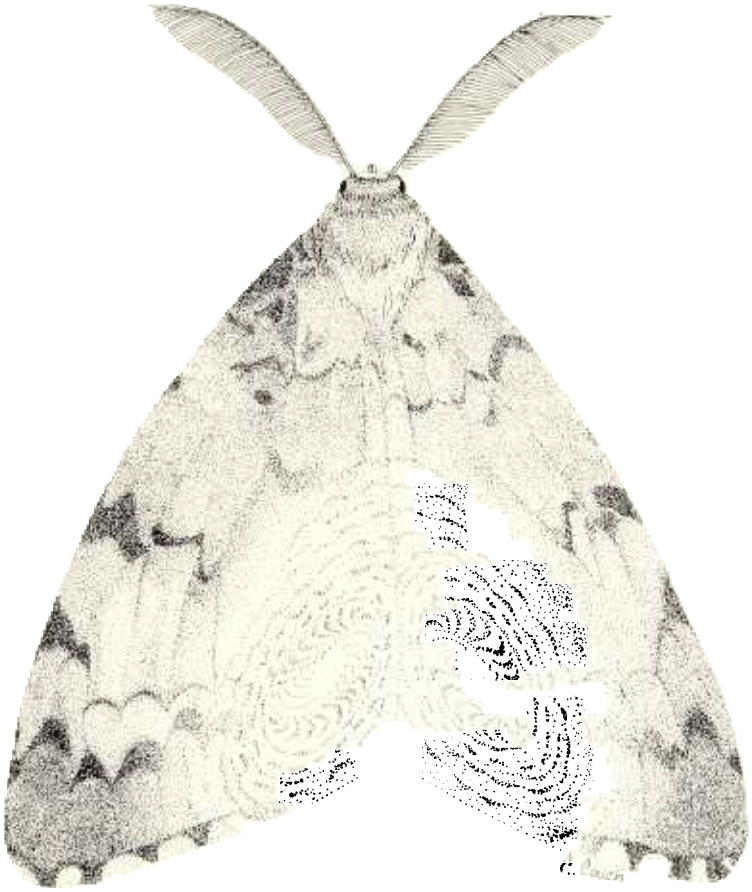
CHAOS AND INSECT ECOLOGY



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CHAOS AND INSECT ECOLOGY

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Papers Presented at the Symposium

Does Chaos Exist in Ecological Systems?

IUFRO XIX World Congress
Montréal, Canada, August 5-11, 1990

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Preface

Jesse A. Logan[1] and Fred P. Hain[2]

Recent advances in applied mathematical analysis have uncovered a fascinating and unexpected dynamical richness that underlies behavior of even the simplest non-linear mathematical models. Due to the complexity of solutions to these non-linear equations, a new mathematical term, *chaos*, has been coined to describe the resulting dynamics. This term captures the notion that in spite of the fact that these equations are purely deterministic, the resulting time dynamics are for all practical purposes indistinguishable from a purely random or stochastic process. A unique aspect to this new revolution in the esoteric arena of non-linear mathematics is the fact that it has captured the imagination of the public at large, and is even the subject of a *New York Times* leading best seller (James Gleik, *Chaos: Making a New Science*). The popular interest in chaos is at least in part due to the fact that solution sets are often represented as fractals, resulting in complex and strangely beautiful geometric patterns (fractals are, themselves, the subject of numerous popular books). Although the subject of chaos has its lighter side, it has also formed the basis of serious science.

Since the accidental discovery of chaos in a simple atmospheric weather model by Edward Lorenz in 1963, chaotic dynamics have been found to be pervasive in **all** of physics. Chaos has been observed in phenomena ranging from the sub-atomic level of organization to cosmic questions such as the orbit of planets in the solar system. The application of non-linear dynamics in physiology has resulted in an impact similar to that in physics. Chaotic dynamics have been found to underlie even those physiological processes that were previously thought to be strictly periodic (e.g., the heart rhythm). Results, primarily from applications in the areas of physics and physiology, have led to prominent review series in the major scientific journals, such as *Science* (1989) and *New Scientist* (1989), and to numerous international conferences. As a result of investigations in physics and physiology, the general characteristics of systems that promote chaotic dynamics are well known.

Ecological systems typically exhibit characteristics that lead to chaos. Non-linearity is the basis of chaotic dynamics. Very few unequivocal statements can be made in science; however, one of the few is that ecological relationships are non-linear. Non-linearity in ecology is a result of fundamental thermodynamics. Malthus recognized this fact in 1826 when he stated, in the sixth edition of his famous essay, that, "... the power of the earth to produce subsistence is certainly not unlimited...." Any system that is based on a finite rate of energy input must at some time become bounded by non-linear feedback. High order dimensionality is another characteristic that predisposes systems to chaotic dynamics. One of the hallmarks of ecological structure is the large number of interactions found in natural ecological associations. In fact, high order dimensionality

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has been proposed to be the most significant difference between physics and physical systems, and ecology and ecological systems. Time-lags are notoriously de-stabilizing in mathematical models. The simplest non-linear difference equation (quadratic) produces well-known chaotic dynamics. Once again, time-lags are a fundamental characteristic of ecological organization. One has to look no further than reproductive time-delays to be convinced of the ubiquitous nature of time-lags in ecology. The final common characteristic that predisposes systems to chaotic dynamics is periodic forcing. The natural world abounds in cyclical patterns that act as periodic forcing variables to ecological systems. Daily cycles function within seasonal cycles that are themselves embedded in solar cycles. In summary, the attributes that lead to chaos are to be found everywhere in the natural ecological world.

If the characteristics of chaotic systems are so ubiquitous in nature, why hasn't chaos been recognized as a fundamental property of ecological structure? Well, in fact, the potential for chaos **has** been demonstrated in almost all realistic **models** of ecological organization. However, empirically demonstrating the existence and/or importance of chaos in ecology is quite another story. The reason that this has been such a hard question to answer is the difficulty in empirically differentiating chaotic dynamics from random dynamics. To convincingly separate the two, it is necessary to have literally thousands of datum points. Such data are relatively easy to generate in physics and physiology, but almost impossible for most ecological systems. Therefore, to date, the debate has largely been waged on theoretical or hypothetical grounds. Convincing theoretical arguments suggest that chaos should not be exhibited in **surviving** ecological associations. Coincidentally, this conjecture does not mean that chaos is not important in ecology, just that it should not be commonly found. Either way the debate is finally resolved, the answer will be interesting and will have important ramifications.

Recognizing the importance of resolving the questions of where and how chaos fits into ecological organization, a symposium was organized by F. P. Hain, North Carolina State University, and J. A. Logan, Virginia Polytechnic Institute and State University, at the 1990 International Congress of the *International Union of Forestry Research Organizations* in Montreal, Canada. The topics discussed in this symposium, titled *Does Chaos Exist in Ecological Systems*, address some of the most important issues facing ecology today. At this symposium, Logan introduced the concept of chaos and described questions that are at issue in determining the importance of chaos in ecology. Turchin and Ellner discussed the problems associated with demonstrating chaos in ecological data, and both offered new and novel approaches to detecting chaos from ecological time series. Berryman presented the case against chaos being commonly exhibited in naturally occurring ecological systems. He further discussed the consequences of ecological disturbance, through intentional management or unintentional disruption, within the context of chaos theory. Stone presented exciting new results from a model based on individual prey and predator behavior in a spatially diffuse system. The results from this experiment suggest that chaos should be expected in simple prey/predator systems, and that tightly bounded chaos could easily be mistaken for "white noise" in populations that are controlled by natural enemies.

The topics of this symposium are timely and have important ramifications for the major ecological issues of today. The major problems of the current "ecological crises," such as climate change, are largely being addressed in chemical or physical terms (e.g., global climate models or the atmospheric chemistry of anthropogenic pollutants). However, they are being expressed

primarily in biological-ecological terms. An improved understanding of chaos and chaotic dynamics will clearly play an important role in predicting the biological consequences of, and in formulating responses to, these ecological perils. We sincerely hope that publication of an international forum, such as that presented in the Montreal IUFRO conference, will have a positive impact on both the future direction of ecological research and the societal response to that research.

Summer 1990

Logan, J. A., and F. P. Hain 1991. Preface, p. v-vii. *In* Chaos and Insect Ecology, ed. J. A. Logan and F. P. Hain. Virginia Experiment Station Information Series 91-3. Blacksburg: Virginia Polytechnic Institute and State University.

Plate 1. (a) Gypsy moth defoliation in Shenandoah National Park, Virginia, USA (photo courtesy M. Carter). Extensive defoliation caused by the advancing wave front of gypsy moth populations. Significant tree mortality has occurred as the gypsy moth extends its range to the south. (b) Southern pine beetle spot, Sam Houston National Forest, Texas, USA (photo courtesy R. Billings). The red top and faded trees are all victims of the southern pine beetle. (c) Mortality from mountain pine beetle, Targhee National Forest, Idaho, USA (photo courtesy G. Amman). The extensive potential for tree mortality from attacks of aggressive bark beetles is well demonstrated in this aerial photograph. (d) A "windrow" of range caterpillars, shortgrass steppe, East of Raton, New Mexico, USA (photo courtesy New Mexico State University). The total standing crop biomass is essentially eliminated by the advancing caterpillars.

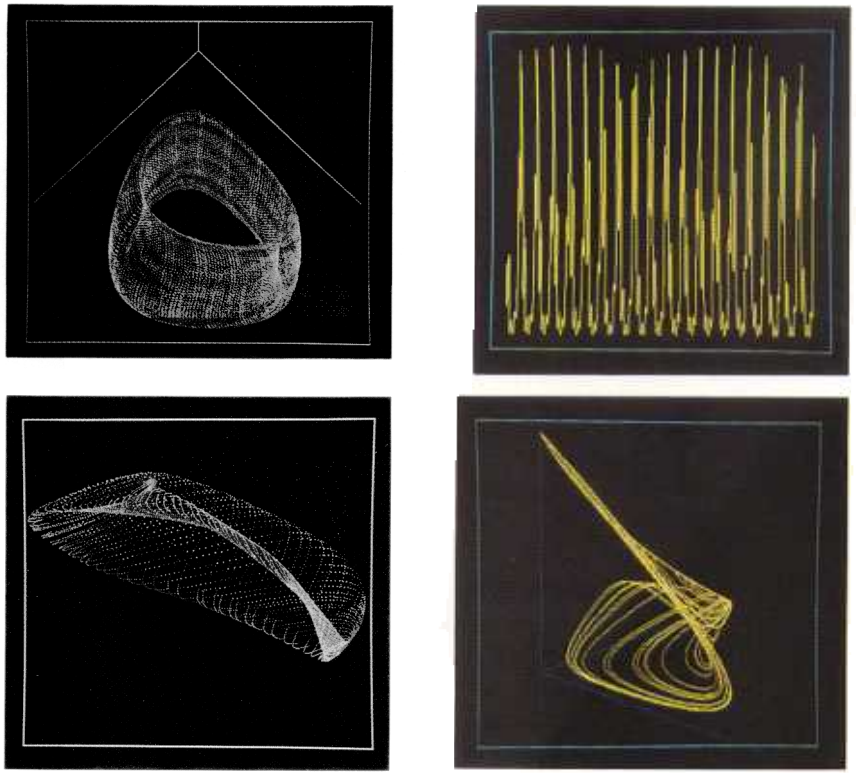

Plate 2. (a) A toris viewed from above. The dynamics of the system result from the system's variables winding around the surface of the toris. This particular toris results from periodic forcing (seasonality) acting on a herbivore/plant interaction (see Schaffer et al., 1988, pp 1.41 for a detailed description). The system is not phase locked for the chosen parameter values. Therefore, the resulting dynamics are quasiperiodic, and the winding action on the toris will eventually cover the entire surface of the attractor. (b) A time series of the complex periodicity that results from the dynamics of a phased-locked system. Note the complex expression of cycles-within-cycles. This system results from a model of a host/pathogen system with seasonal transmission (see Allen 1989). (c) The phase space plot of the toris that resulted in the time series shown in Plate 2B. (d) The strange attractor in the three-dimensional phase space formed by a modeled interaction between one predator and two prey species (Gilpin 1979). Chaotic dynamics result from movement of the system on the surface of the attractor (see text for further discussion).

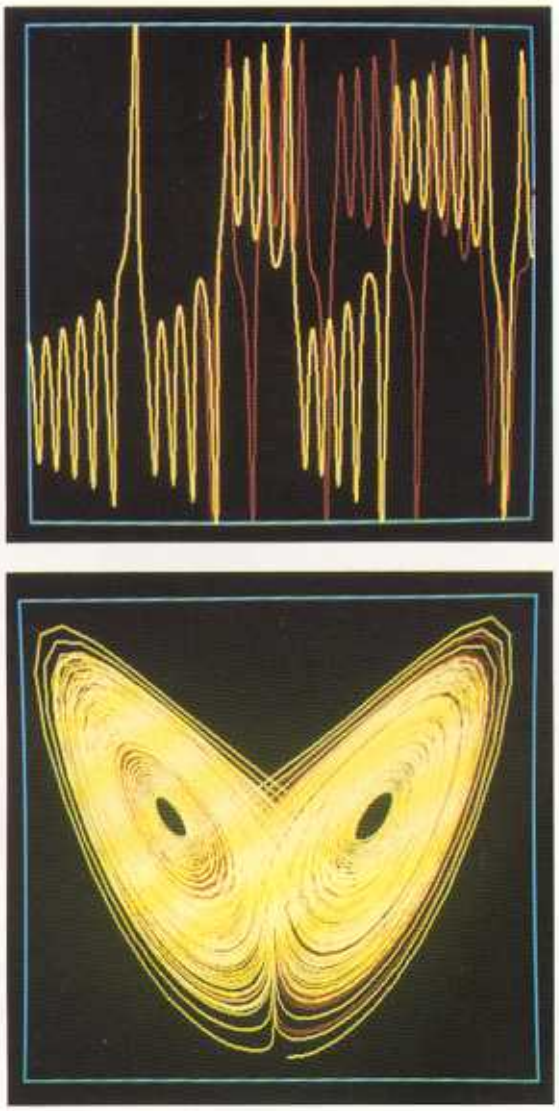

Plate 3. (a) A time trace of two state variables from solutions of Lorenz's famous weather model. The two plots were initialized with a difference in initial state variable values of only 0.001. The small difference in initial condition is magnified at an exponential rate, a characteristic of chaotic systems. (b) The phase-space of the two state variables plotted in A. Note that even though the time trace traces are dramatically different, the phase plots are essentially the same.

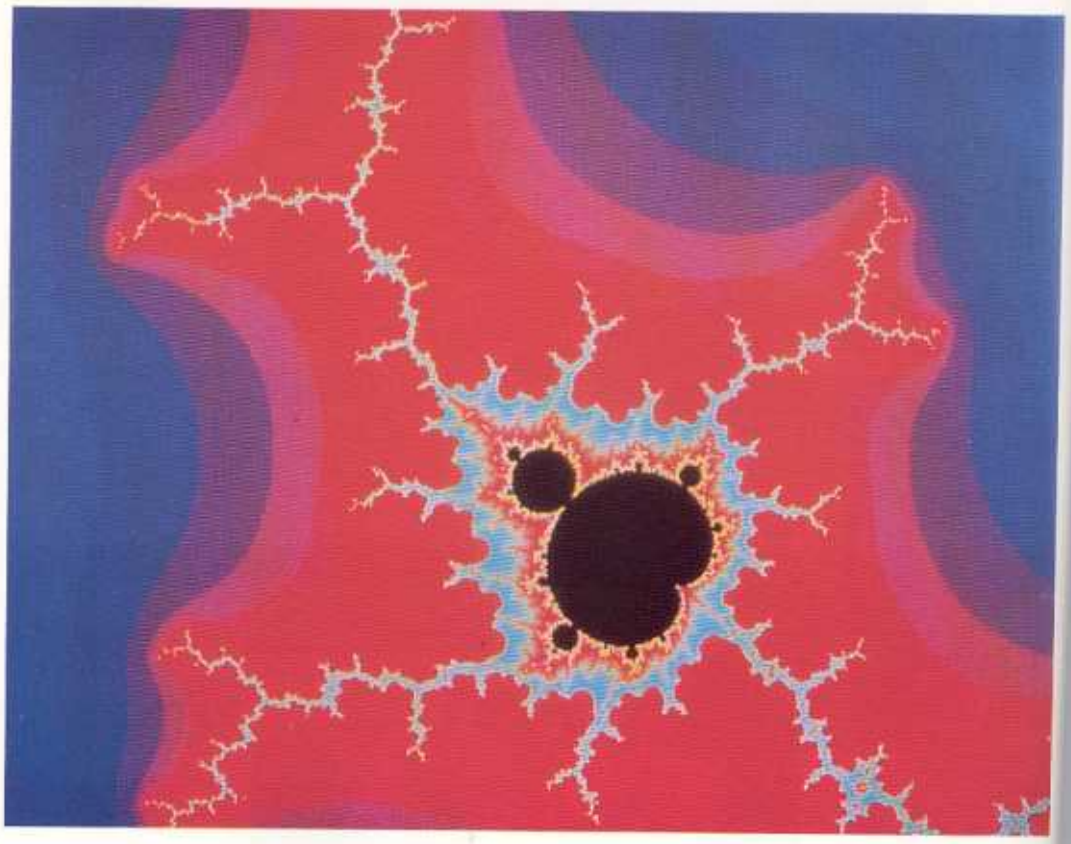

Plate 4. A portion of the famous Mandelbrot set. The mathematics of this fractal are related to the Ricker equation shown in Fig. 4. The pattern arises from assinging different colors to dynamical characteristics of a solution set associated with various combination of parameters. The fractal nature of solutions are well illustrated in this Plate.

Chaos: Much Ado About Something

J. A. Logan[1]

Introduction

The discovery of complex "chaotic" dynamics in simple mathematical models has resulted in widespread interest from a diversity of scientific disciplines. These complex dynamics have been observed in many real world systems, primarily in physics and physiology. As stated in the Preface to this volume, and also indicated by this symposium title, the role that chaotic dynamics may play in real-world ecological systems is less certain. A legitimate question is then, what is the principal motivation for interest in chaos from an ecological point of view, and in particular from that of a Forest Entomologist? The answer to this question, in my opinion, lies in the basic nature of pest management problems in natural resource systems. In a previous publication (Logan 1987), I contrasted the attributes of pest management in rangeland systems to those in intensive agricultural systems. Most of the salient features of this characterization are true for natural resource systems in general, and carry-over to insect pest management in forest systems. The most important attribute with respect to chaos is the time frame of interest. In crop systems management patterns are typically based on a annual rotation. The time frame of interest is therefore short-term, and the important population dynamics of insect pests and their associated biological control agents are of a proximate nature. The contrast to forest pest management is obvious, and the necessity for adopting a long-term view is self apparent. Long-term dynamics associated with forest insect pests are typically complex (see Fig. 1). Several attributes are apparent from the time series shown in Fig. 1, the most obvious of which is the magnitude of differences between endemic or latent phase and the outbreak or eruptive phase. Phase differences for outbreak species of forest pests may be several orders of magnitude; in other words, outbreak densities may be greater than one-million times those of latent phases. Another attribute of the time-traces of Fig. 1 is the lack of true periodicity. The time series is temporally complex.

In addition to the complex nature of temporal patterns, outbreaks of insect pests in natural resource systems are often spectacular events (Plate 1). Outbreaks are both intensive (i.e., greater than 80% mortality with some bark beetles and virtual total defoliation with many lepidopterans) and extensive (thousands of contiguous hc. can be affected). Due to these characteristics, patterns of density and outbreak are both dramatic and enigmatic.

