COMMENTARY

The dynamics of natural populations: feedback structures in fluctuating environments

La dinámica de las poblaciones naturales: estructuras de retroalimentación en ambientes fluctuantes

MAURICIO LIMA

Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago, Chile, e-mail: mlima@genes.bio.puc.cl

ABSTRACT

The fluctuations exhibited by natural populations have fascinated ecologists for the last eighty years. However, a vigorous debate between different schools of population ecologists has hampered reaching a consensus about the causes of such numerical fluctuations. Recent findings and a more synthetic view of population change espoused by ecologists, statisticians, and mathematicians have integrated the role of nonlinear feedback (deterministic) and external environmental (deterministic or stochastic) processes in the dynamics of natural populations. The new challenge for population ecologists is to understand how these two different forces interact in nature. In this commentary, I review some of the basic principles of population analysis during the last 50 years. Finally, this commentary emphasize that one of the most promising approaches in population ecology will be the analysis and interpretation of time series data from several species in the same place, and the integration of demographic analysis and mathematical modeling. In both cases we need long-term data of biological populations and the factors that effect them. The potential insights gained from such an approach will help ecologists to understand better the dynamics of natural populations and will have large implications for applied issues such as conservation, management, and control of natural populations.

Key words: population dynamics, feedback structure, exogenous factors, seasonal regulation, stochasticity, food web structure, climate.

RESUMEN

Las fluctuaciones exhibidas por las poblaciones naturales han fascinado a los ecólogos durante los últimos ochenta años. Sin embargo, las acaloradas controversias entre las dos escuelas de ecólogos poblacionales han retrasado la explicación de dichas fluctuaciones numéricas. Recientes hallazgos y una visión más sintética del cambio poblacional lograda por los ecólogos, estadísticos y matemáticos han integrado el papel de los procesos no lineales (deterministas) y los procesos externos ambientales (deterministas o estocásticos) en la dinámica de las poblaciones naturales. El nuevo desafío para los ecólogos de poblaciones es lograr entender la interacción entre estas dos diferentes fuerzas en los sistemas naturales. En este comentario, reviso algunos de los principios básicos del análisis de poblaciones durante los últimos 50 años. De la misma manera, discuto los recientes hallazgos sobre la interacción entre la estructura de retroalimentación y los factores abióticos externos, enfatizando la fuerza creativa de esta interacción para generar patrones dinámicos. Finalmente, este comentario enfatiza la visión de que una de las aproximaciones más promisorias en la ecología de poblaciones será el análisis e interpretación de series de tiempo de diferentes especies provenientes del mismo lugar, y la integración de análisis demográficos con modelos matemáticos. En ambos casos son necesarios datos de largo plazo de poblaciones biológicas y de los factores que las afectan. La ventajas potenciales de tal aproximación ayudará a los ecólogos a comprender mejor la dinámica de las poblaciones y tendrá implicaciones importantes en aspectos aplicados tales cómo la conservación, el manejo y control de las poblaciones naturales.

Palabras clave: dinámica poblacional, retroalimentación, factores exógenos, regulación estacional, estocasticidad, estructura de la red trófica, clima.

INTRODUCTION

Understanding the dynamic of natural populations is one of the central problems in population ecology (Royama 1977, 1992, Berryman 1981, 1999). Population ecologists have long been troubled by what factors regulate population dynamics, which lead to the hotly debated controversy on the role of density-dependent (intrinsic) vs. density-independent (extrinsic) factors in determining population dynamics (Nicholson 1933, Bodenheimer 1938, Andrewartha & Birch 1954, Royama 1977, 1992, Turchin 1995). Today, most population ecologists agree in that endogenous (density-dependent) and exogenous (density-independent) factors operate simultaneously in natural populations (Murdoch 1994, Turchin 1995, Huffaker et al. 1999) and that population regulation has to be understood within the context of stochastic influences (see Royama 1977, 1992, Turchin 1995 for a detailed discussion). Therefore, demonstrating density-dependence is no longer a key issue in population ecology (Royama 1977, Berryman 1991, Turchin 1995), and has been replaced by the problem of deducing the basic properties and structure of population processes (Royama 1977, 1992, Berryman 1981, 1999, Berryman et al. 1987).

On the other hand, since May (1974) showed that very simple nonlinear deterministic population models can have very complex dynamics (but see Ricker 1954 for a earlier reference), population ecologists have been looking for the signature of nonlinear interactions in nature (Schaffer & Kot 1985, Hastings et al. 1993). Although, recent studies have clearly demonstrated how nonlinear interactions between individuals can lead population fluctuations toward complex dynamics (Constantino et al. 1995, 1997, Dennis et al. 1995, 1997, Cushing et al. 1998). It is still not clear whether determining chaos in natural populations will help us to understand the underlying ecological processes (Stenseth 1999). Most population ecologists are aware that both nonlinear feedback (deterministic) forces and external (abiotic) environmental variability are operating together in natural populations. The basic problems to be faced are; (1) determining the feedback structure and deducing the dominant structure of the food web, (2) determining the nature of the stochastic forces and (3) understand how these two different forces interact to give rise to the observed dynamic patterns.

In this essay, a broad and general overview of some statistical, mathematical and ecological aspects of classical population analysis is presented. I review the development of population analysis, and show the main similarities and differences in philosophy and approach among the different authors. Although (nowadays) ecology seems to be more focused toward theoretical modeling and field experiments, long-term monitoring and time series analysis of population data are (and have been) very important for understanding natural systems. Thus, I highlight some of the advancements made in population dynamics, most of them due to the efforts of collecting population data during long time periods. In fact, the collecting tradition of Eltonian (Crowcroft 1991) and Nordic ecologists (Stenseth 1999) and entomologists (Huffaker et al. 1999) has inspired and supported population dynamic studies for decades. This essay represents only a general comment, especially directed to ecologists interested in population dynamics and those who think that population dynamics studies have a central role in ecology.

MODELLING POPULATION DYNAMICS IN A STOCHASTIC ENVIRONMENT

Let N_t be the abundance (or a proxy thereof) of a population at time t. furthermore, let ε_t be a noise term represented by some randomly distributed quantity (see Engen & Lande 1996, Bjørnstad et al. 1998, 1999a, for a detailed discussion about the error structure of the stochastic forces influencing population dynamics in natural and laboratory systems). A population dynamics model incorporating both system-intrinsic processes (both within the population and between various trophic levels) and stochastic influences may be depicted as:

$$N_t = N_{t-1}F(N_{t-1}, N_{t-2},..., N_{t-p}, \varepsilon_t) \quad (1)$$

where p denotes the number of lags included in the autoregressive process (i.e., the order of the autoregressive process, see Berryman et al. 1987, Royama 1992, Turchin 1995). In the absence of stochastic noise ($\varepsilon_t = 0$, for all t) equation 1 is just a difference equation (linear or non-linear) capable of several dynamical behaviors, ranging from stability (exponential or oscillatory), through limit cycles and quasiperiodicity to chaos (May 1974, Schaffer & Kot 1985, Turchin & Taylor 1992). This noise-free case of equation 1 can be referred to as a skeleton (Tong 1993). The skeleton (function F) represents the individual interactions (within and between populations) or the feedback structure (Berryman 1981, 1999, Royama 1977, 1992). An alternative way to express equation 1 is in terms of the realized per

capita population growth rates that represent the processes of individual survival and reproduction (Berryman 1999). Defining $R_t = \log(N_t) - \log(N_{t-1})$, equation 1 can be expressed as a R-function (sensu Berryman 1999):

$$R_t = f(N_{t-1}, N_{t-2},..., N_{t-p}, \varepsilon_t) \quad (2)$$

This model represents the basic feedback structure and integrates the 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. In the following I will review some of different approaches followed by different authors.

