern Chile.  $N_t$  and  $Seeds_t$  give abundance of rice rats and seeds respectively, while climate (being rainfall, AAOI and SOI) is denoted by  $C_t$ . The ecological functions  $f_N(\cdot)$ ,  $g_N(\cdot)$ ,  $h_N(\cdot)$  and  $j_N(\cdot)$  describe the changes in the rodent population following the ecological interactions given by the arrows and defined by the partial derivatives. Solid arrows denote the interactions considered for modelling. See text for details.

tween the monthly-standardised atmospheric pressure between Tahiti (French territory) and Darwin (Australia). Periods characterised by large negative index-values correspond to El Niño events (wherein warm tropical waters intrude into the western coastlines of America), whereas periods characterised by large positive index-values correspond to La Niña events (when the cold Humboldt and California currents strongly influence the American coastlines; Fig. 1d). In our analyses we used the yearly averaged SOI index. Values of this index are available at an Internet web site (SOI data; <http://www.dnr.qld.gov.au/longpdk/longpdk.htm>; also available from the corresponding author).

In the southern hemisphere, the leading pattern of climate variability is more annular (Thompson and Wallace 1998, 2000). This pattern of variability has been referred to as the High Latitude Mode (Kidson 1988), the Antarctic Oscillation (Gong and Wang 1998, 1999), or more recently the Southern Annular Mode (SAM; Thompson and Wallace 2000). The AAOI refers to a large scale alternation of atmospheric mass between mid-latitude surface pressure and high latitude surface pressure, and it seems to be an acceptable index to represent the atmospheric circulation condition in high southern latitudes (Gong and Wang 1999). The AAOI index has shown a decreasing trend and a clear periodic component of 4–5 yr since 1960 (Fig. 1e) and it seems to relate to the rainfall inter-annual variability in southern Chile (Stenseth et al. 2002b). Values of the AAOI are available at the internet web site (<http://www.cpc.ncep.noaa.gov/products/precip/CWlink/all-index.html>).

Monthly precipitations for Valdivia town were obtained from The Global Historical Climatology Network at [[http://www.ncdc.noaa.gov/pub/data/ghcn/v2/zipd/ghcnftp\\_zipd.html](http://www.ncdc.noaa.gov/pub/data/ghcn/v2/zipd/ghcnftp_zipd.html)].

In addition, we evaluated the effects of climate during the two different parts of the year. Winter conditions are defined by the SOI, AAOI and rainfall data based on the months through May to September, and summer conditions based on the months through November to March.

### Population dynamic model

Population dynamics of small rodents are the result of the feedback structure, climatic and stochastic forces. To understand how these factors may determine small rodent population fluctuations, we consider the scenario of Fig. 1f. The arrows define the potential ecological forces influencing the population dynamics of long-tailed rice rats. The first-order feedback of rodents is defined by the partial derivative of the ecological function  $\partial f_N / \partial N$ . The trophic effect of plants (seeds) is given by the partial derivative of the func-

tion  $\partial g_N / \partial P$  and the direct and indirect climatic effects by the partial derivatives  $\partial h_N / \partial C$  and  $\partial j_N / \partial C$  (Fig. 1g).

We can represent these ecological relationships using a very general model in terms of reproduction and survival of individuals (Berryman and Gutierrez 1999), which represent a variant of the Ricker (1954) discrete-time logistic model influenced by food, climate and stochastic forces. We can represent the population dynamics of rice rats using the following formulation;

$$N_t = N_{t-1} \cdot e^{[a_N + f_N(N_{t-1}) + h_N(\text{Climate}_t) + j_N(\text{Climate}_{t-1}) + \varepsilon_t]} \quad (1)$$

where  $N$  is the small rodent abundance, and  $\text{Climate}$  is a variable representing the climate state. The functions  $f_N(\cdot)$ ,  $h_N(\cdot)$  and  $j_N(\cdot)$  represents the effects of rodent density and direct and indirect climatic forces on rodent population dynamics and  $\varepsilon_t$  represent normal distributed stochastic perturbations. An alternative way to express Eq. (1) is in terms of the realized per capita population growth rates, which represent the processes of individual survival and reproduction that drive population dynamics; this is the R-function (Berryman 1999). Defining  $R_t = \log(N_t) - \log(N_{t-1})$  Eq. (1) can be expressed as a R-function (Berryman 1999):

$$R_t = a_N + f_N(N_{t-1}) + h_N(\text{Climate}_t) + j_N(\text{Climate}_{t-1}) + \varepsilon_t \quad (2)$$

