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Second-order feedback and climatic effects determine the dynamics of a small rodent population in a temperate forest of South America

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Abstract The multiannual cyclic fluctuations exhibited by arvicoline rodents in the Northern Hemisphere have attracted the attention of population ecologists. However, despite the abundant information on small rodent dynamics in South America, there are no studies reporting cyclic population dynamics. Here, we report evidence of cyclic population dynamics in a South American small rodent, the longhaired field mouse (*Abrothrix longipilis*) from southern temperate forests in Chile. The time-series analyses showed that longhaired field mice dynamics are better represented by a second-order autoregressive model characterized by 3-year cyclic dynamics. The 3-year cycles are clearly shown in the autocorrelation factor (ACF) pattern and in the dominant frequency of the spectral analysis. In addition, we determined nonlinear effects of the Antarctic Oscillation Index (AAOI). The results shown here pointed out that we need the integration of studies about cyclic small rodent populations from the different continents and beyond the Northern Hemisphere to resolve the enigma underlying the cyclic population dynamics exhibited by many small rodent species.

Key words Longhaired field mouse · Population cycles · Climate

Introduction

The multiannual cyclic fluctuations exhibited by arvicoline rodents (voles and lemmings) in the Northern Hemisphere

have attracted the attention of population ecologists since Elton (1924). In particular, multiannual cyclic dynamics in voles and lemmings have been widely reported in Fennoscandia (Henttonen et al. 1985; Hanski et al. 1993; Bjørnstad et al. 1995), in central Europe (Saucy 1994; Tkadlec and Stenseth 2001), Scotland (Lambin et al. 2000), and Hokkaido, Japan (Saitoh 1987). Most studies on fluctuating populations of small mammals in the Northern Hemisphere have focused on the analysis of the first- and second-order feedback structure (Turchin 1993; Turchin and Hanski 1997; Stenseth et al. 1996; Stenseth 1999). In particular, the role of trophic interactions (specialist predators) (Hanski et al. 1993; Turchin and Hanski 1997) and seasonality (Stenseth et al. 1998, 2002a) have been studied as potential general causes of small rodent cycles. Otherwise, in contrast with Northern Hemisphere studies in South America most of the studies had been focused on the climatic effects on population dynamics (Stenseth 1999). Moreover, although there are many data on small rodent dynamics from South American small rodents (Pearson 1975; Murúa et al. 1986; Meserve et al. 1996; Lima et al. 1999) and several species showed large population fluctuations, there is no evidence of cyclic population dynamics.

Here, we report evidence of cyclic population dynamics in a South American small rodent, the longhaired field mouse (*Abrothrix longipilis*) from southern temperate forests in Chile. In consequence, we revealed the existence, to our knowledge for the very first time, of cyclic population dynamics in a South American small rodent.

