CHAOS IN ECOLOGY: Is Mother Nature a Strange Attractor?*

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Abstract

We review the role of chaos and the study of chaos in ecology. We use sensitive dependence on initial conditions as the best heuristic definition of chaos. This definition forms the common theme for our review of approaches for demonstrating the importance of chaos in ecology. We emphasize that this

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definition of chaos can include the effects of noise, and that there is no dichotomy between stochasticity and chaos.

We review three classes of approaches for studying chaos in ecology: models, analysis of time series, and experiments. Current ideas from modelling approaches demonstrate the plausibility of chaos. New approaches for analyzing time series are based on using the presence of a positive Lyapunov exponent to indicate sensitive dependence on initial conditions. The methods can deal with relatively short time series that include the effects of noise, with chaotic dynamics appearing in at least some cases. Experimental work is just beginning, spurred by modelling results and the new methods for analyzing times series. We suggest directions for further work in each of these approaches.

INTRODUCTION

May's early work on discrete time models in population ecology (85–87, 92) was one of the first studies of chaos in any discipline. These papers attracted a tremendous amount of attention among theoreticians and workers in chaos in other disciplines, but chaos as an ecological phenomenon was overlooked by most researchers for a number of years. An early paper by Hassell et al (58) may have been influential in this: their work lent support to the view that chaos was unimportant in natural populations. However, Schaffer & Kot (124–129, 131) emphasized the possibility of chaos in ecology and rekindled interest in the topic. Chaos in ecology has been the subject of several recent reviews (39, 50, 81, 82, 88, 90, 119, 130). Despite these efforts, we assert that the role of chaos in the study of ecology needs to be still further clarified. Part of the need arises because a clear definition of chaos is not part of the training of most ecologists, especially those without a heavy theoretical bent. The inaccessibility of the technical literature renders entry into the field virtually impossible for nonspecialists. More accessible literature is, however, beginning to appear—we strongly recommend the "picture" book by Abraham & Shaw (3) and the recent volume by Peitgen et al (110) to any reader who wants an introduction to chaotic dynamics.

The best definition of chaos is that chaos is a sensitive dependence on initial conditions (and not just for some special initial conditions), a point emphasized by Ruelle (120, 121). We make this definition more formal below, but even the verbal definition we have just given allows us to explore further what chaos is and what chaos is not, and to explain why the study of chaos in ecology is important. Finally, we proceed from these topics to describe what we believe will be the most successful approaches for detecting chaos in natural ecological systems. We offer ways to answer the question posed in the title, rather than the answer itself.

Our assertion that the role of chaos in ecology is not clearly defined follows

from our belief that equilibrium concepts, other than those approaches focusing on chaos explicitly, continue to dominate ecological thinking (30). This equilibrial view may have been influenced by the most common approach used in theoretical ecology during the past 20 years, as emphasized in the work of May (84). (May was, however, one of the first to point out difficulties with an overemphasis on equilibria—85–87, 92.) In this framework, the focus is on simple deterministic difference or differential equations describing the dynamics of population sizes. A natural first line of investigation for such models is finding equilibria—i.e. population sizes that do not change through time—and determining their stability.

Underlying the focus on stable equilibria is the assumption that the communities we observe in nature correspond, at least loosely, to stable equilibria of the model systems. Prediction of long time behavior is based on the notion of approach to stable equilibria. In such systems, the precise value of initial conditions typically is unimportant.

In contrast, for chaotic systems, asymptotic solutions have the property that two points lying close to each other will, in general, diverge and spread apart over time. Thus, in chaotic systems, predictions can be made over short time scales because the dynamics are deterministic. However, predictions cannot be made over a long time scale. This inability to predict over the long term is the hallmark of chaos. We define this property below by saying that the system has a positive Lyapunov exponent, which is a measure of the rate of spread of two nearby initial conditions. Lyapunov exponents represent a natural extension to more complex solutions of eigenvalues evaluated near an equilibrium. We define and discuss Lyapunov exponents in more detail below.

Care should be taken in understanding the assertion of a lack of predictability over long time scales. First, the system has an attractor, a concept we define formally below, so solutions (i.e. population sizes) will remain between upper and lower bounds. Second, we argue below that this lack of predictability in itself is not a good basis for detecting chaos in observed time series, although calculation of the Lyapunov exponent is an appropriate approach.

Are endeavors to find chaos in ecological systems likely to succeed? Several methods, each with its own advantages and disadvantages, can be used to answer this question. These techniques can be classified along a continuum, depending on both the certainty one has in a model for the system under consideration and the data that are available. Toward one end are methods that involve estimating the parameters of simple population models from experiments and observations, and then observing the dynamic behavior of the parameterized model (58, 153). The results obtained usually depend critically upon the choice of the model (96). For this approach to be valid, great confidence is required in the biological realism of the chosen model. The primary advantage of this method is that a time series of data is not required.

A related approach, which would offer strong support for the existence of chaos in natural systems, would be to show that chaos exists for a wide range of reasonable models (with sensible parameter values) depicting ecological interactions. The contention among physical scientists has been that chaotic dynamics are likely to be the rule rather than the exception in the nonlinear models which describe many physical systems (110). We argue that this is also likely to be true for multispecies models in ecology.

A second approach in the middle of the continuum is based on fitting a series of related models to the data from a time series. One then chooses the "best" model and uses it to characterize the dynamics as chaotic or nonchaotic (e.g. by calculating the largest Lyapunov exponent). We discuss this approach in great detail below. This approach can be applied to some of the longer time series collected in ecology—on the order of 50 data points or fewer.

At the other end of the continuum of approaches for studying chaos, one could try to calculate the Lyapunov exponent from the data directly, an approach used by physical scientists who may have time series of 1000 or more points. This requires more data than the approach just outlined, but makes somewhat fewer assumptions. Calculating Lyapunov exponents directly from data requires a longer time series than ecologists typically can gather and assumes that stochasticity plays a limited role.

The determination of evidence for chaos from time series is an extremely active area of research, as summarized in other recent reviews emphasizing applications to physical sciences (1, 26). Almost certainly, new and more effective methods will be discovered in the next few years. Even now, however, methods for detecting chaos can be applied successfully to relatively short data series. Therefore, attempts to detect chaos in ecological systems are likely to yield new insights into the behavior of natural systems.

CHAOS: CONCEPTIONS AND MISCONCEPTIONS

It is necessary to have both an intuitive understanding of chaos and precise definitions before examining the role of chaos in the dynamics of natural populations. We begin with both an intuitive and a formal definition of chaos, and a discussion of characteristics of the consequences of chaotic dynamics that are important for ecologists.

A Definition of Chaos

The simplest and most intuitive definition of chaos is extreme sensitivity to initial conditions. If a system has chaotic dynamics, then the difference between the trajectories of two populations that have slightly different initial conditions grows until this difference is essentially as large as the variation in either trajectory. The difference between trajectories grows exponentially (as in simple exponential growth) through time. In other words, if there is an

error in the determination of the initial conditions, the error grows until the error is as large as the signal.

DEFINITION OF AN ATTRACTOR   To define chaos precisely, we need to make formal the definition of an attractor. First, we introduce the concept of phase space (3, pp. 38–41). In dynamic models equilibria often are depicted using phase space diagrams in which the size of one population is plotted against the sizes of a second and third population, without explicitly including the time axis. Thus, in phase space, an equilibrium consists of a single point. More complex solutions that appear in ecological models are limit cycles, which are represented by closed curves in phase space. Still more complex are quasiperiodic solutions composed of periodic variation with two or more incommensurate frequencies, so in phase space solutions trace out the surface of a "doughnut," and the time series for any single dependent variable exhibits oscillations on fast time scales within an oscillating envelope on a slower time scale. The most complicated solutions such as those that arise in chaos typically will have more complex geometrical shapes in phase space.