This model represents the basic feedback structure and integrates the climatic and stochastic forces that drive population dynamics in nature. The basic idea for population analysis is to choose a family of functional forms for  $f$ ,  $h$  and  $j$  using time series data. This model formulates Eq. (2) as an additive non-linear model (see Bjørnstad et al. 1998 for an ecological example). Model 2 represent a Generalized Additive Model (GAM; Hastie and Tibshirani 1990). The choice of the functional form of the functions can be approached using natural cubic splines (Stenseth et al. 1997, Bjørnstad et al. 1998, 2001). The complexity of the curve (the number of degree of freedom) was 3 and the number of terms was tested by using 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 npar represents the number of parameters and nobs the number of observations in the fitted model. This is equivalent to select the best model by deducing the relative importance of first-order feedback  $f_N(\cdot)$  and the direct and indirect climatic effects  $h_N(\cdot)$  and  $j_N(\cdot)$ . In consequence, we can use this statistical modeling approach to select the climatic influences and the model structure.

## Results

### Population dynamics

Population dynamics of rice rats were characterised by irregular numerical fluctuations (Fig. 1b), in particular rice rats irrupted during winter of 1994, after a large seed input in the system due to a bamboo masting event in summer 1993–1994 (Murúa et al. 1996). On the other hand, the partial rate correlation function (PRCF; Berryman and Turchin 2001) strongly suggests a first-order dynamic (Fig. 2a). The per capita population growth rate is a non-linear decreasing function of the log population density (first-order regulation; Fig. 2b), non-linear and non-monotonic direct effects of the annual AAOI (Fig. 2c) and negative non-linear indirect effects of the SOI (Fig. 2d). This model with three terms explains 95% of the variation in per capita population growth rates. However, a model using the AAOI and SOI during summer appears to describe better the exogenous effects than the annual indexes (Fig. 2e, f and g; Table 1).

### Discussion

One important result of this study is that first-order feedback structure captures the essential features of population dynamics of long-tailed rice rats. This regulatory structure strongly suggests that long-tailed rice rats are regulated by intra-specific competition (for food or space; Murúa et al. 1986, 1996, González et al. 1989, 2000). Mechanisms such as territoriality and spacing behaviour, observed in other small mammal species, may regulate population dynamics operating as density-dependent factors on maturation and recruitment (Stenseth et al. 1996, Prévot-Julliard et al. 1999, Lima et al. 2001a, b, 2002a). In addition, the first-order dynamics observed in long-tailed rice rats strongly suggests that Hantavirus have no harmful effects on survival or reproductive processes. If Hantavirus influences negatively survival and/or reproduction we would have found a second-order effect on population dynamics (Royama 1992, Berryman 1999, Bjørnstad et al. 2001, Lima 2001). However, if long-tailed rice rats are regulated chiefly by food competition, as suggested by the strong responses to bamboo masting events, then predators will have very weak influences in the regulation of this species' population fluctuations. Specialist raptors like *Strix rufipes* and *Tyto alba* showed high proportions of long-tailed rice rats in their diets (Martínez and Jaksic 1996), which may be related to competition for enemy-free space (Holt 1977).