Additional attributes of pest management in forest systems are based in economic rather than ecological terms. Due to the lower per-unit monetary return from natural resource systems, the management options available to Forest Entomologists are more restrictive than those that are available to Crop Protection Entomologists. In many cases, Forest Pest Management must rely on the augmentation of natural forces rather than the more simplistic approach of direct intervention. Monetary constraints on the viability of heavy-handed control tactics necessitate that managers have a more in-depth understanding of the system to be managed, and the nature of forest

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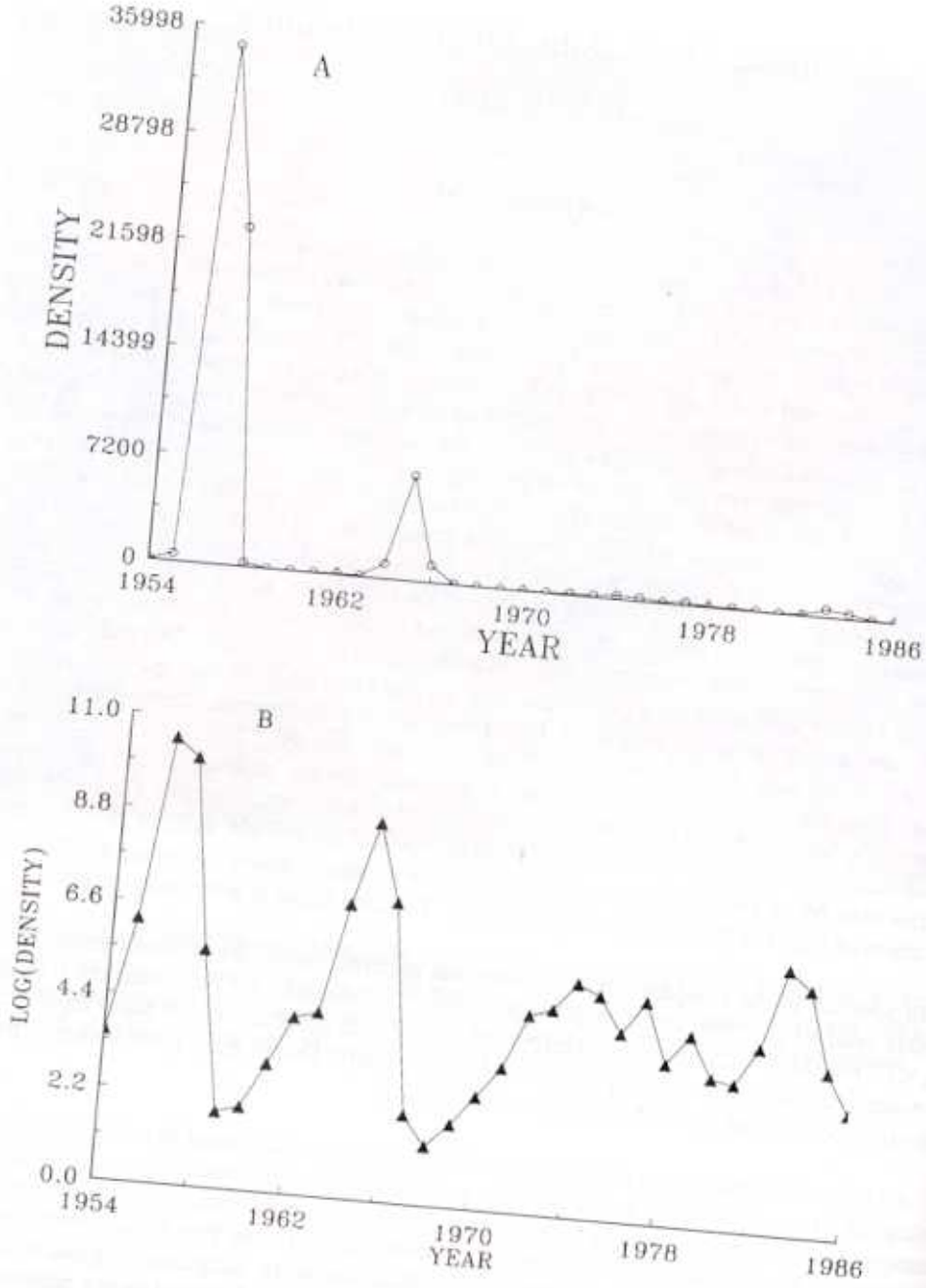

Figure 1. (a) Gypsy moth population density for the years 1954 to 1986. Density estimates from annual measures of gypsy moth egg masses/ha in Yugoslavia (source: Sisojevic 1975 with data update communicated by M. E. Montgomery, USDA-FS, Northeastern Experiment Station, Hamden, Connecticut). (b) Log_e of the density data in 1a.

rotation necessitates that this understanding include long-term population dynamics. The attributes of pest management in natural resource systems undoubtedly poses a challenge to development of effective management strategies and tactics, but it also provides for significant scientific opportunities. The requirement for understanding basic ecological relationships combined with the intrinsic and extrinsic value of forest systems provides both the motivation and the resources to undertake ambitious scientific enterprise. Forest entomologists have a long and rich history of contribution to basic insect ecology. Many of these contributions have been of a quantitative nature. For reasons of necessity (time frames of interest that rival or exceed the professional life of a scientist), economy, and intellectual return, mathematical reasoning and modeling have played a prominent role in the scientific contributions of Forest Entomologists.

Application of computer modeling technology began to have a major impact on Forest Entomology during the mid 1960s. Forest pests, in particular bark beetles, were one component of the famous Huffaker Project. This historically important research project was part of an even more ambitious[2] research program, the International Biological Program (IBP). The central unifying theme of the IBP was development of detailed computer models that faithfully simulated entire ecosystems or even biomes. The strong commitment to computer simulation models carried through to the Huffaker Project; of twelve specific objectives, seven were directly related to development of simulation models (Stone 1989). The Huffaker Project was largely responsible for formulating the philosophy of pest management in North America as it continued to evolve during the 1970s and 1980s. This philosophical basis continued to have a strong computer modeling component, as illustrated by the central role of computer models in the "Big Bug" projects funded by the U.S. Forest Service. The U.S. Forest Service during the past 20 years has provided resources for accelerated research on several important North American forest insect pests, including tussock moth, southern pine beetle, spruce budworm, and gypsy moth. The central role of modeling in these efforts has fulfilled expectations with respect to research organization and synthesis (Brookes, et al. 1978, 1987), but has not resulted in improved power to predict outbreaks (e.g. Berryman 1991).

In general terms, prediction of insect pest outbreaks in natural resource systems remains an elusive goal. This statement is true in spite of efforts by some of the most talented entomologists (including C.V. Riley, the "founding father" of Applied Entomology in North America), expenditure of substantial dollars, and application of the most advanced computer technologies. What is going on here? Perhaps the reason for our lack of predictive power lies in the prevailing modeling paradigms, as suggested by Berryman (1991). However, it may also be due to something much more basic. New mathematical discoveries in non-linear dynamics indicate that this situation may not be entirely due to the maladroitness of those asking the questions, but rather may result from the very nature of the problem itself. Results indicate the characteristics of ecological organization and structure predispose these systems to the complex dynamics that have become known as deterministic chaos. The continuing frustration in lack of predictive power, then, is the reason for my interest in non-linear dynamics and chaos. The inability to predict outbreaks in even seemingly straightforward systems has prevailed throughout my personal work in natural resource systems, experience that includes grasshoppers in the short grass steppe, bark

2 Total U.S. funding for the IBP was in excess of $55 million in 1970s US dollars; personal communication, J. T. Callahan, Associate Director, NSF Ecosystems Studies

beetles in the coniferous forests of the West, and gypsy moth in the deciduous forests of the East. The chance that innate properties of Forest/Pest interactions negate prediction of outbreaks is simply too important to ignore.

In the remainder of this Chapter, I will first attempt to introduce the somewhat esoteric notion of deterministic chaos. Then I describe more fully the characteristics of chaotic systems, provide a review of the search for chaos in insect population dynamics, and discuss contributions that other authors in this volume make toward a more complete understanding of chaos in insect population systems.

Non-linear dynamics and Chaos - What is Chaos?

Several recent reviews introduce the concept of chaos (Crutchfield et al. 1986, Gleick 1987, Holden 1986, Jensen 1987, Krasner 1990, Stewart 1989). Treatment of the subject in these articles and books ranges from a popular *New York Times* best seller (Gleick 1987) to rigorous mathematical developments (Devaney 1986). The approach I will take is to provide more rigor than the popular accounts, but remain comprehensible to an interested insect ecologist. *Webster's New World Dictionary*, College Edition, defines *chaos* as" any great confusion or great disorder," and *chaotic* as, "in a complete confused or disordered condition." As with many common words that have been appropriated by mathematicians, the mathematical meaning of chaos is only obliquely related to the standard usage of the term. In the mathematical sense, chaos does not imply "completely disordered" but instead refers to a very special and complex type of ordering. Perhaps the best way to gain an appreciation for the mathematical meaning of chaos is through a series of progressively more complex dynamics, leading to what Schaffer and Kot (1985b) have termed a "taxonomy of motion."

Before I proceed with a "taxonomy of motion" for dynamical systems, it is first necessary to introduce the notion of a "phase space." Phase space is a graphical way of representing the dynamical properties of a system that may at first be confusing to ecologists, but is valuable for characterization of a system's long-term dynamics. Ecologists have traditionally thought in terms of the time series as a way to represent population dynamics (Fig. 2a). Although conceptually straightforward, a time series plot is often of limited value for representing long-term dynamics, and may in fact not provide much insight into the dynamical structure of the system. As an alternative to a time series, mathematicians typically plot concurrent values of state variables on independent axes (see Fig. 2b). The state-variable space generated by this process is called *phase space*, and the graph of state variables in phase space is termed a ***phase plot***. Plotting system dynamics in phase space as opposed to a time series has the distinct advantage of collapsing the systems dynamics along the time axis, thereby solving the logistic problem of plotting long-term behavior. More important, structure that is opaque in a time-dimensioned plot may become obvious in a phase plot. For this important reason, plotting long-term dynamics of a system in phase space is an essential step in dynamical systems analysis. Adopting the phase space prospective also facilitates thinking of ecological systems in qualitative terms, a perspective that is essential for assessing the impact of complex non-linear dynamics on ecological structure.

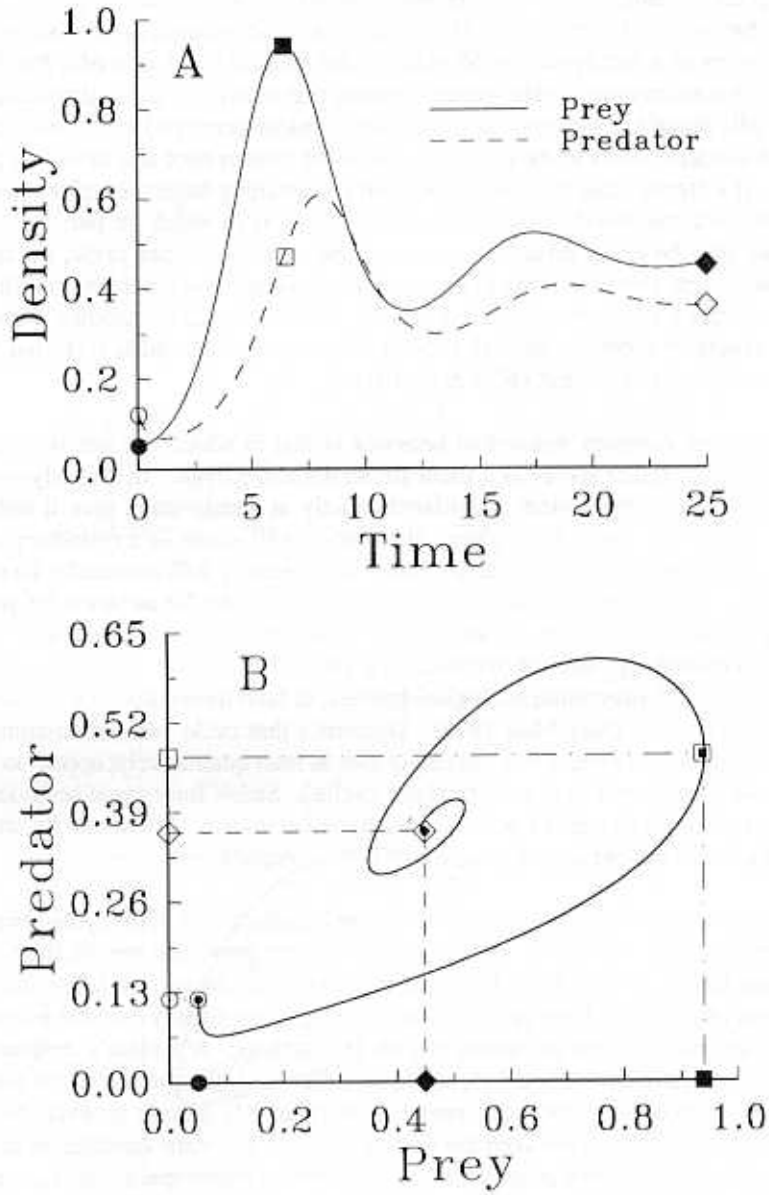

Figure 2. (a) Time series for a typical prey-predator interaction. (b) The phase-space plot of the time series shown in 2a. Each point in A maps to a corresponding point in B. Symbols (open for predator, closed for prey) in A indicate points that map to points on B that are indicated by the same symbol. Time progresses from the circle symbols, to the square symbols, and finally ends at the diamond symbols.

The simplest dynamics in our classification scheme is that of a stable system. The dynamical requirement for such a system is the existence of a steady-state that acts as an attractor. The ecological concept of a steady-state is identical to the mathematical term of a *fixed-point*, both of which refer to a combination of state-variable values that result in a static, time-invariant dynamic. The system will remain at steady-state indefinitely unless perturbed by an external force. The concept of an *attractor* refers to the time behavior of the system once it is moved or perturbed from steady state. If a steady-state is an attractor, then the resulting trajectory of the perturbed system will always be back towards the steady-state value. The way in which the perturbed system returns to steady-state may be either directly without cycling or as a damped cycle, the important point being that the system always returns to its steady-state value. Such behavior is illustrated in Fig. 2, which represents a stable prey-predator system. The existence of stability is implicit to many of the basic tenets of ecology, such as Clementsian succession, and is reflected in the popular concept of the "balance of nature" (Ellis et al. 1991).

The next, more complex dynamical behavior is that in which the steady state no longer is itself an attractor but rather serves as a focus for an attracting cycle. In these dynamics, a steady-state still exists, and if the system is initiated exactly at steady-state, then it will remain there indefinitely. However, even the slightest disturbance will result in a trajectory *away* from the steady-state. After deflection from steady-state, the trajectory will eventually be captured by an attracting cycle. The cycle, instead of the steady-state, acts as the attractor for points in phase-space that are outside the cycle as well as for those that are inside the cycle (Fig. 3). The mathematical terminology for such dynamics is a *stable limit cycle*. Stable limit cycle behavior has been the subject of substantial ecological interest, in both theoretical (e.g. Volterra 1926, May 1981) and applied terms (Noy-Meir 1975). Dynamics that cycle without damping, but that are none-the-less bounded, are intuitively appealing and, at least qualitatively, appear to be common in the natural ecological world (e.g. prey-predator cycles). Stable limit cycle behavior is a result of non-linearity and, in fact, requires non-linearity to be expressed. *Non-linearity*, in turn, refers to the effects of a state-variable upon a system that is *non-proportional*.

Dynamics that are similar, but potentially more complex, than limit cycle behavior are those that result from motion on a *toris*. A toris is a geometric figure that results from the interaction of at least three forces, and has been described as a doughnut-like surface (Plate 2a). In ecological systems, a toris often results from periodic forces acting on an already cyclical interaction, or from the natural resonance of three (or more) trophic interactions. A system's dynamics result from points in phase-space being attracted to, and winding around, the surface of the toris. Dynamics resulting from motion on a toris can range from relatively simple to exceedingly complex, depending on the relationship between the forcing variable and state-variables or that between the state variables themselves. For example, if the trajectory in phase-space winds around the toris an integer number of times while winding around the axis another integer number of times, then the system is said to be *phase-locked* and the resulting dynamics are truly periodic, although the period can be lengthy and complex (Plates 2b and 2c). Conversely, if the ratio of the two periods cannot be expressed as a ratio of two integers, then the resulting dynamics will never close upon itself and become periodic. The dynamics in this latter case are said to be *quasiperiodic* (Plate 2a).

Toridal flow does not always result in simple doughnut-shaped figures, but can produce complex and beautiful attractors such as that shown in Plate 2c. Likewise, the dynamics that

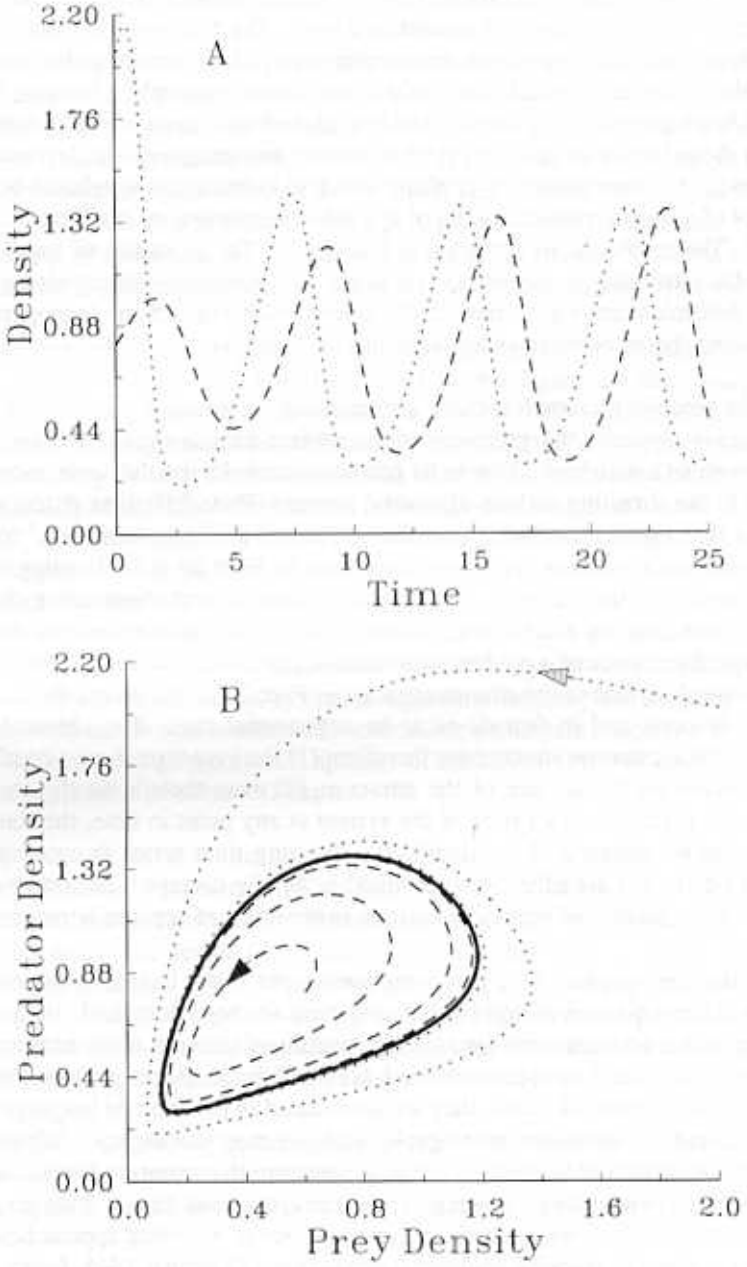

Figure 3. (a) Time series for a prey-predator interaction that results in limit cycle dynamics. (b) The phase-space plot of the time series shown in 3a. Note that points from within the cycle spiral outward (dashed line, dark arrow), and those from outside the cycle spiral inward (dotted line, light arrow). The limit cycle trajectory is shown as the heavy, solid line.

result from motion on a toris are highly variable; in fact, perhaps all dynamics short of chaos may be described as some manifestation of motion on a toris. The ecological implications are clear. It has often been the case that population time-series superficially appear to be periodic, but upon closer inspection are found to lack true periodicity. As an example, Uvavrov, in his classical *Locusts and Grasshoppers* (1928) stated, "The first idea of most authors was to discover a definite periodicity, or the existence of definite cycles of years, coinciding with the decrease or increase of locust numbers . ... On the contrary, everything seems to indicate that we should be better justified in speaking not of a regular periodicity but of *irregular fluctuations* of numbers of a given species in a country." The emphasis, by the way, is Uvavrov's. The existence of fuzzy or messy time series is usually attributed to the effects of stochastic variation. Recognizing that complex, quasiperiodic dynamics can result from strictly deterministic interactions (endogenous rather than exogenous effects) should be more widely appreciated by ecologists.

As with the preceding examples, chaos also results from points in phase-space being attracted to a surface but in this case the geometry of the surface cannot easily be categorized by some simple shape such as a doughnut. Due to its geometric complexity, the name *strange attractor* has been attached to the attracting surface of chaotic systems (Plate 2d). One description of chaos is "the dynamics that result from motion on the surface of a strange attractor," although not all strange attractors result in chaos. An important aspect of Plate 2d is the bending and folding that occurs on the surface of the attractor. The complex dynamics that characterize chaos are a direct consequence of this bending and folding. These dynamics are so complex that they are virtually indistinguishable from those of a random or stochastic process. Another characteristic that results from the convoluted surface of the strange attractor in Plate 2d is that points that are initially close together soon diverge, and in fact do so at an exponential rate. The characteristics that are embodied by a chaotic strange attractor are therefore: (1) the long-term dynamics of the system are bounded by motion on the surface of the attractor; (2) even though the dynamics are strictly deterministic (i.e. given the exact state of the system at any point in time, the state at any future point in time can be uniquely determined), the resulting time series is apparently random or stochastic; (3) points that are initially close together rapidly diverge. The combination of these factors results in the paradox of regularity existing in the midst of apparently random behavior.