Probably the first time series analysis of a population dynamic process was made by Moran (1953a) who focused on the lynx fur-returns data. Moran (1953a, 1953b) fitted a linear second-order autoregressive model to the log-transformed lynx data, which provides an important insight on two essential aspects of the lynx dynamics. The first, was the order of the feedback structure and the second was the cause of the synchrony of the cycles among regional populations. The order of the feedback structure represents an appropriate and useful way to deduce the food web structure (see Stenseth et al. 1997, Berryman 1999). The second insight of Moran's study was related to the effect of a correlated density-independent stochastic factor on the synchrony of regional populations ("the Moran's effect", see Royama 1992). Despite of the implications of Moran's studies they were largely ignored in the ecological literature for decades. One year later, Ricker (1954) introduced the concept of "reproduction curves" as the relationship "...between the existing stock and the future stock which the existing stock produces". The author describes the different types of reproduction curves (discrete maps) that may be found in nature, and develop two important issues for population dynamics. One was how the shape of the reproduction curve determines the kind of deterministic dynamics of a population. In fact, Ricker (1954) was the first ecologist who showed that negative feedback can give rise to regular and irregular population oscillations (cycles and chaos). The second insight of Ricker's monographs was his intention to link the type of reproduction curves (and the subsequent population dynamic patterns) to some explicit biological mechanisms, such as, predation, competitive interactions and cannibalism. In addition, Ricker was very interested in the interaction between (stochastic) disturbances and reproduction curves, and how the relative importance of both factors influences population fluctuations.

Although, Moran (1953a, 1953b), Ricker (1954) and also Morris (1959) described the basic structures of the population dynamics processes, that is the order and the shape of the feedback structure. These insights were ignored in most of the ecological literature (but many entomologists were involved in these issues in the 60's and 70's, see Berryman 1978 for details) for more than twenty years. However, they were clearly expressed in the Royama (1977) influential work on population dynamics and the notions of density-dependence and basic population structures (see Royama 1977 pp. 6-7). These basic structures are the components of the factors that determine R (per capita population growth rate), that is the R-function of equation (2), which represent a general form of the "reproduction curves" of Ricker (1954). Following Royama's (1977) notations, the factors that determine R can be classified as density uninfluenced or "exogenous" (Z) and density influenced or "endogenous" (F). Royama's scheme represents the basic structures of population dynamic processes and they can be linked to ecological time series data using equation (2). The factors belonging to the F category are those which conform the feedback structure of the population processes. The F factor involves the idea of first-order and second-order negative feedback (Morris 1959, Varley et al. 1973, Berryman 1981, 1999). Determining the structure of the system (F factors), that is the sign (+ or -) and order of the feedback structure, is the key issue in population dynamic studies, and in linking such studies to food web structure (Berryman 1999), a fact not widely appreciated by ecologists.

The approaches followed by the different authors to choose the type of f models to represent the structure of population dynamics have been varied. Some authors have used log-linear models to describe population dynamics (Royama 1992, Bjørnstad et al. 1995, Stenseth et al. 1996a, 1996b, 1997, Lima & Jaksic 1999). These kinds of models are one of the simplest representations of population dynamic processes. Log-linear autoregressive models are very useful to determine the density-dependent structure (the order of the density-dependent feedback), particularly in short time series (15-20 points). In addition, the feedback coefficients (first- and second-order) can be used for comparisons among populations or species (Bjørnstad et al. 1995, Stenseth et al. 1996a) and to link time series and mathematical models (Stenseth et al. 1996b, 1997). However, linear models have an unrealistic ecological property, the per capita population growth rate is unbounded and also cannot exhibit complex dynamics (Royama 1992). Another option is to use

theoretically-based models, such as the discrete non-linear logistic model (Berryman 1991, 1992, Royama 1992), or the two-lag linear modification of the discrete logistic model (Turchin 1990). Theoretically based time series models have the advantage that parameters have a direct biological interpretation, fulfill some basic biological and logical properties, have a parsimonious structure and also enable extrapolation beyond the data (Royama 1992). The cost comes from assuming a specific functional form for f. However, one can fit several alternative theoretical models and use model selection tools, such as cross validation or Akaike Information Criteria (AIC) (see Burnahm & Anderson 1998) to choose the best model according to the available data.

A more complex approach is to choose the functional form of f using the response surface methodology (Turchin & Taylor 1992) and neural nets (Ellner & Turchin 1995). Recently, non-parametric autoregressive models with non-Gaussian error have been used to determine the feedback structure (Bjørnstad et al. 1998). This kind of model may be estimated using the framework of Generalized Additive Models (GAM) (see Stenseth et al. 1997, Bjørnstad et al. 1998, 1999a for applications to population dynamics):

$$R_t = f_1(N_{t-1}) + f_2, (N_{t-2}) + ... + f_d (N_{t-d}) \quad (3)$$

The basis functions f_i of the additive terms are natural cubic-B splines smoothers (Bjørnstad et al. 1998). However, there are some problems, one is overfitting when there are not enough data points, and the other is the biological interpretation of the model parameters and extrapolation (see Royama 1992). Taking in consideration that population data are mostly short (15-30 points), and that some essential aspect of population dynamic structures and processes in natural systems are unknown, the use of simple theoretical models has clear advantages and merits.

INTERACTIONS BETWEEN FEEDBACK STRUCTURES AND STOCHASTICITY

A very interesting type of interaction between deterministic and stochastic processes was proposed by Bjørnstad et al. (1999b) and Stenseth et al. (1999a) for explaining the two-peaked spectrum (cycles and trends) observed in the recruitment time series of a cod (*Gadus morhua*) population. These authors argued that the short-term cycles and long-term trends are the results of stochastic (white noise) recruitment echoed through the age structure of the population. In this case stochastic recruitment appears to interact with population-intrinsic density dependent processes (inter-cohort competitive interactions) to produce a dynamical pattern that is very different to that predicted by the purely deterministic or stochastic models. In ecological terms, the effect is caused by the inter-cohort interaction operating as a "resonator" for the variability in recruitment. As a consequence, the dynamics of this cod population would be the result of the combined age-structured deterministic processes and stochastic forces. In fact, other marine populations appear to have the potential to give rise to this type of complex dynamics when inter-cohort interactions are strong enough (Lima et al. 2000). The recruitment dynamics of the yellow clam (*Mesodesma mactroides*) in Uruguayan coasts is an interesting example of how density-dependent structure and stochasticity can interact to give rise to complex dynamics for determined values of inter-cohort interactions.