Material and methods

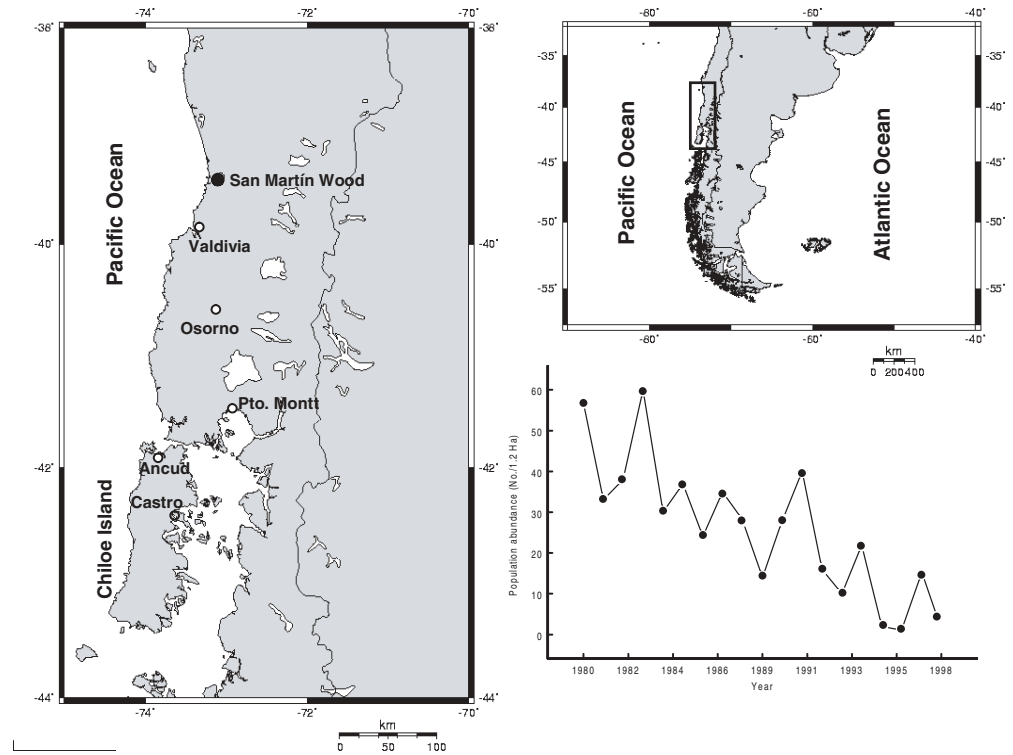
The species, the study area, and data

The longhaired field mouse (*Abrothrix longipilis*) is a common small rodent inhabiting forest habitats in central and southern Chile. This small rodent is mainly omnivore (Meserve et al. 1988); adult weight is about 50–80 g, and breeding occurs during late summer and autumn.

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Fig. 1. Southern South America. The enlarged inset is the southern Chile temperate rain forest area, the Experimental San Martín Wood Station, situated 72 km north of Valdivia City, Chile (39°38'S; 73°07'W). The annual time-series of the longhaired field mouse (*Oligoryzomys longicaudatus*) (lower right) shows population size in the time-series, the minimum known alive (MNKA) estimate of individuals per 1.2 ha



The study site is located in Bosque Experimental San Martín, 72 km north from Valdivia City, Chile (39°38'S; 73°07'W; Fig. 1). The area experiences mild wet winters and short dry summers. Annual precipitation in the vicinity of the study area ranges from 1440 to 3000 mm (mean, 2240 mm). Temperatures range from a monthly mean of 7.3°C in winter to 17.5°C in summer. The area is characterized as a Valdivian temperate rain forest, dominated by evergreen trees, dense understory vegetation, epiphytes, and lianas (Murúa et al. 1986). The data presented here are based on a long-term monitoring study of small mammals spanning from 1980 to 1998 at San Martín (Biological Station) Experimental Preserve. Small mammals were live-trapped monthly. The study site contained a 12 × 12 live-trapping grid with stations located 10 m from each other (thus covering 1.2 ha). One Sherman live-trap protected by a wooden shelter and baited with rolled oats was located at each station (total traps = 144). Each trapping period consisted of 4 days; on initial capture, each individual was marked, 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). The density of the population was expressed as the minimum number known alive (MNKA; Krebs 1966), based on capture–mark–recapture techniques.

Statistical analyses

The time-series of the longhaired field mouse was ln transformed and linearly detrended by regressing N_t against year and adding the mean value (Berryman 1999) because of the observed nonstationarity in the time series. We calculated the mean abundance and the s index (standard deviation of \log_{10} abundances). We used two different approaches to select the best order: first, the partial rate correlation function (PRCF) (Berryman and Turchin 2001), and second, the Akaike's information criterion (AIC) (Burnham and Anderson 1998) to select the order of the linear feedback processes using autoregressive models in a log scale [$X_t = b_0 + (1 + b_1)X_{t-1} + b_2 X_{t-2} + \varepsilon_t$; Royama 1992]; smaller values of AIC indicate more parsimonious models, where X is the natural logarithm of the density and the coefficients b_1 and b_2 are the strengths of the first- and second-order feedback on the per capita population growth rates ($R_t = X_t - X_{t-1}$). This analysis was implemented using the function AR in S-PLUS (2000). The autocorrelation function (ACF) and spectral analysis plot assessed the existence of cyclic dynamics (Berryman 1999; Bjørnstad et al. 1995).

