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Reviewed work(s):

Source: *The American Naturalist*, Vol. 145, No. 3 (Mar., 1995), pp. 343-375

Published by: [The University of Chicago Press](#) for [The American Society of Naturalists](#)

Stable URL: <http://www.jstor.org/stable/2463024>

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CHAOS IN A NOISY WORLD: NEW METHODS AND EVIDENCE FROM TIME-SERIES ANALYSIS

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Submitted May 4, 1993; Revised April 12, 1994; Accepted April 22, 1994

Abstract.—Chaos is usually regarded as a distinct alternative to random effects such as environmental fluctuations or external disturbances. We argue that strict separation between chaotic and stochastic dynamics in ecological systems is unnecessary and misleading, and we present a more comprehensive approach for systems subject to stochastic perturbations. The defining property of chaos is sensitive dependence on initial conditions. Chaotic systems are “noise amplifiers” that magnify perturbations; nonchaotic systems are “noise mufflers” that dampen perturbations. We also present statistical methods for detecting chaos in time-series data, based on using nonlinear time-series modeling to estimate the Lyapunov exponent λ , which gives the average rate at which perturbation effects grow ($\lambda > 0$) or decay ($\lambda < 0$). These methods allow for dynamic noise and can detect low-dimensional chaos with realistic amounts of data. Results for natural and laboratory populations span the entire range from noise-dominated and strongly stable dynamics through weak chaos. The distribution of estimated Lyapunov exponents is concentrated near the transition between stable and chaotic dynamics. In such borderline cases the fluctuations in short-term Lyapunov exponents may be more informative than the average exponent λ for characterizing nonlinear dynamics.

Ecologists continue to be intrigued by chaos, the erratic and seemingly unpredictable behavior that can result from nonlinearity even in a completely deterministic system. Population dynamics, whether in the lab or the field, are always characterized by some degree of irregularity. The discovery that simple deterministic models can also exhibit random-looking behavior (May 1974, 1976; May and Oster 1976) raised the hope that simple explanations may be found for the apparent complexities, at least in some populations and ecosystems.

The importance of chaos in population ecology, however, goes beyond satisfying our intellectual curiosity. Chaotic population oscillations are more predictable over short time scales than fluctuations driven by purely exogenous factors such as weather (Hastings et al. 1993). Clearly, the ability to forecast the change in population numbers is critical in natural resources management and conservation. Moreover, in chaotic oscillations the degree of predictability often varies in

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a predictable manner (Smith 1992), which makes it possible to recognize and exploit the circumstances in which accurate prediction is possible and also to recognize when prediction is less likely to succeed. The widespread occurrence of nonlinear and nonequilibrium behaviors in natural ecosystems would also require a substantial revision of the current ecological theory, which is largely based on equilibrium paradigms. A striking example of this is the recent demonstration by Allen et al. (1993) that chaos may reduce, rather than promote, species extinction in a metapopulation system.

Although chaos offers temptingly simple solutions to complex questions, ecologists recognize that the systems they usually study are small parts of a very much larger world. This has made it difficult for ecologists to accept the relevance of concepts and models that apply only to perfectly deterministic systems, unaffected by external perturbations. Chaos is usually presented to ecologists as an alternative to random effects in attempting to explain complicated dynamics; indeed, in the primary literature on chaos, "chaos" is almost invariably a shorthand for "deterministic chaos" and refers to nonlinear difference or differential equations without any randomness. Simple deterministic models can be valuable theoretical constructs for developing ecological principles, but such models are understood to be deliberate oversimplifications that omit, in particular, any stochastic factors affecting the system.

What possible role can there be for chaos, then, in the "noisy" world that ecologists study? This question has been a part of ecology's involvement with chaos from its early days (Smith and Mead 1980) to the present (Hansson 1991).

Our first purpose in this article is to argue that the use of "chaos" to mean only "deterministic chaos" and the consequent strict separation between chaotic and stochastic dynamics are unnecessary and potentially misleading. A more comprehensive approach is possible, based on mathematical theory for random nonlinear systems (Kifer 1986). This approach allows a mathematically precise definition of chaos for systems with random components and leads to data analysis methods that explicitly allow for randomness and have a firm basis in statistical theory.

Our approach for distinguishing between chaotic and nonchaotic dynamics is based on the Lyapunov exponent, λ . The Lyapunov exponent is the rate of growth over time of the effects of a small perturbation to the system's state (we give a formal definition below). Thus, a system with $\lambda > 0$ has the property of *sensitive dependence on initial conditions* and is chaotic. Intuitively, a chaotic system is a noise amplifier (Deissler and Farmer 1992): after a perturbation occurs, the effects of the perturbation are magnified over time by the system's intrinsic dynamics. Thus, both the system itself and external perturbations contribute to the system's unpredictability. A nonchaotic system ($\lambda < 0$) is a noise muffler: the effects of external perturbations decay asymptotically to zero over time. Any unpredictability is solely due to perturbations. The value of λ is also meaningful for nonchaotic systems, since then the amount of time until the effects of a given perturbation die out is roughly proportional to $1/|\lambda|$.

Testing time-series data for chaos by estimating Lyapunov exponents is an established approach. For example, Schaffer et al. (1990) used a modification of

the Wolf et al. (1985) method to estimate λ for childhood disease epidemics, and the nonlinear forecasting method of Sugihara and May (1990) is based on the relationship between λ and forecasting accuracy in deterministic systems. However, these and the other commonly used methods for estimating λ implicitly make the a priori assumption that the data come from a noise-free, strictly deterministic system. Consequently, these methods are prone to false positives in which nonchaotic data are misidentified as being chaotic (see, e.g., Sayers 1990; Ellner 1991; Theiler et al. 1992). The variety of methods that have been proposed to detect deterministic chaos, and their limitations, are reviewed for biologists by Hastings et al. (1993).

The methods we present here explicitly allow for a random component in the dynamics. The methods are based on statistical theory for parameter estimation in nonlinear time-series models. Use of these methods to detect chaos is new and not yet perfected, but the approach is entirely within the domain of statistical time-series analysis. Simulation studies indicate that our methods are robust to realistically high levels of noise without requiring excessive amounts of data, so they can be applied to many available ecological data sets. We therefore believe that our methods provide more objective and reliable answers to questions about the prevalence of chaos versus stability in population dynamics than answers based on the theory of strictly deterministic chaos.

Our second purpose is to present the results of applying our methods in a consistent manner to a collection of long-term ($n \geq 50$) data sets on population fluctuations, in the wild and in the laboratory. As Morris (1990) has recently emphasized, when a simple model with a few parameters is fit to time-series data, the results may depend mainly on the investigator's choice of model and parameter estimation criterion. We address this concern by using three general families of time-series models (described below) that encompass a range of model complexities and by using data-based objective criteria to select specific models within each family. Each of the model families can approximate a wide range of shapes, and all work well in simulation studies with a variety of different systems. Still, the methods are new and still being improved, so it is virtually certain that our results will not be the last word on these data sets.

We have deliberately adjusted our methods so that the results are conservative with respect to detecting chaos. We nonetheless find chaos occurring in some populations, and we also observe both weakly and strongly stable dynamics. There is also a wide range in the relative importance of noise, with some populations appearing to have unpredictable fluctuations that are almost entirely random, while others are highly predictable based on current and past population densities. We find a clustering of populations near the border between stability and chaos, for both field and laboratory populations. This clustering could have significant implications for attempts to make short-term predictions of population changes. It also suggests that a concentration on the precise dividing line between chaos and nonchaos may be less informative than looking directly at nonlinear aspects of population dynamics, which would be evident and significant for dynamics near the transition to chaos.

THEORETICAL BACKGROUND

Early investigations of chaos in ecology employed simple one-dimensional models of the form

$$N(t + 1) = f(N(t)) \quad (1)$$

(see, e.g., May 1974, 1976; May and Oster 1976). Here $N(t)$ is the population abundance in year (or generation) t . Equation (1) specifies the rule by which the population density in the next year is determined from the current density and thus constitutes a dynamic system: given some initial density N_0 , we can iterate equation (1) and determine the trajectory of the system (i.e., the population values at all future times).

The model (1), however, is a great simplification of the dynamics of most real-life populations. The abundance of any species in a community will be influenced by the abundances of its resources, competitors, and predators. In addition, many populations are physiologically structured—there could be individuals belonging to several different age or stage classes present at the same time. This means that we need a multidimensional system of equations to fully describe these interactions:

$$\begin{aligned} s^1(t + 1) &= f^1(s^1(t), \dots, s^k(t)) \\ s^2(t + 1) &= f^2(s^1(t), \dots, s^k(t)) \\ &\vdots \\ s^k(t + 1) &= f^k(s^1(t), \dots, s^k(t)). \end{aligned} \quad (2)$$

Here each $s^i(t)$ is a state variable, such as the number of individuals in a particular age or stage class of each species in the community. Using vector notation, we can rewrite equations (2) as

$$\mathbf{S}(t + 1) = \mathbf{F}(\mathbf{S}(t)), \quad (3)$$

where $\mathbf{S}(t) = s^1(t), \dots, s^k(t)$ is the vector of state variables. Although equation (3) is expressed as a discrete-time system, our discussion applies equally to continuous systems, since we can sample such systems at discrete time intervals.

The functional relationships in equation (3) encapsulate the *endogenous* structure of the system, or the dynamic feedbacks regulating its behavior. No ecological system, however, exists in complete isolation. This means that there are also *exogenous* variables acting on the system (exogenous variables affect the system state $\mathbf{S}(t)$ but are not themselves affected by it; thus, unlike endogenous variables they are not part of the feedback structure of the system). Exogenous variables may have regular (e.g., seasonal), irregular, or stochastic patterns of fluctuation. Examples of exogenous variables include external disturbances such as immigration events, pathogen invasions, or mortality due to storms; seasonal patterns of change in parameters affecting the dynamics such as temperature, metabolic and reproductive rates, and predator activity levels; and factors internal to the system that cannot be predicted from the state variables (e.g., demographic stochasticity

or genetic drift in small populations). Including a vector of exogenous variables $U(t)$ in our general model, we have

$$S(t + 1) = F(S(t), U(t)). \quad (4)$$

Any random components of the exogenous variable $U(t)$ are called *dynamic noise*. It is essential to recognize that dynamic noise is very different from measurement errors. Dynamic noise is an integral part of the system's dynamics, affecting how the state variables change over time (e.g., a cold snap that delays or prevents an insect outbreak). Dynamic noise can even move a system into or out of chaos (Crutchfield et al. 1982; Rand and Wilson 1992). Therefore, chaos cannot be defined for systems with dynamic noise simply by deleting the noise from equation (4) and applying deterministic chaos theory.