The feedback structure of long-tailed rice rats raises some optimistic view for developing outbreak-forecasting strategies. For example, this feedback structure explains why long-tailed rice rats respond in a propor-

tional manner to the dramatic increases in food resources during the bamboo blooming events, which occur every 11–15 years in southern Chile (González et al. 2000, Jaksic and Lima 2003), and result in the rodent outbreaks called “ratadas” (Hershkovitz 1962, Gallardo and Mercado 1999). During bamboo blooming events food availability increases in several orders of magnitude (Murúa et al. 1996, 2002b), consequently, the periodic event of bamboo flowering and mast seeds (Hershkovitz 1962, Murúa et al. 1996, Gallardo and Mercado 1999, Jaksic and Lima 2003) represent a fundamental factor to consider in population forecasting. For example, the flowering period of *Chusquea valdiviensis* occurs during spring and mast-seeding during summer of the following yr (ca 18 months later). As a consequence, long-tailed rice rats irrupt during autumn and winter of the masting year (or two years after the bamboo blooming; Gallardo and Mercado 1999, Jaksic and Lima 2003). A recent review showed that in southern Chile and Argentina *Chusquea* spp. bloomed on average every 12–14 years (Jaksic and Lima 2003). However, bamboo blooms appear to not only have a periodic component but also seem to be spatially patterned (Gallardo and Mercado 1999, González and Donoso 1999, Jaksic and Lima 2003). According to Jaksic and Lima (2003), the latest bloom in Chile was first detected in Osorno province, and then it spread north to Valdivia and south to Llanquihue provinces, and to the east toward Peulla, finally reaching the southernmost provinces of Chiloé and Palena over two years (González and Donoso 1999, Jaksic and Lima 2003). The important consequence for managing and forecasting long-tailed rice rats outbreaks in southern Chile and Argentina is that the timing and magnitude of the rodent increases can be predicted one or two years before. That is because of the delay between bamboo flowering and seed release (almost 18 months). Therefore, bamboo flowering may be used as a signal for forecasting long-tailed rice rat outbreaks and implementing information and health policies to avoid human-rodent contacts in specific areas. In our study site there was no seed production of *Chusquea valdiviensis* until December 1993, and it peaked by middle January 1994 (51.3 million of seeds per hectare), while long-tailed rice rats peaked in May–June 1994 (Murúa et al. 1996).

Two large-scale climatic variable factors appear to influence population fluctuations of rice rats in southern Chile, the Southern Oscillation (SOI) and the Antarctic Oscillation (AAOI). It is interesting that we do not find any important effects of rainfall on long-tailed rice rats dynamics, which suggests that AAOI may be related to other weather variables, such as temperature (minimum or maximum), winds, humidity and cloudiness. In addition, the non-linear indirect (lagged) effect of SOI means those El Niño years