On the other hand, recent studies have shown the importance of global and local climatic variables in determining the dynamics of natural populations. Large northern ungulates (Post et al. 1997, Forchhammer et al. 1998, Post & Stenseth 1999), small mammals (Merrit et al. 2001) and song birds (Saether et al. 2000) populations are influenced by a large-scale climatic variable such as the Northern Atlantic Oscillation (NAO). In the same vein, small mammal populations in semi-arid regions of western South America are strongly influenced the El Niño Southern Oscillation (ENSO) phenomena (Jaksic et al. 1997, Lima et al. 1999a, 1999b). However, understand and predicting the dynamical consequences of these climatic influences on population change is not an easy task. First, because population responses to environmental forces depend of the type of feedback structure (Royama 1992). Also, the relation between demographic responses and climate variability can be highly nonlinear implying that population change may show large responses to small climatic changes and vice versa (Saether et al. 2000). On the other hand, global climate has its own complex temporal dynamics that can be the result of a nonlinear dynamical system driven by random fluctuations (Stone et al. 1998). For example, the strong aperiodicity (every 3-7 years) observed in the El Niño Southern Oscillation ENSO (Allen et al. 1996) may result from stochastic resonance via chaotic dynamics induced by external noise (Stone et al. 1998). Otherwise, the NAO is closely associated with global fluctuations in temperature and an increasing trend of this index has been observed during the last 30 years (Hurrel 1995). This trend in climate change

will have positive effects on ungulate (Forchhammer et al. 1998, Post & Stenseth 1999) and bird (Saether et al. 2000) populations in northern Europe, but negative consequences for small mammal populations in eastern North America (Merrit et al. 2001).

CHANGES OF THE FEEDBACK STRUCTURE

Natural populations are potentially embedded in a web of interaction with other species so that many feedback loops can be created, and a complex feedback structure is expected. However, the empirical evidence from time series analysis suggests that natural populations have feedback structures characterized by dimension one or two. This is an indication that population dynamics are controlled by simple feedback structures and that only certain feedbacks in the food web dominate the dynamics of natural populations (see Berryman 1993, 1999 for details). This phenomenon is related to the concept of limiting factors or the "law of the minimum" (Liebig 1840), and it has been integrated within a population dynamic framework by Berryman (1993, 1999). However, although only one feedback is able to dominate population dynamics close to equilibrium, this can change from time to time, given some external or internal factors. Consequently it is possible to find complex regulatory structures and alternative stable states (meta-stable dynamics, see Berryman 1999) in natural populations.

For example, the feedback structures may change according to some population density threshold. This phenomenon has been clearly represented by a kind of modeling approach using Threshold Autoregressive models (TAR, see Tong 1993). These models are piecewise Taylor approximations to more general nonlinear models (Stenseth 1999), the fitting procedures are well developed (Tong 1993), and they have been applied recently in an ecological setting (Framstad et al. 1997, Grenfell et al. 1998, Stenseth et al. 1998). The model depicted by equation (1) may be simplified in several ways. The function $F(\bullet)$ may be represented by an exponential function (e.g., Stenseth et al. 1996a, 1996b; i.e., $F(\bullet)$ = $\exp(f(\bullet))$, where f is some function of the same variables as F. It may further be argued that it is appropriate to consider the f-function to be represented primarily as a function of $X_{t-1} = \log_e (N_{t-1})$; $X_{t-2} = \log_e (N_{t-2})$, etc. (Berryman 1992, Royama 1992, Turchin 1995, Stenseth et al. 1996a). A log-linear TAR model can be expressed as (see Stenseth 1999):

$$R_1 = \beta_{1,0} + \beta_{1,1} \cdot X_{t-1} + \beta_{1,2} \cdot X_{t-2} + \sigma_1 \cdot \varepsilon_t \text{ if } X_{t-d} \leq \theta \quad (4)$$
$$R_2 = \beta_{2,0} + \beta_{2,1} \cdot X_{t-1} + \beta_{2,2} \cdot X_{t-2} + \sigma_2 \cdot \varepsilon_t \text{ if } X_{t-d} \leq \theta$$

where $\beta_{i,j}$ (i = 1 and 2) are the autoregressive parameters for the two domains. Notice that ε_t represent a noise term normally distributed and σ_1 is a positive parameter representing the degree of stochasticity in the two domains. The assumption about the error structure is based on the fact that natural populations are generally lognormal or gamma distributed (Engen & Lande 1996) and thus the variance is stabilized by a log-transformation (Sen & Sivrastava 1990). The biological meaning of this model lies in that a different feedback structure exists for each domain (θ), and that the threshold represents some critical density level (Fig. 1). For instance, a TAR model with population density as the threshold to separate the two domains has been used to describe population dynamics of the lynx (Stenseth et al. 1998a) and sheep (Grenfell et al. 1998). In this case, there are two different density-dependent structures depending on the actual or some lagged population density. If these population systems are faced with some external environmental perturbations (be it deterministic or stochastic), the density-dependent structure can switch from one state to the other depending on the magnitude of the perturbation. For example, Grenfell et al. (1998) showed that the feedback structure of soay sheep populations can be represented by a first-order feedback above the population threshold, while below the threshold the realized population per capita growth rate is constant and positive (exponential growth) (Fig. 1A). On the other hand, the observed population dynamics of the lynx across northern Canada appears to be the result of a common TAR structure (first- and second-order feedback), but second-order feedback are stronger above the population threshold (Stenseth et al. 1998) (Fig. 1B).

Another approach to the problem of feedback dominance, thresholds and shift in the feedback structures is based on the interaction between negative and positive feedbacks (Berryman 1999). Because the opposed forces of negative (e.g., competition) and positive (co-operation) feedbacks complex R-functions can be produced with three (or more) equilibrium points (Fig. 2A). The population dynamics of such feedback structure can shift from one to other stable state given the existence of an unstable intermediate equilibrium point or escape threshold where positive feedbacks dominate (Fig. 2A). This kind of dynamics is called meta-stable (Berryman 1999) and can be approached by using two different R-functions
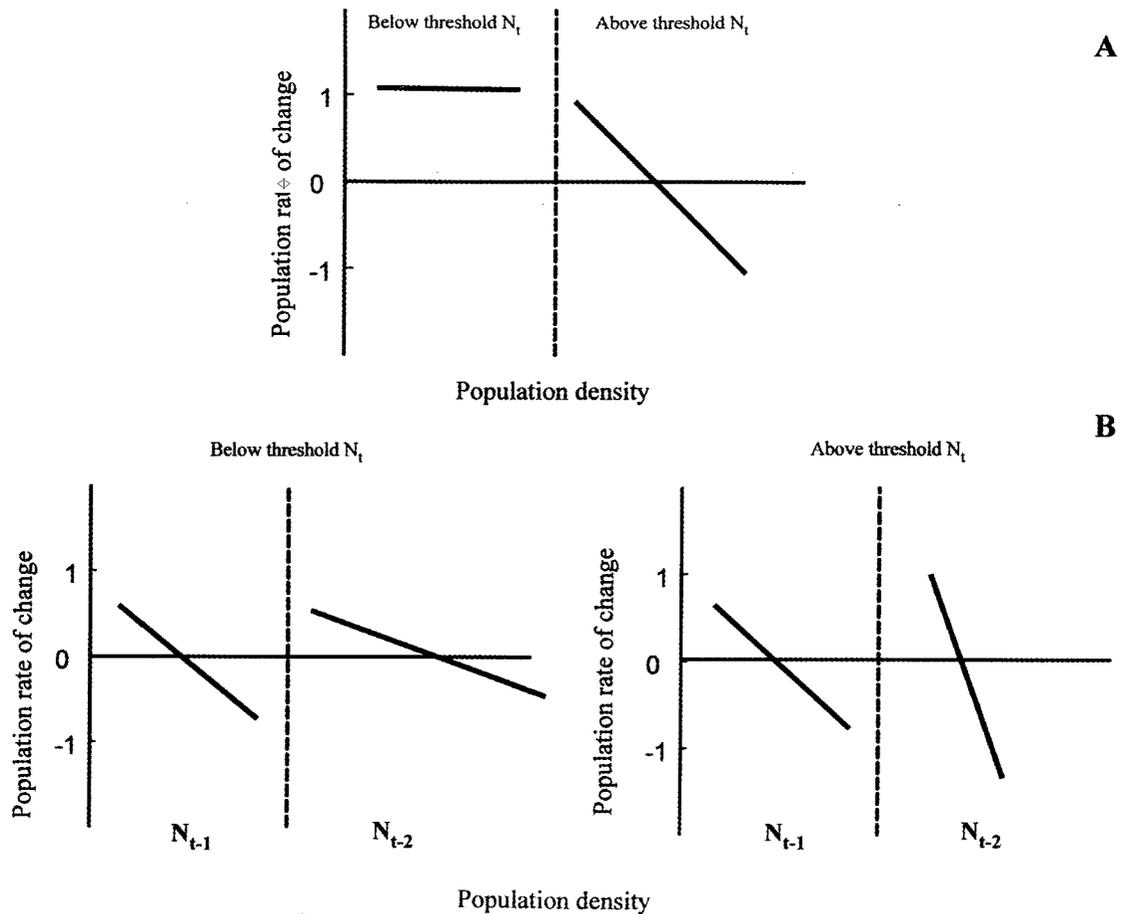
Fig. 1: Changes in the feedback structure according to population density. (A) The population rate of change (R-function) is constant (exponential growth) below the population threshold and there is a negative feedback above the population threshold (see Grenfell et al. 1998 for details). (B) Below the population threshold (left inset) the realized per capita growth rate showed first-order (N_{t-1}) and weak second-order (N_{t-2}) feedback, while above the population threshold (right inset) the second-order feedback is stronger (see Stenseth et al. 1998 for details).