An attractor is a set of points in phase space (e.g. population sizes in a model) that represent a stable set of final dynamics for the system. These dynamics are final in three senses. First, once the state of the system or model is in this set, it does not leave this set. Second, all points of the set are reached. Finally, any trajectory starting near enough to the attractor approaches the attractor. For a simple discrete time model, depending on the parameters, the attractor can be a single point (an equilibrium), two points (a two-point cycle), four, eight, or a larger finite number of points (a more complex cycle), a closed curve, or a chaotic attractor. Chaotic attractors of deterministic systems also are usually strange attractors, which are defined below. Likewise, for a continuous time model, attractors can be simple points, limit cycles, or more complex.

DEFINITION OF LYAPUNOV EXPONENTS   The notion of exponential divergence can now be quantified using the concept of a Lyapunov exponent. Suppose that a point, p, (i.e a vector of population levels) lies on the attractor of a system. Consider what happens to a small cloud of possible population levels near p. Follow both p and the cloud of nearby initial conditions through time as the population levels change according to the model. The distance from p to points in the cloud will either grow or shrink. The (long-term) average rate of change of this distance can be decomposed into rates of (exponential) change along principal axes in the cloud of points. Each one of these rates of change is a Lyapunov exponent. Thus there are as many Lyapunov exponents as there are variables in the phase space (in differential equation or difference equation models).

DEFINITION OF CHAOS USING LYAPUNOV EXPONENTS   The attractor is chaotic if (and only if) at least one of the Lyapunov exponents is positive (120, 121). This corresponds to the intuitive definition used earlier: points in the cloud near p will eventually diverge. (Note that in continuous time differential equation systems there must also be at least one negative Lyapunov exponent for the attractor to attract.)

The definition of Lyapunov exponents, and thus of chaos, can be extended to include noisy systems (33, 69), which is of vital importance when describing natural populations. In fact, stochasticity can change a system from the nonchaotic regime to the chaotic regime or vice versa, as has been demonstrated for some epidemiological models (115). The Lyapunov exponent is still defined as the average rate of trajectory divergence caused by the endogenous component, but now, using two trajectories that start near each other and that are affected by the identical sequence of random shocks. The relation of this definition to the more familiar features of strictly deterministic chaos (e.g. fractal attractors) is presented graphically in (103).

Under this definition, the Lyapunov exponent, λ, tells us whether the endogenous part of the mixed deterministic/stochastic system amplifies or dampens over time the effects of exogenous perturbations. A chaotic system ($\lambda > 0$) is a "noise amplifier": the effects of perturbations are compounded and cannot be ignored in predicting the future state of the system. A nonchaotic system ($\lambda < 0$) is a "noise muffler": the effects of a perturbation are transient and asymptotically have no effect on the system's long-term dynamics. Recent advances now make it possible to study chaos in systems that include stochastic components.

CHARACTERISTICS OF CHAOS   Another characteristic of chaotic behavior is the existence of an attractor to which all sufficiently nearby solutions converge, given sufficient time. Thus, a chaotic system is stable (which does not mean that an equilibrium is approached) by its very definition. Further, if population levels on the attractor remain sufficiently far from zero, the system may persist indefinitely even though the population levels fluctuate widely.

Another typical characteristic of chaotic solutions is the geometric form of the attractors. The attractors typically are twisted and "strange," meaning that they have fractional (fractal) dimension, although this is not necessarily the case. The dimension of an attractor is typically computed using an algorithm (51, 52) based on the notion that the fraction of points on the attractor that are within ϵ of any specified point on the attractors proportional to ϵ^d, where d is the dimension. For a deterministic chaotic attractor, the dimension (i.e. the so-called fractal dimension) would typically be a fraction (e.g. 1.26 rather than 1 or 2), whereas for a stochastic system, the dimension would typically be equal to the dimension of the phase space. Computation of the dimension

of an attractor was the first practical method of data analysis for determining if a system was chaotic, but more recent work has shown that other methods are more useful.

INVARIANTS   The two characteristics of chaotic systems just noted, dimension and Lyapunov exponents, are both invariants: they are unchanged by nonlinear coordinate changes. Invariants are important since they are the quantities most appropriate to use when attempting to characterize systems as chaotic or not.

Approaches for Detecting Chaos

Chaos can be detected using several approaches we discuss below; visual inspection of time series is not a reliable method for detecting chaos. Two factors may be responsible for the notion that chaos can be detected by visual means. First, graphs of population densities versus time in chaotic systems appear to lack a perceptible pattern. This has led to the origin of an "intuitive, but technically vague" definition of chaos that refers to the presence of irregular oscillations (119). Second, some of the tools used to analyze chaos are graphical. However, visual methods can be misleading and may be insufficient to distinguish between chaos and stochasticity. We demonstrate this below.

Chaos and Stochastic Dynamics

Several prevalent misconceptions about chaos pertain to its relationship to stochastic behavior. One such misconception either equates chaos and noise, or includes stochasticity as a special type of chaotic behavior. In reality, chaos and stochasticity are not equivalent: not only do the underlying mechanisms differ, but the consequences for observers are very different. In deterministic systems, if information is complete, then predictions made from the governing equations will be perfect. Chaotic systems are predictable over short time scales because they are deterministic; the lack of predictive power over long time scales stems from lack of complete information about the exact location of initial conditions. In contrast, systems that are stochastic are unpredictable over any time scale because of the probabilistic nature of the components. Further, systems can have endogenous dynamics that are chaotic in the presence of exogenous stochastic perturbation. Such interaction between systems with chaotic dynamics and stochasticity leads to new and interesting behavior (33, 114, 115) which we discuss below.

So ... Why Bother?

To many ecologists, investigating chaos and dynamical systems may seem like an esoteric fad pursued only by theoreticians suffering from a severe case of physics envy (although ecologists did it first). We strongly believe that the

study of chaos will yield important insights for ecologists. First, most natural systems and the interrelationships therein are too complex to be easily comprehensible. In such cases, models and quantitative methods are useful tools for synthesizing and organizing observations about nature. Historically, ecological models ignored nonlinear effects in per capita growth rates because of the analytical tractability of linear models. The analyses of these models have been based on the notion that the communities observed in nature correspond to stable equilibria in these models, e.g. (112). However, nonlinear effects are realistic, and the evidence for equilibrium behavior is inconclusive (30). Including nonlinear effects can make substantial qualitative changes in behavior, including the appearance of chaos, even in continuous time models. Thus, ecological paradigms based on models that assume linearity or on stability analyses of equilibrium points should be regarded with caution, a point emphasized early on in the development of the subject (87, 92).

The premise that ecological phenomena are inherently nonlinear (e.g. saturating predation rates and Allee effects) implies that the existence of complex dynamics in natural systems cannot be ruled out. Recent theoretical advances render application of dynamical systems theory in ecology more feasible. The application of these tools to a broad spectrum of formulations used to describe ecological phenomena has led to the observation of chaotic dynamics in a wide variety of models.

Second, the existence of chaos in the models suggests that examining data on the dynamics of natural populations may be worthwhile. Here, time series approaches are becoming better suited for application in ecology. The earliest methods used to study chaos in empirical time series were developed for physical applications and assume noise-free dynamics and perfectly accurate data. Ecologists cannot make these assumptions. Uncritical use of purely deterministic models has contributed to a rejection of nonlinear dynamics ideas by many ecologists, e.g. (57). Ecological applications require methods that can incorporate nonlinearity and dynamical noise or that are robust to the effects of noise. Such methods have been developed. Thus, ecologists will be able to understand the relative roles of deterministic and stochastic forces in determining the apparently irregular dynamics of most natural systems (30, 50).

