Nonlinear Time-Series Modeling of Vole Population Fluctuations

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Abstract. A central goal of population ecology is to understand and predict fluctuations in population numbers. Until recently, much of the debate focused on the issue of population regulation by density-dependent factors. In this paper, I describe an approach to nonlinear modeling of time-series data that is designed to go beyond this question by investigating the possibility of complex population dynamics, characterized by lags in regulation and periodic or chaotic oscillations. The questions motivating this approach are: what are relative contributions of endogenous vs. exogenous components of dynamics? Is the irregular component in fluctuations entirely due to exogenous noise, or do nonlinearities contribute to it, too? I describe the philosophy and the technical details of the nonlinear modeling approach, and then apply it to a collection of time-series data on vole population fluctuations in northern Europe. The results suggest that population dynamics of European voles undergo a latitudinal shift from stability to chaos. Dynamics in northern Fennoscandia are characterized by positive Lyapunov exponent estimates, and a high degree of short-term (one year ahead) predictability, suggesting a strong endogenous component. In more southerly populations estimated Lyapunov exponents are negative, and there is no one-step ahead predictability, suggesting that fluctuations are driven by exogenous factors.

Key words: chaos, nonlinear dynamics, population oscillations, stability, time-series analysis, vole.

Introduction

One of the central goals of population ecology is to understand and predict fluctuations in population density. Historically, development of the field has been dominated by one issue: the relative importance of density-dependent vs. density-independent factors, with the debate focusing on two opposing viewpoints (e.g., Nicholson 1954; Andrews and Birch 1954): that populations are regulated around stable point equilibria by density-dependent mechanisms vs. the view that population change is largely driven by density-independent factors (for a recent review, see Turchin 1995). Even if we admit that these two viewpoints are only extremes of a continuum, we are still left with what one could call the "one-dimensional paradigm of population regulation" (Turchin and Taylor 1992). The fundamental flaw in the one-dimensional view of population regulation is that it ignores the possibility of complex population dynamics.

The emphasis on simple population dynamics—either monotonic approach to equilibrium, or random walk, or a combination of the two—has resulted from an over-reliance on linear models in ecology in the past. Historically, most ecological models focused on equilibria and tended to ignore nonlinear effects because of analytical tractability of linear models. However, a linear model is at best an approximation near an equilibrium point, because population dynamics are inherently nonlinear (Royama 1992; Hastings et al. 1993). The problem with the emphasis on linear models is that they have a limited range of dynamical behaviors, being either globally unstable (population density growing to infinity, or declining to extinction), or characterized by a globally stable point equilibrium. Nonlinear models, by contrast, can also exhibit complex deterministic behaviors, such as limit cycles, quasiperiodicity, chaos, and multiple attraction domains. In addition, nonlinear models with noise can generate dynamics characterized by a complex mixture of determinism and stochasticity. For example, a nonlinear model that is characterized by a stable equilibrium in the absence of noise, may become chaotic when a small stochastic exogenous component is added (Rand and...
based on different modeling approaches, we can shift the different results about whether a system is chaotic or not. The practical benefit of this interpretation is that when we get chaotic according to the commonly used understanding of repeat itself. In other words, such a population cannot be chaotic is that in most cases population numbers is a discrete variable (since populations consist of individuals). If there is a finite number of states that a population can be in, then sooner, noise will be present and will have to be filtered out. It has been successfully employed to persuade chemists that chemical chaos is possible (Argoul et al. 1987), and there are several promising ecological systems that may be amenable to such experiments (e.g., see Costantino et al. 1995). The second approach is to estimate parameters of an a priori model and demonstrate that the parameters put the model in a chaotic regime. Many such attempts are reviewed in Hastings et al. (1993). The third approach, on which I focus in this paper, is to analyze time series of population fluctuations.

Before we delve into the technical details of nonlinear time-series modeling, I want to make two general comments. First, I want to emphasize that all three approaches in the search for “holy chaos” have an explicit modeling component. The goal of the time-series analysis, in particular, is to fit some model to data (that is why I refer to the approach as nonlinear time-series modeling). This emphasis on models is because, in a sense, chaos is not property of “the real world”, but a property of a model we might develop for a particular system. One difficulty with saying that a particular ecological system is chaotic is that in most cases population numbers is a discrete variable (since populations consist of individuals). If there is a finite number of states that a population can be in, then sooner or later the trajectory will repeat itself. In other words, such a population cannot be chaotic according to the commonly used understanding of what chaos is. Thus, I would argue that when we say that a particular ecological system is chaotic, what we mean is: “the best model we have for this system is chaotic”. A practical benefit of this interpretation is that when we get different results about whether a system is chaotic or not based on different modeling approaches, we can shift the emphasis of the argument from a largely unproductive argument on whether it really is chaotic or not, to a more interesting argument on which of the two is a better model. The second direction is more productive, because it leads to discussion of what the purposes of the rival models are, how we evaluate their usefulness, and how our personal biases may have affected their construction.

My second general comment is that chaos is only one kind of complex dynamics. A narrow emphasis on chaos—e.g., claiming that everything is chaos—is as counterproductive as the opposite attitude that chaos is irrelevant to ecological issues. Investigations of nonlinear dynamics in ecology should not narrowly and exclusively focus on chaos. Rather, we should ask what relative contributions of endogenous vs. exogenous components are, what mechanistic causes drive fluctuations, and how well we can forecast populations, in addition to whether dynamics are chaotic or not. The approach I discuss below was developed to provide some partial answers to these questions, based on analyzing ecological time-series data.

Time-series data—records of organism abundance in a certain locality over a period of time—contains much information about the pattern of population fluctuations, and is frequently available in both basic and applied situations. At the most basic level, time-series data can be used to quantitatively summarize the pattern of population fluctuations. For example, we can compare different populations by measuring the amplitude of fluctuations, by calculating, for example, the standard deviation of the log transformed numbers, S (Lewontin 1966; Stenseth and Framstad 1980). We can also use autocorrelation analysis (Finerty 1980; Turchin 1990; Royama 1992) to detect periodicity. If periodicity is present, then we can estimate its average period by observing at which lag the autocorrelation function (ACF) reaches a peak, and its strength by the magnitude of ACF at the period.

There also are many other interesting questions, beyond simple characterization of fluctuation patterns, that time-series data can help us answer:

1. What are relative contributions of endogenous vs. exogenous components of population dynamics? And how do these components interact?
2. Are dynamics characterized by sensitivity to initial conditions? In other words, does the endogenous component work to amplify or dampen perturbations introduced by exogenous factors?
3. What can we conclude about possible mechanisms responsible for population fluctuations? In particular, are dynamics best described as one-dimensional, two-dimensional, or higher-dimensional?
4. How well, and how far ahead can we forecast population numbers?

These questions can be asked at many different levels of...