Time-Delay Coordinates

Although the dynamics of typical ecosystems are multidimensional, the available data are usually univariate—either one of the state variables or some function of the state variables, $N(t) = h(S(t))$. For example, $N(t)$ could be the total abundance of one species in the community, that is, the sum of abundances of each stage or age class. This raises the question, How can we analyze data on one component of the multidimensional system such as that given by equation (4), without knowing how all the other components behave?

For the deterministic system (3), the classical answer is *reconstruction* of the state vector using time-delay coordinates (Packard et al. 1980; Takens 1981). Recently, Casdagli (1992) derived the important result that reconstruction also applies to stochastic systems such as those described by equation (4). Specifically, under our assumption $N(t)$ follows a nonlinear autoregressive model

$$N(t) = f(N(t - 1), N(t - 2), \dots, N(t - d), e_t). \quad (5)$$

Here d is the *embedding dimension* (i.e., how far in the past we must look for an explanation for current changes in N), and e_t is a vector of the exogenous variables over some finite interval of the past.

Ecologists, in fact, have traditionally used variants of equation (5) in the analysis of population censuses. A one-dimensional version of equation (5) using only $N(t - 1)$ provides the basis for the analysis of direct density dependence (see, e.g., Varley and Gradwell 1960). A two-dimensional variant of equation (5) employing both $N(t - 1)$ and $N(t - 2)$ has been used (Turchin 1990) to assess the frequency of delayed density dependence in a collection of population data sets. The equivalence between equation (5) with $d = 2$ and a predator-prey system has been established by Murdoch and Reeve (1987). More generally, equation (5) says that past values of $N(t)$ can serve as surrogates for the unobserved state variables in $S(t)$, whether they are population abundances of predators or unobserved age or stage classes.

Defining X to be the vector of lagged N , $X_t = (N(t - 1), N(t - 2), \dots, N(t - d))$, we can rewrite equation (5) in vector notation as

$$X_t = F(X(t - 1), e_t), \quad (6)$$

where F is defined to reproduce the structure of equation (5). Thus, we have a reconstructed system expressed in terms of the observed variable, which is in a certain way equivalent to the system (eq. [4]) that actually drives the population fluctuations of the species in the community. More specifically, mathematical theorems (Sauer et al. 1991; Casdagli 1992) tell us that if d is large enough, then the qualitative dynamics of equation (6) will be the same as the dynamics of equation (4). In particular, both systems will have the same Lyapunov exponent. As usual in reconstruction, the equivalence between the original and reconstructed systems holds with probability one (Sauer et al. 1991). Exceptions occur, but they are as unlikely as getting only heads in infinitely many tosses of a fair coin (Stoppard 1967).

Chaos and Lyapunov Exponents

Following Eckmann and Ruelle (1985), we define chaos as bounded fluctuations in the state variables with sensitive dependence on initial conditions. Chaos is often defined differently for deterministic systems, but this definition has two advantages. First, it applies equally well to systems with or without dynamic noise. Second, it focuses on the property of chaos that is most likely to be important for prediction and management.

In order to understand this definition, let us first consider a purely endogenous deterministic system, such as that described by equation (3). For example, our dynamic system could be a population model that has been implemented as a computer program. We initiate the system by providing it with a vector of initial states, $\mathbf{S}(0)$, and observe how the system evolves (e.g., by solving the model on the computer). Next, we reinitiate the system at a new initial state vector $\mathbf{S}^*(0)$ that is near the original starting point $\mathbf{S}(0)$ and again observe how the system evolves with time. We now compare the two trajectories: if they are diverging from each other, then we have sensitive dependence on initial conditions and thus, by definition, chaos (assuming that trajectories are bounded, that is, that they do not diverge to infinity). By contrast, in nonchaotic dynamic systems such as ones with stable equilibrium points or periodic solutions, the trajectories will either converge toward each other or their distance apart will settle down to small, bounded oscillations.

The sensitivity or insensitivity to initial conditions is quantified by the dominant Lyapunov exponent λ . Here λ is defined to be the long-term exponential rate of divergence between two trajectories with an infinitesimally small difference in their initial conditions. Positive λ , thus, is the defining characteristic of chaotic systems, while negative or zero λ characterizes nonchaotic systems.

For systems with exogenous perturbations, the above definition has to be modified. Consider, for example, a system influenced by dynamic noise. No matter what the endogenous structure of the system is, two trajectories starting nearby will always diverge if they are influenced by different sequences of random perturbations. The same can also occur even if the perturbations are deterministic. Thus, the key to defining chaos in systems with exogenous elements is to observe whether nearby trajectories diverge when subjected to exactly the same exogenous inputs.

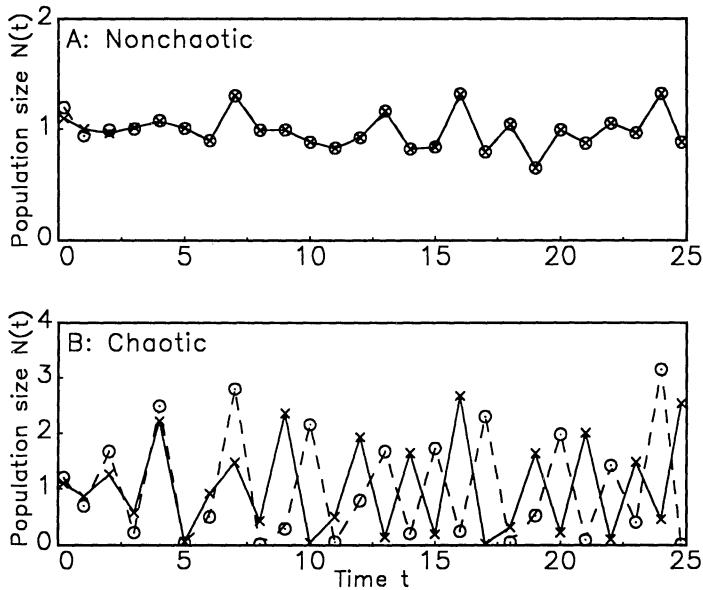


FIG. 1.—Chaotic vs. nonchaotic dynamics in the presence of dynamic noise. The plots show trajectories of a Ricker model with lognormal fluctuations in recruitment, $N_{t+1} = N_t \exp[r \cdot (1 - N_t) + 0.15 \cdot Z_t]$, where N_t is the population size, and Z_t is a Gaussian random variable with mean zero and variance one. A, $r = 1.5$ (nonchaotic); B, $r = 3$ (chaotic). The same sequence of values for the dynamic noise Z_t was used for all four trajectories.

As an example, consider our imaginary model referred to above. Suppose we now include a stochastic exogenous component in it and again want to determine whether the system is chaotic. First, we generate a sequence of random perturbations for the system and save it. Then we start two trajectories from similar initial conditions and subject both trajectories to the saved sequence of random perturbations. Both trajectories will move somewhat erratically, because they are affected by noise. But if the system is stable they will converge, while if it is chaotic they will diverge. In the latter case, we will conclude that some part of the observed irregularity is due to the endogenous component. Figure 1 shows an example of this kind of experiment. With nonchaotic dynamics (fig. 1A), the trajectories quickly converge and thereafter undergo the identical pattern of noise-driven fluctuations; with chaotic dynamics (fig. 1B) the trajectories soon diverge, leaving no hint of their initial similarity.

To summarize, for systems with exogenous components, λ is defined by considering trajectories that start near each other and are affected by the same sequence of exogenous shocks, e_t . Consequently, the sign of λ tells us whether the system's endogenous dynamics, represented by F , amplifies or dampens over time the effects of exogenous perturbations. Calculating λ for a system is thus (metaphorically) akin to a qualitative analysis of variance on the unpredictability in the observed dynamics. In a nonchaotic system any long-term unpredictability is

entirely due to the actions of exogenous factors. In a chaotic system, some (or possibly all) of the long-term unpredictability is internally generated by nonlinear causal relationships among the endogenous variables. The definition of chaos for stochastic systems is discussed more fully by Casdagli (1992) and Nychka et al. (1992).

Estimating the Lyapunov Exponent

The first (and best-known) methods were based on the definition of λ in terms of trajectory divergence. The data set is searched to find similar pairs of state vectors, and the divergence rate of the subsequent trajectories (averaged over the attractor) is an estimate of λ (Guckenheimer 1982; Wolf et al. 1985). However, this approach is not robust to effects of dynamic noise. The paired trajectories will diverge even if $\lambda < 0$, simply because they did not experience the same sequence of random shocks, so the estimate of λ is positively biased (Sayers 1990).

For systems with dynamic noise, a preferable approach is to estimate λ indirectly, by estimating the map F . Using the estimated map, we can then perform on the computer the thought experiment of starting a second trajectory near the one observed in our data set and calculating how the trajectories would diverge if they were exposed to the same random shocks. A further improvement is to take the limit as the initial separation between the trajectories decreases to zero. The limiting value can be expressed in terms of the derivatives of the map. In appendix A we give the formula for the resulting estimate of λ and the mild technical assumptions needed for its validity. (For full details, see Ellner et al. 1991 and McCaffrey et al. 1992.)

MODELING THE ENDOGENOUS DYNAMICS

The most important conclusion from the theory reviewed above is that nonlinear time-series modeling can be used to estimate quantities that characterize a system's dynamics, including the Lyapunov exponent λ , whose sign indicates the presence or absence of chaos. However, there remains the practical task of fitting a model to the data in a way that gives reliable estimates. It is essential to recognize that a good fit for some purposes may be a bad fit for others. Lyapunov exponents are derived from the partial derivatives of the estimated function f , and a method that gives accurate estimates of f may give poor estimates of the partial derivatives and correspondingly poor estimates of λ . For example, a piecewise constant approximation can come arbitrarily close to a smooth function f , just as a staircase with many tiny steps can approximate a straight line with constant slope. But the derivative of this staircase approximation is zero at all points between steps and undefined at the steps, so it cannot be used to estimate derivatives.

A variety of time-series models give reliable estimates of the Lyapunov exponent for deterministic systems, given moderate amounts of data (1,000 or so values) (Briggs 1990; Brown et al. 1991; Abarbanel et al. 1992; McCaffrey et al. 1992). For shorter time series (50–500 values) from low-dimensional systems with

dynamic noise, three models have been identified as reliable in simulation studies: the response surface method (Turchin and Taylor 1992), thin-plate splines (TPS) (Wahba 1990), and feedforward neural networks (FNN) (McCaffrey et al. 1992; Nychka et al. 1992).