Finally, the distinction between stochastic and deterministic dynamics has important practical applications. If fluctuations in population sizes are driven primarily by deterministic factors, and if those factors are understood, then the dynamics are predictable over short time scales. Management of such populations is feasible. On the other hand, if fluctuations are driven primarily by exogenous stochastic forces, then prediction and management become much more difficult.

In the following sections, we review general deterministic models that have

been important in ecology. We then turn to time series approaches and the use of experimental techniques to study chaos. Finally we discuss our forecasts for future directions.

HOW CAN WE INVESTIGATE CHAOS IN ECOLOGY-MODELS

We argue that chaotic dynamics are likely to be common rather than the exception in ecological systems by looking for chaos in ecological models, focusing only on biologically reasonable interactions and parameter values. By showing that the presence of chaotic dynamics does not depend critically on either the choice of model, as long as it is sufficiently complex (in terms of the number of species), or the choice of parameter values, we make a strong case for the potential importance of chaotic dynamics in natural systems.

   We begin our study of chaos in ecology with strategic models, which are both a logical and a historical beginning. The first studies of chaos in ecology began with the recognition that simple discrete time models for single species could lead to chaotic behavior (85, 87, 92). These models represent a logical beginning for several reasons. First, as we shall show, one of the surprises of nonlinear dynamics is a kind of universality to chaos: dynamical features present in the simplest models appear in a wide variety of more complex models. The simple models are the best way to introduce concretely some of the general features of chaos. Second, the parameterization of simple models of natural or laboratory populations is one way to determine whether chaotic dynamics are merely a possible outcome of ecological interactions described in models, or whether they actually occur in nature. Third, simple models already show the plausibility of chaos.

Discrete Time Models

We begin with one of the simplest examples of a discrete time model that exhibits chaos (85–87, 92). Let N_t be the number of individuals in a population at time t, $\tilde{r}$ be the intrinsic growth rate, and K the carrying capacity. Then one version of the discrete time logistic model (85) is:

$$N_{t+1} = N_t[1+\tilde{r}(1 - N_t/K)].\qquad\qquad 1$$

   One important feature of chaos is that often the exact details of the model are not critical, so the behavior we describe below is repeated for a wide variety of similar models (87). We simplify this model by letting $x_t = N_t\tilde{r}/[(1$

$+ \tilde{r}K]$ and $r = 1 + \tilde{r},$ *so* x_t is a rescaled measure of the size of the population which satisfies

$$x_{t+1} = rx_t(1 - x_t). \qquad 2$$

The simplest way to study this equation is simply to iterate it on a computer by picking values for r (between 1 and 4, with some between 3.5 and 4) and values for x_0, and then finding x_1, x_2, and and so on. Notice that for $r < 3$, solutions approach a stable equilibrium. For $r > 3$, the solutions oscillate between two or more points. Moreover, the number of points on the cycle increases as r increases. Specifically, the solution to the logistic equation has period two for r near 3, then 4, then 8, and so on, as r increases. Finally, for most (but not all) values of $r > 3.57$ (or thereabouts), the results have no apparent pattern: long-term predictions are impossible even for a deterministic model because any imprecision in the initial conditions gets magnified. In Figure 1, we have demonstrated this by looking at the outcome of applying Equation 2 twenty times to each of 9999 equally spaced initial conditions. Note that there is no apparent relationship between the initial conditions and the outcome at this time scale, even though the dynamics are completely predictable on a time scale of one to a few generations. The graph of x_1 vs
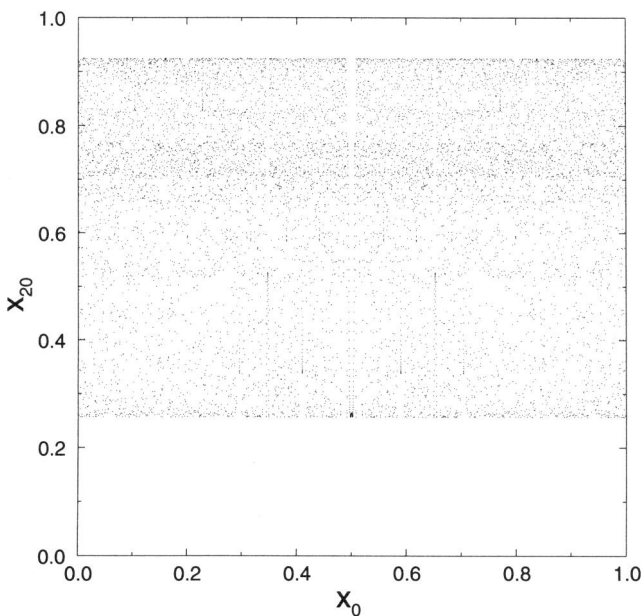

Figure 1   Population levels in a chaotic model after 20 time steps, x^{20} as a function of initial conditions, x^0. The logistic model, Equation 2, is iterated 20 times for $r = 3.7$.

x_0 is simple while the graph of x_{20} vs x_0 is extremely complex. This spread of solutions that start close to each other is the outcome of a positive Lyapunov exponent, the hallmark of chaos (120, 121). However, we emphasize that a graphical approach is insufficient to unambiguously classify a system as chaotic: it is essential to use more precise definitions and methods.

Another way of looking at the dynamics is the construction of a bifurcation diagram, e.g. (87), which displays information about the dependence of the dynamics on a single parameter. To construct a bifurcation diagram is a straightforward process. Start with a fixed value of a parameter, such as r in the logistic model. Then, look at the asymptotic behavior of the model for that parameter value, by iterating the system for a long time (say 100 time steps), and then plotting the next 32 time steps. Increase the value of the parameter slightly and repeat the process. The bifurcation diagram consists of plotting the long-term values of the dependent variable (population size, x, in this case) against the parameter (in this case, r) as in Figure 2. Apparent in the bifurcation diagram is the presence of simple periodic behavior for some parameter values in the region $r > 3.57$. The presence of period doubling, a solution first of period two, then four, eight and so on, is also apparent from the bifurcation diagram.

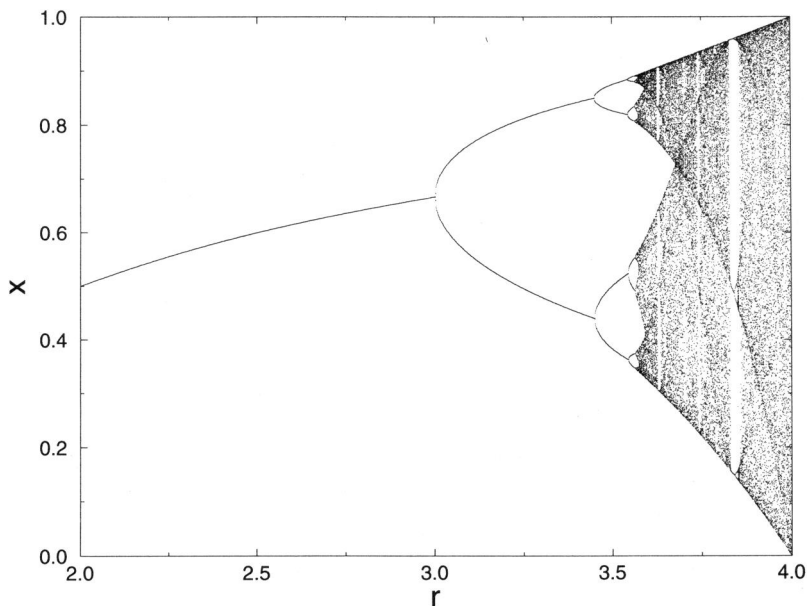Period doubling is an example of a "route to chaos"—how the dynamics