The classification scheme of the preceding paragraphs is not inclusive; there are other, more subtle dynamical consequences of non-linearity that have not been described. In fact, there is every reason to believe that undiscovered dynamical possibilities underlie many reasonable ecological models. It is also clear that I have characterized, but not defined, chaos. Although there are several possible rigorous definitions of chaos, they are formulated in the esoteric language of topology or ergodic theory, and are therefore incomprehensible to most ecologists. While lacking rigor, presenting familiar examples from the ecological literature that progress from simple to complex dynamics is intended to provide an appreciation for the *concept* of chaos. This progression is also intended to demonstrate that chaos is a natural consequence of modeling approaches that have been used for over a century to describe ecological associations (Verhulst 1845, Lotka 1925, Volterra 1926). In the natural evolution of theoretical ecology, it has been necessary to include nonlinearity, time delays, periodic forcing, etc. to more realistically represent ecological structure. With each additional increase in ecological realism, there has been a concurrent increase in the potential for dynamical complexity. Chaos is simply the most recent addition to the dynamical possibilities of ecologically motivated models.

Characteristics of Chaotic Systems

In the previous section, the basic characteristics of chaotic systems were described. In this section the consequences of those characteristics will be discussed in greater detail. Since chaos results from motion on an attracting surface, chaotic systems are bounded by the limits of the attractor in phase space. Boundedness within ecologically reasonable limits is required for a feasible ecological model. This ecological constraint may or may not be violated by chaotic systems, depending on the characteristics of the particular attractor in question. Therefore, the ecological necessity of remaining within reasonable limits, i.e. neither growing without bounds nor decaying to zero, is neither necessarily violated nor satisfied by chaotic systems.

The rapid divergence of points that are initially close together is illustrated by the two time series that are plotted in Plate 3a. The time series in this figure are the result of numerical solution to Lorenz's[3] (1963) famous weather model. The two different numerical solutions were obtained from initial starting values that differed by only 0.001. As is apparent in Plate 3a, the time series are indistinguishable for a short period of time, but once they begin to diverge they rapidly become totally out of synchrony, and in fact do so at an exponential rate. The exponential magnification of small differences is one of the most characteristic attributes of chaotic systems, and is directly responsible for the lack of long-range predictive power. A measure of the rate at which close points diverge is known as the *Lyapunov exponent*. For a n-dimensional system, there will be n Lyapunov exponents, only one of which needs to be greater than zero for the system to be chaotic. The condition of at least one positive Lyapunov is, therefore, necessary (but not sufficient) for chaos. For a defined system of equations the complete Lyapunov spectrum can be obtained. Techniques are also available for estimating the largest Lyapunov exponent from an empirical time series, although the typical sparsity of ecological time-series data is a significant limitation to the application of these techniques.

Motion that is restricted to the surface of a chaotic attractor is responsible for the order that lies at the heart of "chaotic" randomness. Plate 3b offers an excellent example of the nature of this order. Even though the two time series in Plate 3a are completely out of synchrony and appear to be unrelated, the plots that result from their 2-dimensional projections in phase-space are essentially indistinguishable. This is an important result for ecologists, because it clearly illustrates that the "classical" way of viewing dynamical properties of a system result in an misleading plot (Plate 3a), while viewing the dynamics in a somewhat different light (the phase-space of Plate 3b) result in the emergence of an underlying order.

Another attribute underlying deterministic chaos is the existence of a non-integer *fractal dimension*. The statement that chaotic systems have fractal (or fractional) dimension is confusing because of the standard use of the term dimension to describe the number of state-variables that

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[3] Lorenz's classical experiment with a simple weather model dates the beginning of the modern (computer- assisted analysis) era of nonlinear dynamics. Through a series of simulation experiments with a simple, non-linear model of the weather, Lorenz discovered never-repeating, aperiodic cycles in which long-term prediction was not possible due to an exponential growth of initial error. An excellent popular account of Lorenz's work can be found in Gleick (1987) and a mathematical account in Sparrow (1982).

define a system. For example, a prey-predator system has dimension 2, and a prey-predator-pathogen system has dimension 3. Used in this sense, dimension corresponds to the order of the system or, equivalently, the Euclidian dimension of the system. Other concepts of dimension, such as fractal dimensions, defy such simple description. The consequences that result from a non-integer fractal dimension are, however, comprehensible. Self-similarity is one characteristic of systems with a non-integer fractal dimension, and refers to complexity that is not necessarily related to the scale by which the system is observed (Gordon and Greenspan 1988). For example, Fig. 4 was obtained by plotting the dynamics of a chaotic system at progressively higher levels of resolution. Although the scale in the last frame in Fig. 4 is over 5 orders of magnitude smaller than that of the first, there has not been a concurrent reduction in the complexity of the dynamics. The fractal nature of chaotic systems also leads to complex and beautiful geometric patterns. The complexity and beauty of plots such as Plate 4 have been responsible for much of the popular attraction of chaos (i.e. Gleick 1987). Since a non-integer fractal dimension is one hallmark of chaos, calculation of the fractal dimension provides a diagnostic tool for evidence of chaos in empirical time series. Additionally, for the ecologist, the fact that the complexity of chaotic systems is irreducible with respect to scale may have important consequences regarding attempts to determine an "appropriate" scale to view various ecological phenomena.

Although I have yet to formally define chaos, the characteristics of chaotic systems (bounded-aperiodic behavior, sensitivity to initial conditions, positive Lyapunov exponents, non-integer fractal dimension) provide criteria to evaluate the likelihood of chaos in a particular system. Demonstrating chaos is more often a case of accumulating evidence for or against chaotic dynamics rather than obtaining unequivocal "proof" of chaos. This statement is particularly true for empirical systems. Establishing the existence and/or importance of complex non-linear dynamics in empirical ecological associations necessitates the accumulation of qualitative (evaluation of the particular ecological attributes of the association in question) as well as quantitative information (Ellner, these proceedings).

Chaos and Insect Population Ecology

May's (1974) discovery of chaotic dynamics in one of the simplest and most and widely applied ecological models motivated numerous subsequent articles that explored existing ecological models for evidence of chaotic dynamics [see Logan and Allen (1992) for a recent review]. The result of this work was that the potential for chaos existed in almost every case. In Berryman's words (these proceedings), "the seeds for chaos underlie all reasonable ecological models." These results have provided fertile grounds for both active empirical investigation and theoretical conjecture.

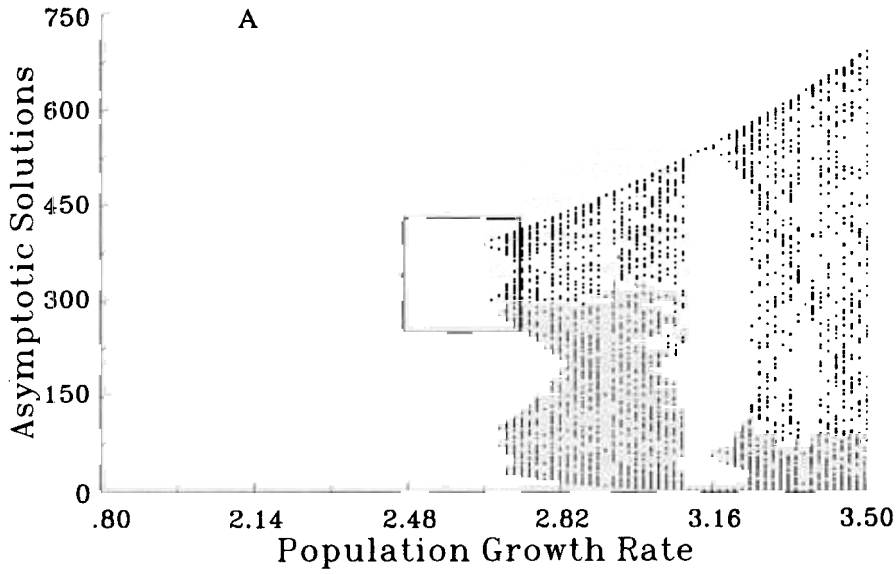
The first, and until recently one of the few, empirical studies that attempted to examine field data on insect temporal abundance patterns for indications of complex nonlinear dynamics was by Hassell et al. (1976). In this historically important paper, they reviewed time-series field-collected data for 24 insect species. Through the use of a simple single-species population model (a discrete analog of the logistic model), they estimated population growth and density dependent feedback parameters for each species. They then classified the dynamical characteristics for each species, and found that almost all fell within a region of stability. In fact, only one gave indications of

complex nonlinear behavior (a stable limit cycle) and none fell within the region of chaos. Subsequent work (Bellows 1981, Thomas et al. 1980), which generally replicated Hassell et al.'s approach, served to reinforce their results. Although Hassell et al. were careful to point out the limits of their analysis, their results have been widely cited in support of the view that complex dynamics, and in particular chaos, are seldom expressed in nature (e.g. Berryman and Millstein 1989).

The major limitation to Hassell et al.'s work, as they were careful to point out, was that their model explicitly excluded trophic interactions with other populations. Naturally occurring populations are invariably embedded within a matrix of nonlinear interactions with other populations. It has long been recognized that analysis of a complex ecological system in reduced dimensionality and a single time lag will tend to obscure complex dynamics (Guckenheimer et al. 1977). The problem, of course, is that it is typically difficult enough to accurately sample one insect population, much less the complete community within which it is embedded. Fortunately, due to a theorem of Takens (1981), which confirmed a previous conjecture by Packard et al. (1980), the dynamic behavior of a complex system is often identical to that of the time-lagged series in one of its state variables. Takens' theorem has been routinely applied in the analysis of physical systems (Argoul et al. 1987, Roux et al. 1983). Schaffer and coworkers (1984, 1985a, 1985b, 1986) were the first to recognize the implications of Takens' results to ecological systems, although the analysis of time-lag structure per-se has a long tradition in population ecology (Berryman 1978, Hutchinson 1948, Moran 1953, Royama 1977). Graphical analysis (by Poincaré section) of the lagged time series, in view of Takens' theorem, has resulted in the discovery of probable complex nonlinear dynamics underlying the behavior of insect systems that had previously been thought to be random (Schaffer and Kot 1985b). Other graphical procedures have also been used (Sugihara and May 1990) to demonstrate the existence of low-dimensional attractors (chaos) in ecological data. Ellner, in these proceedings, reviews the validity of these techniques for analysis of ecological time series.

In recent work, Turchin (1990, this volume) applied a time-lagged methodology (Turchin and Taylor 1991) to analyze the time series of 13 forest insect pests. This work, which is reviewed and expanded upon in these proceedings, resulted in the following breakdown of dynamics: no regulation, 1 case; exponentially stable, 2 cases; damped oscillations, 6 cases; limit cycles, 3 cases; chaos, 1 case. Turchin's results are in marked contrast with Hassell et al.'s (1976) earlier conclusions, indicating the general importance of complex nonlinear dynamics in forest insect populations. In particular, Turchin suggested that complex dynamics resulting from density-dependence may in fact underlie population fluctuations that had previously been attributed to stochastic and/or exogenous effects.

Analysis of empirical insect population data for the signature of chaos presents a significant dilemma. On the one hand, the "standard" techniques of mathematical analysis are unrealistically data intensive. Although development of new methodology for detecting chaos in small data sets is currently an active area of research in mathematical analysis, there are potential problems in ecological application of this work, as illustrated by a recent quote from this literature. Ramsey and Yuan (1989) provide an optimistic statement that, ". . . one should be able to get a reasonably



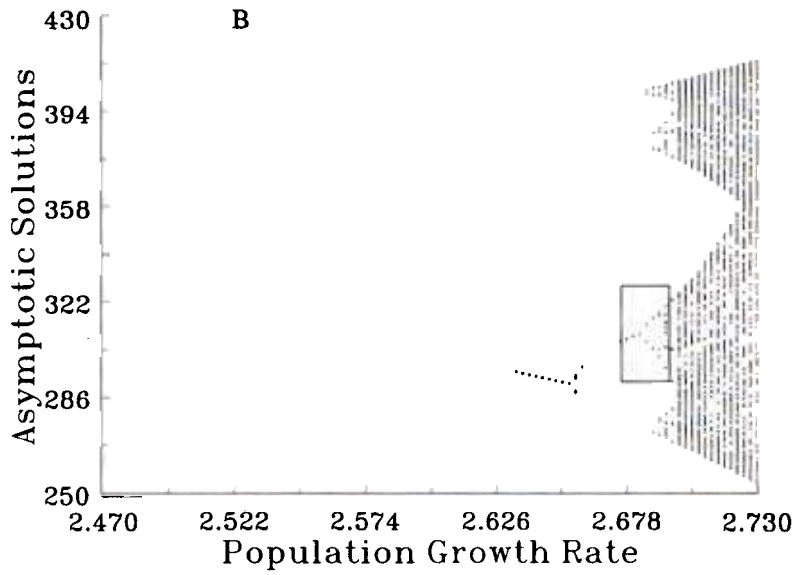


Figure 4. (a) A Bifurcation plot of the Ricker equation. This type of plot is generated by iterating a model for enough time steps to allow convergence of the system to its long-term dynamics. The long-term dynamics are then plotted for a large number of iterations. The value of one parameter in the model is then increased by a small amount and the same procedure is repeated. This method allows examination of the effects of varying a parameter on the long term dynamical behavior of the model. Repeated plotting of the same point (which forms one line as the parameter is increased) indicates single-point steady-state behavior, two points indicate a two-point cycle, four points a four-point cycle, etc. The points at which one level of complexity branches

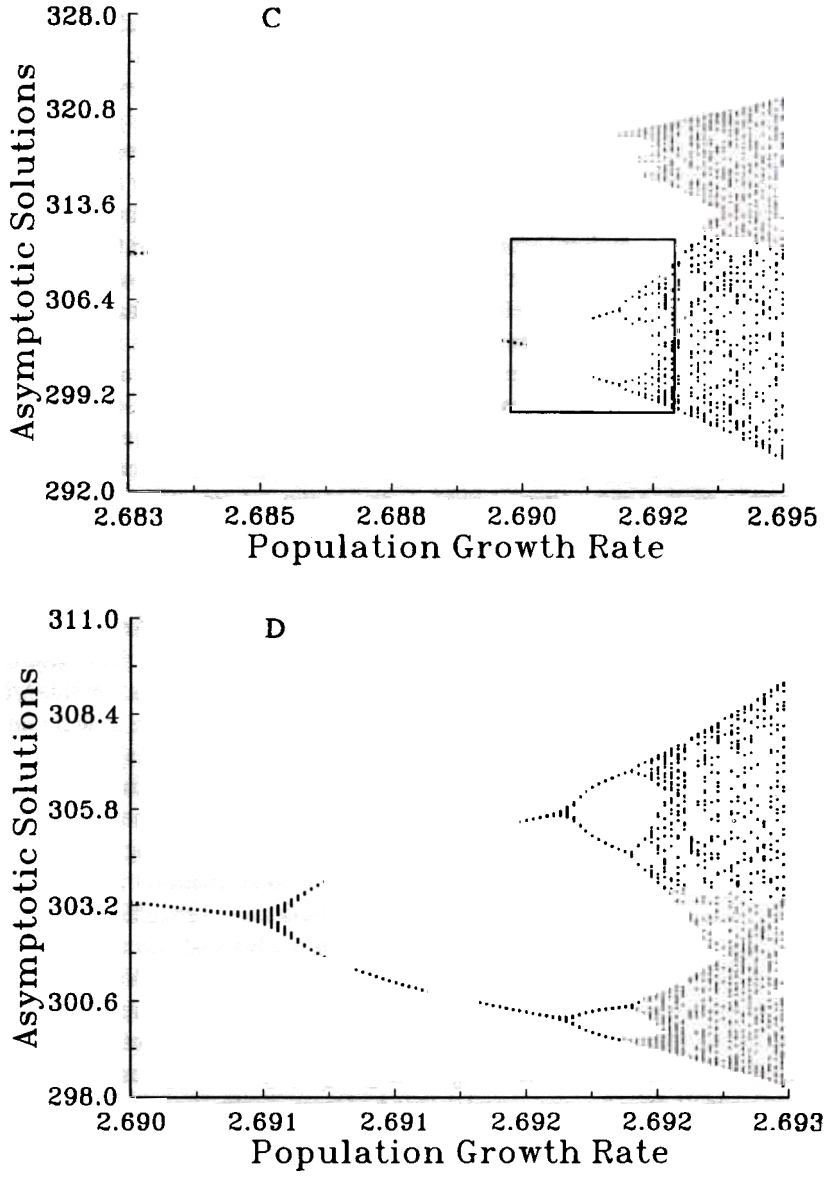


Figure 4. (continued) into more complex dynamics are called "bifurcation points," hence the name bifurcation plot. Chaos results in a "smear" of points. As the parameter for population growth rate is increased, the dynamics become increasingly complex. Note that in chaotic regions, some population values are very close to zero (extinction), and that low population levels become increasingly close to zero as the critical parameter is increased (see Berryman and Millstein 1989). (b) An enlargement of the region contained in the box of A. (c) An enlargement of the region contained in the box of B. (d) An enlargement of the region contained in the box of C. See text for further discussion.

clear idea of whether one has an attractor or not with **only a few thousand** observations... ." Obviously, the concept of "small data set" is relative. Ecologists feel lucky to measure data in terms of tens rather than thousands!

On the other hand of the dilemma are problems inherent in estimating parameters for single-species population models from empirical data, and then determining if the parameterized model is chaotic (e.g. Schaffer et al.1990). The problem of deciding which generally accepted model to use further complicates the serious difficulty of accounting for high order dimensionality. Through analysis of insect life-table studies, Morris (1990) has recently demonstrated that the choice of model, and the method used to parameterize the model selected, can both have significant effects on the conclusions that are drawn. These effects can span the full range of dynamical behavior (from stable equilibrium through chaos) for the same data set.

One alternative to the dilemma presented by empirical analysis of time series data is to use process level simulation models to generate data that are then subjected to quantitative analysis. In this approach, data from a validated simulation model can be used in several ways. First, time series data from such models can be used directly for estimation of parameters that are characteristic of chaotic systems (i.e fractal dimension, positive Lyapunov exponents, etc.). Since the data result from simulation, the large data requirements for such analysis no longer pose constraints. Stone (1990; this volume) has used such an approach to analyze a spatially distributed, insect prey-predator system. This work involved analysis of a deterministic version of a previously published stochastic model describing the interaction between *Campoletis sonorensis* preying on the tobacco budworm, *Heliothis virescens* (Makela et al. 1988). Stone further elaborates on this work in these proceedings.

Another application of validated simulation models has been their use for parameter estimation in more analytically tractable models. The analytic model is then subjected to mathematical analysis designed to provide insights into dynamical properties. A modeling paradigm that utilizes a systematic process of developing progressively more analytically tractable models from simulation models is the development of composite models (Logan 1982, 1989; Plant and Mangel 1987). This approach has been successfully applied for analysis of the outbreak dynamics of several important insect pests (Logan 1982, Ludwig et al. 1978, Wollkind et al. 1988). Application of the composite modeling paradigm for analysis of a spider mite-Phytoseiid [*Tetranychus mcdanieli* McGregor and *Metaseiulus occidentalis* (Nesbitt)] interaction resulted in the discovery of complex dynamics underlying a simple prey-predator interaction, including the existence of sub-critical stability in a model that had previously been thought to have a more restricted dynamical behavior (Collins et al. 1990, Logan 1982, Wollkind et al. 1988). Further analyses that have included the effects of temperature cycles on model parameters uncovered even more complex aperiodic cycles that appear to be chaotic (J. A. Logan, unpublished). The significance of this work was that the complex dynamics resulted as an emergent property from ecological analysis. There was no a priori goal of building a chaotic model; rather the goal was to elucidate the role of temperature on the prey-predator interaction and the resulting biological control of *T. mcdanieli* (Logan 1976).

Several general principles have emerged from dynamical analysis of insect population models. First and foremost is that specific modeling constructs and estimated parameter values should be

based on real life interactions. As indicated in the previous section, the potential for chaos is ubiquitous in the generally accepted ecological models. Therefore, demonstration of chaos in a real system through use of a model is credible only if the model is a reasonable representation of the system and if parameter values are in a realistic range. In any case, due to the difficulties I have discussed with empirical data analysis, simulation-generated data will continue to play an important role in analysis of insect population dynamics.