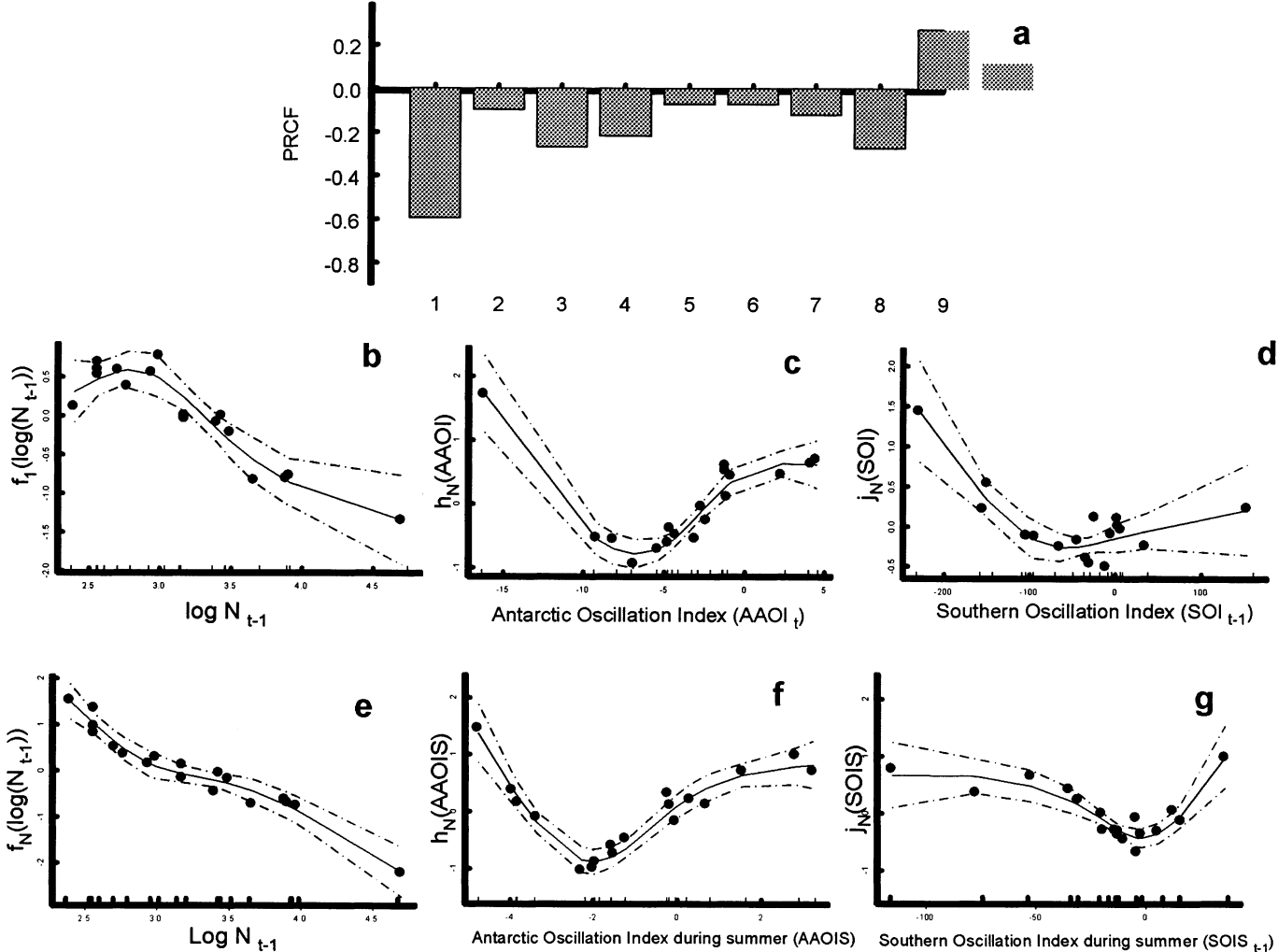


Fig. 2. a) Partial rate correlation function (PRCF) for the rice rats time series. b, c and d) The model representing the R-function and the direct and indirect effects of annual large-scale climatic variables (AAOI and SOI) for rice rats (*Oligoryzomys longicaudatus*). Partial non-parametric regression line for log population density (b); partial non-parametric regression line for the annual AAOI (c) and partial non-parametric regression line for the annual SOI (d). e, f and g) The model representing the R-function and the direct and indirect effects of summer large-scale climatic variables (AAOI and SOI) for rice rats (*Oligoryzomys longicaudatus*). Partial non-parametric regression line for log population density (e); partial non-parametric regression line for summer AAOI (f) and partial non-parametric regression line for summer SOI (g). The model was fitted by using natural cubic splines with 3 df, dashed lines are 95% confidence intervals.

Table 1. The best population dynamic models for long-tailed rice rats; we present the statistical optimal models chosen by using 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 npar represents the number of parameters and nobs the number of observations in the fitted model. The model parameters were estimated by regression analysis in S-Plus (2000). Where p = probability value,  $R^2$  = coefficient of determination, BIC = BIC criterion value and the value of  $\Delta\text{BIC}$  is the difference in the Schwarz's Bayesian criterion (SBC) from the most parsimonious model. The model notations are:  $\log N_{t-1}$  = log population density; Rain = Annual rainfall; SOI = Annual Southern Oscillation Index; AAOI = Annual Antarctic Oscillation Index; Rainw = winter rainfall; Rains = summer rainfall; SOIw = winter Southern Oscillation Index, SOIs = summer Southern Oscillation Index; AAOIw = winter Antarctic Oscillation Index, AAOIs = summer Antarctic Oscillation Index, see text for details. Bold face indicates the most parsimonious model.