A second step in our analysis was to test for nonlinearity in the feedback structure and climatic effects in the small rodent population dynamics. We represented population dynamics 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 (*sensu* Berryman 1999). Defining $R_t = X_t - X_{t-1}$ and $X_t = \ln(N_t)$, a population dynamic model can be expressed as an R function (*sensu* Berryman 1999):

$$R_t = A_n + f_1(N_{t-1}) + f_2(N_{t-2}) + f_3(C_{t-d}) + \varepsilon_t \quad (1)$$

This model represents the basic feedback structure (N) and integrates the climatic (C) (direct $d = 0$ and indirect $d = 1$ effects) 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 to fit time-series data. This model formulates Eq. 1 as an additive nonlinear model (see Bjørnstad et al. 1998 for an ecological example). Model 1 represents a generalized additive model (GAM; Hastie and Tibshirani 1990). The choice of the functional form of the f_i functions can be approached using natural cubic splines (see Bjørnstad et al. 1998 for ecological examples). In consequence, we can use this statistical modeling approach to select the climatic influences and the model structure. To select the generalized additive models (the degrees of freedom of the smoothing terms), we used penalized regression splines and generalized cross validation (GCV) (Wood 2001). Smoothed terms are represented using penalized regression splines with smoothing parameters selected by GCV.

As climatic covariables, we used the annual precipitation for Valdivia town obtained from The Global Historical Climatology Network at [http://www.ncdc.noaa.gov/pub/data/ghcn/v2/zipd/ghcnftp_zipd.html], the Southern Oscillation Index (SOI) obtained from [<http://www.longpaddock.qld.gov.au/SeasonalClimateOutlook/SouthernOscillationIndex/SOIDataFiles/>], and the Antarctic Oscillation Index (AAOI) obtained from [http://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/aao/aao_index.html].

Results

The population dynamic pattern of the longhaired field mouse was characterized by a significant negative trend in time ($F_{1,17} = 34.08$; $P < 0.0001$; $R^2 = 0.67$). The detrended time-series showed a cycle amplitude of 2.75, and the s index was 0.31, indicating a less fluctuating pattern than Fennoscandian cyclic voles. The PRCF showed that a two-order feedback structure appears to describe well the longhaired field mouse dynamics (Fig. 2a). In addition, a second-order log-linear autoregressive model was the best fit for the detrended time-series ($\Delta AIC = 3.72$ between a first-order and a second-order autoregressive process); the parameter estimates of the AR(2) process indicate that rodent dynamics exhibits clear 3-year cycles (Fig. 2b). The 3-year cycles are clearly shown in the ACF pattern (Fig. 2d) and in the dominant frequency of the spectral analysis (Fig. 2e).

A GAM model with nonlinear negative first-order ($\chi^2 = 148.53$; estimated $df = 3.68$; $P < 0.0001$; Fig. 3a) and nonlinear negative second-order feedback ($\chi^2 = 55.12$; estimated $df = 3.9$; $P < 0.0001$, Fig. 3b) and nonlinear lagged ($t - 1$) effects of AAOI ($\chi^2 = 14.28$; estimated $df = 2.73$; $P = 0.0019$; Fig. 3c) explains 98% of the total variation in per capita population growth rates (Fig. 3).

Discussion

In this study we have reported the existence of cycles in a small rodent population from the southern temperate forests of South America. The period of the multiannual cycle was around 3 years, which is in close agreement with the 3- to 5-year vole cycles observed in Fennoscandia and Hokkaido Island (see Stenseth 1999). Although vole and lemming cycles are one of the most studied areas in population dynamics, the existence of cycles in small rodent populations from South America is a new finding.

One important element of the cyclic fluctuations of longhaired field mice is that the amplitude of the cycles appears to be much lower than the value observed in the Northern Hemisphere vole cyclic populations (Stenseth 1999). We think that the low amplitude of the cycles may be one reason that no previous references to cyclic dynamics have been recorded from South American small rodents. On the other hand, the general cause of cyclic dynamics is a second-order regulation structure, as in every dynamic system (Berryman 1999), likely to be related to trophic interactions (predator-prey dynamics). Longhaired field mice represent an important and common small rodent in the temperate forests of southern Chile. It is the third species in abundance in the southern part of Chile (Murúa et al. 2003). This small rodent is preyed upon by two predators in San Martín, by the gray fox in higher proportion than is expected (Martinez et al. 1993) and also by rufous-legged owls (Martinez and Jaksic 1996).