Since neither empirical data analysis nor model results have definitively demonstrated the importance of chaos in insect population dynamics, the issue provides fertile grounds for theoretical debate and conceptual conjecture. On one side lies the evidence that ecological structure abounds in characteristics that lead to complex dynamics and chaos, and on the other side is the historical tradition that stability (consistency) is a desirable (i.e. has positive selection value) ecological trait (Berryman and Millstein 1989). The arguments against chaos (and by implication complex nonlinear dynamics) being expressed in extant ecological associations are based on the assumption that chaos would lead to population extinction. This assumption is based on the observation that for some models oscillations in the chaotic parameter region lead to a high probability of extinction (Berryman and Millstein 1989, Thomas et al. 1980). The counter to this argument is that the behavior of one class of equations does not generalize to all ecological models (Rogers 1984). In particular, systems of equations, including simple prey-predator equations, can exhibit chaotic behavior that is tightly bounded (Stone, these Proceedings). In fact, for some ecological models the dynamics of populations in chaotic regions are more closely bounded than those in nearby non-chaotic regions (Allen 1989). Examples from laboratory (Pimentel and Al-Hafidh 1965, Pimentel and Stone 1968) and field experiences (Fenner and Myers 1978) can be cited to support the view of selection for stability. Conversely, the body of literature on the dynamics of "outbreak" insects (e.g. Barbosa and Schultz 1987) provide numerous examples of populations with violent density fluctuations that are none-the-less persistent.

In summary, the empirical search for chaos in ecological systems has involved three approaches: (1) use of time series data to estimate parameters in simple population models, (2) phenomenological construction of a multidimensional attractor from time-lagged data, and (3) the construction of statistical models (RSM technology) from time-lagged data. All three approaches are limited by large data requirements or potential inconclusiveness of results. Related to these purely empirical approaches has been the use of validated simulation models to generate data that are then subjected to dynamical systems analysis. Although data sets generated from simulation models are not restricted by the constraints of real-world time frames, results from these studies are subject to the limitations and criticisms of simulation studies in general. Therefore, much of the evidence for or against chaos and complex dynamics has a basis in conceptual or theoretical arguments. Once again a convincing case (using selected examples) can be made either for or against chaos. From this diffuse information, however, one consistent pattern does emerge: and that is, the deeper one looks into the dynamics of insect populations, the more likely one is to find evidence for complex nonlinear effects.

Important Issues

The difficulty in empirically demonstrating chaos in ecological data leaves the important question of the existence of chaos in ecological systems unresolved. Resolution of this question is important for reasons both philosophical and practical. The remaining chapters in this proceedings address both the conceptual and the practical issues relating to chaos in ecology.

In this chapter, I have noted that those characteristics which predispose systems to chaotic dynamics are commonly found in ecological structure. I anticipate that as the ramifications of deterministic chaos become more fully understood, chaos will be found to be an important component of many ecological associations. This expectation is by no means universal. An underlying theme of natural history since antiquity has been the "balance of nature" (Egerton 1973), which has led to a strong equilibrium-based paradigm for population ecology. This paradigm is implicit to some of the most basic ecological concepts such as Clementsian succession and Darwinian selection (Ellis et al. 1991). Many ecologists have found chaos to be incompatible with the prevailing equilibrium paradigm. Thomas et al. (1980), for example, state: "We argue that chaos and stable limit cycle behavior are maladaptive ... "; or Berryman in these proceedings: " ... ecological systems evolve naturally into ordered, stable structures... . In the next chapter of this volume, Berryman presents the case for the equilibrium viewpoint that holds chaos to be maladaptive. He further elucidates the management tactics that are de-stabilizing to equilibrium systems.

The practical issues of chaos revolve primarily around prediction, and in particular what may be termed the *paradox of prediction* that results from chaotic dynamics. As we have seen, insect population phenomena such as outbreaks of forest pests have been notoriously difficult to predict. Lack of predictive power has historically been attributed to stochastic noise or other chance events that are truly unpredictable. If, however, this "noise" results from deterministic chaos, then it is possible to predict short term events if the strange attractor can be reconstructed (Farmer and Sidorowich 1987, Schaffer and Kot 1985b), or from time series data alone (Casdagli 1989, Farmer and Sidorowich 1987). As summarized by Schaffer and Kot (1986), "... one could thus predict the severity and timing of the next irruption from knowledge of the last ... ." For many outbreak insects this would indeed be a significant advance in predictive power. The paradox is that prediction in the classical sense is more futile than we had previously thought but, conversely, variation that was previously thought to result from unpredictable stochastic effects may in fact be predictable if the system is viewed from an appropriate perspective. Before the perspective that allows prediction in the face of uncertainty can be utilized, however, it is necessary to differentiate between time series that are chaotic from those that are simply noisy.

Two chapters in these proceedings address the problems of inferring the dynamical properties of a system from its time series. Turchin begins his paper with a brief discussion of the polemic that has historically surrounded the topic of population regulation. The conclusion of this review is that complex, nonlinear dynamics are counter to the prevailing view of regulation around a stable equilibrium, the "equilibrium" argument. He further notes the influence that Hassell et al.'s (1976) work has had on this controversy. Turchin points out that a major weakness in Hassell et

al.'s work was the a priori assumption of a single species model[4]. He then proposes a multidimensional, time-lag-based model and applies this model to time series from several important forest insect pests. Turchin concludes that complex dynamics are more common that has previously been recognized. Following Turchin's contribution, Ellner provides a thorough review of some of the dangers of looking for chaos in short time-frame data sets that are characteristic of ecological studies. In particular, he demonstrates that many of the characteristics of chaotic systems can also arise from simple, non-chaotic stochastic models. Ellner's work serves to emphasize the necessity of placing the analysis of ecological time series within the ecological context of the system under examination. In other words, what are the plausible controlling mechanisms of the system under consideration and are they consistent with (or counter to) chaos as an explanation for the observed time-series? Ellner concludes his contribution by noting that significant progress has been made toward development of analytic tools for distinguishing chaos from random noise in the types of data sets typical to ecology, but that the task is by no means completed. His paper is an eloquent plea for further development of such techniques.

The papers of Turchin and Ellner serve to point out the challenges of empirically demonstrating chaos in ecological systems. Their contributions provide motivation for the empirical analysis of time series that result from well considered ecological models in which the underlying governing rules are uniquely defined. Due to the accessibility of powerful personal computers, it is now possible to construct models of ecological associations that are far more detailed than has previously been reasonable. In the final chapter of these proceedings, Stone takes a novel approach to simulation of prey-predator dynamics. He departs from traditional modeling approaches by developing an object-oriented programming simulation of the behaviors of **individuals** that comprise the population. Through this approach, Stone is able to examine the dynamics of the prey-predator interaction at an unprecedented level of resolution. In a further departure from previous individual-based simulations, Stone bases behavior entirely on if-then rules that contain no random or stochastic elements. This latter point is particularly germane to the topic of this symposium since any dynamics that emerge from the model could be attributed solely to deterministic forces. Since the model was not cast in the traditional difference or differential equation model, analysis of model results can follow approaches similar to those used for the analysis of real ecological data. However, since large, long-term data sets can be easily generated through computer simulation, the typical constraints of ecological data are avoided. In other words, through simulation, results from Stone's work meet the conditions in Ellner's paper for reliable detection of chaos (i.e. (1) abundant data, (2) small (nil) measurement error, and (3) data result from a purely deterministic system). Stone's work identifies a chaotic strange attractor that is an emergent property from his simulated prey-predator system. Stone further notes that dynamics resulting from motion on this strange attractor would be diagnosed as resulting from stochastic forces acting on non-chaotic, logistic growth. The basic result from Stone's paper is, therefore, in some sense the mirror-image to that of Ellner's; it is also quite easy to misclassify chaotic behavior as stable.

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[4] Hassell et al. acknowledged that real-world population dynamics result from complex trophic interactions and that their results should be viewed with caution for this reason. This caveat has largely been ignored in subsequent work that has cited the Hassell et al. paper.

In this paper I have tried to provide motivation for interest in chaos from a forest entomologist's point of view. I have also attempted to provide a basic description of the concepts of chaos and chaotic dynamics, and to review the entomological status of chaos research to date. The remaining chapters in these proceedings advance the state of current knowledge, particularly with respect to assessing the importance of chaos in insect ecology.

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Chaos in Ecology and Resource Management: What Causes It and How To Avoid It

Alan A. Berryman[1]

Nowadays, as Logan notes in the first chapter of this volume, there is "much ado about chaos." Articles regularly appear in the major journals, books are published in profusion, chaos is hailed as a "new science" (Gleick 1987), ranking in importance to "relativity and quantum mechanics" (Fisher 1985). Despite all this excitement, however, chaos remains mysterious to many people. The purpose of this paper is to provide ecologists and resource managers with an elementary understanding of the phenomenon called chaos. In the first section I describe chaotic motion and explain what causes it. Then I address three important questions about chaos in ecology and resource management - Does chaos occur naturally in ecological systems? Can human actions cause chaos? How can chaos be avoided in managed ecosystems?

What is Chaos?

In the book *Chaos: Making a New Science*, Gleick (1987) cites several definitions of chaos, e.g., "complicated, aperiodic, attracting orbits of certain dynamical systems; a kind of order without order; apparently random recurrent behavior; irregular, unpredictable behavior of deterministic, non-linear dynamical systems."

Most experts would probably agree that chaos is a type of behavior that emerges from dynamic (time-varying) systems containing non-linear relationships (as most biological systems do). Classical dynamics recognizes two major types of deterministic (non-random) behavior – equilibrium points or point attractors (Fig. 1a), and periodic orbits or cyclic attractors (Fig. 1b). I should explain that attractors are regions in the phase-space of two or more variables (the inserts in Fig. 1) that attract nearby trajectories; i.e., a magnet is a point attractor to an iron nail. Chaos is a third kind of behavior in which the trajectories are not drawn towards a single point or orbit but rather to a definable region of phase-space called a "strange attractor" (Fig. 1c). Because orbits on a strange attractor do not repeat themselves, or repeat only after long time intervals, they sometimes appear to have random motion. In fact, if we take a system that has a cyclic attractor (Fig. 1b) and place it in a noisy (variable) environment, we obtain behavior that is difficult to distinguish from chaos (Fig. 1d). A major problem, therefore, is to separate chaos from non-chaotic noisy trajectories (see Ellner's contribution in this volume).

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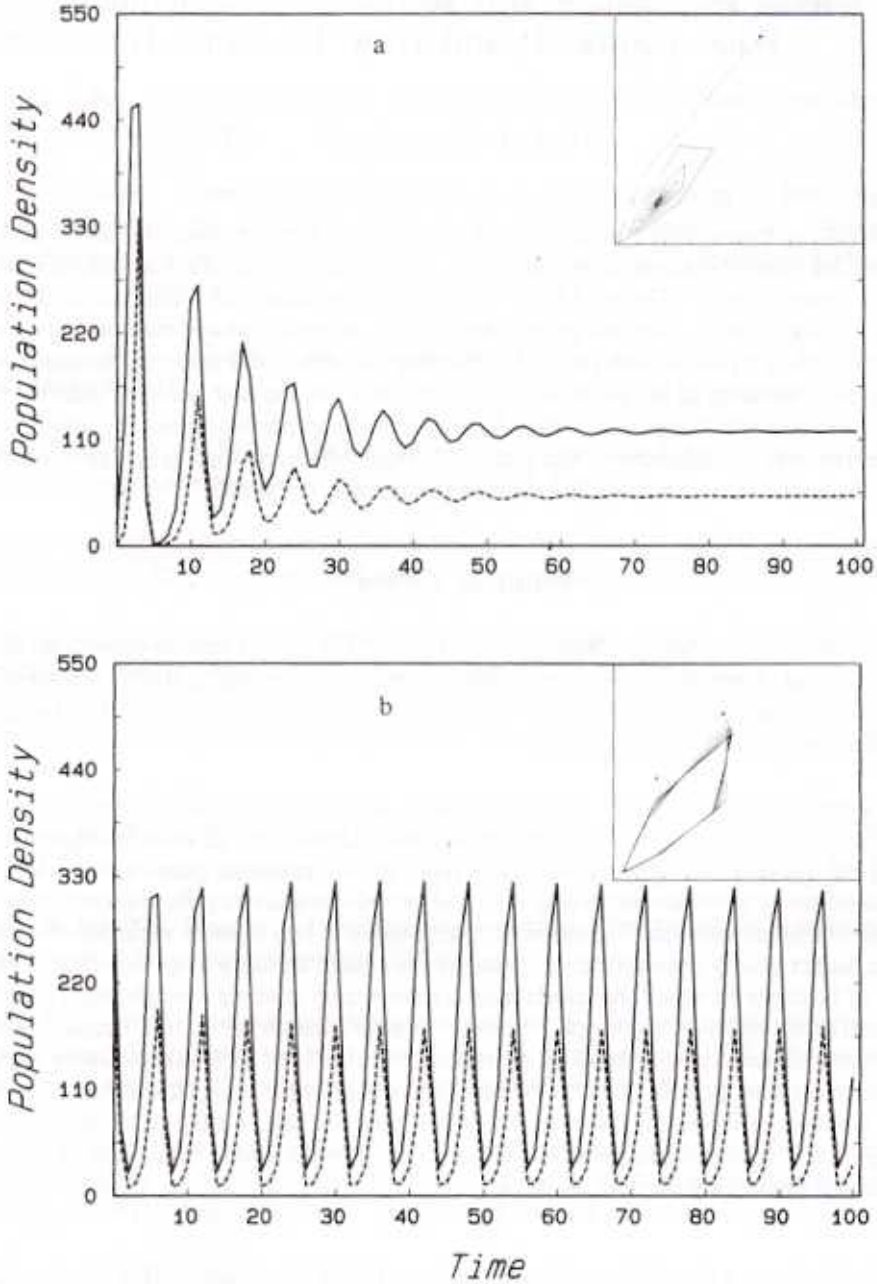


Figure 1. Dynamics of a simple non-linear logistic model fit to data from a population of blackheaded budworms interacting with a guild of larval parasitoids (Berryman 1990). (a) Single damped-stable equilibrium or point attractor resulting from a model derived from the data (Morris 1959). (b) Cyclic behavior obtained when the budworm growth rate parameter is increased.

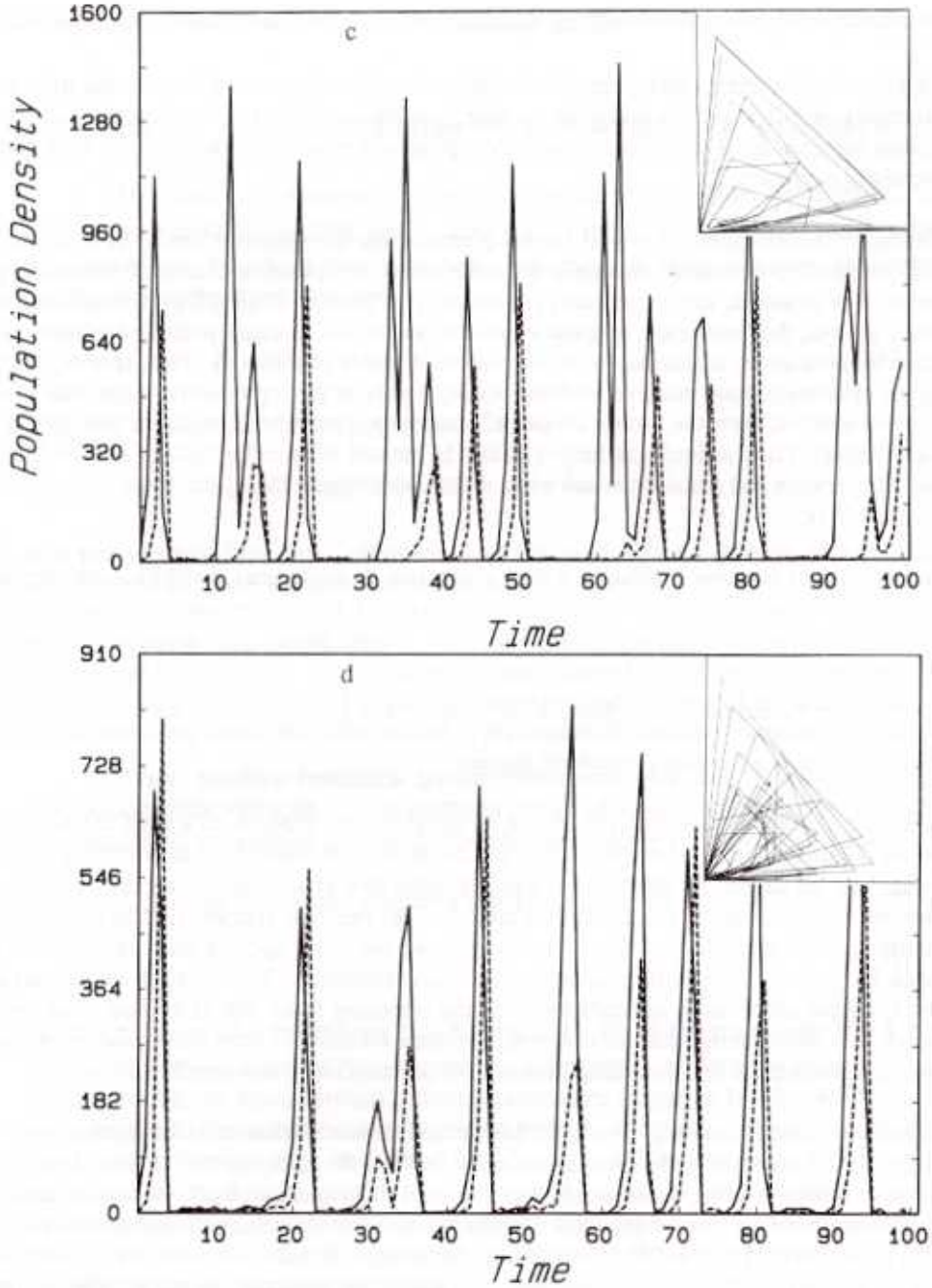


Figure 1. (continued) (c) Chaotic behavior resulting from an even larger budworm growth parameter. (d) Uneven cycles similar to chaos arising when the model (b) is run in a variable environment. Inserts show the phase plots, or the density of parasitoids plotted against the density of budworms.

What Causes Chaos?

Perhaps the best formal definition of chaos arises from the observation that chaotic trajectories are extremely sensitive to their initial, or starting, conditions. In fact, if we start two trajectories very close together on a strange attractor, their positions relative to one another will diverge exponentially over time.

Deviation amplification is a well-known phenomenon in systems science. It is created by systems engineers, or caused naturally in ecosystems, by positive feedback (autocatalytic) processes. For example, the "population explosion" is a positive feedback growth process, as is economic growth, the "arms race," organic evolution, and so on. Because positive feedback causes deviation amplification, it can also be an ingredient of chaos (see Box I). Furthermore, since all ecological systems contain positive feedback loops, if only in the reproductive capacities of their constitutive species, then the "seeds of chaos" must lurk everywhere in nature (Berryman and Millstein 1989a). Positive feedback loops can also be created when individuals or species help one another (cooperation and mutualism) and when species harm each other (inter-specific competition) (Berryman 1981).

In contrast to positive feedback, which gives rise to ecological instability and deviation amplification, negative feedback usually induces stability by ironing out deviations from the steady-state (deviation attenuation) (Berryman 1981, 1989). In fact, it is negative feedback that defines the attractor onto which dynamic trajectories converge. In ecological systems, negative feedbacks are created by competition between individuals for food or territories (intra-specific competition), consumer-resource (predator-prey) interactions, and other processes that oppose population growth in a "density-dependent" manner.

The type of attractor that emerges from a dynamic system depends, to a large extent, on time lags in the dominant negative feedback loops and the strength or intensity of the feedback response. Time-lags can be caused by discrete life-cycle events, like synchronized breeding periods and overwintering stages, and by feedbacks that involve more than one species, such as predator-prey interactions, nutrient cycling, and so on. In general, the more species that are involved in a feedback loop, the longer is the lag in the feedback response. The strength of the negative feedback, on the other hand, depends more on the opposing force that is applied, with violent counter-action often being termed overcompensatory feedback. Overcompensatory negative feedback can also lead to deviation amplification, the trademark of chaos (see Box I).

When the controlling negative feedback in a dynamic system acts instantaneously (no time-lag), a point attractor is always created, irrespective of the force applied. If time-lags exist in the negative feedback loops, as we would expect in most ecological systems, then point attractors, limit-cycle attractors, or strange attractors can arise under different parametric conditions. Given a time-lag greater than zero, a stable point attractor can change (or bifurcate) into a cyclic attractor as certain parameters reach critical values, and then the cyclic attractor can itself bifurcate into a strange attractor at other critical values of the same parameters (Fig. 2). Dynamic systems are particularly sensitive to their positive feedback

Box I. Chaos, Deviation Amplification, and Feedback

In chaotic systems, small differences in initial conditions, Δ_o, diverge exponentially so that $\Delta_t \approx \Delta_o \exp(ht)$ at time t, provided that the Lyapunov exponent $h > 0$. This phenomenon, however, is also present in positive feedback amplifiers, of the form

$$X_t = HX_{t-1}\ , H > 1 \qquad (1)$$

a difference equation with the general solution

$$X_t = X_o \exp(ht)\ , h = \ln(H). \qquad (2)$$

It is easy to see that small differences in initial conditions diverge exponentially with time when the Lyapunov exponent $h > 0$; i.e.,

$$\Delta_t = \Delta_o \exp(ht) \qquad (3)$$

where $\Delta_o = X_{1,0} - X_{2,0}$ and $\Delta_t = X_{1,t} - X_{2,t}$; $X_{i,t}$ = position on trajectory i at time t.