Cambios en la estructura de retroalimentación en relación con la densidad poblacional. (A)La tasa de cambio poblacional (función-R) es constante (crecimiento exponencial) debajo de la densidad umbral y presenta una retroalimentación negativa arriba del nivel de densidad poblacional umbral (véase Grenfell et al. 1998 por detalles). (B) Debajo del umbral (parte izquierda de la figura) la tasa de cambio realizada presenta una retroalimentación de primer (N_{t-1}) y segundo orden (N_{t-2}), mientras que arriba del umbral poblacional la retroalimentación de segundo orden es mayor (véase Stenseth et al. 1998).

for each domain (equation 4) because natural populations are almost never observed near unstable equilibrium (Fig. 2B). Population dynamics regulated by two different first-order feedbacks exhibit sudden transitions from low- to high-density dynamics, while catastrophic "boom and bust" dynamics are produced if second-order feedback dominate at high-densities (Berryman 1999). One of the best examples of a meta-stable system is population dynamics of bark beetles and how they escape tree defenses (by positive feedback) producing massive tree mortality in forest ecosystems (Berryman et al. 1984).

A somewhat different kind of change in the feedback structure has been recently proposed for explaining rodent outbreaks in semiarid Chile. It has been proposed that the frequent (but aperiodic) rodent outbreaks ("ratadas") are the outcome of shift in feedback dominance mediated by El Niño disturbances (Lima, Stenseth, Crespin, Yoccoz & Jaksic unplublished results). A strong first-order feedback will dominate population dynamics during low-rainfall periods (competition for food limitation) producing low population density and saw-toothed oscillations (Fig. 3A), while second-order feedback, suggestive of
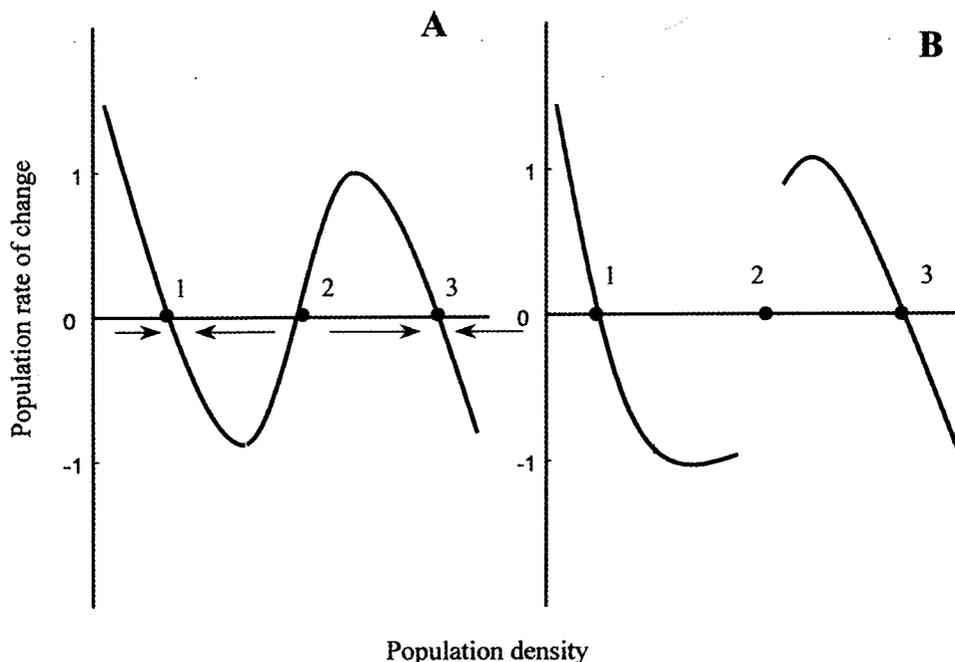
Population density

Fig. 2: (A) Example of a complex R-function, which is characterized by negative feedback at low densities, positive feedback at intermediate densities and at high-density population is limited again by a negative feedback. This R-function is characterized by showing two stable (1 and 3) and one unstable (2) equilibrium. Predators that switch or aggregate in response to prey densities are able to create this feedback structure in prey populations (see Berryman 1999 pp. 75 for details). (B) Approximation to this complex R-function by two first-order stabilizing R-functions because natural populations are almost never observed near unstable equilibrium.

(A) Ejemplo de una función-R compleja caracterizada por retroalimentación negativa a bajas densidades, positiva a densidades intermedias y negativa de nuevo a altas densidades. Esta función-R está caracterizada por dos puntos equilibrios estables (1 y 3) y un punto de equilibrio inestable (2). Depredadores capaces de agregarse o cambiar de presa en respuesta a la densidad de las mismas pueden crear este tipo de estructura de retroalimentación en las presas. (véase Berryman 1999 pp. 75 para más detalles). (B) Aproximación a esta compleja función-R por medio de dos funciones-R de primer orden dado que las poblaciones naturales casi nunca son observadas cerca del punto inestable de equilibrio.

trophic interactions (predators or plants), dominates during high-density and high-rainfall years and causes low frequency dynamics (Fig. 3B). Consequently, rodent outbreaks ("ratadas") in semiarid Chile may be caused by the interaction between climatic variability (ENSO), intra-specific interactions and food web structure.