An important point to note is the strong first-order negative feedback exhibited by this rodent, although in most studies of cyclic vole dynamics the role of second-order feedback (delayed density dependence) has been emphasized (trophic interactions and specialist predators) (but see Stenseth et al. 1996). The classic 3- to 5-year cycles of voles are basically structured from a strong first-order feedback coupled with a second-order term (but weaker); the findings in this study are consistent with this view, suggesting that intraspecific competition is the most important biological factor underlying the regulatory structure of these small rodent populations (Berryman 1999). This intraspecific competition is supported by the large proportion of animals with body wounds found in this species (Murúa et al. 2003).

In addition, we showed a nonlinear lagged effect of AAOI on population dynamics of longhaired field mice. This lagged effect can be a proxy for the climatic influences (temperature, humidity, rainfall, etc.), but most likely represent the indirect influence of climate through lower trophic levels (fungus in autumn and winter and fruits and plants during summer) (Bozinovic and Muñoz-Pedrerros 1995). It is interesting that we did not find any important effects of rainfall on longhaired field mouse dynamics, which suggests that AAOI may be related to other weather variables, such as temperature (minimum or maximum), wind, humidity, and cloudiness, in spite of the fact that AAOI appears to be closely related to the rainfall pattern in southern Chile (Stenseth et al. 2002b). This result appears to be consistent with the idea that climate does not affect