Models	F (d.f)	P	R <sup>2</sup>	BIC	$\Delta\text{BIC}$
First-order feedback, direct and indirect rainfall effects					
$R_t = f_N(\log N_{t-1}) + h_N(\text{Rain}_t) + j_N(\text{Rain}_{t-1})$	1.50 (9, 8)	0.29	0.63	55.61	38.15
$R_t = f_N(\log N_{t-1}) + h_N(\text{Rainw}_t) + j_N(\text{Rainw}_{t-1})$	1.29 (9, 8)	0.37	0.59	57.29	39.83
$R_t = f_N(\log N_{t-1}) + h_N(\text{Rainw}_t) + j_N(\text{Rains}_{t-1})$	1.48 (9, 8)	0.30	0.62	55.79	38.33
$R_t = f_N(\log N_{t-1}) + h_N(\text{Rains}_t) + j_N(\text{Rains}_{t-1})$	0.95 (9, 8)	0.54	0.52	60.37	42.91
$R_t = f_N(\log N_{t-1}) + h_N(\text{Rains}_t) + j_N(\text{Rainw}_{t-1})$	0.92 (9, 8)	0.55	0.51	60.60	43.14
First-order feedback, direct and indirect large-scale climate effects (SOI and AAOI)					
$R_t = f_N(\log N_{t-1}) + h_N(\text{SOI}_t) + j_N(\text{SOI}_{t-1})$	2.83 (9, 8)	0.078	0.76	47.63	30.17
$R_t = f_N(\log N_{t-1}) + h_N(\text{SOI}_t) + j_N(\text{AAOI}_{t-1})$	2.41 (9, 8)	0.11	0.73	49.80	32.34
<b><math>R_t = f_N(\log N_{t-1}) + h_N(\text{AAOI}_t) + j_N(\text{AAOI}_{t-1})</math></b>	<b>4.78 (9, 8)</b>	<b>0.019</b>	<b>0.84</b>	<b>40.06</b>	<b>22.60</b>
$R_t = f_N(\log N_{t-1}) + h_N(\text{AAOI}_t) + j_N(\text{SOI}_{t-1})$	17.88 (9, 8)	0.0002	0.95	18.52	1.06
$R_t = f_N(\log N_{t-1}) + h_N(\text{SOIw}_t) + j_N(\text{SOIw}_{t-1})$	1.54 (9, 8)	0.28	0.63	55.30	37.84
$R_t = f_N(\log N_{t-1}) + h_N(\text{SOIw}_t) + j_N(\text{SOIs}_{t-1})$	1.35 (9, 8)	0.34	0.60	56.76	39.30
$R_t = f_N(\log N_{t-1}) + h_N(\text{SOIs}_t) + j_N(\text{SOIs}_{t-1})$	1.98 (9, 8)	0.17	0.69	52.30	34.84
$R_t = f_N(\log N_{t-1}) + h_N(\text{SOIs}_t) + j_N(\text{SOIw}_{t-1})$	1.75 (9, 8)	0.22	0.66	53.84	36.38
$R_t = f_N(\log N_{t-1}) + h_N(\text{SOIw}_t) + j_N(\text{AAOIw}_{t-1})$	4.17 (9, 8)	0.028	0.82	42.11	24.65
$R_t = f_N(\log N_{t-1}) + h_N(\text{SOIw}_t) + j_N(\text{AAOIs}_{t-1})$	1.31 (9, 8)	0.36	0.60	57.10	39.64
$R_t = f_N(\log N_{t-1}) + h_N(\text{SOIs}_t) + j_N(\text{AAOIw}_{t-1})$	4.10 (9, 8)	0.03	0.82	42.36	24.90
$R_t = f_N(\log N_{t-1}) + h_N(\text{SOIs}_t) + j_N(\text{AAOIs}_{t-1})$	1.79 (9, 8)	0.21	0.67	53.60	36.14
$R_t = f_N(\log N_{t-1}) + h_N(\text{AAOIw}_t) + j_N(\text{AAOIw}_{t-1})$	2.62 (9, 8)	0.095	0.75	46.71	29.25
$R_t = f_N(\log N_{t-1}) + h_N(\text{AAOIw}_t) + j_N(\text{AAOIs}_{t-1})$	1.48 (9, 8)	0.30	0.62	55.78	38.32
$R_t = f_N(\log N_{t-1}) + h_N(\text{AAOIs}_t) + j_N(\text{AAOIs}_{t-1})$	3.26 (9, 8)	0.055	0.79	45.70	28.24
$R_t = f_N(\log N_{t-1}) + h_N(\text{AAOIs}_t) + j_N(\text{AAOIw}_{t-1})$	4.34 (9, 8)	0.025	0.83	41.52	24.06
$R_t = f_N(\log N_{t-1}) + h_N(\text{AAOIw}_t) + j_N(\text{SOIw}_{t-1})$	1.24 (9, 8)	0.39	0.58	57.72	40.26
$R_t = f_N(\log N_{t-1}) + h_N(\text{AAOIw}_t) + j_N(\text{SOIs}_{t-1})$	1.71 (9, 8)	0.23	0.66	54.09	36.63
$R_t = f_N(\log N_{t-1}) + h_N(\text{AAOIs}_t) + j_N(\text{SOIw}_{t-1})$	3.84 (9, 8)	0.036	0.81	43.33	25.87
<b><math>R_t = f_N(\log N_{t-1}) + h_N(\text{AAOIs}_t) + j_N(\text{SOIs}_{t-1})</math></b>	<b>19.01 (9, 8)</b>	<b>0.00018</b>	<b>0.96</b>	<b>17.46</b>	<b>0.00</b>