Thus, positive feedback growth processes give rise to what engineers call "exponential instability." It is perhaps not so obvious that initial deviations are also amplified in systems containing overcompensatory negative feedback.

Consider the simple negative feedback operator

$$X_t = 1 - HX_{t-1}. \qquad (4)$$

which produces an equilibrium ($X_t = X_{t-1}$) at $1/(1 + H)$. If the parameter $H < 1$, then oscillations about the equilibrium point die out, while if $H > 1$ they grow in size, a condition that we have termed overcompensatory negative feedback. Now it is fairly simple to show that deviations of two trajectories starting close to each other near equilibrium are also described by equation (3). In this case, however, we have what is called oscillatory instability, where oscillations due to overcompensatory negative feedback amplify over time. Thus, the two amplifying properties, growth through replication and overcompensatory regulation, provide the driving forces for chaotic motion.

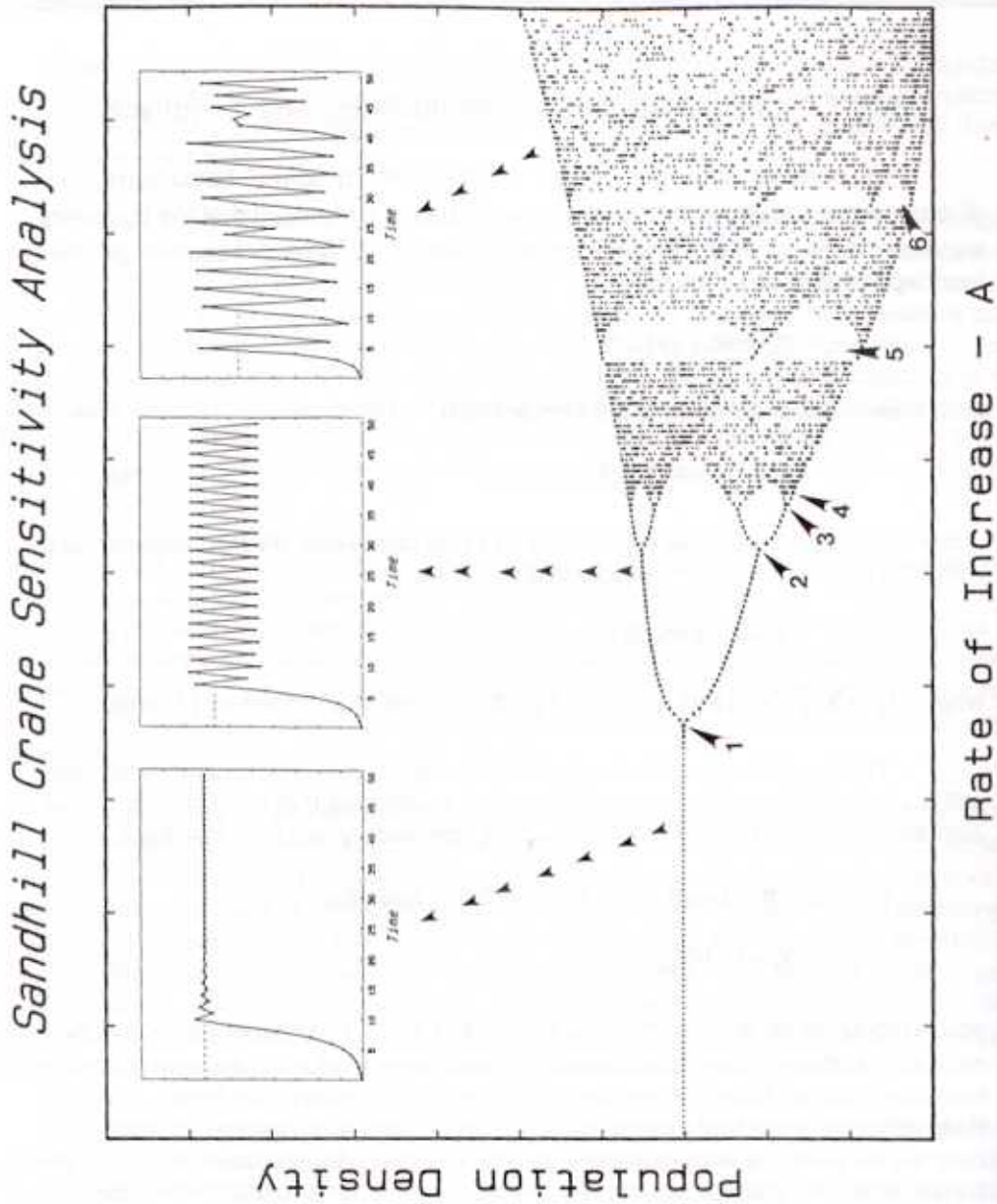


Figure 2. Sensitivity of a simple model of sandhill crane population dynamics to changes in its per-capita rate of increase, showing bifurcations (arrows) from a point equilibrium into a 2-point cycle (arrow 1), then into 4-point (arrow 2) and 8-point (arrow 3) cycles, and finally into chaos (arrow 4). Notice the presence of orderly windows in the chaotic region (arrows 5 and 6) (model derived from data in Buller 1979, using methods described in Berryman and Millstein 1990).

growth parameters as well as to parameters determining the strength and inertia of the feedback response, both of which create the deviation-amplifying requirements for chaotic motion.

In summary, it is possible for ecological systems to exhibit the major types of equilibrium behavior – point equilibria, periodic cycles, and aperiodic chaotic motion. The behavior around equilibrium becomes more irregular and unpredictable (more chaotic) as time-lags get larger and as the intensity or strength of the negative feedback reactions increase and, of course, as the positive feedback growth parameters become large.

Does Chaos Occur Naturally in Ecological Systems?

Following May's (1974) observation of chaos in simple ecological models, an obvious question was: "Do ecological systems display this complex and unpredictable deterministic behavior?" In other words, is the irregular and apparently random behavior observed in many natural populations (Fig. 3) due to chaos (Fig. 1c), or to random disturbances of non-chaotic trajectories (e.g., Fig. 1d)? For a number of technical reasons, the usual methods of attractor reconstruction cannot be applied to most ecological data (e.g. see, Ellner's contribution in this volume and the discussions by Nisbet et al. 1989 and Berryman and Millstein 1989b).

An alternative approach is to fit theoretically reasonable ecological models to the data and then determine if the parameters fall into the chaotic domain. When this approach is applied to data from natural and laboratory populations, chaotic parameters are rarely encountered (see Hassell et al. 1976, Thomas et al. 1980, and Turchin's contribution in this volume). I have analyzed numerous sets of field data in a similar way and have only once found parameter values in the chaotic domain. For example, when the data in Figure 3 are fit to a theoretical two-species model, the estimated parameters give rise to point attractors (Fig. 4, left), even though the model, with different parameters, is capable of producing chaotic motion (Fig. 1c). However, the trajectories are very similar to the observed dynamics when the models are run in a variable environment [c.f. Figs. 3 (left) and 4 (right)]. Thus, although some see chaos in ecological data (e.g., Schaffer and Kot 1986), the empirical evidence suggests that ecosystems are usually quite stable and that the irregular fluctuations often observed are due to external random perturbations rather than to internal chaotic motion.

Besides the empirical evidence, there are strong evolutionary reasons why ecosystems should not behave chaotically. First, chaotic population trajectories often spend considerable time far from their equilibrium points, sometimes declining to extremely low densities where extinction is likely (Thomas et al. 1980, Berryman and Millstein 1989a). Conventional wisdom argues that species should evolve parameter values that minimize the likelihood of extinction; i.e., non-chaotic parameters. This viewpoint is supported by modeling exercises (Nisbet et al. 1989, Mani 1989), and by laboratory and field experiments. For example, Pimentel and his associates grew populations of houseflies and parasitic wasps in the laboratory and observed that the amplitude of population fluctuations decreased significantly over time (Pimentel and Al-Hafidh 1965, Pimentel and Stone 1968). Examples of evolving stability can also be found in the biological control of pest organisms. One of the best documented cases is the biological control of rabbits in Australia by the myxoma virus (Fenner and Myers 1978). Shortly after introduction

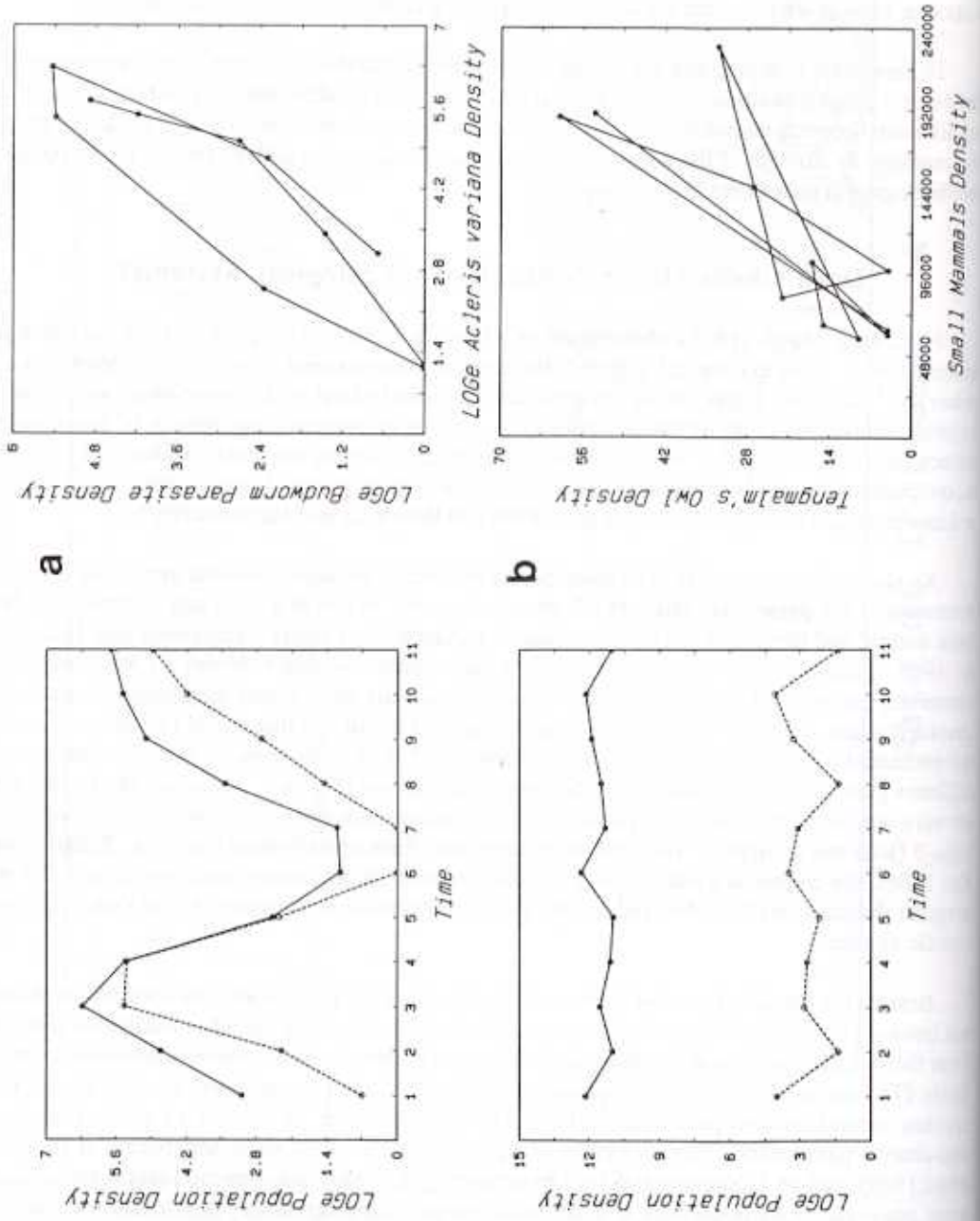


Figure 3. Trajectories of several natural populations observed in time-series and phase-space. (a) Densities of blackheaded budworm larvae (solid line) and parasitoids (broken line) per 100 m^2 of fir foliage (Morris 1959). (b) Densities of small mammals (solid line) and Tengmalm's owls (broken line) per 100 ha (Korpimäki and Norrdahl 1989).

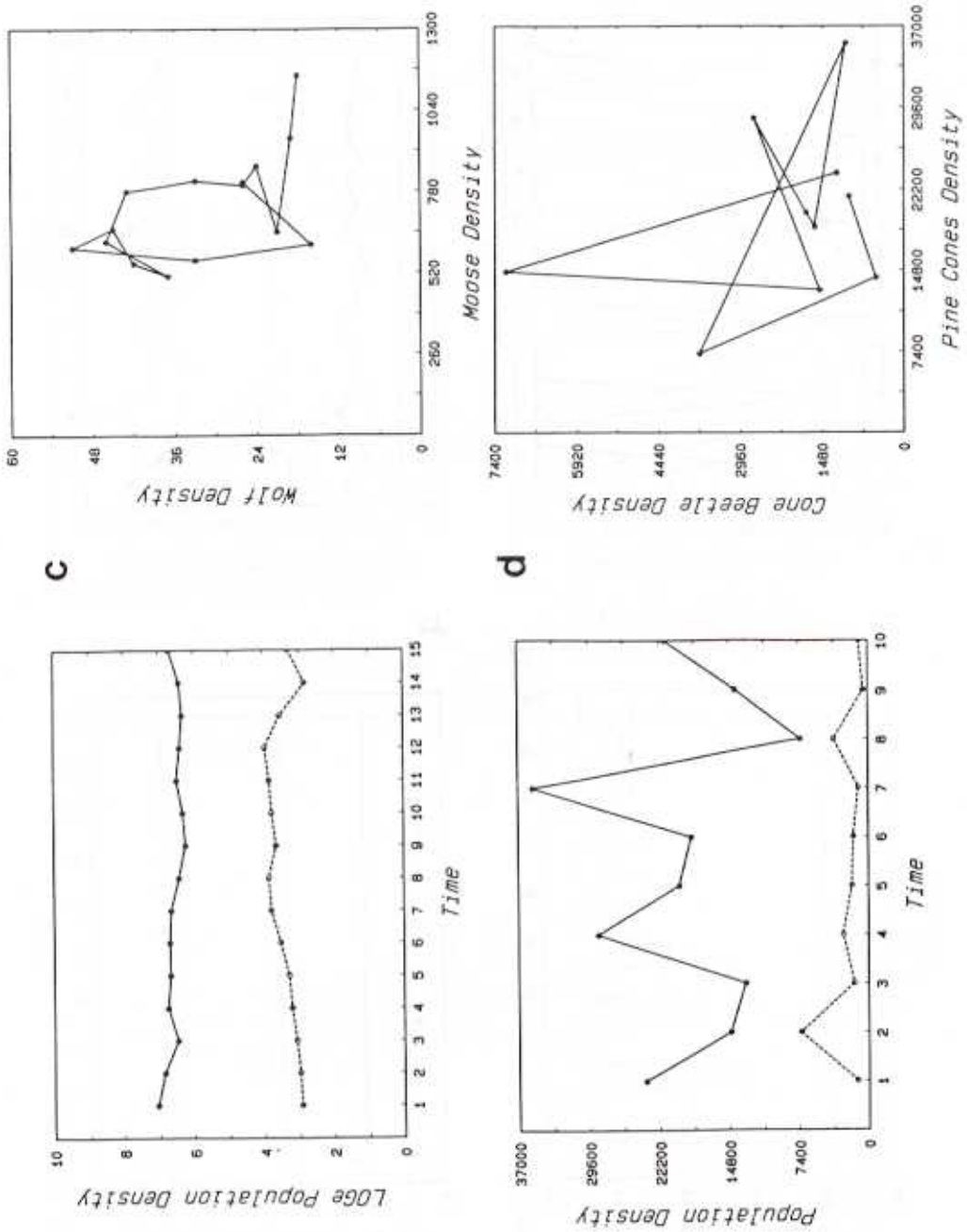


Figure 3. (continued) (c) Moose (solid line) and wolves (broken) on Isle Royale (Peterson et al. 1984). (d) Red pine cones (solid line) and cone beetles (broken) per hectare (Mattson 1980).

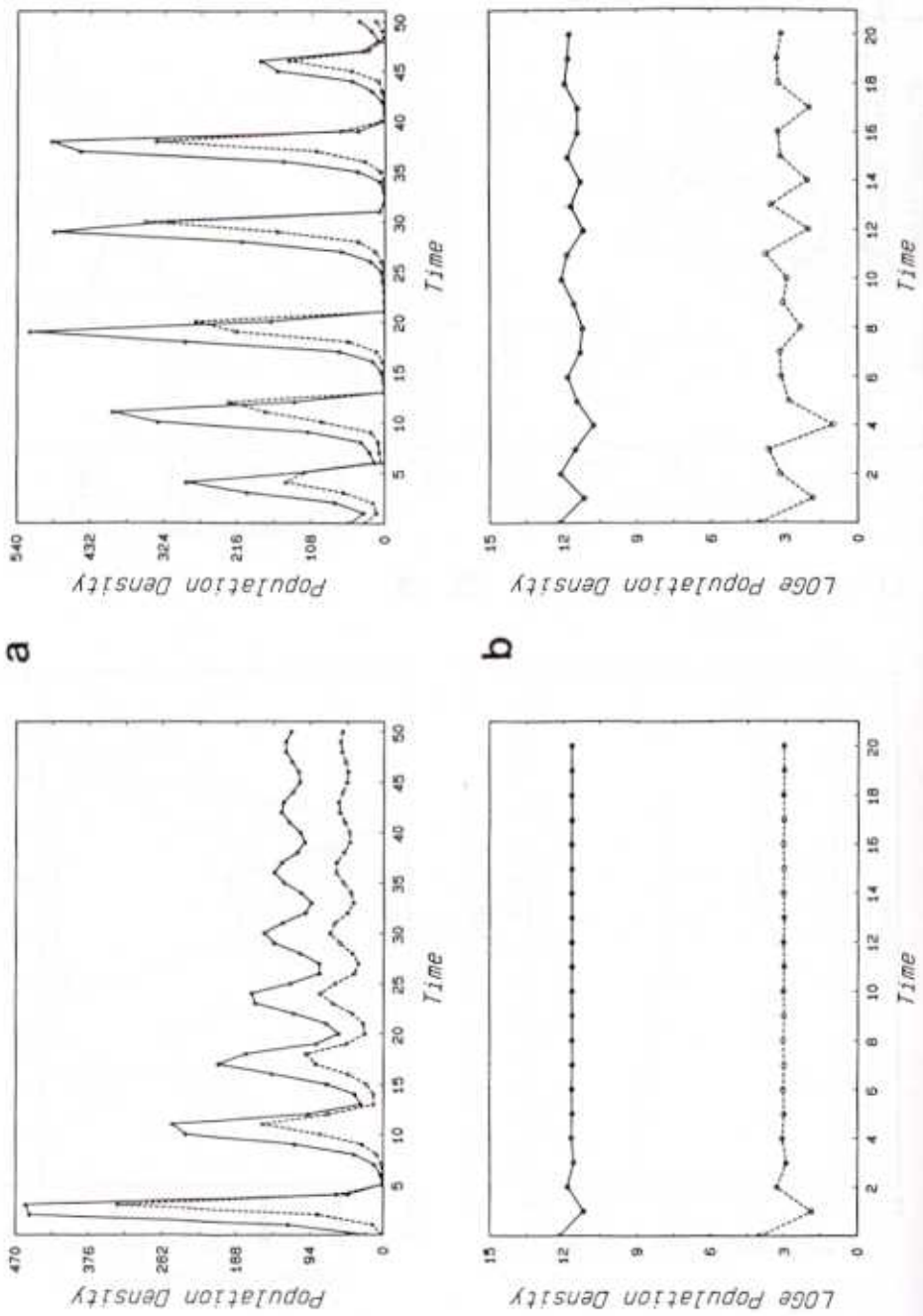
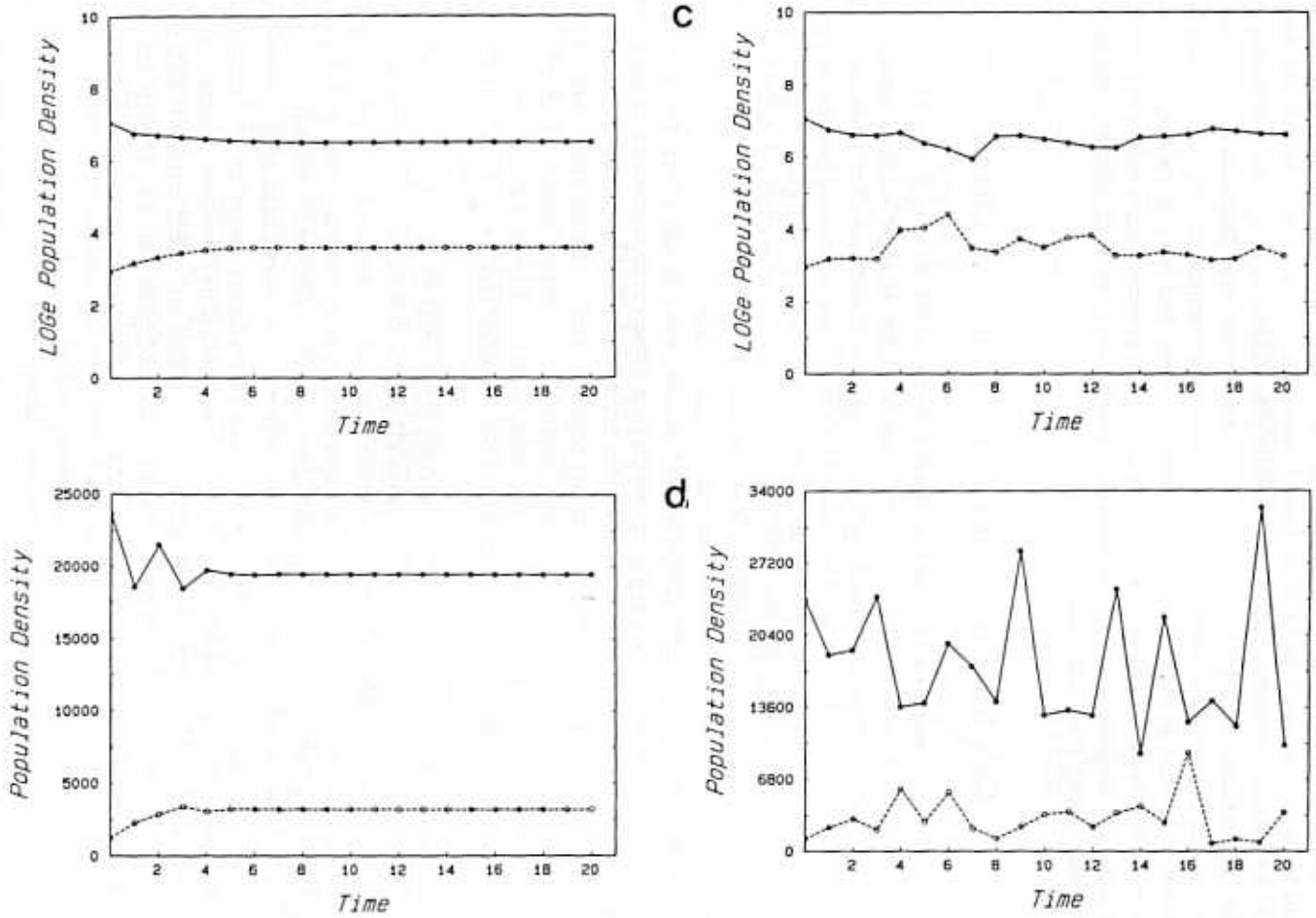