Response Surface Method

Response surface method (RSM) is based on generalizing polynomial regression by allowing Box-Cox transformation of the independent variables, as suggested by Box and Draper (1987). The dependent variable fitted by RSM is the per capita replacement rate N_t/N_{t-1} . Simpler functions and thus fewer parameters are needed to fit the replacement rate, compared with fitting N_t , because most ecological processes are per capita rates of population change (Turchin and Taylor 1992). The replacement rate is log transformed because this tends to normalize the errors (Turchin and Taylor 1992). Thus, the form of the model is

$$\log(N_t/N_{t-1}) = P_q(N_{t-1}^{\theta_1}, N_{t-2}^{\theta_2}, \dots, N_{t-d}^{\theta_d}) + e_t, \quad (7)$$

where P_q is a polynomial of degree q . The transformation parameters θ_i , the polynomial degree, and the coefficients are determined from the data by least squares. The model must be fit by nonlinear methods if the θ_i are allowed to vary continuously. However, a simpler and nearly as accurate method is to fit the polynomials by ordinary least squares for all combinations of discrete values of θ_i and select the power transformations that produced the highest r^2 . Following earlier work (Turchin and Taylor 1992), θ_i were allowed to take values $-1, -0.5, 0, 0.5, \dots, 3$, where $\theta = 0$ is log transformation.

Feedforward Neural Networks

“Neural networks” refers to a class of nonlinear models inspired by the neural architecture of the brain. The form of this model is

$$N_{t+1} = \beta_0 + \sum_{i=1}^k \beta_i G\left(\sum_{j=1}^d \gamma_{i,j} N_{t-j} + \mu_i\right) + e_t, \quad (8)$$

where G is a sigmoid function such as the logistic distribution $G(u) = e^u/(1 + e^u)$. In the neural interpretation of equation (8), each $G(\cdot)$ term represents the firing rate of a single neuron as a function of the stimuli it receives. In our application, the stimuli are past values of population density, and the predicted N_{t+1} is a weighted sum of the firing rates of all the neurons. (As with RSM, we used log-transformed N to stabilize variances.) The parameters $\gamma_{i,j}$ represent the connection strength between stimulus j and neuron i , the β_i are the weights assigned to the different neurons, and μ_i is an external input to neuron i .

The neural interpretation has no real relevance here. We use FNN simply as a statistical model, based on practical experience in a variety of applications, which has shown that the FNN model is often quite successful for modeling nonlinear and chaotic time-series data (see, e.g., Casdagli and Eubank 1992). In particular, for estimating Lyapunov exponents, the FNN model is especially robust against errors in choosing the embedding dimension (McCaffrey et al. 1992).

More general versions of the FNN model are possible, in which there are secondary, tertiary, and so forth, layers of neurons, but statistical applications have mostly used a single layer as in equation (8). Even the single-layer model can become much more complex than RSM because the number of analog neurons (k in eq. [8]) is one of the parameters to be estimated. If the value of k is not limited a priori, then FNN can approximate with arbitrary accuracy any smooth function on a bounded region in d -dimensional space (Cybenko 1989; White 1989; Barron 1991a; Gallant and White 1992).

Theoretical results on the large-sample accuracy of FNN (Barron 1991b) suggest that FNN will outperform traditional nonparametric models (such as splines, discussed below) if the function being estimated is high dimensional but otherwise fairly simple, in the sense of not having any high-frequency wiggles. Thus, FNN complements RSM by allowing us to fit higher-dimensional dynamics. However, FNN requires orders of magnitude more computer time, because each possible value of d and k requires a separate nonlinear least-squares estimation of the other parameters.

Thin-Plate Splines

Splines are most widely known as piecewise polynomial curves in one variable. Thin-plate splines also use piecewise polynomial curves, but the estimated function is a compromise between fitting the observed data and smoothness of the estimated function. The TPS estimate of f is the function \hat{f} that minimizes

$$\text{MSE}(\hat{f}) + \rho I_m(\hat{f}),$$

where MSE is the mean square prediction error using \hat{f} , ρ is a positive constant, and I_m is a measure of \hat{f} 's roughness based on the mean square magnitude of its m th order partial derivatives (Wahba 1990).

The complexity of \hat{f} is determined by the value of ρ . Large values of ρ produce a very smooth estimate at the expense of not fitting the data closely, which is appropriate when the random errors have a large variance. In the opposite limit $\rho \rightarrow 0$, \hat{f} interpolates the data, which is appropriate for data with little or no noise. Schluter and Nychka (1994) discuss TPS in more detail, in the context of estimating multivariate fitness surfaces.

The TPS model is the most flexible of our three models. Like FNN it is able to approximate any smooth function on a bounded region with arbitrary accuracy. However, the minimum number of parameters grows rapidly with the dimension of the model: 15 parameters for $d = 4$ and 56 parameters for $d = 5$, for the smallest allowable value of m (i.e., the smallest such derivative estimates are consistent; see Wahba 1990). We therefore used TPS only for $d \leq 4$. The TPS model complements RSM by allowing us to fit models that are low dimensional but too complex to be approximated well by RSM.

Selecting smoothing and reconstruction parameters.—Fitting a time-series model involves choosing the values of one or more *smoothing parameters* that control the complexity of the fitted model. Here the smoothing parameters are the polynomial order q for RSM, the values of ρ and m for TPS, and the number of neurons (k in eq. [8]) for FNN. Choice of smoothing parameters is critical to

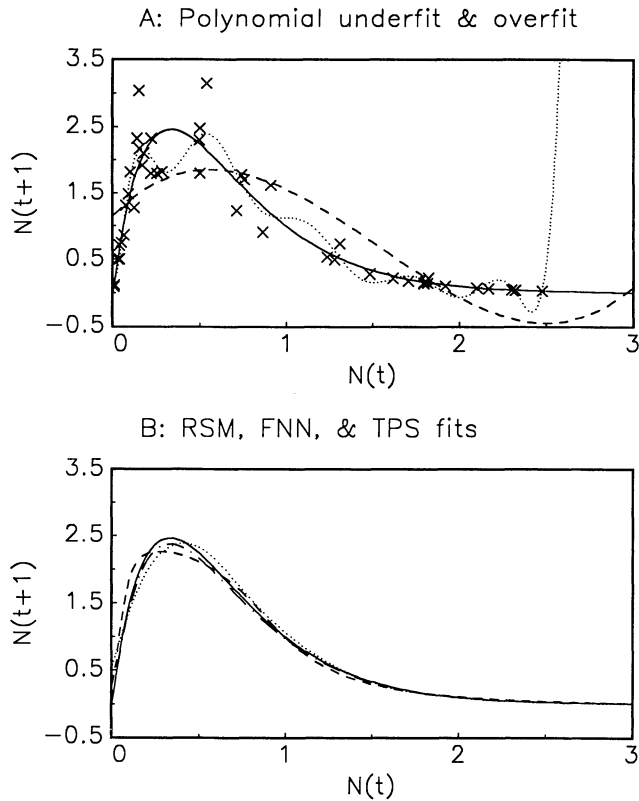


FIG. 2.—Fitting a model to simulated data from a noisy chaotic population model. The population model is a one-dimensional Ricker equation with random fluctuations in recruitment, $N_{t+1} = N_t \exp[3 \cdot (1 - N_t) + 0.2Z_t]$, where N_t is the population size and Z_t is a Gaussian random variable with mean 0 and variance 1. *A*, The true endogenous component of the dynamics $N_{t+1} = N_t \exp[3 \cdot (1 - N_t)]$ (solid line), the simulated data (\times), and two estimates of the endogenous component from least-squares fitting of polynomials to the data: cubic polynomial (dashed line) and fourteenth-order polynomial (dotted line). The cubic polynomial is not flexible enough and underfits the data. The fourteenth-order polynomial is too flexible and overfits: it wiggles to “fit” random scatter and behaves wildly outside the range of the data. *B*, Estimates for the same data with model complexity chosen automatically by the generalized cross validation (GCV) criterion. The neural net, spline, and RSM models all give accurate fits to the true relationship (solid line), without any spurious wiggles. All models slightly underestimate the sharpness of the peak, which would cause a small negative bias in estimating the Lyapunov exponent.

obtaining accurate results. Models with too few parameters, or too low an embedding dimension d , may not be able to approximate the dynamics. On the other hand, a model with too many parameters will fit the noise instead of only fitting the endogenous feedbacks (fig. 2A).

There is no general prescription available for making an optimal choice of smoothing parameters (Hastings et al. 1993). However, we can adopt procedures that penalize complex models in a way that biases the selection slightly toward

simpler, nonchaotic models. The resulting choice is not right, but it is wrong in the right direction (i.e., it minimizes the chances of false positives in the search for chaos). The procedures are data based and quantitative, with no subjective intervention by the user.

The technical details and rationale for our procedures are given in appendix B. An example of their performance is shown in figure 2B. For each of our three time-series models, the fitting criterion does a good job of identifying the complexity of the true relationship underlying the observed dynamics and of choosing model parameters to approximate the shape.

Model complexity and accuracy are also affected by the choice of independent variables. If N_t and N_{t-1} are tightly correlated, it would be redundant to include them both in the model, and using fewer variables is desirable because it reduces the number of parameters. A strategy based on the ideas of attractor reconstruction in the chaos literature is to consider models of the form

$$N_{t+T_p} = f(N_t, N_{t-L}, N_{t-2L}, \dots, N_{t-(d-1)L}), \quad (9)$$

where T_p is the prediction time, and L is usually called the time delay. We choose L based on the autocorrelation of the time series and set $T_p = L$ (see app. B for details).

Computational methods.—Parameters for FNN were estimated by nonlinear least squares using procedures described elsewhere (Ellner et al. 1992). FORTRAN source code and a user's manual are available at no charge (with no guarantee) by anonymous ftp on lyapunov.ucsd.edu in directory /pub/ncsu. To fit TPS we used GCVPACK (Bates et al. 1987). The RSM parameters were estimated by ordinary least squares. Equation (A2) was used to calculate estimated Lyapunov exponents.

TESTS ON SIMULATED DATA

The main advantage of the approach described here is that noise is built-in from the beginning. This allows our methods to cope with moderately high levels of noise, so long as the endogenous components of the dynamics can still be detected and estimated. Tests on simulated data have been presented elsewhere (Nychka et al. 1992; Turchin and Millstein 1993), so we give here only one example to illustrate how our methods perform in the presence of appreciable dynamic noise.