SEASONAL DENSITY-DEPENDENT STRUCTURE

Recent studies on cyclic species of voles show an important consequence of seasonality; namely, density-dependent regulation that differs between seasons (Mallorie & Flowerdew 1994, Hansen et al. 1999). In northern Fennoscandia winter regulation appears to be the crucial factor in the production of multi-annual cycles of the vole community (Hansen et al. 1999). Also, many small rodent populations living in seasonal environ-

ments experience different sequential density dependent processes within a year (Nelson et al. 1991, Hörnfeldt 1994, Morris 1996). Hansen et al. (1999) represented the seasonal feedback structure using an autoregressive model that considers spring and autumn abundances as separate variables. Let S_t and F_t be the log abundances in the year t at spring and fall respectively, the population growth rates of winter and summer can be written as a linear function of their seasonal densities:

$$R_{wt} = S_t - F_{t-1} = a_1 F_{t-1} + a_2 S_{t-1} + a_3 F_{t-2} + a_4 S_{t-2} + \varepsilon_{wt}$$

$$R_{st} = F_t - S_t = b_1 S_t + b_2 F_{t-1} + b_3 S_{t-1} + b_4 F_{t-2} + \varepsilon_{st} \quad (4)$$

R_{wt} and R_{st} represent the population growth rates during winter and summer respectively. The a_i parameters represent the feedback acting during the winter and the b_i parameters the feedback
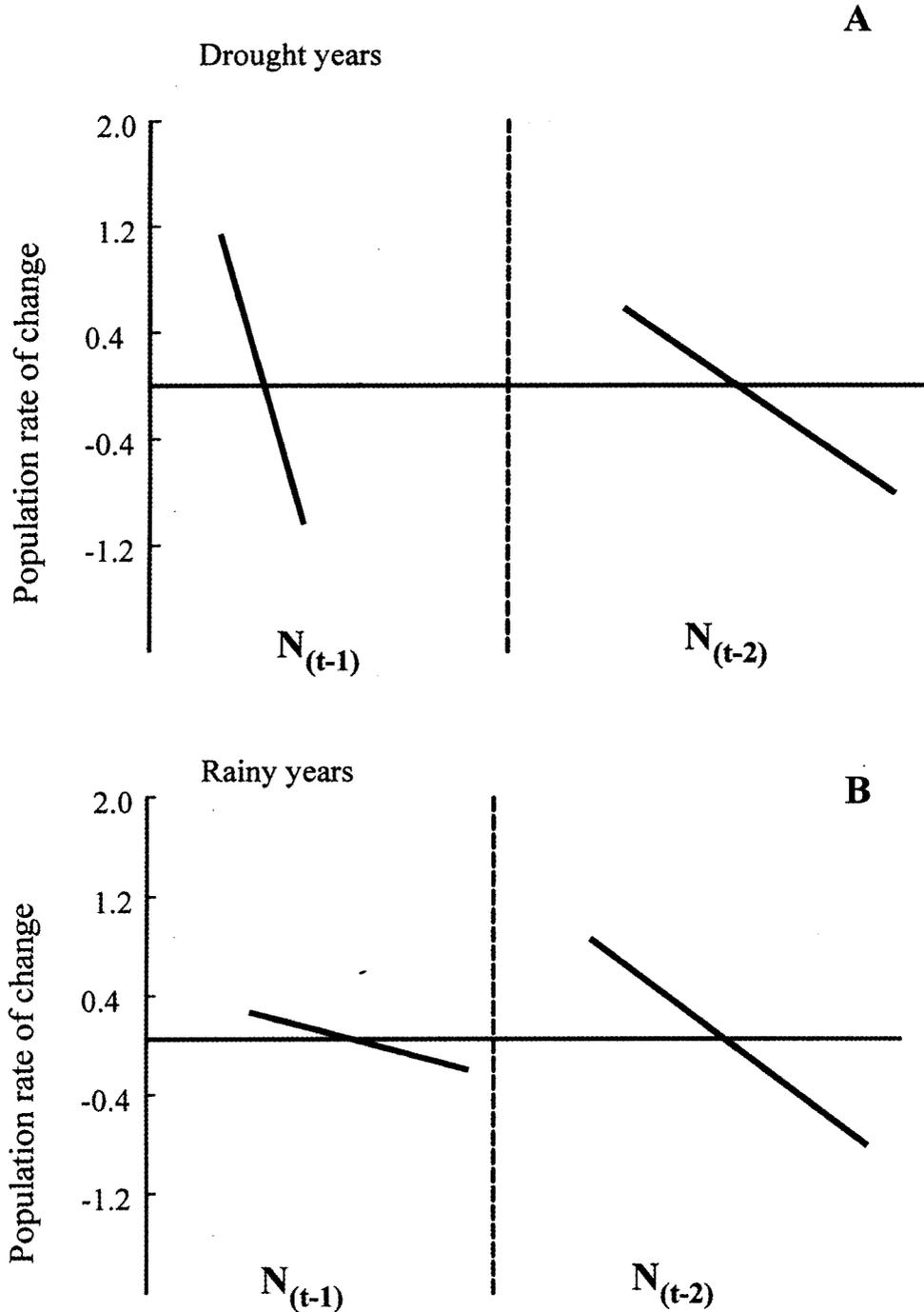
Fig. 3: Changes of feedback structure according to some exogenous perturbation (e.g., El Niño) for leaf-eared mice (*Phyllotis darwini*) population dynamics. The population rate of change (R-function) changes the feedback structure in relation with the rainfall level. Note that during low-rainfall years (La Niña drought-years) a first-order feedback (N_{t-1}) dominates the R-function and population dynamics, while during high-rainfall years a second-order feedback (N_{t-2}) become dominant.

Cambios de la estructura de retroalimentación en respuesta a una perturbación exógena (e.g., El Niño) en la dinámica poblacional del lauchón orejudo (*Phyllotis darwini*). La tasa de cambio poblacional (función-R) modifica su estructura de retroalimentación con el nivel de precipitaciones. Durante años de bajas precipitaciones (La Niña) la función-R y la dinámica poblacional son dominadas por una retroalimentación de primer orden (N_{t-1}), mientras que durante los años lluviosos (e.g., EL Niño) una retroalimentación de segundo orden (N_{t-2}) se vuelve dominante.

during the summer. The parameter a_1, a_2, b_1 and b_2 measure first-order feedback, while second-order feedback is represented by the other parameters and the noise terms are represented by ε_{wt} and ε_{st}.