Figure 4. Trajectories of a two-species model (Berryman 1990) fit to the data shown in Figure 3 and run in a constant (left) and a variable (right) environment.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of the virus a virulent strain generated an epizootic that killed most of the rabbits. After this high-amplitude oscillation, however, less virulent strains (and more resistant rabbits) began to predominate and the populations settled into a muchmore stable condition. Selection for less virulent virus strains seems to have occurred because the virulent strains killed their hosts too quickly for effective transmission in sparse rabbit populations. These studies demonstrate that unstable populations (perhaps even chaotic ones) will evolve over time into more dynamically stable systems through the modification of species-specific parameters such as fecundity, feeding efficiency, resistance to attack, virulence, competitiveness, and intra-specific aggression. The evidence, both empirical and theoretical, is that ecological systems evolve naturally into ordered, stable structures, and that any irregular behavior is usually due to unpredictable external forces that continuously disturb them from their steady states.

Can Human Actions Cause Ecological Chaos?

Although most natural co-evolved ecological systems do not seem to behave chaotically, the fact remains that all ecosystems contain the "seeds of chaos" in their feedback structures and, therefore, it is always possible to push them into their chaotic domains (Berryman and Millstein 1989a, Allen 1990). Instability can be introduced into any system containing positive and negative feedbacks by increasing the time lags in the negative feedback loops or by changing the values of certain parameters, particularly the birth and death rates. For example, I have argued that instability in Dungeness crab populations in the oceans off Northern California could have been induced by delayed feedback between the crab population and the economic system (Berryman 1991); i.e., the abundance of crabs affects harvest success, which in turn affects profits, which are then used to purchase new boats and gear, which then impact crab abundance in the following fishing season (= time lag) (Fig. 5). Many more examples of human actions that could induce delayed negative feedback on future populations could be cited, including global warming, ozone depletion, destruction of tropical forests, and buildup of radioactive waste. Feedbacks such as these, which may not have an impact for a long time, should be expected to decrease the stability of ecological systems, and could create an environment in which chaos reigns (see Box II).

Instability can also be introduced by modifying certain ecological parameters. For example, species-specific growth rates can have very strong effects on stability, with large reproductive rates giving rise to greater instability (Fig. 2). Growth rates can be increased by improving growing conditions for the species in question (habitat improvement) or by breeding faster-growing or more fecund strains (genetic improvement and biotechnology) (Berryman and Millstein 1989a). Instability can also be induced by increasing the strength of the interactions between species (see Box II), i.e., increasing the efficiency or virulence of predators, parasites and pathogens, or increasing the degree of competition or cooperation (mutualism) between species. Thus, the engineering of more efficient or virulent pathogens can induce ecological instability and, perhaps, even chaos. This message should not be lost to biotechnologists who are currently engineering more virulent viruses for use in insect pest control.

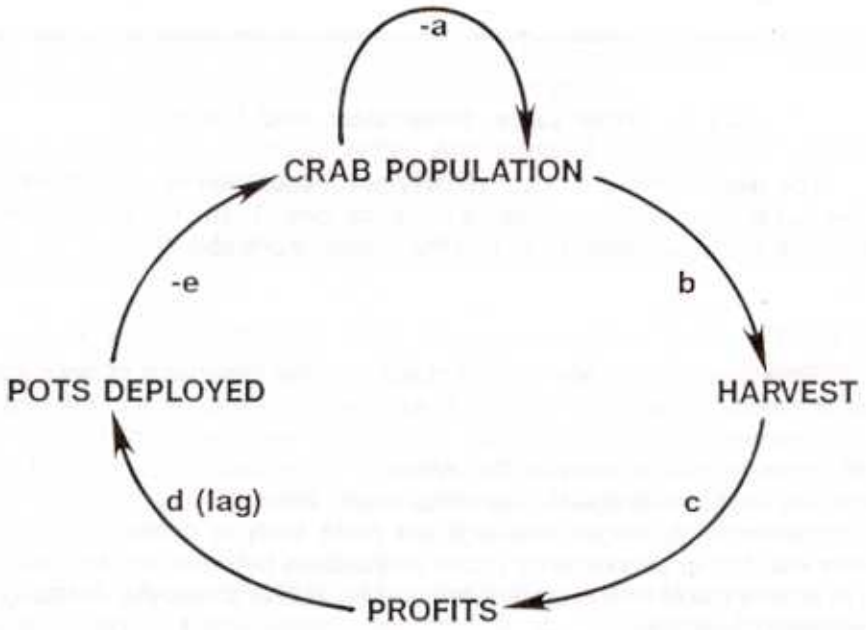

Figure 5. Hypothesized delayed negative feedback between the northern California Dungeness crab population and the economics of the fishery (after Berryman 1991).

How Can We Avoid Chaos?

The lessons for the resource manager about chaos and chaos avoidance are fairly obvious from the preceding discussion, avoid long time-lags, large growth rates, and highly efficient predators and parasites. Some specific suggestions that immediately come to mind are:

1. Minimize the time-lag between management decisions and their implementation (reduce time-lags in the control loops involving stand treatments, pest control, etc.).
2. Try not to create new feedback loops with strong interactions with other system components; e.g., don't insert new pollutants, pesticides, or strong economic incentives into the system (see Box II).
3. Refrain from disturbing populations far from equilibrium where chaos-producing positive feedback growth can take over; e.g., use pesticides to obtain optimal rather than maximal kill (Berryman 1986).
4. Be cautious about introducing organisms into habitats that are very favorable for their reproduction and survival, thereby increasing their positive feedback growth parameters; e.g., introducing pests into exotic habitats or creating monocultures of susceptible plants.
5. Avoid creating harsh or violent interactions between system components, say by bioengineering more virulent pathogens with high reproductive rates.
6. Avoid over-reacting to changes in the system that can result in harsh, overcompensatory feedback. In other words, react quickly but gently to changes that you observe in the ecosystems you are managing.

Box II. Time Lags, Dimension, and Instability

The neighborhood or local stability of an equilibrium point depends on the time-lag in the stabilizing negative feedback loop, T, and the strength of the negative feedback parameter H, so that the system is unstable if

$$HT > 1 .$$

Time-lags are actually representations of the dimension of the system, where dimension means the number of mutually interacting parts of the system, i.e., components (species) that are part of the feedback structure or that contribute to feedback loops in the system. In general, systems with more dimensions (interacting species) are less stable because long feedback loops with correspondingly longer time-lags are more likely to occur. In addition, systems with higher connectance (more connections between species) are also likely to be less stable for the same reasons. May (1972) shows that instability will almost certainly result if

$$H(MC)^{1/2} > 1$$

where M is the number of components (species), C is the connectance, or the probability that any pair of components will interact, and H is the mean interaction strength. Obviously, human activities can increase connectance and decrease stability by interacting with more species or by having "too many fingers in the pie."

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Nonlinear Modeling of Time-Series Data: Limit Cycles and Chaos in Forest Insects, Voles, and Epidemics

Peter Turchin [1]

Although the emphasis of this conference is on chaotic population dynamics, in this paper I will address the broader issue of complex dynamical behaviors in ecosystems. ``Simple" refers to dynamics whose endogenous (density-dependent) component is characterized by a stable-point equilibrium. In such systems fluctuations around the equilibrium point are primarily, or entirely, due to exogenous (density-independent) factors. Thus, ``complex" dynamics are bounded, endogenously-driven fluctuations that do not settle to a stable-point equilibrium. Examples include limit cycles, quasiperiodic dynamics, and chaos. It is important to consider limit cycles and chaos together because both dynamical behaviors have the same implications for the population-regulation debate (more on this later). Another source of complexity is the interaction between the nonlinear endogenous component and the environmental noise. My main argument will be that both ecologists and forest managers need to pay more attention to the possibility of complex dynamical behaviors in natural ecosystems.

The current debate about complex population dynamics revolves around the issue of whether or not such dynamical behaviors are found in nature. A small, but vocal, group of ecologists (notably W.M. Schaffer and coworkers) have argued that complex dynamics, and chaos in particular, are commonly found in nature. On the other hand, many ecologists appear to subscribe to the view that if populations are regulated at all, they are characterized by stable-point equilibria, and complex dynamics are no more than a mathematical curiosity. This view has been expressed by both experimentalists, e.g. ``the rarity with which populations fluctuate cyclically in nature..." (Hairston 1989, p. 6), and theoreticians, e.g. ``deterministic stability is the rule rather than exception, at least with insect populations" (Nisbet and Gurney 1982, p. 55).

Whether or not complex dynamics are common in nature has a bearing on one of the central issues in population ecology: the perennial debate about population regulation. Willingness to ignore the possibility of complex dynamics leads to a certain mind set with which many ecologists view the debate, which I will call ``the one-dimensional paradigm of population regulation." According to this view, all natural populations lie within the spectrum ranging from completely unregulated populations at one extreme to tightly regulated populations at the other extreme. Since ``regulation" is usually limited to ``regulation around a stable-point equilibrium," any population fluctuations around the mean must be due to lack of regulation, in other words, to exogenous (density-independent) perturbations. Clearly, complex dynamical behaviors do not fit within this framework; thus violently fluctuating populations, even if the fluctuations are caused by endogenous (density-dependent) factors, are by default classified as poorly regulated.

If complex dynamics were rare or absent in nature, then there would be no need to modify the one-dimensional paradigm. The most frequently cited empirical evidence for rarity of complex population behaviors comes from the paper by Hassell, Lawton, and May (1976). Hassell et al.

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[1] Southern Forest Experiment Station, USDA-Forest Service, Pineville, Louisiana, 71360, USA.

(1976) used a simple one-species model to assess the frequency of various dynamical behaviors among 24 natural insect populations. They concluded that all but one population were stable (22 cases of exponential and 1 case of oscillatory damping). There was only one case of a limit cycle, and no cases of chaos.

A major flaw in the Hassell et al. (1976) analysis is that they used a single-species model without delayed density dependence. Using such a simple model biases the results in favor of stability, since complex dynamics are much more likely in higher-dimensional systems, and mistakingly analyzing such systems in fewer dimensions will tend to hide this complexity (Guckenheimer et al. 1977, Schaffer and Kot 1985a). Natural populations are multidimensional systems, since any given population typically affects, and is in turn affected by, other populations in the community (i.e. resources, competitors, and natural enemies). Additional dimensionality may arise as a result of population structure (e.g. age-structure). Hassell et al. (1976) acknowledged this problem, but lacked the tools for dealing with it. Despite this caveat, the results of Hassell et al. (1976) are still being used as evidence against complex dynamics and, in particular, chaos (Berryman and Millstein 1989; Berryman, this volume).

Nonlinear modeling of time-series data

The above discussion highlights a major difficulty associated with assessing the type of dynamics in natural populations. In order to understand and predict population change, we need information about the abundances of interacting species. The problem is, usually data are available only for the target population, and we never have the complete data for all species in the community. It turns out, however, that actions of other species in the community can be detected by considering the influence of lagged (past) population densities on the current rate of population change. To illustrate this idea, consider a very simple community consisting of a single predator and a single prey species, both species having one generation per year (see Fig. 1). The population density of the next generation of prey, N_{t+1}, will be influenced directly by the current density of prey, N_t. This influence will consist of the effect of reproduction, and any direct density-dependent effects such as intraspecific competition. In addition, there is going to be an indirect effect of the lagged density N_{t-1} mediated by the predator population. If N_{t-1} was high, then

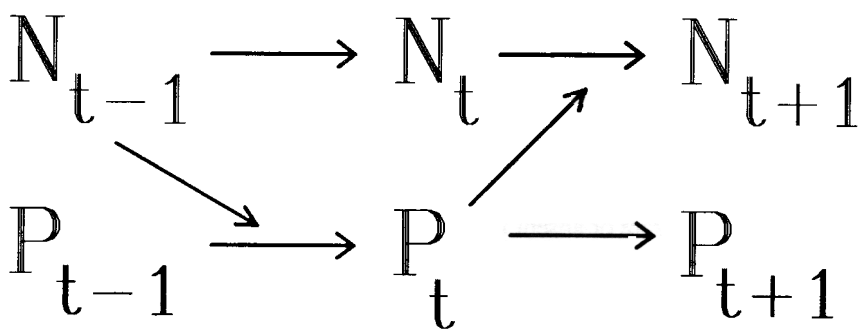

Figure 1. Delayed density regulation in a predator-prey system.

predators at generation t-1 had plentiful prey, and predator numbers have increased between t-1 and t, negatively impacting the prey population at t+1. Alternatively, if N_{t-1} was low, then predator population has been decreasing, which will have a positive effect on N_{t+1}. Thus, the system of two equations describing the dependence of N_{t+1} and P_{t+1} (predator) on N_t and P_t can be rewritten as a single equation describing the dependence of N_{t+1} on N_t and N_{t-1}:

$$N_{t+1} = F\,(N_t, N_{t-1}).$$

In general, if there are p interacting species in a community, then N_{t+1} will depend on p previous lags (Royama 1977). In addition to species interactions, lags can arise as a result of age structure, maternal effects, and other kinds of population structure. Fortunately, in practice a few lags (2 or 3) may be sufficient in many situations (Schaffer and Kot 1985a). Analyzing lag structure of population regulation is a venerable tradition in population ecology (Hutchinson 1948, Moran 1953, Royama 1977, 1981, Berryman 1978, 1986, Turchin 1990).

The method of reconstruction with lags provides the basis for recapturing the dynamics of a multivariate system when only a univariate time series is available. I will call this approach, described below, ``the nonlinear time-series modeling" of data. Nonlinear time-series modeling of ecological data was independently proposed by Ellner and coworkers (Ellner, this volume; see also Ellner et al. 1991, McCaffrey et al. 1991, Nychka et al. 1991), and by Turchin and Taylor (1992; see also Turchin 1991, 1992). This approach is similar to the methods of Eckmann and Ruelle (1985, Eckmann et al. 1986) and Farmer and Sidorowich (1987, 1988) that were proposed for physical applications. Its major departure from the physical methods is its explicit treatment of noise (the exogenous component) as an integral part of dynamics.

The general model underlying the approach is:

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

where ε_t is the exogenous component, or the noise term. Note that I have changed the subscripts to reflect the fact that we are fitting a model to the observed change for the year t as a function of previous lags t-1, t-2, and so on. The basic idea of the approach is to use the time-series data to approximate F. If F has been accurately approximated, then the dynamics of the studied system can be characterized by simply iterating F on the computer, or more formally by calculating the dominant eigenvalue and the dominant Lyapunov exponent. The function F can be approximated in a variety of ways. One approach that seems to work well is the response surface methodology (RSM) of Box and Draper (1987). RSM is similar to fitting polynomials to data, but both the response (dependent) and predictor (independent) variables are transformed using the Box-Cox transformation (Box and Cox 1964). For biological and technical reasons (see Turchin and Taylor 1992) it is better to use the realized per capita rate of population change $r_t \equiv \ln(N_t/N_{t-1})$ as the predictor variable. This variable was fitted with a quadratic surface using the first two lags:

$$r_t = a_0 + a_1X + a_2Y + a_{11}X^2 + a_{22}Y^2 + a_{12}XY + \varepsilon_t\,, \qquad (1)$$

where $X = N_{t-1}^{\theta_1}$ and $Y = N_{t-2}^{\theta_2}$ are transformed lagged densities, and the parameters of the Box-Cox transformation θ_1 are estimated from data (for more details see Turchin and Taylor 1992). I emphasize that nonlinear modeling is a phenomenological approach, since parameters a_i have no biological meaning apart from defining a response surface. The goal is to develop an objective method for extracting endogenous dynamics from data, rather than gain understanding into the mechanisms that generate fluctuations. Nevertheless, visually examing an estimated response surface, as well as calculating the dynamical quantities described below, provides a useful diagnostic tool that may suggest possible mechanisms for subsequent study (for an example see Turchin et al. 1991).

Once the shape of F has been approximated (by fitting r_t), we can characterize its dynamical behavior with two numbers: the dominant eigenvalue of the Jacobian of F evaluated at the equilibrium, λ, and the dominant Lyapunov exponent, Λ. The dominant eigenvalue characterizes the stability of the endogenous component of dynamics when the level of noise is set to zero: if its magnitude $|\lambda| \leq 1$ then the point equilibrium is stable; otherwise it is unstable (see Edelstein-Keshet 1988 for a readable introduction to the stability analysis). The Lyapunov exponent is a generalization of λ for dynamics that do not settle on a stable point attractor. It measures the ``sensitive dependence on initial conditions," so that a system with bounded fluctuations and $\Lambda > 0$ is chaotic. The definition of the Lyapunov exponent can be extended to cover noisy systems (McCaffrey et al. 1991, and Ellner, this volume). I calculated Λ numerically, using a modified method of Wolf et al. (1985). The Wolf et al. (1985) method estimates Λ as the rate of trajectory divergence averaged over all points on the attractor (in practice, one needs only to follow one trajectory long enough to ``sample" the attractor). This method assumes that data were generated by a deterministic system without noise (there can be observation errors, but no dynamical noise). Including an exogenous component, however, affects the amount of time the system spends in various regions of the phase space. In other words, the shape of the attractor is changed, and the rate of trajectory divergence will need to be averaged over a different set of points compared to the attractor of the deterministic system. To measure Λ of a stochastic system, I modified the Wolf et al. (1985) method by adding noise to the equation for generating trajectories. In the modified method, Λ is the average rate of divergence between two nearby trajectories generated by the model (1) with a random but *identical* sequence of errors $\{\varepsilon_t\}$. When defined this way, Λ measures trajectory divergence due only to the endogenous component of dynamics. That is, in systems with positive Λ, trajectories diverge both as a result of and endogenous and exogenous dynamics. In systems with negative Λ, endogenous dynamics will cause trajectories to converge, this tendency being counteracted by divergence due to noise. In order to estimate Λ using this method, in addition to an estimate of the endogenous component one also needs an estimate of noise. I modelled the exogenous component as a Gaussian random variable with mean zero, and the variance estimated by the variance of the residuals from fitting the model (1) to data. Each estimate of Λ was an average of three values obtained by starting with random initial conditions, discarding the first 100 iterations, and then measuring divergence/convergence rate for the next 1000 iterations. The units of Λ are binary bits per iteration, and the numerical scheme measured Λ with a standard error of approximately 0.01 bit/iteration.