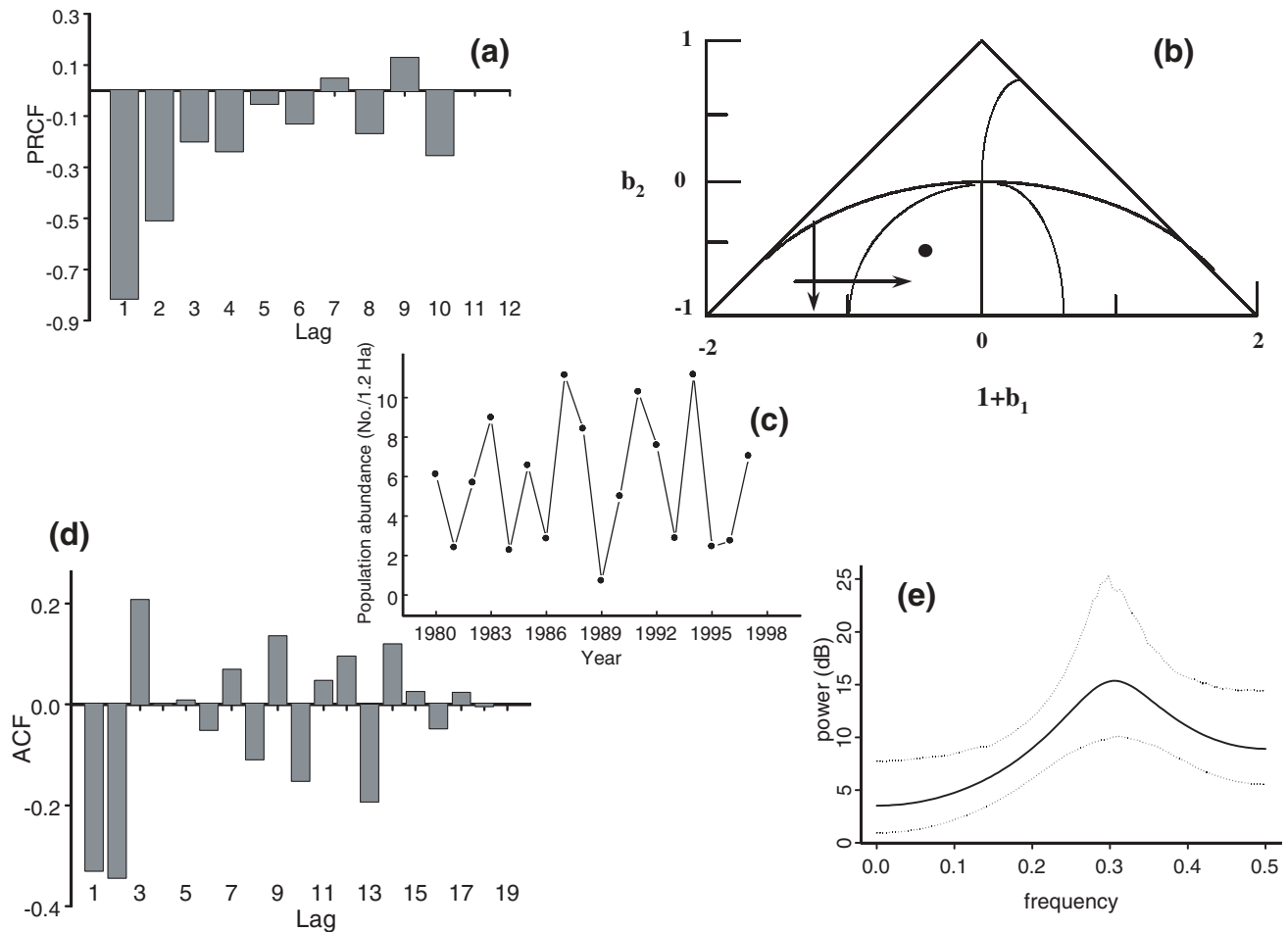


Fig. 2. **a** Partial correlation rate function (*PRCF*) plot for the detrended time series of longhaired field mice. **b** Dynamics of the second-order linear autoregressive model based on the values of the parameters $1 + b_1$ and b_2 . Values of parameters *outside the triangle* lead to extinction, and *inside the triangle* the dynamics are point stability or damped fluctuations. Below the *semicircle* the dynamics are cyclic, and the length of the periodicity increases toward the right-hand corner of the triangle. *Arrows* indicate the gradients from short to long periodicity, which are given through a reduction in b_2 (stronger delayed

density dependence) and an increase in $1 + b_1$ (weaker direct density dependence); the *lines* given are contour lines and the periodicity changes continuously inside the *semicircle*. **c** Detrended time-series of abundance. **d** Autocorrelation function (*ACF*) plot of the log-transformed time-series of longhaired field mice. **e** Spectral density of the ln-transformed and detrended times-series of longhaired field mice. The spectral density is estimated using the function *specar.ci* coded by Ottar Bjørnstad and Wilhelm Falck [<http://asi23.ent.psu.edu/>] using *S-PLUS* (2000)

populations through a single weather variable but rather through a blend of weather features (Stenseth et al. 2002b). In particular, the use of 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). In particular, the lagged AAOI could represent a proxy for the interannual variability in the food basis. However, the long-term decline in this population appears to be associated with an important change in habitat structure in the study site. In fact, the known trend toward lower rainfall levels in southern Chile since the middle of the 1950s would have important effects on longhaired field mouse equilibrium density. For example, the gradual reduction in abundance observed in the past 15 years in San Martín is coincident with the extinction of a sister species, *Abrothrix sandborni* (Murúa, unpublished data). Both small rodent

species are typical of closed and mature forests (Murúa et al., personal observation), and they have disappeared and declined in the study area probably because of the gradual environmental desiccation and changes in vegetation structure.

The nonlinear effects of AAOI on population growth rates of longhaired field mice represent a new and interesting finding for understanding the population dynamics of this rodent. Nonlinear effects of climate on population dynamics have been recently described for ungulates (Grenfell et al. 1998) and also for rodents in semiarid Chile (Lima et al. 2002). This result points out some of the problems of predicting population responses to large-scale climatic changes when nonlinear climate effects are present (Mysterud et al. 2001). In addition, the longhaired mouse is characterized by a second-order feedback structure that can mask the climatic signals.