(during summer months) has a positive impact on population dynamics of rice rats. It seems that El Niño years (negative SOI values) are related with negative anomalies in summer precipitation in southern Chile (Montecinos et al. 2000, Montecinos and Aceituno 2003), which may influence vegetation growth during summer–autumn and seed availability during the next winter (breeding season). The non-linear effects of AAOI and SOI on population growth rates of rice rats represent a new and interesting finding for understanding population dynamics of this rodent. Non-linear effects of climate on population dynamics have been recently described for ungulates (Myserud et al. 2001) and also for rodents in semi-arid Chile (Lima et al. 2002c). In fact, these two large-scale climatic oscillations appear to describe better the influence of climatic variation than local weather variables, such as yearly and seasonal rainfall.

This result appears to be consistent with the idea that climate does not affect populations through a single weather variable, but rather through a blend of weather features (Stenseth et al. 2002b). In particular, the use of these two large-scale climatic indexes appears to provide a more robust assessment of the ecological

effects of climate fluctuations due to the more holistic account of the climate systems (Namias and Cayan 1981). For example, the strong non-linear effect of AAOI represents a new and very interesting finding, previously it has been described a relationship between AAOI and annual rainfall in southern Chile (Stenseth et al. 2002b). Our result point out to the problems of predicting population responses to large-scale climatic changes when non-linear climate effects are present (Myserud et al. 2001), particularly for a species that represents the major reservoir of Hantavirus in southern South America.

## Conclusions

The numerical fluctuations of long-tailed rice rats show a first-order feedback structure, which could be interpreted as the signature of a population regulated by intra-specific competition by food, space or enemy-free space. This feedback structure is consistent with the dramatic responses of long-tailed rice rats to bamboo blooms in southern Chile and Argentina. In addition, we detected non-linear direct and indirect effects of two

large-scale climatic indexes that influence climatic variability along southern Pacific Ocean, the AAOI and the SOI, especially during the summer months. This study emphasizes the role of considering non-linear feedback structures and climatic forces for understanding small rodent population dynamics. Considering that long-tailed rice rats represent the major Hantavirus reservoir in southern Chile and Argentina, we need to gain an in-depth understanding of the structure and functioning of these small rodent populations in face of the potential consequences of global change and climatic oscillations.

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