One important result is that winter regulation appears to be the crucial element in producing multi-annual cycles in gray-sided vole populations (Hansen et al. 1999) (Fig. 4). The comparison of this result to the seasonal dynamics of southern red-backed voles in eastern North America showed some interesting insights on seasonal regulation in vole population dynamics

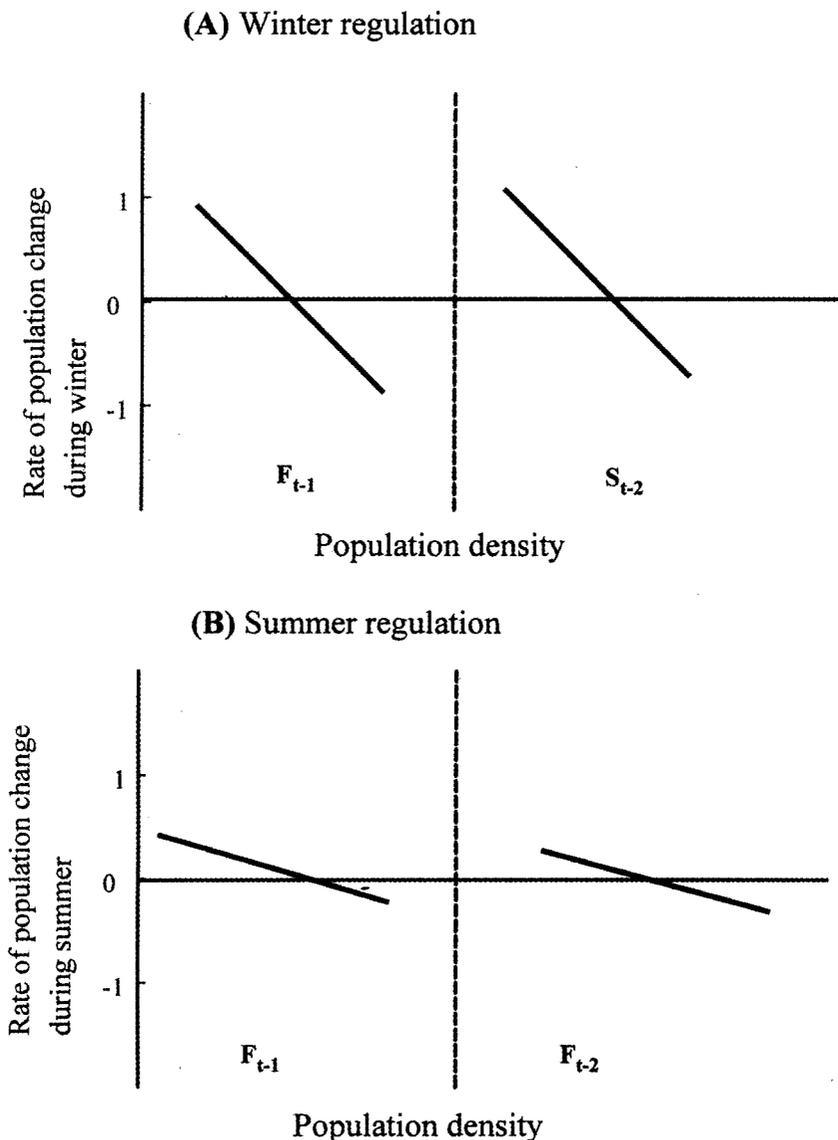## (A) Winter regulation

(B) Summer regulation

Fig. 4: Seasonal feedback structure of gray-sided voles (*Clethrionomys rufocanus*) in Fennoscandia (from Hansen et al. 1999). (A) Winter regulation characterized by strong first- and second-order negative feedback (R_{wt} = population growth rates during winters; F_{t-1} = previous autumn density; S_{t-2} = spring density two years before). (B) Summer regulation characterized by weak first- and second-order negative feedback (R_{st} = population growth rates during summers; F_{t-1} = previous autumn density; F_{t-2} = autumn density two years before).

Estructura de retroalimentación estacional del roedor (*Clethrionomys rufocanus*) en el norte de Finlandia (Hansen et al. 1999). (A) Regulación durante el invierno caracterizada por una fuerte retroalimentación de primer y segundo orden (R_{wt} = tasa de cambio poblacional durante los inviernos; F_{t-1} = densidad durante el otoño previo; S_{t-2} = densidad durante la primavera dos años antes). (B) Regulación durante el verano caracterizada por una débil retroalimentación de primer y segundo orden (R_{st} = tasa de cambio poblacional durante los veranos; F_{t-1} = densidad durante el otoño previo; F_{t-2} = densidad durante el otoño dos años antes).

(Merrit et al. 2001) (Fig. 5). Hansen et al. (1999) found that one of the most important factors that may explain cyclic dynamics in gray-sided voles is a seasonal change in the strength of regulation. They found that the gray-sided vole seasonal dynamics at Fennoscandia was characterised by a stronger first- and second-order negative feedback structure in winters than in summers, implying that a major part of the regulation occurs during winter (Fig. 4). However, seasonal regulation in southern red-backed voles switches from first- and second-order feedback in winter to only first-
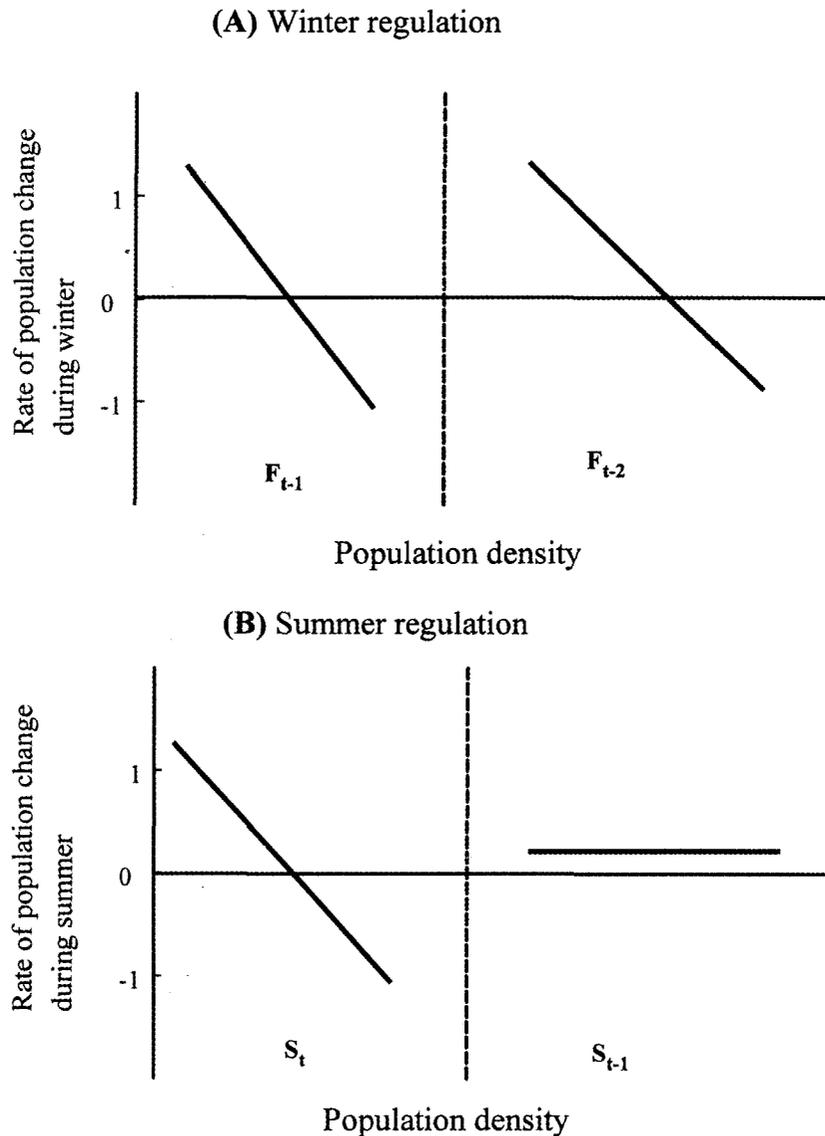
(A) Winter regulation

(B) Summer regulation

Population density

Fig: 5. Seasonal feedback structure of southern red-backed voles (*Clethrionomys gapperi*) in Pennsylvania (Merritt et al. 2001). (A) Winter regulation characterized by strong first- and second-order negative feedback (R_{wt} = population growth rates during winters; F_{t-1} = previous autumn density; F_{t-2} = autumn density two years before). (B) Summer regulation characterized only by strong first-order feedback (R_{st} = population growth rates during summers; S_t = previous spring density; S_{t-2} = spring density two years before).