Figure 2   Bifurcation diagram for the quadratic model, Equation 2. Long-term population levels, x, are plotted as a function of the growth parameter, r.

of a system change as a parameter is changed, leading ultimately to the appearance of chaos. The concept is useful because only a small number of well-defined routes to chaos (110) have been found. These include the period doubling scenario we have just described as well as the breakup of quasi-periodic behavior. Another possibility is the change of a chaotic set from repelling to attracting through a tangent bifurcation, which would show up as the sudden appearance or disappearance of a chaotic attractor as a parameter is varied. (This, too, can be seen in Figure 2.) A bifurcation diagram that corresponds to one of the well-known routes to chaos is a good indication of the presence of chaos in a model. The use of bifurcation diagrams can be extended in obvious ways to systems with more than one population or dependent variable and to continuous time systems, as in the ecological examples (61, 74).

The bifurcation diagram illustrates several other points. First, the attractor is bounded—there are both upper and lower limits to the population level when the model is chaotic. Second, within the chaotic region of parameter space, some parameter values lead to simpler behavior.

Not surprisingly, chaotic dynamics have been found in a number of more complex discrete time models as well. Chaotic dynamics have been found in models with age structure (36, 54, 79, 80), models with two species (5–9, 13, 14, 85, 92, 99), simple models of parasites (89), host-parasitoid-pathogen systems (65), demographic models with two sexes (27), and models incorporating frequency dependent selection (10, 32, 91). Studies of the influence of periodic variation in parameters, caused for example by annual cycles, on discrete time models show that chaotic dynamics remain and more complicated behavior can result (75). Other "routes to chaos" can also appear in these models, e.g. the breakup of quasiperiodic behavior rather than period-doubling. The important question—Is chaos "more likely" with more species or with age structure?—does not yet, and may never have, a definitive answer.

Continuous Time Models

Chaotic dynamics are not a property of discrete time models. The first modern investigation of chaotic dynamics was that of Lorenz (83), who demonstrated the existence of chaotic dynamics in a continuous time model (three differential equations) now known as the Lorenz equations, which caricatures equations from fluid dynamics. One difference between continuous time models and discrete time models is that, in the absence of seasonality, at least three variables are needed for chaos to occur. Given the emphasis of ecological models on two species, it is not surprising that the occurrence of chaotic dynamics in continuous time has not received as much attention from ecologists.

One technical tool useful for the study of dynamics in continuous time

models is the Poincaré map. The word map just refers to a discrete time system; the map is the function giving the state of the system next time in terms of the state this time. The construction of a Poincaré map provides a way to relate continuous time systems to the universal properties observed in discrete time systems, by looking at the system not at fixed intervals of time, but instead at each time the system passes through a particular set of values for the dependent variables. For three-dimensional continuous time systems, the simplest Poincaré maps are given by looking at successive intersections (in the same direction) of the solutions of the system with a Poincaré section consisting of a plane in the phase space. The construction of Poincaré maps in ecological contexts is discussed in (61, 105, 125, 126, 128). The Poincaré map of a continuous system is also a useful diagnostic tool for detecting chaos in a model. If the continuous system is chaotic, the Poincaré map often will resemble a one-dimensional, chaos-producing map like the logistic map discussed above (Equation 2) (125, 126, 128).

One of the first demonstrations of chaotic dynamics for a continuous time model in ecology was that of Gilpin (49), who showed that chaos could occur in a Lotka-Volterra model for one predator and two competing prey species with self-damping terms. Gilpin initially concluded that the dynamics were chaotic by looking at the solution graphically. Further study of this model by Schaffer (126) has confirmed that the dynamics are indeed chaotic. Other studies of Lotka-Volterra systems with three or more species have also found chaos (47, 146).

More recent work by Hastings & Powell (61) on a three species food chain has reemphasized the possibility of chaos in continuous time ecological models. This model describes a plant species growing logistically that is fed upon by an herbivore which is in turn fed upon by a carnivore, incorporating Type II functional responses. Hastings & Powell (61) argued that the intuitive reason that the dynamics in this model were chaotic was the interaction between two cycles of different period. Because cycles of different periods would be generated by population interactions, this reasoning would suggest that chaos is likely the rule rather than the exception in the dynamics of all but the simplest ecological communities.

This work has been recently extended by Klebanoff & Hastings (70) who showed that chaos is expected in general food chain models without restricting attention to a specific model. More specifically, they showed that for parameter values where the top predator has a small population level and the two lower trophic levels would have a small amplitude oscillation in the absence of the top trophic level, chaos should occur in essentially any food chain model with nonlinear functional responses. Other authors (133, 158) have also emphasized the presence of chaotic dynamics in a wide variety of simple continuous time models of interacting species. Several studies have

demonstrated chaotic dynamics in models of larger communities (37, 158). Thus, chaos may be widespread.

SEASONALITY OR PERIODICITY   Biological populations frequently are influenced by periodic processes such as seasonality, tides, and daily changes in the environment. Exogenous periodic forcing can interact with intrinsic population processes to produce interesting dynamics that often are chaotic. Two lines of investigation have been emphasized by ecologists: models of periodically forced chemostats, and models of epidemics. Seasonal models of interacting species are discussed in detail in (116, 117).

The simplest model for a chemostat considers one nutrient, one species of bacteria, and one species of protozoa preying on the bacteria, with the predation described by a Monod function, or a Type II functional response. In the absence of periodic forcing, the behavior of this model is quite simple, with the outcome either a limit cycle or a stable equilibrium. Two recent studies (74, 109) have examined the effect of periodic forcing in this model. One basic mechanism for chaos is present—periodic forcing of a system which is already periodic (53). Both conclude that chaotic dynamics are quite likely, even though the choice of the periodic term in each case is different—either the flow rate (109) or the nutrient concentration (74).

Epidemic models represent another specific well-studied case. Schaffer, Kot, Olsen and colleagues (77, 104, 105, 125, 128, 132) have conducted extensive studies of epidemic models in a seasonal environment. These models are appropriate for modeling most so-called childhood diseases such as measles, mumps, rubella, or chickenpox. Changes in seasonal behavior of children is assumed to lead to a periodic contact rate. This model, like the chemostat model, has innate periodicity plus a periodic forcing term. Extensive studies of this class of models have indicated that chaos occurs for reasonable parameter values. Below we review approaches to detecting chaos from the extensive (at least by ecological standards) time series of disease incidence records available for childhood diseases from a number of major cities.

DETAILED MODELS   Strategic models can only suggest the possibility of chaos in natural systems. More specific models, including the epidemic models and chemostat models just discussed, can provide another way to argue for the presence of chaos in the systems they describe. These models are specific enough that parameter estimates suggesting that the model's dynamics are chaotic may be an indication of chaos in the ecological system.

Other systems are also appropriate for this kind of detailed modeling. Attempts to model specific laboratory entomological systems, such as Nicholson's blowflies, have also led to strategic models that have been shown

to be chaotic (106, 107). We discuss this particular experimental system in more detail when we review experimental approaches. A detailed simulation model of a stored-products pest, (*Ptinus techtus,* Coleoptera), has exhibited chaos (102).