In the following section I will discuss the analysis of population time series in three data sets. First, I will discuss time series data for 13 tree and forest insects (this is largely a subset of the

data analyzed in Turchin and Taylor 1992). Nonlinear modeling of these data leads to a conclusion very different from that reached by Hassell et al. (1976). Next, I will analyze two other data sets, for which the evidence indicates chaotic fluctuations: small rodents in the Arctic, and measles in American and European cities.

Forest insects

Unlike the results of Hassell et al. (1976), our analysis revealed a complete spectrum of dynamical behaviors in the forest insect data set, ranging from stability to chaos. Of the 13 forest insect cases, only 2 were classified as exponentially stable (Table 1). Six cases were classified as damped oscillations. However, in one of these cases, *Bupalus piniarius* , increasing the number of lags from two to three indicated quasiperiodicity, suggesting that this case may be characterized by higher-dimensional dynamics, that were misclassified by the two-lag response surface. Another case, *Dendroctonus frontalis* , exhibited oscillations of increased amplitude that appear to become chaotic during the second half of the series (see below). There were one limit cycle and three cases of quasiperiodic dynamics (these are similar to limit cycles, but have an irrational period, so that the solution never repeats itself; see Schaffer and Kot 1985a for a classification of various dynamical behaviors). Finally, one case was classified as chaos. In sum, almost half of the cases exhibited evidence of complex dynamics. I will now examine several selected cases in greater detail with the goal of checking on how plausible these results are.

Choristoneura fumiferana (spruce budworm) is the only case for which the extracted dynamics (exponential stability) did not resemble the observed dynamics (Fig. 2). It has been suggested that this population undergoes periodic outbreaks as a result of some delayed density-dependent process (Royama 1977, 1984). However, a regression analysis did not detect any signs of density-dependent regulation, either direct or delayed (Turchin and Taylor 1992). One alternative to Royama's hypothesis of endogenously generated cycles is that the population may be tracking a long-term periodic trend in its food base (Turchin and Taylor 1992). It is too early to attempt to distinguish between these two (or any other) explanations, since the quantitative data are available for only one outbreak.

In another case, the population of *Dendroctonus frontalis* (southern pine beetle) in East Texas, there is a well-documented environmental trend. During the last 30 years this beetle's food base has grown several-fold (Turchin et al. 1991). It is possible that such a resource enrichment led to an increased instability in the southern pine beetle populations in the South. Note that during the recorded history of SPB outbreaks the mean population density did not change much, while the amplitude of outbreaks has increased, with the peaks getting progressively higher and the troughs progressively lower (Fig. 3). Since the environmental conditions have changed over the observed period, fitting the response-surface model to these data directly may have led to overestimating the degree of stability in this population (non-stationarity tends to bias response-surface results in favor of stability; see Turchin and Taylor 1992). Fitting a response surface to the first and second halves of the series separately, we obtained diverging oscillations and chaos, respectively. This result is consistent with the idea that the SPB population is becoming progressively more unstable as its environment changes.

Table 1. Results of fitting two-lag quadratic response surfaces (equation 1) to the insect data.

Species (reference)	Length	$\|\lambda\|$	Dynamics[1]	Λ
Choristoneura fumiferana (Royama 1981)	28 y	0.71	ES	-0.24
Panolis flammea (Schwerdtfeger 1941)	60 y	0.58	ES	-0.91
Dendrolimus pini (Varley 1949)	60 y	0.69	OS	-0.11
Hyloicus pinastri (Schwerdtfeger 1941)	50 y	0.61	OS	-0.43
Lymantria monacha (Bejer 1988)	42 y	0.78	OS	-0.01
Hyphantria cunea (Morris 1964)	22 y	0.97	OS	-0.06
Bupalus piniarius (Schwerdtfeger 1941)	60 y	0.73	OS	-0.24
Dendroctonus frontalis (Turchin *et al.* 1991)	30 y	0.94	OS	-0.15
Drepanosiphum platanoidis (Dixon 1990)	19 y	1.31	LC	-0.30
Operophtera brumata (Varley *et al.* 1974)	19 y	1.01	QP	-0.07
Lymantria dispar (Montgomery and Wallner 1988)	24 y	1.03	QP	-0.01
Zeiraphera diniana (Baltensweiler and Fischlin 1988)	38 y	1.07	QP	-0.10
Phyllaphis fagi (Dixon 1990)	19 y	1.40	Chaos	0.20

[1] Dynamics obtained by iterating model (1) without noise.

Data were detrended prior to fitting where doing so resulted in a substantial increase in the degree of fit. ``Length" column gives the length of the time series in years. Columns labeled ``$|\lambda|$" and ``$\Lambda$" list the estimated dominant eigenvalue and Lyapunov exponent, respectively. The type of dynamics exhibited by the estimated response surface without noise (obtained by iterating equation (1) with $\varepsilon_t = 0$) is listed in the column labeled ``Dynamics". ES = exponential stability, OS = oscillatory stability, LC = limit cycle, QP = quasiperiodicity.

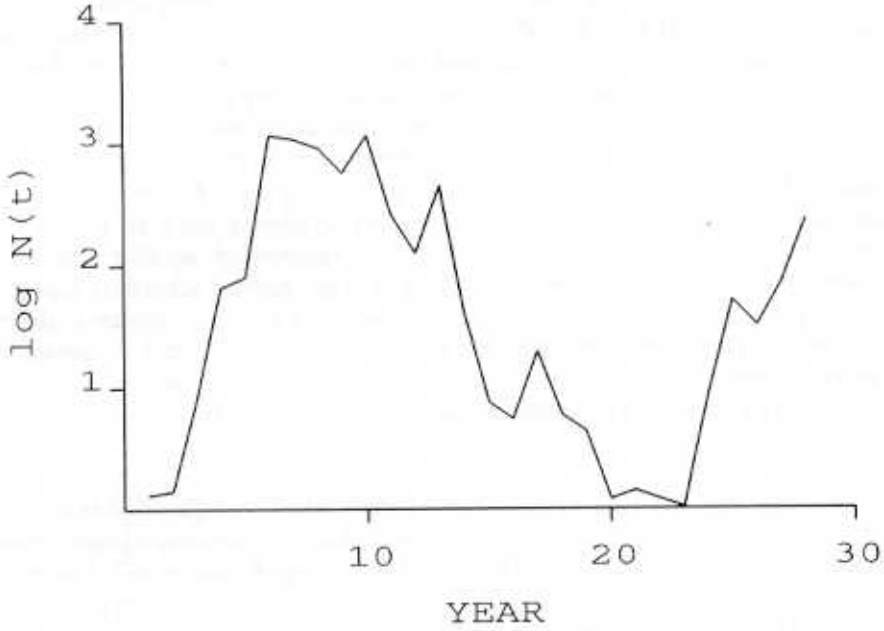

Figure 2. The time series of *Choristoneura fumiferana* .

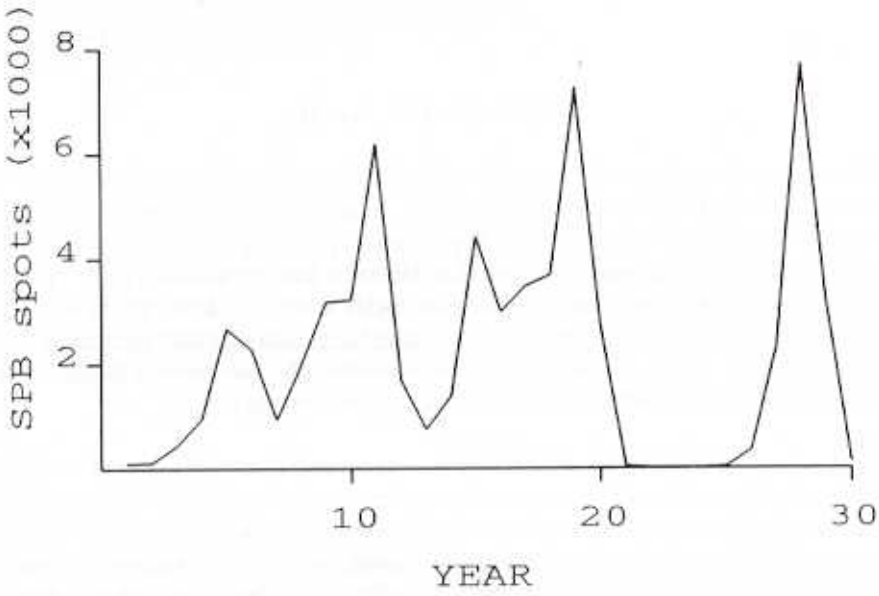

Figure 3. Population fluctuations in *Dendroctonus frontalis* .

The populations of *Drepanosiphum platanoidis* (sycamore aphid) and *Zeiraphera diniana* (larch budmoth) provide arguably the best examples of periodic dynamics among insects (Fig. 4 and 5). Both visual examination and more formal analyses (e.g. estimating the autocorrelation functions; see Turchin and Taylor 1992) suggest that these two populations are characterized by complex periodic dynamics. Such cyclic populations provide an opportunity to test the ability of nonlinear modeling to accurately reconstruct complex dynamics from time series of real insect populations. The logic here is that if the method is not capable of reconstructing limit cycles and quasiperiodicity from data, than there is little hope that we can use it to detect chaos. If, on the other hand, we can accurately reconstruct complex dynamics such as limit cycles and quasiperiodicity, then confidence in our ability to reconstruct another kind, chaos, is correspondingly enhanced. Thus it is encouraging that the method accurately classified both populations (Fig. 4 and 5). Moreover, the extracted dynamics were very similar to the observed time series. First, RSM correctly indicated the period of dynamics: 2 years for sycamore aphid, and ≈ 8 years (observed: ≈ 9 years) for larch budmoth. Second, the relative amplitude of the oscillation was also accurately represented, especially when a stochastic exogenous component is included (Fig. 4 and 5).

The final case is that of *Phyllaphis fagi* (beech aphid), which was classified as chaotic. As in the case of limit cycles, the pattern of extracted dynamics has many features resembling the actual time series. Extracted dynamics were characterized by exponential growth for 3-4 years followed by crashes, interspersed by periods of rapid oscillations (Fig. 6). The observed series exhibited a similar pattern. However, the data did not exhibit a rigid regulatory ceiling that characterized the response surface simulations. We conclude that while the response-surface results are suggestive, the case for chaos in the beech aphid population is yet far from proven. Clearly, more years of observations, and possibly manipulative experiments, will be necessary before this question can be settled.

Voles in the Arctic

Violent fluctuations in microtine population density have long attracted attention of animal ecologists (e.g. Elton 1942). Subarctic and arctic voles and lemmings seem to be particularly prone to such ``boom and bust" dynamics (for example, cyclicity indices for vole populations in Fennoscandia increase from south to north; see Hansson and Henttonen 1985). There is much controversy surrounding the mechanistic causes of cycles in arctic rodents (Krebs and Myers 1974, Stenseth 1985, Hansson and Henttonen 1988). Some have even disputed the reality of microtine cycles (e.g. Getz et al. 1987). Thus the question of whether the endogenous dynamics of northern voles are stable, periodic, or possibly even chaotic remains unresolved.

Several long-term trapping programs have now generated time-series data of sufficient length for the analysis of population fluctuations in northern microtines. I analyzed time series from three localities: Kola Peninsula (Koshkina 1966), Alaska (Pitelka 1976), and Finnish Lapland (Henttonen et al. 1984, and Henttonen, personal communication). The last two data sets measured vole abundances twice a year: in the spring and in the fall. Having two observations per year creates two problems for time-series modeling of these data: (1) the data are not taken at equal time intervals, and (2) the population change reflects within-year seasonal fluctuations in abundance;

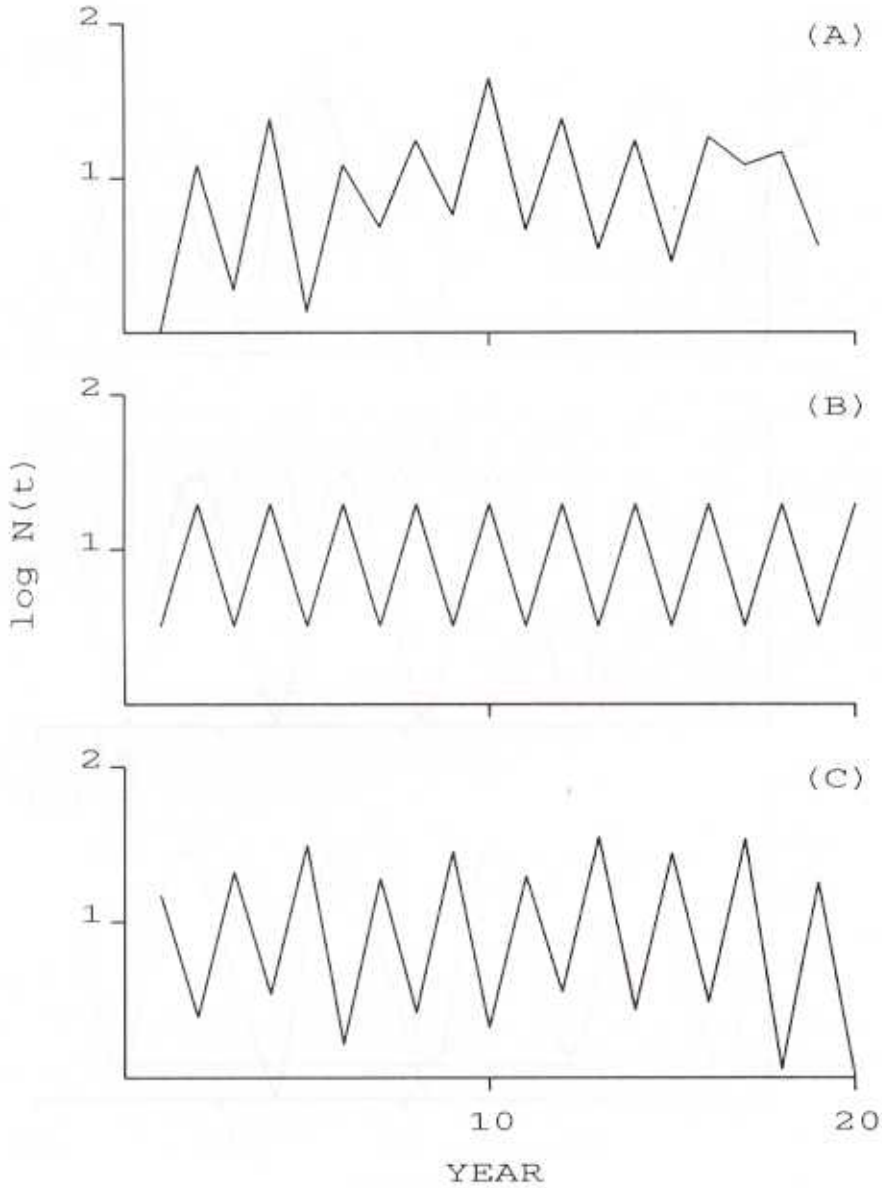

Figure 4. *Drepanosiphum platanoides* : observed time series (a), and trajectories predicted by the model (1) without noise (b), and with noise (c) (ε_t is normally distributed with mean zero and the standard deviation $\sigma = 0.2$).

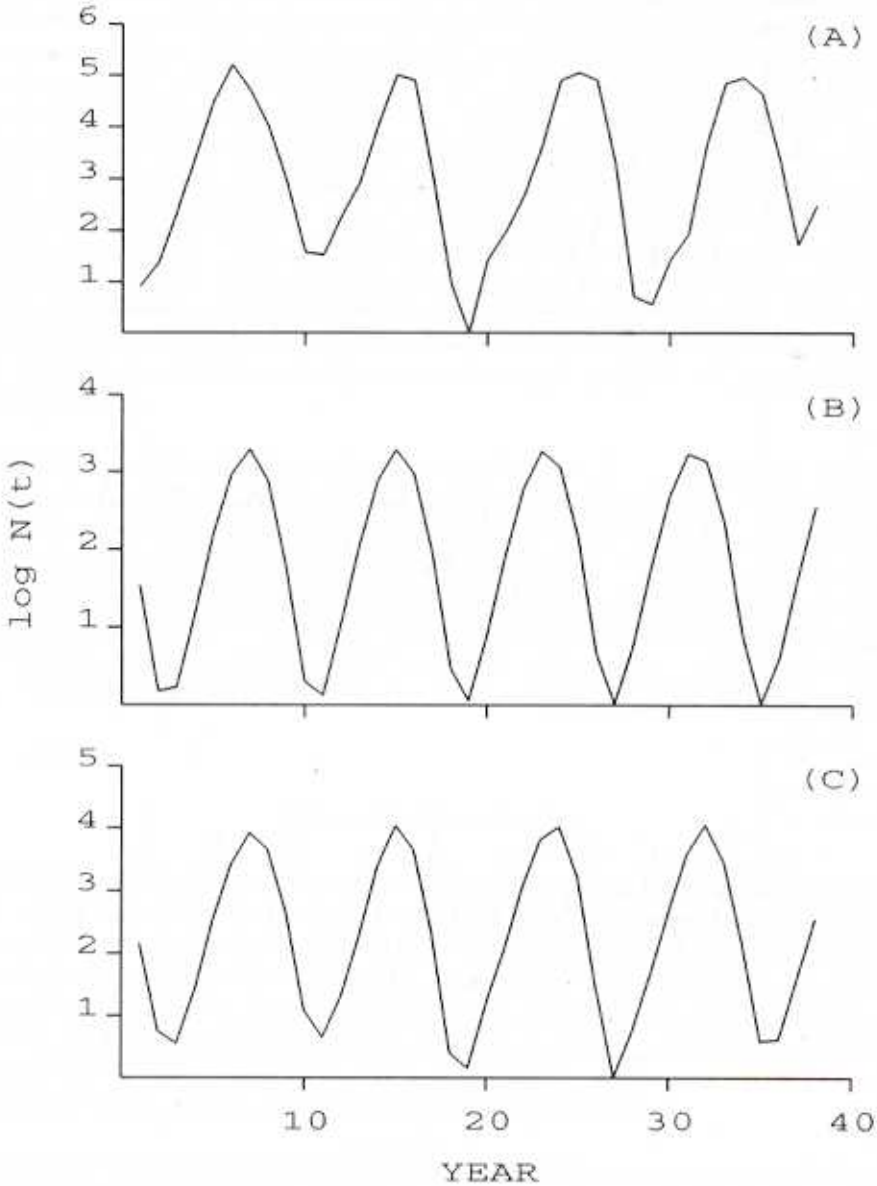

Figure 5. *Zeiraphera diniana* : observed time series (a), and trajectories predicted by the model (1) without noise (b), and with noise (c) (ε_t is normally distributed with mean zero and the standard deviation $\sigma = 0.2$).