The test problem is to distinguish between a chaotic population model with dynamic noise and a stable linear system (also with dynamic noise) chosen to mimic the output of the chaotic model. Figure 3 shows a typical segment of simulated data from each of the models. The chaotic model is a version of the standard delayed-recruitment model for populations with juvenile and adult age classes:

$$N_{t+1} = a_t[N_t + \phi(N_{t-j})]. \quad (10)$$

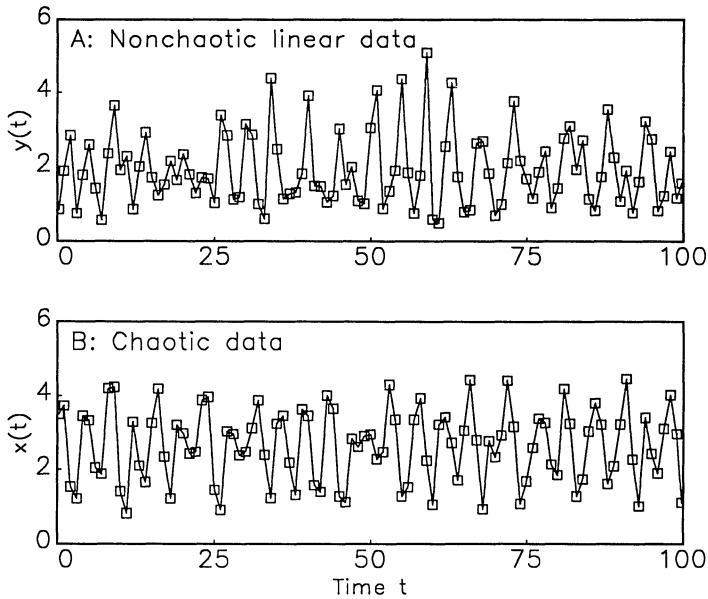


FIG. 3.—Typical simulated data produced by the chaotic and nonchaotic linear models used in the simulation trials. The chaotic model was equation (10), with $\phi(x) = 10x/(1 + x^6)$, $a = 0.2$, and $\sigma = 0.1$. The nonchaotic model was a second-order autoregressive model $y_{t+1} = 0.67627y_t - 0.584356y_{t-1} + 0.362Z_t$, where $\{Z_t\}$ is a series of independent Gaussian variates with mean 0 and variance 1.

Here N_t is the number of adults at time t , a_t is survival rate, ϕ is a nonlinear recruitment function, and j is the time delay between birth and recruitment to the adult population. Mortality during the juvenile period is included in ϕ . Dynamic noise was introduced by letting a_t vary randomly between years, with a lognormal distribution. The linear model was a second-order autoregressive process with parameters chosen by maximum-likelihood fitting to a time series of length 500 from the chaotic model. The true exponents are $\lambda \doteq 0.145$ for the chaotic model and $\lambda \doteq -0.27$ for the linear model.

Figure 4 shows the distribution of estimated Lyapunov exponents with RSM, FNN, and TPS. The numerical estimates are not terribly precise, but the data were correctly classified as chaotic versus nonchaotic in the overwhelming majority of cases. This compares very favorably with the performance of methods developed for deterministic systems. For example, estimates of fractal dimension become inaccurate at much lower levels of dynamic noise (Smith 1992a, 1992b).

The RSM exhibits a small negative bias on the chaotic model, while the more flexible TPS and FNN models are nearly unbiased. On the linear data, both RSM and TPS are nearly unbiased, while FNN has a failure rate of about 25%. Most of the failures are associated with overfitting (more than two lags, or more than one unit). The FNN model is prone to occasionally overfit linear data (Granger and Teräsvirta 1992), which must be kept in mind when interpreting results.

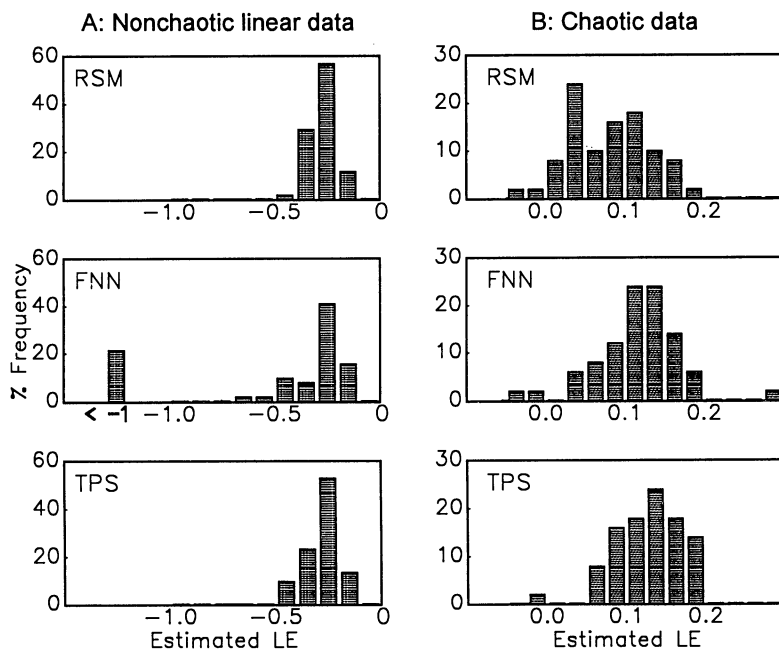


FIG. 4.—Frequency distributions of Lyapunov exponents estimated by RSM, FNN, and TPS, for nonchaotic (A) and chaotic (B) linear time series data. The RSM, FNN, and TPS models were each applied to the same collection of 50 simulated data sets (100 data points each) from the chaotic and nonchaotic models (described in fig. 3 and the text).

The test problem here is admittedly simpler than real population dynamics. However, it illustrates the main advantage of our approach for analyzing data on natural populations: dynamic noise is not a fatal problem. Indeed, since the noise causes the system to explore a wider region of state space, dynamic noise may actually increase our ability to detect nonlinear relationships by time-series modeling (Schaffer et al. 1986).

ANALYSIS OF DATA

Laboratory Populations

We applied our methods to a collection of published data sets on laboratory populations (table 1), originally assembled and provided to us by S. Naeem. We restricted ourselves to data sets with at least 50 values. The data sets were screened (by eye) to eliminate obviously nonstationary data, such as cases in which the dynamics change from one regime to another in the course of the experiments. This included cases in which one of the species became extinct during the experiment or one of the species did not grow above negligible abundance until partway through the experiments, as well as cases with gradual trends in the mean or variance of the fluctuations. One data set (Nicholson's blowflies)

TABLE 1
LABORATORY DATA SETS

Set	<i>n</i>	Species 1/Species 2	Source
3	70	<i>Blattisocius dendriticus</i> / <i>Trhophagus putrescentiae</i> (mite/mite)	Burnett 1964, fig. 3
4	69	<i>B. dendriticus</i> / <i>T. putrescentiae</i>	Burnett 1964, fig. 4
5	70	<i>B. dendriticus</i> / <i>T. putrescentiae</i>	Burnett 1964, fig. 4
6	72	<i>B. dendriticus</i> / <i>T. putrescentiae</i>	Burnett 1964, fig. 4
7	56	<i>B. dendriticus</i> / <i>T. putrescentiae</i>	Burnett 1964, fig. 4
8	51	<i>B. dendriticus</i> / <i>T. putrescentiae</i>	Burnett 1964, fig. 5
9	51	<i>B. dendriticus</i> / <i>T. putrescentiae</i>	Burnett 1964, fig. 6
10	54	<i>B. dendriticus</i> / <i>T. putrescentiae</i>	Burnett 1964, fig. 7a
11	97	<i>B. dendriticus</i> / <i>T. putrescentiae</i>	Burnett 1964, fig. 7b
14	64	<i>Tetrahyma pyriformis</i> / <i>Azobacter vinelandii</i> (protozoa/ bacteria)	Jost et al. 1973, fig. 4
23	67	<i>Didinium nasutum</i> / <i>Paramecium aurelia</i> (protozoa/pro- tozoa)	Luckinbill 1973, fig. 5
35	74	<i>Woodruffia metabolica</i> / <i>Paramecia</i> (protozoa/proto- zoa)	Salt 1967
36	52	<i>Dictostelium discoideum</i> / <i>Escherichia coli</i> (protozoa/ bacteria)	Tsuchiya et al. 1972, fig. 1
37	50	<i>D. discoideum</i> / <i>E. coli</i>	Tsuchiya et al. 1972, fig. 2
38	50	<i>D. discoideum</i> / <i>E. coli</i>	Tsuchiya et al. 1972, fig. 3
39	112	<i>Heterospilus prosopis</i> / <i>Callosobruchis chinensis</i> (parasi- toid 1/beetle)	Utida 1957, fig. 5a
46	68	<i>H. prosopis</i> / <i>C. chinensis</i> / <i>Neocataleccus mamezopha- gus</i> (parasitoid 1/parasitoid 2/beetle)	Utida 1957, fig. 9
49	96	<i>Didinium</i> / <i>Paramecium</i> (protozoa/bacteria)	Vielleux 1979, fig. 8
50	86	<i>Didinium</i> / <i>Paramecium</i> (protozoa/bacteria)	Vielleux 1979, fig. 9
BF	200	<i>Lucillia cuprina</i> (blowfly)	Nicholson 1954, 1957

NOTE.—Here *n*, number of data points. When two species are listed, the first is the “exploiter” (predator or parasitoid), and the second is the “victim” (prey or host). Set numbering refers to a larger collection of data that includes data sets excluded by our screening criterion.

was long enough that we could eliminate any apparent nonstationarity by using only the first 200 observations. We emphasize that screening occurred prior to any estimation of Lyapunov exponents for these data.

The three families of models give essentially the same qualitative conclusion: most of the population fluctuations are nonchaotic (fig. 5; table 2). None of the populations is characterized as chaotic by all three models. Nicholson's blowflies are characterized as weakly chaotic by RSM and FNN and very weakly stable ($\lambda = -0.01$) by TPS, so overall it seems that this population was very near the boundary between stability and chaos. There is also good agreement among the methods for the degree of predictability (as measured by the r^2 of the best-fit model) as well as for the Lyapunov exponent (table 3).