Finally, studies of models from fisheries (such as 80) have shown, not surprisingly, that these systems can also exhibit chaotic dynamics. Models of other fisheries systems, including either more species (35) or economic effects (160) also exhibit chaotic dynamics for reasonable parameter values.

Spatial Structure

Recent efforts have begun to include the effects of spatial structure (11, 29, 59, 62, 63, 72, 73, 76, 139). Kot (73) has shown that period doubling, as in simpler models such as the logistic model discussed earlier, occurs in discrete time, continuous space models. The traveling waves of advance in these models can have a chaotic character. In (29, 59) complex spatio-temporal chaotic solutions are shown for a spatially explicit model of a host parasitoid system. There is also a large and rapidly growing literature in physics on spatial and temporal chaos reviewed in (1).

Preliminary work on spatio-temporal chaos in ecology calls into question many of the generalizations one might draw both from studies of chaos without spatial structure and from studies of spatial structure that do not focus on chaos. Spatial structure can make chaos more likely, through a mechanism of diffusive instability (62, 72). Perhaps more surprisingly, simple diffusion can destabilize chaotic solutions, leaving simple periodic solutions as the only stable ones (63) in a system of two coupled quadratic maps of the form of Equation 2. Coupling much larger numbers of potentially chaotic systems leads to even more possibilities, emphasizing that dynamics can appear chaotic at one spatial scale and temporal scale, but not at another (139).

Stochastic Models

The models we have reviewed so far have all been deterministic, yet stochastic forces are important in ecological systems. As we noted above, it is possible to extend the notion of Lyapunov exponents, and thus a definition of chaos, to include stochastic systems. The number of investigations of chaos in model ecological systems with stochasticity has been quite small. Investigations (114, 127) of a logistic model with noise added showed that chaotic dynamics persisted. Rand & Wilson (115) emphasized how the interaction between the deterministic dynamics and noise can lead to a case where the average Lyapunov exponent is positive, even though the purely deterministic system with the same parameters is not chaotic.

In related work, several investigators (140, 142) have built up from individual-based simulation models to population models that are chaotic.

This work provides further evidence for the ubiquity of chaos, at the appropriate scale, by showing that individual based models can appear deterministic and chaotic at the level of the population.

The Bottom Line

Models have indicated that chaos is a plausible outcome of the interactions among species. Future work on models can proceed from specific ecological assumptions, rather than by having to show in a general sense that chaos can occur. For simple discrete time models, the best summary is still May's (85, 87) observation that strong density dependence will lead to chaos. For continuous time models, interactions between cycles of different periods, due either to exogenous or endogenous effects, are emerging as a ubiquitous source of chaotic dynamics. Another emerging feature is that systems can look chaotic on one temporal or spatial scale, but not on other scales. More work is still needed to understand the conditions most likely to lead to chaos, and to explore the consequences of chaos in the dynamics of more complex models.

INVESTIGATING CHAOS—ANALYSIS OF TIME SERIES

Proceeding along the continuum of approaches we outlined above, we turn our attention now to approaches that begin with observed time series. The strategic models we have reviewed above and the parameterization of other simple models indicate the likelihood of chaos for "reasonable" parameter values. However, to make a stronger case for chaos, this work needs to be supplemented with the analysis of time series. Parameter estimates will have errors. Some parameters may be impossible to measure; and a fundamental difficulty relates to the choice of a particular model. We review methods for detecting chaos in time series in general and specifically discuss these approaches in the context of some of the time series available to ecologists, including the histories of incidences for childhood diseases. Much of the effort at understanding how to analyze time series to look for evidence of chaos has come from the physics community, so we begin by considering these approaches. We dichotomize approaches by focusing first on methods that attempt to detect chaos without formulating a model, and then on those methods based on model formulation.

Model-Free Approaches

RECONSTRUCTION   Ecologists often pose the reasonable question of the role of unobserved variables in determining the dynamics of the population they are currently studying. There is a simple solution to this problem, when looking for evidence of chaotic dynamics. Packard et al (108) demonstrated

that a single time series for a single variable or population could be used to "reconstruct" all relevant information needed to demonstrate chaotic dynamics for a system with more variables (even an infinite dimensional system which could be used to describe age or spatial structure), provided certain technical conditions held (and these are almost always met). This means that the dynamical effects of the unobserved variables of concern to ecologists are incorporated in the observed data. The most popular method is reconstruction in time-delay coordinates (an idea credited to Ruelle), in which the original time series x_t is augmented by the additional state variables $x_t - l$, $x_t - 2l$, . . . for some time delay l and a dimension chosen by the investigator. This creates a multidimensional time series, where, for example, with delay one and dimension three, one point would be $x_t, x_t - 1, x_t - 2$. For ecological examples of this technique, see (39, 105, 125, 129, 131). Other reconstruction methods are discussed and evaluated in (25).

Reconstruction makes it possible to visualize complex dynamics in real data, at least up to three dimensions. Figure 3 shows the strange attractor for a chaotic measles epidemic model (104), reconstructed from the time series of $I(t)$, the number of individuals currently infected. Such plots are suggestive
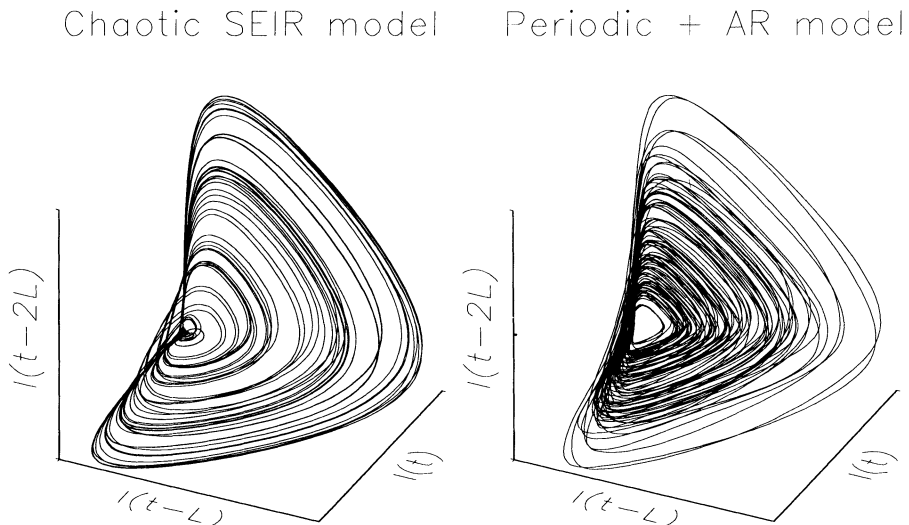

Chaotic SEIR model   Periodic + AR model

Figure 3 Time delay reconstruction in three dimensions, for time series from measles epidemic models. (Left) Chaotic SEIR model with seasonal forcing of the contact rate, as in (104, 132). (Right) Stochastic, nonchaotic model $\log I(t) = p(t) + c(t)$ where $p(t)$ is a periodic function and $c(t)$ is a series of autocorrelated random numbers. Each time series consists of monthly values from a simulation of 100 years. Time delay $L = 3$ months for both. Reconstruction follows the procedures in (104, 132) for measles data: three point smoothing and interpolation with cubic splines.

but they can be misleading: Figure 3 shows a spurious "strange attractor" produced by a random, nonchaotic time series composed of an annual cycle plus correlated noise. To distinguish this series from a truly chaotic time series, more than two time lagged variables are needed. The resulting attractor is more than three-dimensional and therefore cannot be visualized.