Estructura de retroalimentación estacional del roedor (*Clethrionomys gapperi*) en Pennsylvania (Merritt et al. 2001). (A) Regulación durante el invierno caracterizada por una fuerte retroalimentación de primer y segundo orden (R_{wt} = tasa de cambio poblacional durante los inviernos; F_{t-1} = densidad durante el otoño previo; F_{t-2} = densidad durante el otoño dos años antes). (B) Regulación durante el verano caracterizada solo por una fuerte retroalimentación de primer orden (R_{st} = tasa de cambio poblacional durante los veranos; S_t = densidad durante la primavera previa; S_{t-1} = densidad durante la primavera dos años antes).

order feedback in summer (Fig. 5). This dominance of first-order feedback along the year may explain why southern red-backed voles did not exhibit cyclic dynamics as gray-sided voles in Fennoscandia. On the other hand, this kind of approach makes insights about the food web structure of these two ecosystems. Despite of the apparent complexity of the food webs in both systems (boreal and deciduous forests), the realised dynamics of gray-sided voles in Fennoscandia is of order two (due to trophic interactions during winters), while the dynamics of southern red-backed voles is of order one. The paradox is that despite being embedded in a richer small mammal and predator community, the southern red-backed vole dynamics suggest a simpler food web structure, mostly dominated by first order feedbacks.

CONCLUSIONS

The issues discussed above emphasize the importance of determining the feedback structure and the exogenous factors for understanding population dynamics in nature (Royama 1977, 1992, Berryman 1981, 1999, Berryman & Millstein 1994, Turchin 1995, Stenseth et al. 1996b, 1998, Stenseth 1999). It is clear that the underlying mechanisms of the interaction between environmental variation and regulatory structure have not been fully explored in population ecology. There is much work to be done for ecologists, statisticians, and mathematicians in order to develop new conceptual frameworks, statistical methods and mathematical tools to deal with the questions raised by this theme. Although these new questions render population dynamics and demographic studies a little bit more complex, it is certainly true that they also bring new challenges and open new and exciting research opportunities.

I believe that the major advances in the understanding of population dynamics had come from the analysis and interpretations of ecological time series. Of course that mathematical modeling and experimentation are important elements in population ecology, but without time series data and analysis the crucial point in population ecology is lost; that is, the temporal pattern of fluctuation (the population phenomena). Thus, without a clear description and interpretation of the population dynamic pattern, it is very difficult to see how plausible biological hypothesis can be constructed (Berryman 1999). I think that the most promising approach in population ecology will be the analysis and interpretation of time series data from several species in the same place (Berryman 1999) and the integration of demographic analysis and mathematical modeling (Stenseth 1999). In both cases we need long-term data of biological populations and the factors that effect them. The potential insights gained from such interactions will help ecologists to understand better the dynamics of natural populations and will have large implications for applied issues such as conservation, management, and control of natural populations.

LITERATURE CITED

ALLEN R, J LINDESAY & D PARKER (1996) El Niño Southern Oscillation and Climatic Variability. Commonwealth Scientific and Industrial Research Organisation (CSIRO) Publishing, Collingwood, Australia. 405 pp.

ANDREWARTHA HG & LC BIRCH (1954) The distribution and abundance of animals. University of Chicago Press, Chicago, Illinois. 782 pp.

BERRYMAN AA (1978) Towards a theory of insect epidemiology. Researches in Population Ecology 19: 181-196.

BERRYMAN AA (1981) Population systems: a general introduction. Plenum Press, New York, New York. 222 pp.

BERRYMAN AA (1991) Stabilization or regulation: what it all means! Oecologia 86: 140-143.

BERRYMAN AA (1992) On choosing models for describing and analyzing ecological time series. Ecology 73: 694-698.

BERRYMAN AA (1993) Food web connectance and feedback dominance, or does everything really depends of everything else? Oikos 68: 183-185.

BERRYMAN AA (1999) Principles of population dynamics and their application. Stanley Thornes (Publishers) Ltd., Cheltenham, United Kingdom. 243 pp.

BERRYMAN AA & JA MILLSTEIN (1994) Population Analysis System. Single species time series analysis. Ecological System Analysis, Pullman, Washington. 55 pp.

BERRYMAN AA, NC STENSETH & DJ WOLLKLIND (1984) Metastability in forest ecosystem infested by bark beetles. Researches in Population Ecology 26: 13-29.

BERRYMAN AA, NC STENSETH & AS ISAEV (1987) Natural regulation of herbivorous forest insect populations. Oecologia 71: 174-184.

BJØRNSTAD ON, W FALCK & NC STENSETH (1995) A geographical gradient in small rodent density fluctuations: a statistical modeling approach. Proceedings of the Royal Society of London B 262: 127-133.

BJØRNSTAD ON, M BEGON, NC STENSETH, W FALCK, S SAIT & DJ THOMPSON (1998) Population dynamics of the Indian meal moth: demographic stochasticity and delayed regulatory mechanisms. Journal of Animal Ecology 67: 110-126.

BJØRNSTAD ON, J-M FROMENTIN, NC STENSETH & J GJØSAETER (1999a) A new test for density-dependent survival: the case of coastal cod populations. Ecology 80: 1278-1288.

BJØRNSTAD ON, JM FROMENTIN, NC STENSETH & J GJØSAETER (1999b) Cycles and trends in cod populations. Proceeding of the National Academy of Sciences USA 96: 5066-5071.

BODENHEIMER FS (1938) Problems of animal ecology. Oxford University Press, Oxford, United Kingdom. 434 pp.

BURNHAM KP & DR ANDERSON (1998) Model selection and inference: a practical information theoretic approach. Springer-Verlag, New York, New York.

CONSTANTINO RF, JM CUSHING, B DENNIS & RA DESHARNAIS (1995) Experimentally induced transitions in the dynamic behavior of insect populations. Nature 375: 227-230.

CONSTANTINO RF, RA DESHARNAIS JM CUSHING & B DENNIS (1997) Chaotic dynamics in an insect population. Science 275: 389-391.

CROWCROFT P (1991) Elton's ecologists: a history of the Bureau of Animal Population. University of Chicago Press, Chicago, Illinois. 177 pp.

CUSHING JM, B DENNIS, RA DESHARNAIS & RF CONSTANTINO (1998) Moving toward an unstable equilibrium: saddle nodes in population systems. Journal of Animal Ecology 67: 298-306.

DENNIS B, RA DESHARNAIS, JM CUSHING & RF CONSTANTINO (1995) Nonlinear demographic dynamics: mathematical models, statistical methods, and biological experiments. Ecological Monographs 65: 261-281.

DENNIS B, RA DESHARNAIS, JM CUSHING & RF CONSTANTINO (1997) Transitions in population dynamics: equilibria to periodic cycles to aperiodic cycles. Journal of Animal Ecology 66: 704-729.

ELLNER S & P TURCHIN (1995) Chaos in a noisy world: new methods and evidence from time series analysis. American Naturalist 145: 343-375.

ENGEN S & R LANDE (1996) Population dynamic models generating species abundance distributions of the gamma type. Journal of Theoretical Biology 178: 325-331.