The overall results indicate that the populations ranged from strongly stable (an equilibrium or stable periodic orbit) up to and just past the transition to chaos. The proportion of variation explained by the endogenous dynamics varied from nearly none ($r^2 \approx 0$) to nearly all ($r^2 \approx 1$). However, the endogenous dynamics were generally describable by very simple models. With few exceptions, our

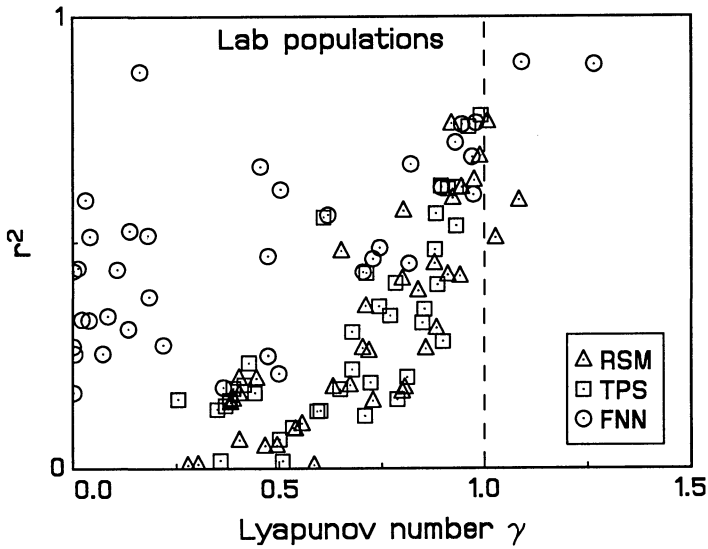


FIG. 5.—Scatterplot summarizing results for the laboratory data sets, using RSM (triangles), TSP (squares), and FNN (circles) time-series models. The X-axis is the Lyapunov number $\gamma = \exp(\lambda)$; the border between stability and chaos occurs at $\gamma = 1$, which is equivalent to $\lambda = 0$. The Y-axis is the r^2 for prediction L time units ahead by the best model ($L = \text{time delay}$), which is a measure of the proportion of the variance in population fluctuations that can be predicted from current and past population densities.

fitting criterion chose one of the simplest models, with few parameters, in each family.

Populations in the wild: annual data.—We applied our methods in the same way to published data on year-to-year fluctuations in natural populations (table 4), using the lists of published data in Witteman et al. (1990) and Krukonis and Schaffer (1991) as starting points. The data were screened by the criteria described above for laboratory populations. We also eliminated data sets covering a large geographical region likely to include many independent populations (e.g., moth population censuses that included migrants to England from the entire European continent), unless there was evidence available of synchronous fluctuations over the region (e.g., the Hudson's Bay Company lynx fur returns). To avoid biasing the results by overrepresenting better-studied species, we analyzed no more than two data sets on a given species, choosing the longest available series meeting our criteria.

The results (summarized in table 5 and fig. 6) are in many ways very similar to those for laboratory populations. There is again a wide range from stability to chaos and from nearly unpredictable to highly predictable, and again the three methods give similar results (table 6). The FNN model gives generally higher estimates of the proportion of variance due to endogenous factors (r^2) than TPS or RSM. In several cases (Lynx, Panolis, Rabbit2, Snowshoe) the higher r^2 is

TABLE 2

RESULTS FOR THE LABORATORY DATA SETS LISTED IN TABLE 1

SET/ SPECIES	<i>L</i>	RSM				TPS				FNN			
		<i>d</i>	<i>q</i>	r^2	λ	<i>d</i>	<i>m</i>	r^2	λ	<i>d</i>	<i>k</i>	r^2	λ
3E	2	2	1	.18	-.22	2	2	.20	-.21	2	2	.49	-.30
3V	2	3	1	.42	-.06	2	2	.15	-.24	4	1	.52	-1.71
4E	1	1	1	.14	-.96	1	2	.13	-1.05	3	1	.44	-4.53
4V	1	1	1	.15	-.95	1	2	.15	-.97	2	1	.25	-2.63
5E	1	1	1	.15	-.32	1	2	.15	-1.37	4	1	.33	-3.26
5V	1	1	1	.18	-.46	1	2	.17	-.95	3	2	.67	-.20
6E	2	1	1	.09	-.62	1	2	.09	-.63	3	1	.27	-1.52
6V	2	1	1	.05	-.77	2	2	.11	-.34	3	1	.31	-2.01
7E	1	1	1	.18	-.40	1	2	.14	-1.00	1	1	.18	-1.01
7V	1	2	1	.48	-.43	2	2	.43	-.34	2	1	.43	-.35
8E	1	1	1	.20	-.91	1	2	.18	-.88	2	1	.44	-7.89
8V	1	2	1	.57	-.22	2	2	.55	-.50	2	1	.59	-3.51
9E	2	1	1	.05	-.71	1	4	.32	-.16	1	1	.17	-6.71
9V	2	1	1	.26	-.35	1	2	.22	-.39	3	1	.56	-.48
10E	1	1	1	.16	-.91	1	2	.17	-.82	1	1	.21	-.70
10V	1	1	1	.20	-.81	1	2	.23	-.85	1	1	.27	-8.70
11E	2	2	1	.26	-.15	1	2	.17	-.43	3	1	.34	-2.48
11V	2	3	1	.39	-.18	2	2	.36	-.30	3	2	.61	-.03
14E	3	2	1	.43	-.09	2	2	.56	-.13	3	3	.89	.24
14V	3	1	1	.59	.08	2	2	.54	-.07	2	3	.88	-1.82
23E	2	3	1	.69	-.01	2	3	.62	-.07	3	1	.72	-.07
23V	2	3	1	.64	-.03	2	2	.41	-.12	3	1	.69	-.03
35E	2	2	1	.36	-.34	2	2	.34	-.26	3	1	.44	-2.24
35V	2	1	1	.17	-.22	2	2	.19	-.33	2	1	.33	-3.85
36E	2	1	2	.31	-.12	2	2	.35	-.16	2	1	.51	-3.21
36V	2	1	1	.01	-1.19	1	2	.02	-1.03	2	2	.62	-.69
37E	2	2	1	.51	.03	1	2	.13	-.51	4	1	.67	-.79
37V	2	1	1	.10	-.59	1	2	.13	-.52	3	1	.53	-1.99
39E	2	2	1	.26	-.33	2	3	.30	-.39	2	2	.47	-.75
39V	2	1	1	.01	-.54	3	3	.28	-.11	3	1	.25	-.75
49E	2	2	1	.60	-.08	2	2	.62	-.11	2	1	.62	-.11
49V	2	2	1	.62	-.06	2	2	.62	-.09	2	2	.76	-.06
50E	2	2	1	.45	-.13	2	2	.48	-.13	2	1	.46	-.32
50V	2	2	1	.76	-.08	2	3	.75	-.04	2	2	.76	-.02
46E#1	2	2	1	.42	-.22	2	2	.41	-.24	2	1	.45	-.20
46E#2	2	1	1	.01	-1.28	2	2	.01	-.68	4	1	.38	-1.69
46V	2	1	1	.06	-.91	1	2	.06	-.69	3	1	.25	-5.51
Blowfly	3	3	2	.77	.01	4	3	.78	-.01	6	3	.90	.09

NOTE.—For each family of time-series models (RSM, TPS, FNN) the table shows the embedding dimension (d), r^2 for the fitted model, model complexity (q , m , or k), and the estimated dominant Lyapunov exponent (λ) for the best-fit model (first minimum of V_2 , as described in the text). For RSM, q is the degree of the polynomial; for TPS, m is the order (see text); for FNN, k is the number of neurons in the network. Units of λ are τ^{-1} , where τ is the time between measurements in the original data set. For multispecies data sets E indicates the predator or parasitoid (exploiter) species, and V indicates the prey or host (victim) species.

TABLE 3

NONPARAMETRIC CORRELATIONS (KENDALL'S τ)
BETWEEN RESULTS FROM RSM, TPS, AND FNN
METHODS APPLIED TO LABORATORY DATA SETS

	RSM	TPS	FNN
RSM68***	.55***
TPS	.58***40***
FNN	.36**	.38***	. . .

NOTE.—Values above the diagonal refer to the estimated proportion of variance explained by the model in one-step-ahead predictions (r^2 of the fitted model); values below the diagonal are for the estimated dominant Lyapunov exponent λ .

** $P < .01$.

*** $P < .001$.

associated with the preferred FNN model being above the upper limits on dimension of the other models or below the minimum number of parameters in TPS. Omitting those cases, all three models suggest that the endogenous predictability (r^2) of natural populations is quite low: 0.25 ± 0.03 for RSM, 0.28 ± 0.04 for TPS, and 0.42 ± 0.04 for FNN.

Populations in the wild: monthly data.—Several of the studies that have figured prominently in the debate about chaos in ecology involve monthly rather than annual censusing of the populations (e.g., *Thrips imaginis*, human childhood diseases). Seasonality creates a regular structure that may generate spurious results for monthly data, including apparent but unreal low-dimensional attractors, low-dimensional Poincaré sections, and deterministic Poincaré maps (Ellner 1991).

A fitted time-series model that ignores seasonality is forced to use population density as a surrogate for the season. While this may work for prediction, it is not good for estimating Lyapunov exponents because time is incorrectly being treated as a state variable in the estimation procedure. We therefore constructed seasonal models by adding a “clock” to the independent variables, giving models of the form

$$N_{t+T_p} = f(N_t, N_{t-L}, \dots, N_{t-(d-1)L}, \cos(2\pi t/12), \sin(2\pi t/12)) + e_t. \quad (11)$$

The importance of seasonality is demonstrated by the large differences between seasonal and nonseasonal models for the same data (table 7; because of the dimensional limits on RSM and TPS, we used only FNN for the comparisons). Adding seasonality generally resulted in a more stable estimated model. It is especially striking that all measles data sets were identified as chaotic when seasonality is ignored but are identified as weakly stable when seasonality is included in the model. Overall, seven of the eight data sets had lower estimated values of λ with the seasonal model.

Populations in the wild: microtine rodents.—We also analyzed three relatively long data sets on population fluctuations of microtine rodents. We included these