Takens's Theorem (122, 145) put time delay reconstruction on a mathematically sound foundation by saying that the reconstructed and true dynamics will be equivalent so long as enough different time delays are used. Consequently, reconstruction reproduces exactly any invariants. In particular, the fractal dimension and Lyapunov exponents are the same in the original and in the reconstructed dynamical system.

ESTIMATING INVARIANTS   Numerical algorithms for calculating invariants were quickly developed and applied in many fields, with fractal dimensions attracting the most attention. In ecology, Schaffer & Kot took the lead, emphasizing population dynamics and childhood disease epidemics; reviews are in (39, 77, 131, 132). The non-ecological literature is vast, but good overviews are available (1, 2, 38, 93, 137, 148).

Eventually, it was realized that "computing fractal dimension is a tricky business" (148, 149). The amount of data needed to compute reliably the fractal dimension of a deterministic system has been estimated under different assumptions (48, 121, 136, 138). The theoretical requirement for efficient methods with accurate data suggest that "a few thousand observations" will be adequate for deterministic systems "if we are not too stringent about the accuracy of the estimates" (138). In practice even several hundred observations may be adequate (4, 64). However, even very small stochastic effects can cause great difficulties (137), and seasonality (i.e. periodic forcing) can give a spurious appearance of low dimensionality in nonchaotic data (39).

Compared with the fractal dimension boom, little effort has gone into determining the data requirements and robustness to noise of methods for computing Lyapunov exponents. *We emphasize again that the Lyapunov exponent quantifies a chaotic system's sensitive dependence on initial conditions; it is therefore a key quantity in characterizing dynamics.* Initially Lyapunov exponents appeared to be estimated less reliably than dimensions (159, 162), but interest in Lyapunov exponents is reviving as better methods are developed. See (17, 20) for methods for deterministic systems.

Schaffer et al (132) review Lyapunov exponent estimates for childhood disease epidemics, based on a modification of the method of Wolf et al (163) to account for seasonality. However, the method (163) assumes a noise-free system, and its estimates of Lyapunov exponents are inflated by dynamical noise (123).

What is particularly important for ecologists is that, unlike fractal dimen-

sions, Lyapunov exponents remain well defined in the presence of dynamical noise and can be estimated by methods that explicitly incorporate noise (40, 103). This knowledge underlies our contention that at present estimating Lyapunov exponents is the best approach for detecting chaos in ecological systems.

NONLINEAR FORECASTING AND SURROGATE DATA   Due to the difficulty of estimating invariants, methods have been developed to test directly for determinism, rather than testing indirectly by estimating invariants. One approach is "nonlinear forecasting": Construct a nonparametric, nonlinear time-series model for the dynamics, reserving some data to evaluate the model's accuracy. The seminal papers (22, 34, 42) showed that very high prediction accuracy, unambiguously indicating a deterministic system, could be achieved on clean chaotic data. Recent work has refined the modeling procedures (26) and has shown that nonlinear forecasting can be used to filter out small measurement errors (43, 56, 71). Sugihara & May (144) developed a nonlinear forecasting method, in which a time-series is identified as chaotic if it is predictable in the short term but unpredictable in the long term; these features are interpreted as revealing sensitive dependence on initial conditions. Kaplan & Glass (67) proposed a statistical test of whether a time series is deterministic, by determining if all trajectories in a small region of state space are pointing in the same direction.

However, measurement errors and dynamical noise also create difficulties for nonlinear forecasting. Even small measurement errors can make a deterministic chaotic series highly unpredictable and effectively stochastic (25). Moreover, an estimate of predictability per se says little unless there is some means of determining whether the cause of unpredictability is external or internal to the system, and if internal, whether it is due mainly to low-dimensional chaos plus measurement errors. This ambiguity seriously confounds Sugihara & May's (144) method. Using this method, measles epidemics are classified as chaotic (143, 164), supporting the conclusions of Schaffer and coworkers (132). However long-term unpredictability could equally well result from the compounding effects of random shocks over time; hence the Sugihara & May method cannot distinguish between chaos and dynamical noise (39).

Another alternative to estimating invariants is to use invariants strictly as sample statistics for hypothesis tests. Bootstrap-like tests have recently been proposed, which involve calculating the same measure for the real data and for many "surrogate" data sets that match certain attributes of the real data (151). For example, Schaffer et al (132) apply the same estimate of the Lyapunov exponent to their data and to surrogate time series generated by randomly shuffling the data. Any null hypothesis can be tested, so long as

surrogates conforming to the null hypothesis can be generated (e.g. having the same linear correlations as the data). Inaccurate estimates of data attributes, which are inevitable when analyzing real data, may cause spurious rejections of the null hypothesis unless precautions are taken (150).

Nonlinear Modeling of Ecological Time Series Data

GOALS OF TIME-SERIES MODELLING   The succession of nonlinear time series methods, from naive estimates of invariants to formal hypothesis tests, has demonstrated that the early hopes for one algorithm to handle all data sets raised by Takens's Theorem were unrealistic. Reconstruction provides the raw material for analysis, but it does not solve the problem of estimating quantities of interest from finite and noisy time series data. Given limited amounts of limited precision data, it is essential to identify the goals and limitations of any analysis: What questions are being asked? What alternative hypotheses are credible, given what is already known about the system? What assumptions can safely be made about the data? For the questions, hypotheses, and data in hand, what methods are acceptably reliable?

Several authors have recently proposed, with ecological applications in mind, extensions of the nonlinear prediction approach that explicitly incorporate a random component in the dynamics. The first step is reconstruction in time delay coordinates. Casdagli (23) has extended Takens's Theorem to systems affected by exogenous variables; for such systems the reconstructed dynamics follow a nonlinear autoregressive model (24),

$$N_t = F(N_{t-1}, N_{t-2,...} N_{t-d}, \epsilon_t). \tag{3.}$$

Here N_t is the population density at year t, d is the embedding dimension (i.e. how far in the past we look for explanation of current population change), ϵ_t is a vector that represents the action of exogenous variables, and F is a function that describes the effects of past population densities and exogenous variables on the present population density. The time interval at which the series is "sampled" does not have to be 1 year, in which case subscripts $t-1, t-2$, etc are substituted with $t-l$, $t-2l$, and so on.

The reconstructed dynamics (Equation 3) resemble some population models with discrete generations, but reconstruction is equally valid if generations overlap. In such cases past values of total population size serve as surrogates for the current age structure, in a way that preserves certain properties such as the Lyapunov exponents.

In principle the exogenous component ϵ_t can include periodic (e.g. seasonal) and systematic long-term changes in environmental factors affecting

the dynamics. However, current approaches in ecology generally assume that the exogenous variables are random and additive when population densities are log-transformed. This is unlikely to hold in all cases but can be regarded as a first approximation. The exogenous term is usually interpreted as environmental stochasticity, but it also contains measurement errors and any other factors that were not included in the model.

Within this approach, questions related to nonlinear dynamics that can be addressed include the following. (i) What is the relative importance of exogenous factors and endogenous dynamics? (ii) Is there evidence for nonlinearity in the endogenous dynamics? (iii) If the system is nonlinear, is there evidence for chaotic rather than stable endogenous dynamics? (iv) What is the interaction between the exogenous and endogenous dynamics (e.g. what is the return time following a perturbation)? (v) How well, and how far ahead, can we make predictions?

Applying this approach to data consists of three steps: deciding on a family of models to fit the endogenous component, F in Equation 3; determining the complexity of the model; and using the fitted model to characterize the dynamics of the data.