FORCHHAMMER MC, NC STENSETH, E POST & R LANGVATN (1998) Population dynamics of Norwegian red deer: density-dependence and climatic variation. Proceedings of the Royal Society of London B 265: 341-350.

FRAMSTAD E, NC STENSETH, ON BJØRNSTAD & W FALCK (1997) Limit cycles in Norwegian lemmings: tensions between phase-dependence and density-dependence. Philosophical Transactions of the Royal Society of London B 264: 31-38.

GRENFELL BT, K WILSON, BF FINKENSTÄDT, TN COULSON, S MURRAY, SD ALBON, JM PEMBERTON, TH CLUTTON-BROCK & MJ CRAWLEY (1998) Noise and determinism in synchronised sheep dynamics. Nature 394: 674-677.

HANSEN TF, NC STENSETH & H HENTTONEN (1999) Multiannual vole cycles and population regulation during long winters: an analysis of seasonal density-dependence. American Naturalist 154: 129-139.

HASTINGS A, CL HOM, S ELLNER & P TURCHIN (1993) Chaos in ecology: is mother nature a strange attractor? Annual Review of Ecology and Systematics 24: 1-33.

HÖRNFELDT B (1994) Delayed density dependence as a determinant of vole cycles. Ecology 75: 791-806.

HUFFAKER CB, AA BERRYMAN, P TURCHIN (1999) Dynamics and regulation of insect populations. In Huffaker CB & AP Gutiérrez (eds) Ecological entomology: 269-312. Academic Press, New York, New York.

HURREL JW (1995) Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. Science 269: 676-679.

LIEBIG J (1840) Chemistry and its applications to agriculture and physiology. Taylor and Walton, London, United Kingdom.

LIMA M & FM JAKSIC (1999) Population dynamics of three Neotropical small mammals: time series models and the role of delayed density-dependence in population irruptions. Australian Journal of Ecology 43: 24-35.

LIMA M, PA MARQUET & FM JAKSIC (1999a) El Niño events, precipitation patterns, and rodent outbreaks are statistically associated in semiarid Chile. Ecography 22: 213-218.

LIMA M, JE KEYMER & FM JAKSIC (1999b) ENSO-driven rainfall variability and delayed density dependence cause rodent outbreaks in western South America: linking demography and population dynamics. American Naturalist 153: 476-491.

LIMA M, A BRAZEIRO & O DEFEO (2000) Population dynamics of the yellow clam (*Mesodesma mactroides*): recruitment variability, density-dependence and stochastic processes. Marine Ecology Progress Series 207: 97-108.

MALLORIE HC & JR FLOWERDEW (1994) Woodland small mammal population ecology in Britain: a preliminary review of the Mammal Society survey of wood mice *Apodemus sylvaticus* and bank voles *Clethrionomys glareolus*, 1982-1987. Mammal Review 24: 1-15.

MAY RM (1974) Biological populations with non-overlapping generations: stable points, stable cycles, and chaos. Science 186: 645-647.

MERRIT JF, M LIMA & F. BOZINOVIC (2001) Seasonal regulation in fluctuating small mammal populations: feedback structure and climate. Oikos (in press).

MORRIS RF (1959) Single-factor analysis in population dynamics. Ecology 40: 580-588.

MORRIS DW (1996) Temporal and spatial population dynamics among patches connected by habitat selection. Oikos 75: 207-219.

MURDOCH WW (1994) Population regulation in theory and practice. Ecology 75: 271-287.

NELSON J, J AGRELL, S ERLINGE & M SANDELL (1991) Reproduction of different female age categories and dynamics in a non-cyclic field vole, *Microtus agrestis*, population. Oikos 61: 73-78.

NICHOLSON AJ (1933) The balance of animal populations. Journal of Animal Ecology 2: 132-178.

POST E & NC STENSETH (1999) Climate change, plant phenology and northern ungulates. Ecology 80: 1322-1339.

POST E, NC STENSETH, R LANGVATN & J-M FROMENTIN (1997) Global climate change and phenotypic variation among red deer cohorts. Proceedings of the Royal Society of London B 264: 1317-1324.

RICKER WE (1954) Stock and recruitment. Journal of Fisheries Research Board of Canada 5: 559-623.

ROYAMA T (1977) Population persistence and density-dependence. Ecological Monographs 47: 1-35.

ROYAMA T (1992) Analytical population dynamics. Chapman & Hall, London, United Kingdom. 371 pp.

SCHAFFER WM & M KOT (1985) Do strange attractors govern biological systems? BioScience 35: 342-350.

SEN A & M SRIVASTAVA (1990) Regression analyses: theory, methods and applications. Springer Verlag, New York, New York. 347 pp.

SAETHER BE, J TUFTO, S ENGEN, K JERSTAD, OW RESTAD & JE SKÅTAN (2000) population dynamical consequences of climate change for small temperate songbird. Science 287: 854856.

STENSETH NC (1999) Population cycles in voles and lemmings: density-dependence and phase dependence in a stochastic word. Oikos 87: 427-461.

STENSETH NC, ON BJØRNSTAD & T FALCK (1996a) Is spacing behavior coupled with predation causing the microtine density cycle? A synthesis of current process-oriented and pattern-oriented studies. Proceedings of the Royal Society of London B 263: 1423-1435.

STENSETH NC, ON BJØRNSTAD & T SAITOH (1996 b) A gradient from stable to cyclic populations of *Clethrionomys rufocanus* in Hokkaido, Japan. Proceedings of the Royal Society of London B 263: 1117-1126.

STENSETH NC, W FALCK, ON BJØRNSTAD & CJ KREBS (1997) Population regulation in snowshoe hare and Canadian lynx: asymmetric food web configurations between hare and lynx. Proceedings of the National Academy of Sciences USA 94: 5147-5152.

STENSETH NC, W FALCK, K-S CHAN, ON BJØRNSATD, M O'DONOGHUE, H TONG, R BOONSTRA, S BOUTIN, CJ KREBS & NG YOCCOZ (1998) From patterns to processes: phase and density dependencies in the Canadian lynx cycle. Proceedings of the National Academy of Sciences USA 95: 15430-15435.

STENSETH NC, ON BJØRNSTAD, W FALCK, J-M FROMENTIN, J GJØSAETER & JS GRAY (1999) Dynamics of coastal cod populations: intra- and intercohort density-dependence and stochastic processes. Proceedings of the Royal Society of London B 266: 1645-1654.

STONE L, PI SAPARIN, A HUPPERT & C PRICE (1998) El Niño chaos: the role of noise and stochastic resonance on the ENSO cycle. Geophysical Research Letters 25: 175-178.

TONG H (1993) Non-linear time series: a dynamical system approach. Oxford University Press, Oxford, United Kingdom. 564 pp.

TURCHIN P (1990) Rarity of density-dependence or population regulation with lags? Nature 344: 660-663.

TURCHIN P (1995) Population regulation: Old arguments and a new synthesis. In: Capuccino N & PW Price (eds) Population dynamics: new approaches and synthesis: 19-40. Academic Press, San Diego, California.

TURCHIN P & AD TAYLOR (1992) Complex dynamics in ecological time series. Ecology 73: 289-305.

VARLEY GC, GR GRADWELL & MP HASSELL (1973) Insect population ecology: an analytical approach. Blackwell Scientific Publications, Oxford, United Kingdom. 211 pp.