TABLE 4
FIELD DATA SETS

Data Sets	Species	Years	Source
Annual census:			
Bupalus	<i>Bupalus piniarius</i> , Letzlingen, Germany	1881–1940	Varley 1949
Cfox	Colored fox	1834–1925	Elton 1942
Dendrol	<i>Dendrolimus pini</i> , Letzlingen, Germany	1881–1940	Varley 1949
Grouse1	<i>Lagopus scoticus</i> (red grouse), Cumberland, U.K.	1848–1904	Middleton 1934
Grouse2	<i>Lagopus scoticus</i> (red grouse), Aberdeenshire, U.K.	1849–1904	Middleton 1934
Gulo	<i>Gulo gulo</i> (wolverine), Alaska and Yukon	1910–1968	Rausch and Pearson 1972
Hare1	<i>Lepus europaeus</i> , Yorkshire estate (b), U.K.	1843–1932	Middleton 1934
Hare2	<i>Lepus europaeus</i> , Norfolk estate (b), U.K.	1862–1932	Middleton 1934
Hyloicus	<i>Hyloicus pinastri</i> , Letzlingen, Germany	1881–1930	Varley 1949
Lynx	<i>Lynx canadensis</i> , Mackenzie River	1821–1934	Elton and Nicholson 1942b
Marten	<i>Martes americana</i> , Hudson's Bay Co.	1820–1900	Jones 1914
Musk1	<i>Ondatra zibethica</i> (muskrat), Northern Department	1821–1891	Elton and Nicholson 1942a
Musk2	<i>Ondatra zibethica</i> (muskrat), Mackenzie River	1849–1927	Elton and Nicholson 1942a
Norfox	Red and arctic fox, all Norway	1879–1930	Elton 1942
Panolis	<i>Panolis griseovariegata</i> , Letzlingen, Germany	1881–1940	Varley 1949
Perdix1	<i>Perdix perdix</i> (partridge), Norfolk estate (a), U.K.	1793–1933	Middleton 1934
Perdix2	<i>Perdix perdix</i> , Yorkshire estate (b), U.K.	1843–1933	Middleton 1934
Rabbit1	<i>Oryctolagus cuniculus</i> , Yorkshire estate (a), U.K.	1867–1928	Middleton 1934
Rabbit2	<i>Oryctolagus cuniculus</i> , Norfolk estate (b), U.K.	1862–1932	Middleton 1934
Snowshoe	<i>Lepus americanus</i> , Hudson's Bay Co. (all Canada)	1849–1904	MacLulich 1957
Weasel	<i>Mustela vulgaris</i> , Perthshire estate (b), U.K.	1879–1930	Middleton 1934
Monthly census:			
Cerop	<i>Ceroplastes floridensis</i> , Hedera, Israel	1929–1936	Bodenheimer 1938
Parlat	<i>Parlatoria camelliae</i> , Hedera, Israel	1930–1936	Bodenheimer 1938
Thrips	<i>Thrips imaginis</i>	1932–1938	Davidson and Andrewartha 1948
Bameas	Measles, Baltimore	1928–1963	Yorke and London 1973
Detmeas	Measles, Detroit	1922–1963	W. M. Schaffer, personal communication
Nycmeas	Measles, New York City	1928–1963	Yorke and London 1973
Copmeas	Measles, Copenhagen	1927–1966	W. M. Schaffer, personal communication

NOTE.—“Years” gives the first and last years included in our analysis; in all cases all intervening years were included.

TABLE 5
RESULTS FOR THE FIELD DATA SETS WITH ANNUAL CENSUS

SPECIES	L	RSM					TPS				FNN			
		d	q	r ²	λ		d	m	r ²	λ	d	k	r ²	λ
Bupalus	2	1	1	.10	-.57		2	2	.19	-.29	2	1	.33	-3.43
Cfox	1	2	1	.15	-.42		2	2	.15	-.49	2	3	.56	-2.06
Dendrol	2	1	1	.29	-.33		1	2	.26	-.34	1	1	.27	-8.19
Grouse1	1	1	1	.49	-.20		1	3	.62	-.20	2	3	.88	.26
Grouse2	1	1	1	.10	-1.13		2	4	.64	-.01	2	1	.35	-.54
Gulo	2	2	1	.36	-.26		1	2	.23	-.37	2	1	.42	-.18
Hare1	2	1	1	.24	-.36		1	2	.25	-.35	2	1	.40	-3.37
Hare2	1	1	1	.18	-1.00		1	2	.19	-.85	1	1	.20	-1.07
Hyloicus	2	2	1	.48	-.16		2	2	.34	-.29	3	1	.54	-.95
Lynx	2	2	2	.65	-.05		2	2	.63	-.08	6	1	.75	-.02
Marten	2	1	1	.19	-.41		2	2	.25	-.31	2	1	.34	-.29
Musk1	2	1	1	.16	-.54		1	2	.15	-.45	1	1	.30	-2.74
Musk2	2	2	1	.43	-.24		1	3	.37	-.42	1	1	.41	-7.44
Norfox	1	3	1	.47	-.15		1	2	.16	-.91	3	1	.47	-.16
Panolis	1	1	1	.24	-.70		1	2	.25	-.68	4	1	.53	-3.38
Perdix1	1	1	1	.10	-1.11		1	2	.08	-1.32	3	2	.39	-.52
Perdix2	1	1	1	.22	-.62		1	2	.20	-.80	3	1	.40	-3.93
Rabbit1	2	1	1	.21	-.40		1	2	.18	-.43	2	1	.39	-4.28
Rabbit2	3	1	1	.25	-.22		1	2	.24	-.23	4	1	.59	-.43
Snowshoe	2	2	1	.40	-.02		2	2	.28	-.15	4	2	.84	.07
Weasel	3	1	1	.22	-.26		2	2	.65	-.23	1	1	.67	-.42

NOTE.—Variables as in table 2.

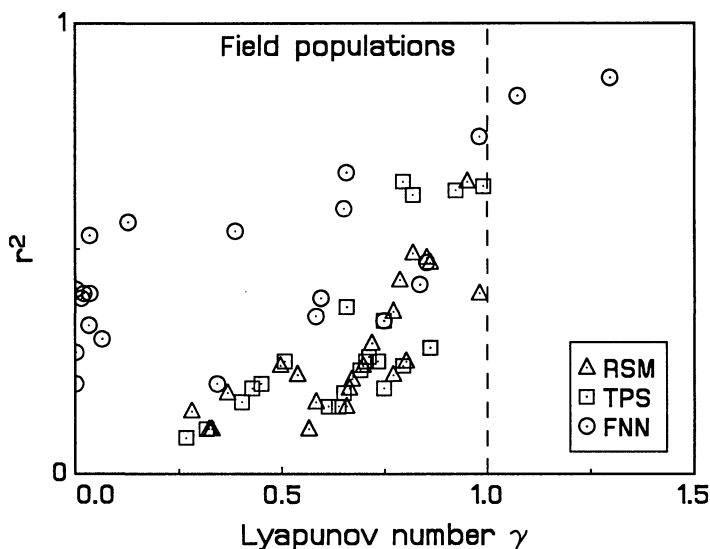


FIG. 6.—Scatterplot, in the same format as fig. 5, summarizing results for the populations in the wild with annual census.

TABLE 6

NONPARAMETRIC CORRELATIONS (KENDALL'S τ)
BETWEEN RESULTS FROM RSM, TPS, AND FNN
METHODS APPLIED TO FIELD DATA SETS

	RSM	TPS	FNN
RSM48***	.50***
TPS	.45**34*
FNN	.37**	.28*	. . .

NOTE.—Format as in table 3. Values above the diagonal refer to the r^2 of the fitted model; values below the diagonal are for the Lyapunov exponent λ .

* $P < .05$.

** $P < .01$.

*** $P < .001$.

TABLE 7

COMPARISON OF NONSEASONAL AND SEASONAL FNN MODELS FOR POPULATION DATA WITH MONTHLY CENSUS INTERVAL

	L	SEASONAL				NONSEASONAL			
		d	k	r^2	λ	d	k	r^2	λ
Measles:									
Baltimore	3	5	4	.83	-.11	8	7	.86	.09
New York City	3	5	3	.93	-.08	6	6	.95	.02
Detroit	3	6	5	.87	-.05	6	6	.82	.02
Copenhagen	3	5	6	.87	-.01	8	6	.85	.06
<i>Ceroplastes</i>	3	2	1	.41	-.52	4	1	.56	-.16
<i>Parlatoria</i>	2	2	2	.84	-.62	2	1	.55	-3.45
<i>Thrips</i>	2	2	1	.73	-1.11	6	1	.74	-.39

NOTE.—Symbols as in table 2.

data sets for comparison purposes, because RSM consistently detects positive Lyapunov exponents in population data of boreal voles (Turchin 1993), but most of the data series are too short for TPS or FNN. The populations were censused two or three times per year. We analyzed two temperate data sets, *Clethrionomys glareolus* in Wytham Wood (Southern 1979) and *Clethrionomys rufocanus* in Hokkaido (Saitoh 1987), and one boreal data set, combined numbers of *Clethrionomys* and *Microtus* voles in Finnish Lapland (Henttonen et al. 1984). The latter data set had only 46 data points but was included because it is the longest boreal time series that we have.

The results (table 8) are qualitatively consistent with previous findings (Turchin 1993): the temperate data sets are identified as being more stable, with less endogenous predictability. Indeed, for the boreal Lapland voles, RSM and FNN agree on a weakly chaotic, low-order model ($q = 1$, $k = 1$) with three lags. The TPS model does not have that option: a cubic model ($m = 3$) is the simplest possible with three lags. If we allow $m = 2$ in TPS (for which the function estimate is

TABLE 8
RESULTS FOR THE MICROTINE RODENT FIELD POPULATION DATA

POPULATION	RSM					TPS				FNN			
	<i>L</i>	<i>d</i>	<i>q</i>	<i>r</i> ²	λ	<i>d</i>	<i>m</i>	<i>r</i> ²	λ	<i>d</i>	<i>k</i>	<i>r</i> ²	λ
<i>Clethrionomys glareolus</i>	1	1	1	.00	-3.77	1	2	.01	-2.63	2	1	.48	-2.98
<i>Clethrionomys rufocanus</i>	1	1	1	.19	-.64	1	3	.17	-.94	1	1	.69	-1.25
Lapland voles	1	3	1	.68	.01	1	2	.83	-.58	3	1	.73	.02

NOTE.—Variables are as in table 2. See text for information about the populations and data sources. For FNN, both seasonal and nonseasonal models were fitted and results are reported for the best-fit model according to the GCV criterion V_2 (seasonal for *C. glareolus*; others, nonseasonal).

consistent but the estimate of λ is not), the preferred model has three lags, $r^2 = 0.65$, and $\lambda = -0.08$. Thus, apart from constraints due to the high lower bound on complexity in TPS, the three methods give similar results on the microtine data and are consistent with the latitudinal trend found earlier (Turchin 1993).

DISCUSSION

Any ecosystem in nature (and for that matter in the laboratory) is affected by noise—unpredictable density-independent perturbations. Practically, the endogenous feedbacks regulating density in populations cannot be isolated completely from unpredictable exogenous factors. We believe that the strict conceptual separation between chaos and noise, which until recently dominated investigations of chaos in ecology, is unnecessary and has had a negative impact on acceptance by ecologists of ideas from nonlinear dynamics.

Investigations of the most compelling and consistent case for chaos in population-dynamic systems—childhood diseases—highlight the difficulty of using deterministic theory for analyzing ecological data. The transmission rate of childhood diseases is influenced by many kinds of factors. Some are predictable, such as seasonality and nonlinear feedbacks. Others are unpredictable and effectively random, such as year-to-year variations in climate and labor disputes affecting the timing and length of the school year. An assumption of 100% deterministic fluctuations is therefore untenable, yet the data have often been analyzed with methods assuming the absence of noise. This leads to a logical inconsistency: how can we decide whether fluctuations are stochastic or chaotic, if the methodology assumes the absence of noise?