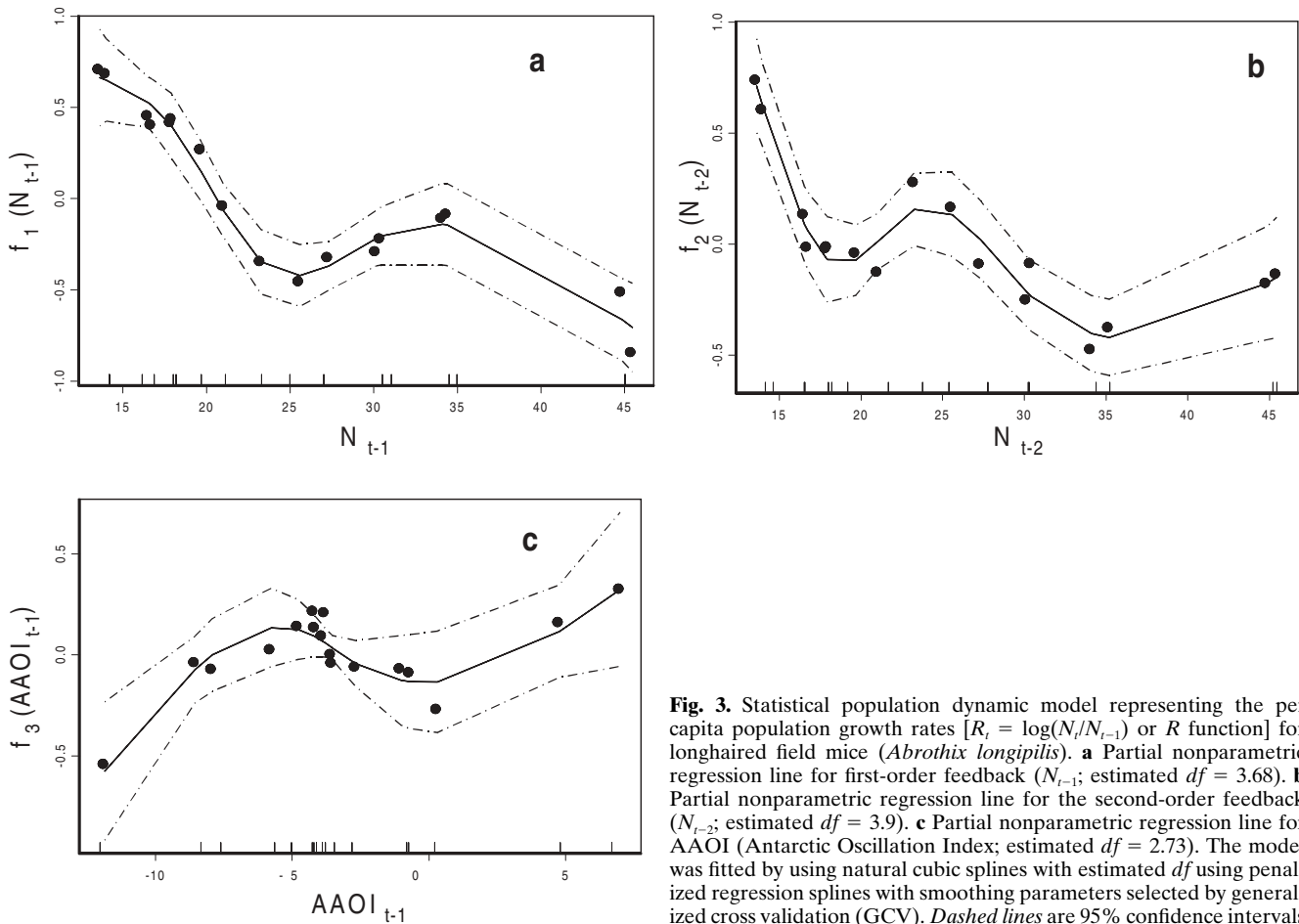


Fig. 3. Statistical population dynamic model representing the per capita population growth rates [$R_t = \log(N_t/N_{t-1})$ or R function] for longhaired field mice (*Abrothix longipilis*). **a** Partial nonparametric regression line for first-order feedback (N_{t-1} ; estimated $df = 3.68$). **b** Partial nonparametric regression line for the second-order feedback (N_{t-2} ; estimated $df = 3.9$). **c** Partial nonparametric regression line for AAOI (Antarctic Oscillation Index; estimated $df = 2.73$). The model was fitted by using natural cubic splines with estimated df using penalized regression splines with smoothing parameters selected by generalized cross validation (GCV). Dashed lines are 95% confidence intervals

To conclude, we have presented for the first time evidence of cyclic numerical fluctuations in a small rodent population from South America. As has been noted previously (Lambin et al. 2000), the results shown here point out the need to integrate studies of cyclic small rodent populations from different continents and beyond the Northern Hemisphere to resolve the enigma underlying the cyclic population dynamics exhibited by many small rodent species.

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