FITTING THE ENDOGENOUS COMPONENT   Early time-series models in ecology either were linear in log-transformed lagged densities (21, 45, 95) or else used only a single time delay (58). Current nonlinear models range from simple parametric models to nonparametric methods with a potentially unlimited number of parameters.

The virtue of a simple parametric model is that the majority of time series in ecology are not long enough to be fitted with more complicated models. POPSYS (15, 16) is a simple parametric model which assumes that the per capita rate of change is affected by both direct and delayed density dependence. Further, all the parameters have a clear biological interpretation. However, the disadvantage of assuming a particular functional form is that the model may not be flexible enough to give good results in many cases. Thus, using a different functional form could result in a very different answer (96).

A more flexible approach relies on the response surface methodology (RSM) for model fitting (154–156). RSM is a generalization of polynomial regression in which the independent variables (N_{t-1}, N_{t-2},...) are transformed using the Box-Cox family of power transformations. Because the parameters do not have a biological interpretation, RSM is intermediate in spirit (as well as data requirements and flexibility) between parametric models like POPSYS and nonparametric methods. Simulation tests using a variety of ecological models indicate that RSM works well with short (20–50 data points) and quite

noisy (up to 50% of the endogenous component) data sets. The price, however, is the ability to classify correctly only low-dimensional dynamics (d≤3). Other approaches (e.g. neural nets) are preferable for higher dimensional dynamics because the number of parameters in those schemes grows more slowly with dimension than RSM.

The most flexible approaches use nonparametric regression to approximate F (22, 24, 40, 103, 144). Several types of methods (thin-plate splines, neural nets, and kernel regression models) appear to work well on moderate amounts of data (50–500 values) from nonlinear systems, even at fairly high noise levels (10–20% of the endogenous component). Nonparametric methods can approximate any functional form, can "smooth" the data when noise is present, and some (neural nets, kernels) can accommodate an arbitrary number of lags. This flexibility increases the amount of data required and also the computational cost of estimating parameters accurately.

Smaller data sets and increased amounts of noise result in high variance of Lyapunov exponent estimates for the nonlinear time series methods. This can be partly compensated by surveying results from a number of similar data sets, e.g. data from different localities.

MODEL SELECTION: HOW COMPLEX SHOULD THE MODEL BE?   Model selection is critical to obtaining accurate results. A model with too few parameters or too small a number of delays in the reconstruction will not be able to approximate the dynamics. A model with too many parameters will "fit the noise" instead of only fitting the endogenous feedbacks, with disastrous consequences.

One popular criterion is to select the model that is best at predicting the data (22, 24, 25, 144). To avoid overfitting, prediction accuracy can be quantified by cross-validation: delete each data point (one at a time), fit the model on the reduced dataset, and then use the fitted model to predict the deleted point. Cross-validation can be used to choose the embedding dimension d (28, 144) and the parameters controlling the degree of smoothing used in a particular model. However, cross-validation is very computer intensive. Criteria have been derived that use the error variance adjusted by the number of fitted parameters to approximate the cross-validated prediction accuracy, but these require modifications to work effectively on time series data (103). Another shortcut is to reserve part of the data for evaluating the model's prediction accuracy (22, 24, 144), but this reduces the amount of data available for parameter estimates. Research is still needed to identify practical and reliable model selection methods.

Finally, the dynamics of the system can be characterized by simulating the model, or by using the model to estimate the dominant Lyapunov exponent λ, with a positive exponent indicating a chaotic system.

WHAT HAVE WE LEARNED SO FAR ABOUT NATURAL POPULATIONS?   What have time-series methods told us about the frequency of chaotic dynamics in nature? Schaffer & Kot (131) surveyed a number of longer ecological time series. They concluded that reconstructed dynamics suggested chaos in four cases: the Canadian lynx cycle, outbreaks of *Thrips imaginis,* a microtine rodent cycle, and measles epidemics (131). Witteman et al (161) extended this approach to 71 population time series that were longer than 50 years, finding several patterns that suggested to them complex dynamics. However, visual examination of "attractors" can be misleading (see Figure 3). Turchin & Taylor (156) examined 14 insect and 22 vertebrate population time series using RSM, and one case, the beech aphid, was classified as chaotic. Subsequent analyses using cross-validation selected a lower-dimensional stable model (P. Turchin, unpublished ms). Most recently, Ellner & Turchin (41) applied neural net, spline, and RSM time series models to a large number of time series. Although they used a conservative method of estimating Lyapunov exponents, they found a wide range of dynamics: from stable (noise-dominated) to apparently chaotic. For example, numerical fluctuations of voles in Finnish Lapland and also of Nicholson's blowflies were characterized by positive Lyapunov exponents. The conservatism of the method employed by Ellner & Turchin (41) argues that such findings of chaos may reflect reality. On the other hand, like any other statistical quantity, the Lyapunov exponent is estimated with error, and thus one should expect a few positive estimates by chance alone, even if there are no chaotic dynamics in nature. The solution to this problem is either to calculate confidence limits for each time series, or, alternatively, to survey a number of time series that are assumed to have similar dynamics. For example, Turchin (157) examined data for several rodent species from six arctic and boreal sites. RSM analysis classified 15 of 23 time series as chaotic, arguing that findings of chaos in northern voles are unlikely to be a chance occurrence.

Time series analysis methods continue to evolve and cannot yet be regarded as supplying unequivocal answers. The most notable conclusion from current methods may be that the extreme positions—that chaos is "always" or "never" at the root of complex ecological dynamics—are not supported. Sharper statements may become possible as sharper tools, and better data sets (e.g. from controlled experiments) may become available.

FUTURE DIRECTIONS FOR TIME SERIES ANALYSIS   The methods for detecting chaos in time series data are very new. A number of key questions remain to be answered. Current approaches usually assume that exogenous factors act as uncorrelated random shocks. Environmental trends and periodic (e.g. seasonal) changes in the environment can be included into models, but it is unclear what are best ways to do so. A number of statistical issues are

unresolved. Are estimates biased and can this bias be corrected? Is the assumption of additive uncorrelated noise adequate, and under what conditions do more complex assumptions regarding error structure need to be made? How do we obtain confidence limits of estimates? Finally and most importantly, we need to test these approaches and determine under what conditions they give correct answers and when they break down.

EXPERIMENTAL APPROACHES

Considering the difficulties of attempting to detect complex dynamics from time series collected in the field, it is natural that ecologists have turned to laboratory systems in their attempts to detect chaotic population dynamics. In the laboratory the abiotic environment is under the control of the experimenter, who also is able to determine the number of interacting species. Unfortunately, laboratory studies are no panacea and have their own particular set of difficulties. In this section we discuss some problems associated with attempts to detect complex dynamics in the laboratory, and then we review the still relatively few studies where this has been attempted.

Problems

The choice of study organism is crucial to the success of any attempt to obtain long runs of population data in the laboratory: it is necessary to maintain replicated populations of reasonable size in culture. The logistics of laboratory experimentation require that the study organism be small, almost certainly an invertebrate or microorganism, and very likely one of the small set of laboratory organisms whose ecology in captivity is very well characterized. Small size normally is correlated with short generation time, which allows long runs of data over many generations to be collected relatively quickly. A logical extension of this argument is to work with microorganisms that have very short generation times. However, there are often great difficulties in sampling microorganisms, especially if densities have to be estimated by counting individuals under a microscope. Automated techniques such as image analyses offer one way of avoiding these problems.