Our goals in this article were to present an approach that allows one to detect and quantify chaos in systems affected by random perturbations and to show that this approach leads to practical methods for analyzing ecological time-series data. Our most significant finding concerning methodology was that the details of fitting a time-series model to the data are not very important, as long as one uses a sufficiently flexible approach and does not attempt to fit the function at the expense of misestimating its derivatives. Three families of models gave similar quantitative conclusions about the degree of predictability (r^2) and stability (λ) exhib-

ited by different data sets. We agree with Morris (1990) that conclusions based on applying a single time-series model must be viewed with suspicion, because different models may give different conclusions in any specific instance. Greater confidence can come from using a variety of models, as we have done here, or by analyzing a series of comparable data sets. Confidence intervals would also be helpful, but reliable methods to generate confidence intervals are not yet available.

Within its limitations on dimension and complexity, RSM gave similar results to those from the more flexible models. We would therefore recommend RSM for shorter population data sets (20–50 points), since the amount of data is not enough to fit high-dimensional dynamics and RSM appears to perform well on low-dimensional dynamics for this amount of data (Turchin and Millstein 1993). Comparative studies (Casdagli and Eubank 1992) and our personal experience suggest that FNN is the preferred method when there are 50–500 data points available (e.g., monthly or weekly data on disease incidence).

Our main empirical finding is that both laboratory and field population data exhibit a wide variety of dynamic behavior. These behaviors cannot be described within a one-dimensional spectrum from noise to chaos. Instead, at least two different axes are needed to characterize them: one for the relative strength of the endogenous/exogenous factors (which we have quantified by r^2 , the proportion of variance in population changes explained by the best-fit model) and the second for the system's damping/amplification rate of exogenous perturbations (quantified by the Lyapunov exponent). Considering the r^2 axis first, we found that population dynamics ranged from essentially noise dominated (r^2 near zero) to almost deterministic (r^2 near one). Similarly, there was a wide spectrum of estimated Lyapunov exponents: negative at one extreme (stability) to positive at the other (chaos).

There was a positive but far from perfect correlation between r^2 and λ . This result is not surprising, since in chaotic or near-chaotic populations the endogenous dynamics can cause large oscillations in population density that would dominate any noise. The same phenomenon underlies the fact that nonlinearity is easier to detect in the presence of noise when the dynamics are chaotic (Schaffer et al. 1986). In addition to dynamics along the diagonal in figure 6, we also observe cases of weakly stable, noise-dominated dynamics (small r^2 , λ near zero). What we appear not to observe is strongly stable dynamics dominated by endogenous factors (large r^2 , $\lambda \ll 0$) (fig. 6). One possible explanation for this pattern is that strongly negative Lyapunov exponents are associated with populations that tend to return rapidly to an equilibrium point after perturbation. In such cases the fluctuations around the equilibrium track the most recent perturbations and cannot be predicted from past values (Royama 1981, 1992; Turchin 1991). This explanation would not apply to strongly stable limit cycles. Apparently we do not observe such dynamics in our data collection. However, this gap is filled by childhood diseases, which frequently have biennial or triennial periodicity and are estimated to fall mostly in the empty part of figure 6 ($r^2 \geq 0.75$, $0.5 \leq \gamma \leq 1$ for quarterly case totals) (Ellner et al. 1995).

Before commenting further on our results, we want to stress that our procedure

was biased against finding chaos. There are two causes of this bias. First, as discussed above, we deliberately used a conservative procedure for selecting model complexity. The current state of the art allows us to choose between deliberate conservatism and an unacceptably high rate of false positives. Given the degree of skepticism about chaos among ecologists, we feel that the conservative approach is preferable.

The second cause of negative bias is something over which we have no control—nonstationarity. Nonstationarity could result from changes in the mean or variance of fluctuations, or the system could shift from one dynamic regime into another. Our field data sets extend over more than 50 yr each, and it is unlikely that some changes did not occur in the environment experienced by the population. This problem is especially acute for the field data sets collected during the twentieth century. Even laboratory populations are not immune to nonstationarity, since the experimenter cannot control evolutionary changes.

Our findings of positive Lyapunov exponents in several data sets, despite the biases in our approach, therefore are a strong indication that ecological systems are capable of chaotic behavior. However, our results do not support any of the extreme positions on the prevalence of chaos that have appeared in the ecological literature (Schaffer and Kot 1985, 1986; Berryman and Millstein 1989): it is not entirely absent, but neither is it the dominant explanation for population fluctuations. If anything, our results provide some support for the hypothesis, recently put forth by some theoreticians (Kaufmann and Johnsen 1990; Ikegami and Kaneko 1992; Kaneko and Ikegami 1992; D. Rand and H. Wilson, unpublished manuscript), that interacting populations should coevolve to dynamics at the “edge of chaos” ($\lambda \approx 0$). For both the laboratory and field data sets, the frequency distribution of estimated Lyapunov exponents has a mode at or near $\lambda = 0$ (fig. 7). A mode at zero in the distribution of estimated Lyapunov exponents was also found for monthly case data on childhood diseases in large cities in the United States and Europe (Ellner et al. 1995).

Alternatively, $\lambda = 0$ will occur if a population is intrinsically stable but driven by a periodic exogenous variable that was not included in the fitted model (the dominant exponent corresponds to perturbing the phase of the exogenous variable). For example, Bulmer (1974) proposed that most cyclic wildlife populations in Canada were driven by the cycle in the snowshoe rabbit. While this hypothesis might explain the mode at zero in our estimates of λ for field populations, it cannot easily account for the modes in lab populations and childhood diseases.

Because of the negative bias in our methods, we cannot place great confidence in the mode at zero. However, if the frequency distributions in figure 7 approximate the situation in nature, this may have significant consequences for predicting population changes and for the study of chaos in population dynamics.

To explain the consequences, we return to the definition of λ in terms of the divergence between trajectories with nearby initial conditions. The definition is based on computing the long-term average divergence rate over the entire future of the system. Thus, λ ignores any transient effects of a perturbation that eventually wash out. To quantify the transient effects, the long-term average divergence rate can be replaced by an average divergence rate over a finite amount of time

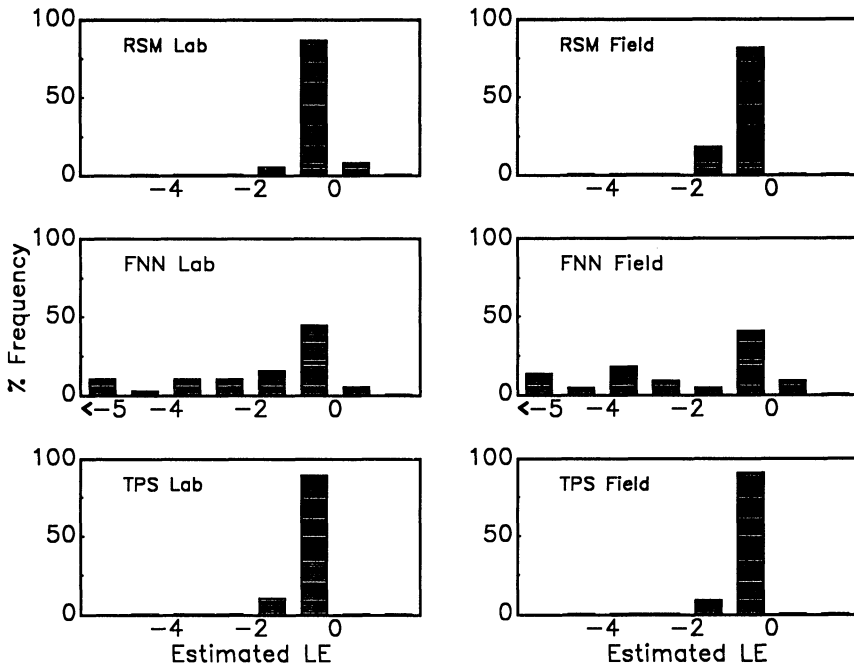


FIG. 7.—Histograms of estimated Lyapunov exponents for laboratory and field population data sets.

M . This quantity is usually called the *local Lyapunov exponent*, denoted $\lambda_M(t)$ (Abarbanel et al. 1991, 1992; Wolff 1992 and references therein); the mathematical definition is given in appendix A. Intuitively, λ_M measures the local (in state space) degree of short-term sensitivity to initial conditions. In nonlinear systems, λ_M will generally depend on the current value of the state variables; hence λ_M will fluctuate over time. In a similar fashion, we can define a local endogenous predictability $r_M^2(t)$.

As an example, figure 8 shows estimated $\lambda_M(t)$ for the blowfly population using FNN, for M equaling roughly half of the average time between peaks. The fluctuations in λ_M are almost exactly out of phase with the fluctuations in $N(t)$. The highest values of λ_M , indicating stronger short-term sensitivity to small perturbations, occur when population size is small, which indicates that the size of the next outbreak is hard to predict. The short-term predictability is highest (so λ_M is smallest) when the population is at a peak, because a crash to nearly zero density is certain to occur.

This perspective has both theoretical and practical consequences. The main theoretical consequence is that the dividing line between chaos and stability at $\lambda = 0$ is not necessarily all that crucial, since the transition to chaos need not involve any abrupt qualitative change in the dynamics. Near $\lambda = 0$, on either side, a nonlinear system will typically produce values of $\lambda_M(t)$ that fluctuate between positive and negative, as in figure 8. Hence the system is sometimes

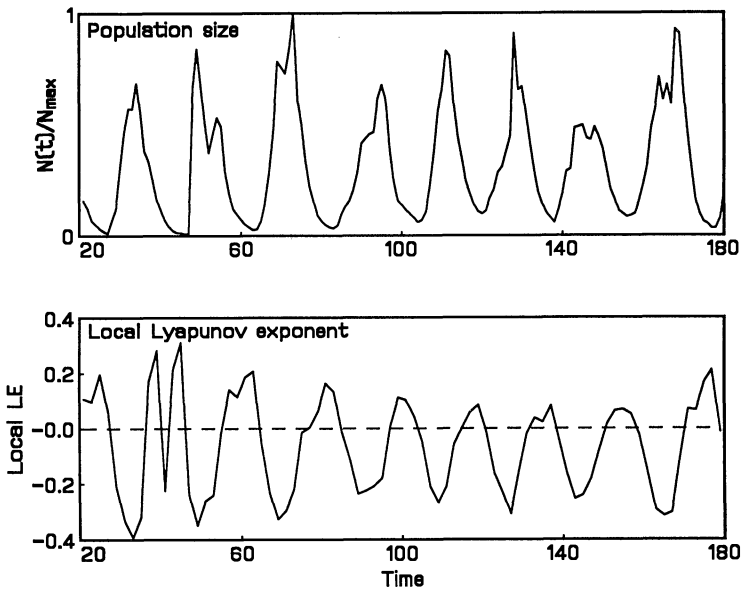


FIG. 8.—Population size $N(t)$ for the blowfly populations (*upper panel*, scaled relative to maximum value in the data set) and the short-term local Lyapunov exponent $\lambda_M(t)$ for $M = 10$ (*lower panel*), using the best-fit FNN model. The value $M = 10$ corresponds to roughly half the time between peaks. Unlike the global exponent λ , the local Lyapunov exponents λ_M are affected by nonlinear coordinate changes; those shown here are for untransformed $N(t)$.

acting as a short-term noise amplifier that will be hard to predict, and sometimes it will be a short-term noise muffler that will be easier to predict. Thus, for example, Schaffer's (1984) finding of "stretching and folding" in lynx fur returns is entirely consistent with our estimate that lynx is weakly stable ($\lambda \doteq -0.05$): dynamics near the transition, whether or not they are chaotic, will tend to have the stretching-and-folding character of chaotic dynamics. Only if the system is 100% deterministic will there necessarily be an abrupt qualitative change at the transition to chaos. In systems with dynamic noise, the change in dynamics between $\lambda = -0.05$ and $\lambda = +0.05$ need not be very different from the change in dynamics between $\lambda = -0.1$ and $\lambda = -0.05$.

The main practical consequence is that we can expect endogenous and exogenous factors to vary in their relative contribution to a system's unpredictability, depending on the system's current state. This situation would affect not only the accuracy with which we can predict but also the best allocation of effort for improving predictions. When endogenous factors are the main component of predictability (λ_M and r_M^2 are large), the way to get better forecasts is to measure more state variables or measure them more accurately. When exogenous factors are dominant (λ_m and r_M^2 are small), effort spent measuring the system's state is wasted, and only additional information on exogenous factors (if it can be gathered) would increase prediction accuracy.

The take-home from these considerations is that for population dynamics, it may be more productive to ask, When, and how often, is this system chaotic? rather than, Is this system chaotic? The former question may be easier to answer and also may give us more information about the predictability of changes in the system. Quantities such as the range of $\lambda_M(t)$ and $r_M^2(t)$ values, their frequency distribution, and their autocorrelation and correlations with state variables may tell us more than long-term average measures such as λ and r^2 that have been emphasized up to now, and more than the simple dichotomies of deterministic versus random, stable versus chaotic.

ACKNOWLEDGMENTS

This work was partially supported by National Science Foundation grant DMS-9217866 to D. Nychka, S.E., and A. R. Gallant. We thank H. Henttonen, S. Naeem, W. M. Schaffer, and S. Pimm and A. Redfearn for sending us data on voles, laboratory predator-prey experiments, diseases, and field populations, respectively; K. Tsai for assistance with literature search and data entry; D. Nychka and D. McCaffrey for the thin-plate spline code; the North Carolina State University Biomathematics chaos group (D. Nychka, A. R. Gallant, D. McCaffrey, B. Bailey, G. Bobashev, and S. Peck) for their input over many years of weekly discussions; and the editors and referees for insisting that we explain ourselves more clearly.

APPENDIX A

DEFINITION AND ESTIMATES OF GLOBAL AND LOCAL LYAPUNOV EXPONENTS

For the system in equation (6), the Lyapunov exponent can be defined as follows. Let $\{X_0, X_1, X_2, \dots\}$ be a trajectory of the system, and let $J_t = DF(X_t, e_t)$, the Jacobian matrix of F 's partial derivatives with respect to the variables in X . Let $\|A\|$ denote the norm of the matrix A (any operator norm can be used). Then

$$\lambda = \lim_{t \rightarrow \infty} \frac{1}{t} \log \|J_t J_{t-1} \dots J_1\|. \quad (\text{A1})$$

This definition seems to depend on the trajectory used to define J_t , but under mild regularity conditions, the limit in equation (A1) is constant with probability one so long as the process (X_t, e_t) is stationary and ergodic (Kifer 1986). The limit is also independent of the choice of norm and invariant under smooth coordinate transformations, because their effects are at most order $1/t$ and therefore vanish in the limit in equation (A1).

The connection between this formal definition and the heuristic definition in the text is that the J_t 's describe the divergence between our baseline trajectory X_t and a second trajectory X_t^* in which the initial separation is infinitesimally small. In that limiting case, the divergence is governed for all time by the linear variational system given by J_t .

Here all of the models used to estimate F assume additive noise, so J_t is independent of e_t . We can therefore compute an estimate of J from an estimate of the map F and the observed values of X_t , without estimating the exogenous component of the dynamics. Our estimate of λ based on the estimated Jacobians $\hat{J}_t = D\hat{F}(X_t)$ and n observed data vectors is then

$$\hat{\lambda}_n = \frac{1}{n} \log \|\hat{J}_n \hat{J}_{n-1} \dots \hat{J}_1 v\|, \quad (\text{A2})$$

where \mathbf{v} is a vector of length one, usually $\mathbf{v} = (1, 0, 0, \dots, 0)$. Deleting \mathbf{v} from the right-hand side of equation (A2) gives an alternative (and larger) estimate of λ . In our simulation studies the difference between these is minor for $n \geq 50$, but equation (A2) has lower bias without any increase in variance.

The Lyapunov exponent λ is global in the sense that it averages the divergence rate over all trajectories and over infinite time. Local Lyapunov exponents eliminate these averages and look at trajectory divergence over a finite time horizon, from a single initial location in state space.

There are several different formal mathematical definitions of local exponents in current use. Here we have used a definition adapted to the case of dynamics in a time-delay reconstruction based on a single-variable time series $\{N_0, N_1, N_2, \dots\}$ but general enough to encompass systems with or without dynamic noise. Let M be the time horizon (the number of time steps over which divergence is monitored). The time- M local exponent at N_t is defined by perturbing N_t to $N_t^* = N_t + \epsilon$ and following the subsequent trajectories until time $t + M$:

$$\lambda_M(t) = \lim_{\epsilon \rightarrow 0} \frac{1}{M} \log\{|N_{t+M}^* - N_{t+M}|/\epsilon\}. \quad (\text{A3})$$

The limit can be computed from the partial derivatives of F using the chain rule.

If the system is deterministic, then $\lambda_M(t)$ depends only on N_t (rather than on N_t and the random shocks between times t and $t + M$), and we can therefore define local exponents $\lambda_M(N)$ as a function of N . For stochastic systems, the local Lyapunov exponents $\lambda_M(t)$ are a second time series, changing along with the data series N_t .

APPENDIX B

SELECTION OF SMOOTHING AND RECONSTRUCTION PARAMETERS

SMOOTHING PARAMETERS

One popular criterion in time-series modeling is to select smoothing parameters to maximize prediction accuracy (see, e.g., Casdagli 1989, 1992; Sugihara and May 1990). To avoid overfitting, prediction accuracy can be quantified by cross validation: delete each data point (one or a few at a time), fit the model to the reduced data set, and then use the fitted model to predict the deleted point. The average error in these predictions is the measure of the prediction accuracy at the given values of the smoothing parameters.

Cross validation is widely used in nonparametric regression (see, e.g., Wahba 1990), but it is known to have a high variability and sometimes drastically overfits the data. Nychka et al. (1992) found that overfitting could be avoided on noisy chaotic data, without creating a large bias, by overweighting the number of parameters in the GCV criterion. For a model fitted to n data points, let p be the number of parameters (or the effective number of parameters; see Wahba 1990) and RMS the root mean square prediction error. The modified generalized cross-validation function is

$$V_c = \left\{ \text{RMS} / \left(1 - p \frac{c}{n} \right) \right\}^2. \quad (\text{B1})$$

Here V_1 (i.e., $c = 1$ in equation [B1]) is the standard GCV criterion; as sample size increases, GCV is asymptotically equivalent to ordinary cross validation for TPS (Wahba 1990). Here we use $c = 2$ for choosing smoothing parameters, based on Nychka et al. (1992).

RECONSTRUCTION PARAMETERS

Several criteria for choosing an optimal time delay have been proposed, but none is generally accepted and the criteria often give very different results on the same data (Ellner

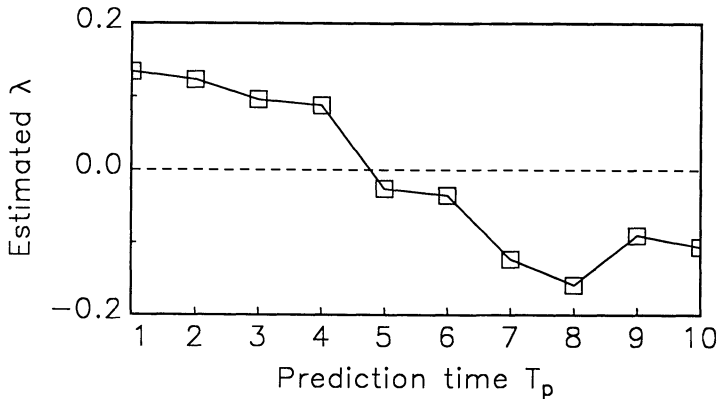


FIG. B1.—Estimated Lyapunov exponent $\hat{\lambda}$ as a function of the prediction time T_p used in fitting a time-series model. The time-series model here was TPS with $m = 3$ and two lags with time delay $L = 1$; the data were 100 points from the noisy chaotic population model used in fig. 3.

1991). One appealing idea is to choose L and T_p along with the smoothing parameters to optimize prediction accuracy, but there are serious pitfalls in implementing this proposal (Nychka et al. 1992). When models with different T_p 's are compared, smaller values of T_p are almost invariably favored because either chaos or dynamic noise make it difficult to predict far into the future. But when T_p is so small that N_t and N_{t+T_p} are strongly correlated, the best predictor is usually a linear function of one or two recent values that ignores the long-term dynamics that are the actual object of interest. In addition, when many models are being compared, overfitted models would be favored because they overestimate the prediction accuracy, which thus biases the results toward a finding of chaos.

To avoid these pitfalls, while eliminating redundant lags from the model, we have chosen to set L and T_p both equal to the minimum time lag such that the autocorrelation between $\log N_t$ and $\log N_{t-L}$ is ≤ 0.5 . An unavoidable cost of our rule is that a greater degree of smoothing is required in order to compensate for the compounded effects of dynamic noise over L time units. Therefore the results will tend to be conservative with regard to detecting chaos (i.e., estimates of λ will be negatively biased). Figure B1 shows an example of this effect: λ is estimated very well by fitting models based on one-step-ahead or two-step-ahead prediction accuracy, but for five or more steps ahead, the cross-validated smoothing parameters produce simpler, nonchaotic models and fail to detect that the system is chaotic. To reduce the chance of overfitting by including too many lags, we used the first local minimum of V_2 as a function of d rather than the global minimum; this is a standard tactic in smoothing parameter selection (S. Marron, personal communication). Again, this tends to bias our results toward simpler, nonchaotic models.

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Associate Editor: Stephen W. Pacala