The population dynamics of organisms in the laboratory obviously differs from their dynamics in the field. This raises the question of how to interpret the success or failure of attempts to detect chaos in the laboratory. One line of argument suggests that chaos is easier to detect in artificial experiments. Laboratory ecosystems are relatively simple. Cycles (and possibly chaos) are easier to find in simple ecosystems such as the arctic than in complex ecosystems in temperate and tropical regions. On the other hand, the reduced species diversity of laboratory systems, and the lack of any significant spatial dimension, means that processes known from theoretical studies to generate

complex dynamics cannot operate in the laboratory. There are also more mundane problems with laboratory experiments. In nearly all experiments, in one form or another, food must be regularly added to the system. The resource renewal regime may determine and dominate the observed dynamics. This is especially likely to be a problem in experiments with comparatively large organisms, such as insects, whose resources are added in relatively infrequent pulses. For example, the adults of some laboratory insects are harvested each generation and then placed on fresh resources to lay eggs. Such artificial rearing protocols have a huge effect on dynamics and may give rise to patterns of population change that are very different from those exhibited by the same species in natural systems.

The laboratory is a strange environment for most organisms and one to which they are to some extent poorly adapted. In consequence, natural selection may operate over the course of a long-term experiment. Indeed, an experiment that allows sufficient time to reveal complex dynamics is almost certainly long enough to allow Darwinian evolution. If natural selection influences demographic parameters, then any attempt to characterize the underlying dynamic attractor, or to fit a model to the time series, may be chasing a moving target. In effect the whole time series may be an evolutionary transient. Of course, evolutionary changes may be included in the dynamical description of the system, but the slower timescale of evolutionary changes probably makes the experimental studies of such systems infeasible, at least for eukaryotes.

Despite these caveats, we believe that experiments will eventually be able to demonstrate unequivocally the existence of chaotic dynamics in simple ecological systems. Here we discuss some existing data sets in light of the approaches we have advocated.

Experiments

The Australian entomologist A. J. Nicholson was unaware of chaos when in the 1950s he initiated a series of long-term experiments in which he kept populations of blowflies (*Lucilia cuprina*) in cages under a variety of resource renewal regimes (100, 101). In one experiment, which lasted for over 700 days, the numbers of adult blowflies fluctuated with irregular cycles for the first 400 days. Subsequently, the fluctuations became much more irregular, and the average population density increased. The data from this experiment have been subject to repeated analysis using a wide range of different techniques (19, 55, 106, 107, 141). There is general agreement that the dynamics over the first 400 days can be explained by perturbed limit cycles. However, it is unclear whether the variability in the cycles is best explained by a model with a chaotic component or by noise (12). The pronounced change in dynamics toward the end of the experiment may have been caused by

natural selection acting on the demographic parameters. Stokes et al (141) estimated the parameters of a delay-differential model using data from the beginning and the end of the time series. They found that fecundity decreased toward the end of the experiment, but that tolerance to crowding increased. In a computer simulation, a mutant with the parameters estimated from data collected at the end of the experiment was able to invade a population characterized by the parameters associated with the beginning of the experiment.

The question of whether natural selection reduces the frequency of chaos in nature has prompted a series of experiments with *Drosophila* maintained in serial culture (46, 97, 98, 111, 113, 118, 152). Most analyses of *Drosophila* have fitted relatively simple population models to runs of data of between 8 and 15 generations and concluded that the population dynamics are deterministically stable, although they frequently display damped oscillations (154). In a few cases, models fitted to one or a few replicates show cyclic or chaotic dynamics, but the statistical significance of these observations is unclear (98, 113, 154). A recent model by Ferriere & Gatto (44) has shown how chaos can result from natural selection.

Laboratory cultures of several other insect species display interesting dynamics. Cultures of flour beetles (*Tribolium*) nearly always have cyclic dynamics (31), almost certainly due to asymmetric interactions between different age classes (60). However, no evidence for chaotic dynamics has been found in this system (A Hastings & RF Costantino, unpublished), although the dynamics may be quite complex. Long-term cultures of bean weevils (*Callosobruchus*) and their hymenopteran parasitoids display irregular fluctuations. Detailed, behavior-rich simulations of the host–parasitoid interaction are chaotic and produce dynamics that at least superficially resemble the laboratory data (14).

Experiments have investigated the long-term dynamics of freshwater organisms such as the cladoceran *Daphnia* in the laboratory. In one of the first such experiments, Slobodkin (134, 135) observed irregular fluctuations in time series that lasted between 200 and 400 days. Application of the approaches for analyzing time series by computing Lyapunov exponents discussed in the previous section indicate that these time series are essentially periodic, as all Lyapunov exponents are negative (A. Hastings, unpublished results). This is evidence of the difficulty of relying on visual evidence for chaos. Other experiments lasting over 200 days (68) have observed both constant and variable opulation densities. McCauley & Murdoch (94) noted that cyclical dynamics often occur in laboratory populations of cladocerans. However, they did not attempt to determine whether population fluctuations were consistent with the influence of periodic forcing, endogenous stable cycles, or more complex dynamics. Kot is currently attempting to detect chaos

in aquatic microcosms (M Kot, unpublished), because such systems are excellent candidates for this type of investigation.

Recent work on a simple plant system which has used the approach of parameter estimation in a simple model (153) has argued for the presence of chaos. Although this study has the difficulties of choice of models discussed earlier, no other approach seems feasible, because the time scale of the annual dynamics is too long to permit the collection of a time series.

WHAT SHOULD ECOLOGISTS DO ABOUT CHAOS

There are several stages in the development and maturity of a subject when a review can be written. In the initial stage of the development, a review can provide one individual's insights and attract others. After most of the questions in an area have been answered, a review can provide a summary so that the results can be used to move on to new subjects. We feel that the study of chaos in ecology lies between these extremes. What we have tried to do here is to bring together ideas from many approaches, indicating those we feel will prove successful in the future, and those we feel have not stood the test of time. Yet, much work needs to be done. We hope that this review will prove outdated in five years, although we hope as well that our suggestions for future directions will prove correct.

The reader will have noticed that we have skirted the answer to the question in the title. We have demonstrated that chaos is quite likely, but much more work is needed to obtain a fuller answer to the question. We have, however, shown ways to proceed to get the answer.

We conclude with brief suggestions for experimentalists and theoreticians. We believe that the study of chaos is important for ecology because the lessons of nonlinear dynamics will provide very different answers than the linear models traditionally emphasized by ecologists. Also, we believe that the use of equilibrium approaches needs to be circumscribed carefully.

To study chaos in ecology, experimentalists need to determine ways to obtain long enough time series, so that the presence of chaotic dynamics can either be confirmed or rejected. We have indicated some of the difficulties with this approach above, but simultaneously we have shown that the length of time series needed may be less than widely believed (50 data points may be sufficient). Thus, there is a real possibility of achieving this goal. Experimentalists also need to be aware of the potential implications of chaos for long-term predictions, and the fact that sustained "irregular" fluctuations may be due to chaos. Perhaps evidence for chaos can come from approaches based on parameter estimates for detailed models of laboratory populations, since these models may be well justified.

There are several challenges for theoreticians as well. Analyses of models

need to get away from equilibrium approaches. This will of necessity lead to changes in the development of ecological theory in many areas, from the study of population dynamics to food web theory. Here, both numerical methods and new analytic approaches will prove useful. Analyses of chaos focussing on transients (147) and local Lyapunov exponents (1) will likely prove useful. Another particularly promising development is the use of permanence (66), instead of asymptotic stability, as a mathematical definition of the intuitive ecological notion of stability. Also, we assume that there will be improvements in techniques for the computation of Lyapunov exponents, and perhaps approaches will be developed that can make use of data collected across space over shorter time scales than would be needed for data collected at a single point in space.

The challenges are many, yet the chance of success is high.

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