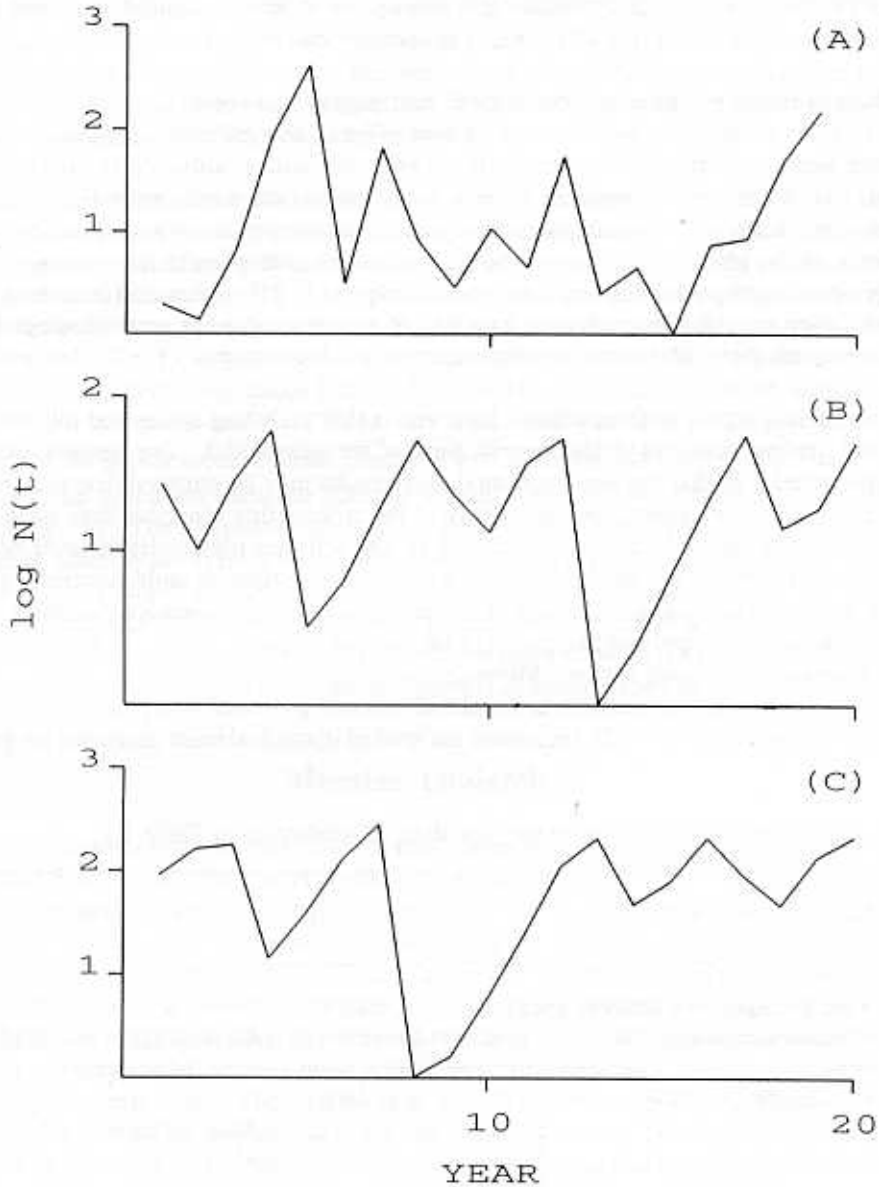

Figure 6. *Phyllaphis fagi* : observed time series (a), and trajectories predicted by the model (1) without noise (b), and with noise (c) (ε_t is normally distributed with mean zero and the standard deviation $\sigma = 0.2$).

that is, the process is non-stationary. In order to avoid these problems, I analyzed the spring and the fall series separately. This procedure also resulted in an increased number of time series for analysis, although fall and spring series are, of course, not true replicates.

Results of fitting response surfaces to these data suggest that population fluctuations of arctic voles may have a chaotic endogenous component. Out of five estimated Lyapunov exponents, three were positive (Table 2). Interestingly, in one case with positive Λ, the data from Kola Peninsula, the deterministic dynamics without noise settled onto a quasiperiodic attractor. This result suggests that environmental noise may force the population density to spend more time in those areas of the phase space where nearby trajectories diverge, and less where trajectories converge, resulting in overall divergence when averaged. If this explanation is correct, then the Kola population provides an interesting example of how nonlinear but non-chaotic endogenous dynamics may interact with exogenous stochasticity to produce chaos.

One troubling aspect of these results, however, is that analyzing spring and fall series in the Alaska and Lapland data sets yields opposite signs of the estimated Λ. One possible explanation of this discrepancy is that the nonlinear modeling results may be conservative with respect to detecting chaos. For example, non-stationarity of the process that generates data, or insufficient flexibility of response surface resulting in lack of fit, will bias the results in favor of stability (Turchin and Taylor 1992). I have already discussed how investigating multi-dimensional systems with low-dimensional models will result in mistakingly classifying complex dynamics as stable. This problem may well apply to the results of the two-lag response surface if the dimensionality of vole dynamics is three or higher. Moreover, noise also can mask chaotic dynamics, as was suggested by fitting response surfaces to simulated data sets generated by a predator-prey model in the chaotic regime (Turchin 1992). Increasing the level of dynamical noise decreased the proportion

Table 2. Fitting response surfaces to the vole data. (Columns as in Table 1.)

Source of data and species		Length	$\lvert\lambda\rvert$	Dynamics[1]	Λ
Kola Peninsula (Koshkina 1966)		25 y			
Clethrionomys spp.			1.06	QP	0.29
Alaska (Pitelka 1976)		18 y			
Lemmus	Spring		1.36	Chaos	0.55
Lemmus	Fall		0.61	OS	-0.48
Finnish Lapland (Henttonen *et al.* 1984)		25 y			
All species	Spring		0.86	OS	-0.16
All species	Fall		1.07	Chaos	0.03

[1] Dynamics obtained by iterating model (1) wihtout noise. OS = oscillatory stable, QP = quadsiperiodic.

of simulated data sets that were correctly classified as chaotic from 80% to 30%. By contrast, increasing noise level in the generating model with stable endogenous dynamics did not increase the proportion of data sets that were misclassified as chaotic; this proportion stayed below 1%. In short, it appears that any mechanism that increases the scatter of data points around the response surface will bias the results in favor of stability. Thus finding two of the five real-world data series classified as stable is perhaps not surprising.

A close examination of one of the data series, the fall numbers of voles in Finnish Lapland, provides further insights into the nature of vole population fluctuations. Between 1964 and 1986 the population underwent four well-defined outbreaks (Fig. 7a). However, the outbreak duration varied from three to six years (Fig. 7a). The autocorrelation function rapidly decays to zero, indicating that periodicity is not very strong (Fig. 7a). A two-lag quadratic response surface fits the data very well (Fig. 8), suggesting that a large proportion of variation in population change is explained by the action of endogenous factors ($R^2 = 0.81$). The intrinsic rate of increase of this population, r_0, is estimated as 5.5. This is very high -- for example, simple one-dimensional models such as the Ricker model become chaotic at $r_0 \approx 2.7$ (May and Oster 1976). The dynamics generated by the estimated response surface without noise are very similar to the observed dynamics (Fig. 7b). The Lyapunov exponent of the system without noise is relatively small at 0.10. Adding noise to the system further decreases it to 0.03, suggesting that in this case noise makes the system more stable. Interestingly, the attractor characterizing the estimated deterministic dynamics consists of four distinct pieces. In short, these results suggest a case of ``weak chaos": a system not very far from a bifurcation point between a four-point limit cycle and chaos, with strong periodicities still evident in temporal dynamics (see Fig. 7b).

Measles epidemics

Measles epidemics have recently received much attention as possible cases of chaos in ecology (Schaffer and Kot 1985b, Olsen et al. 1988, Olsen and Schaffer 1990). The case for chaos in measles is supported by two complementary lines of evidence: analyses of time-series data using the reconstruction technique, and *a priori* modeling using the SEIR (susceptible-exposed-infectious-recovered) framework (for review see Schaffer et al. 1990). Olsen et al. (1988) have also calculated Lyapunov exponents for a number of data sets. However, they defined the Lyapunov exponent as the rate of trajectory divergence due to combined effects of endogenous dynamics and noise. This definition is not very useful, because noise will always cause trajectory divergence, and therefore positive Lyapunov exponents. Thus, Olsen et al. (1988) estimated positive Lyapunov exponents both for measles and for the disease that is not chaotic, chicken pox. The definition of Λ that I use here does not suffer from this problem, and thus it could be instructive to apply the method of non-linear modeling to measles data sets.

Measles data sets consist of monthly cases reports. Analyzing monthly data directly, however, has a disadvantage in that the generating process is not stationary, since there is a systematic seasonal variation in contact rates. Seasonally driven variation in contact rates causing annual peaks is well understood (London and Yorke 1973). The interesting question is whether interannual fluctuations are chaotic (at least in part), or whether the irregularity in fluctuations is due entirely to exogenous factors. Accordingly, I aggregated monthly cases into the total number

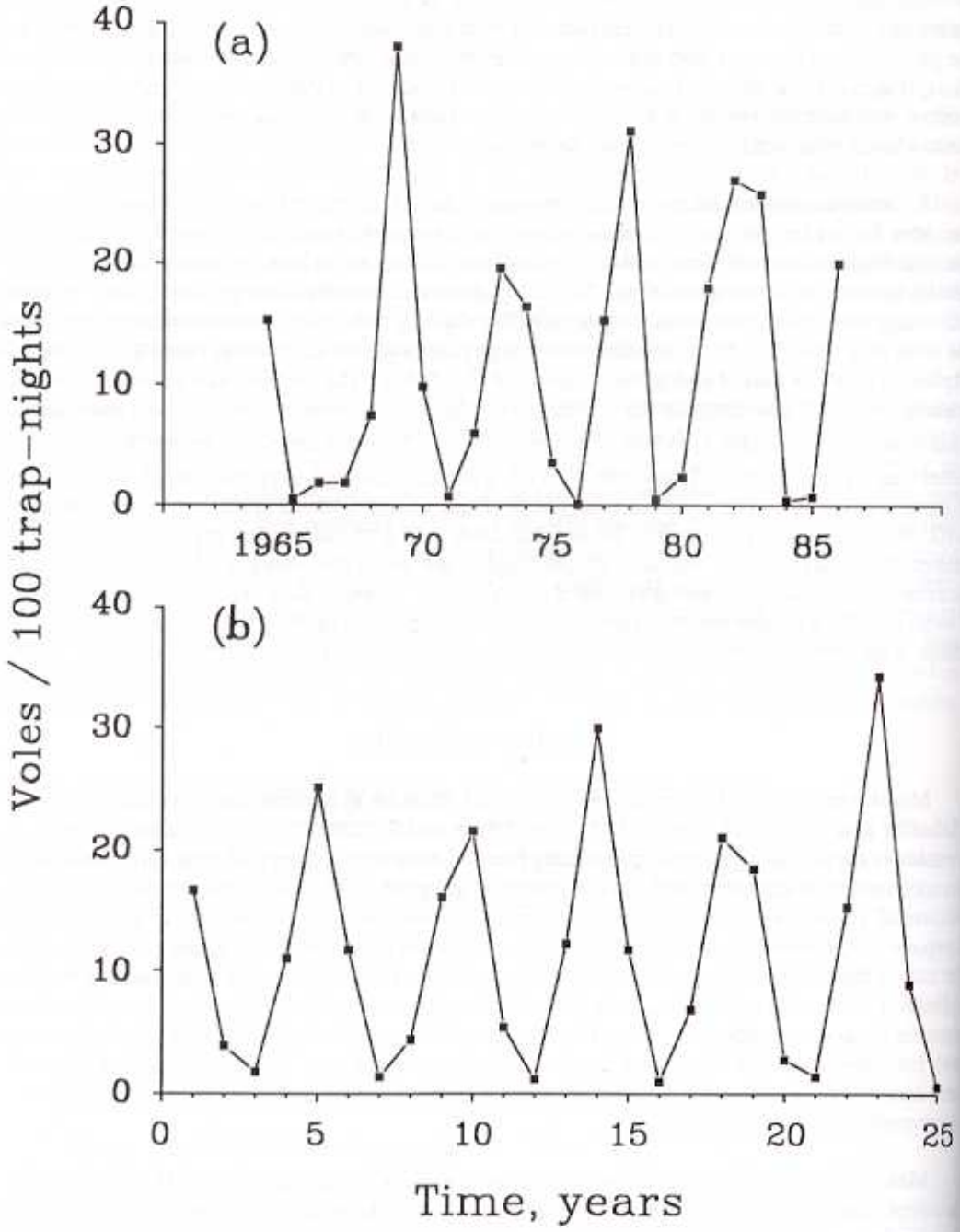

Figure 7. (a) Time series of vole population density in Finnish Lapland. (b) A sample trajectory generated by the model (1) without noise with parameters estimated by fitting vole data.

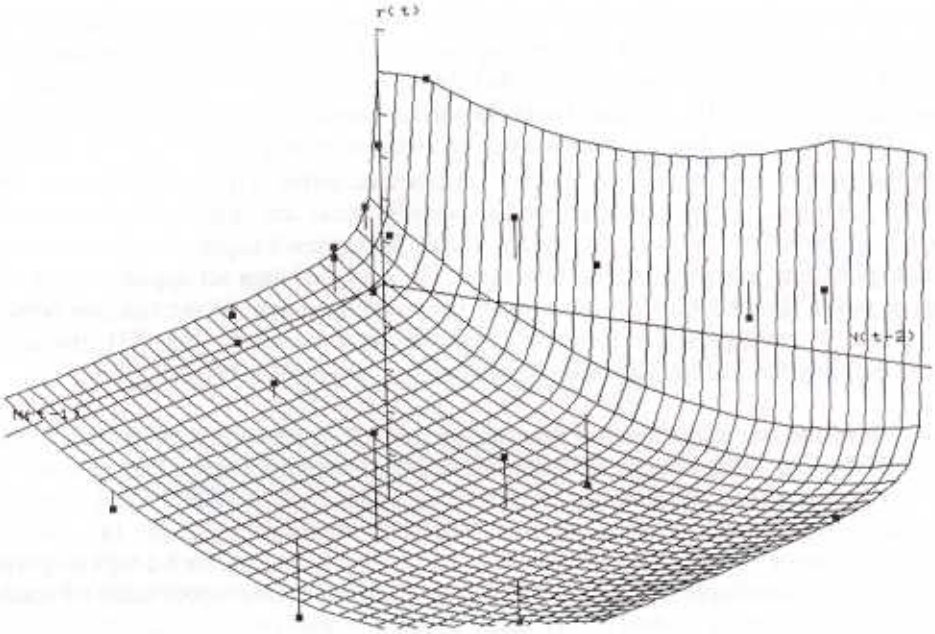

Figure 8. The response surface estimated for r_t as a function of N_{t-1} and N_{t-2} (voles in Finnish Lapland). Data points are plotted as triplets (r_t, N_{t-1}, N_{t-2}) in the three dimensional space. The length of the line connecting each data point to the estimated surface indicates the magnitude of the residual.

of cases reported each year. This procedure also has the advantage of reducing the influence of observation errors present in each monthly report, as well as any systematic biases that could cause under-reporting in some months compared to others.

I begin with a detailed analysis of one data set, measles in Baltimore. This time series illustrates the problem common to many long-term data sets: lack of stationarity. For the first 25 y (1928-1952) the population trajectory appears to be stationary, undergoing erratic fluctuations with approximately the same mean and variance (Fig. 9). After 1952, however, the nature of fluctuations changes: the system goes into a 2-point oscillation of decreasing amplitude and then it converges almost to a steady state. During the mid-sixties another change takes place: the number of reported cases declines dramatically. The cause of the latter change is known: widespread use of vaccination in the early 1960s (London and Yorke 1973). The paradox exemplified by this data set is that many data points are necessary to accurately quantify the nature of dynamics. The longer the time series, however, the more likely it is that environmental conditions will change, which could in turn change the dynamics. One possible approach is to break up long data series into several shorter pieces, and model each separately. This is the approach that I will follow here. Another approach is to add the time dimension to the space within which the time series is embedded. This approach (currently under investigation) is promising because it could allow us to explicitly model temporal changes in dynamics.

Estimating a response surface for the first 25 y of Baltimore data yields a striking result: although temporal fluctuations look very erratic, suggesting noisy dynamics, embedding the time series in three-dimensional space reveals that the data points are clustered close to a two-dimensional surface (Fig. 10). The fitted response surface captures a high percentage of variance in r_t: $R^2 = 0.91$ (also note that the intrinsic rate of increase is very high: $r_0 = 5$). This result suggests that the primary cause of fluctuations in this time series may be endogenous. Indeed, trajectories generated by the estimated surface without noise are chaotic (Fig. 11b), and the estimated Λ of the noisy system is 0.42 bit / y, one of the highest Lyapunov exponents extracted from ecological data sets discussed in this paper. In sum, this data set appears to provide an example of how a simple functional relationship between population change and past population density (Fig. 10) can produce very complicated temporal dynamics (Fig. 11), the idea that motivated the early fascination with chaos in ecology (e.g. May 1974, 1976).

Analysis of the rest of the measles data sets reveals a high proportion of positive Lyapunov exponents (Table 3). To ameliorate the influence of nonstationarity, I broke long data sets (more than 40 y) into two pieces, and analyzed each piece separately (e.g. Bornholm 1 and 2 in Table 3). I have also detrended series where doing so substantially improved R^2 of the fit. The results indicated that 7 out of 13 series were characterized by positive Λ. Again, such a high proportion of positive Λs is a strong indication that measles dynamics tend to be chaotic, since the method is biased in favor of finding stability, and many apparently non-chaotic cases may have been misclassified as a result of a too low embedding dimension and noise. In fact, a more detailed analysis of the New York data showed that increasing the embedding dimension to three produces a positive estimate of Λ. This result agrees with the conclusions of Ellner (this volume), who also found that one needs at least three lags to correctly estimate Λ for New York measles (see Ellner's Fig. 9).

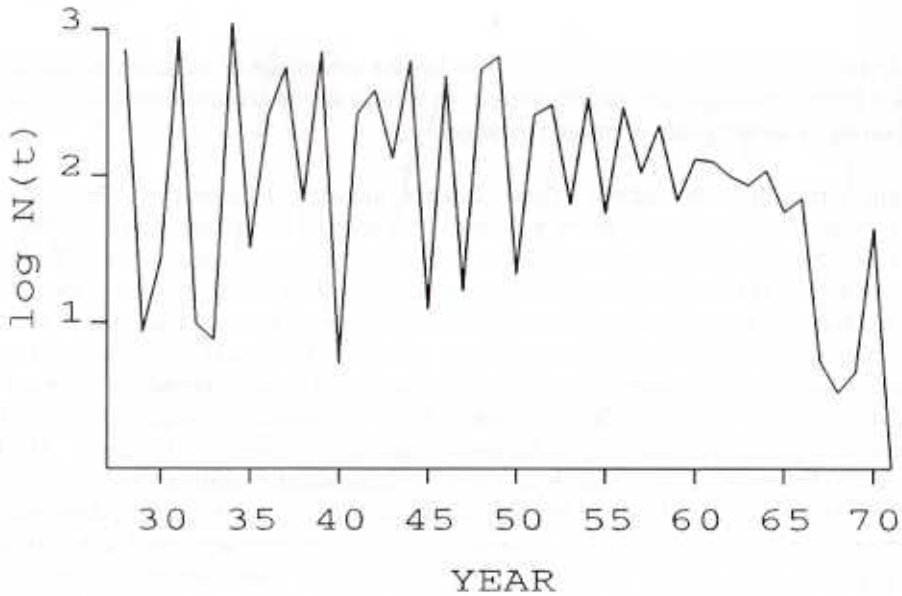

Figure 9. Annual cases reports of measles in Baltimore, 1928-1972.

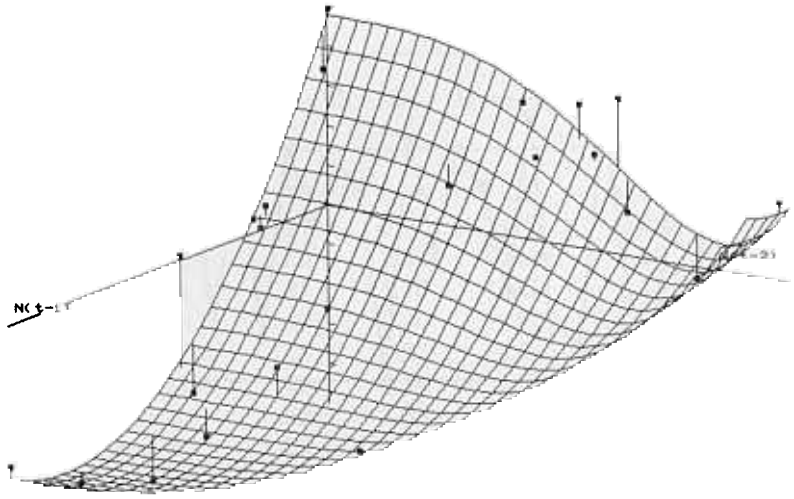

Figure 10. The response surface estimated for the Baltimore measles data (1928-1952).

Conclusion

In summary, nonlinear modeling of ecological time series reveals a rich spectrum of complex dynamical behaviors. In two data sets, voles and measles, the frequency of positive Lyapunov exponents appears to be too high to be easily explained away as spurious. There is also a real possibility that many higher-dimensional complex dynamical behaviors have been misclassified as noisy stability. On the other hand, the data sets analyzed here represent organisms with high intrinsic rates of increase, whose dynamics frequently exhibit violent fluctuations in population density. It is likely that complex dynamics will be more frequent in such systems.

It is often argued that populations characterized by chaotic dynamics will be eliminated by natural selection, because such populations would go through periods of low density, during which population extinctions would be likely (Berryman and Millstein 1989). One can argue in the same fashion about populations characterized by limit cycles, since they would also go through periods of low density. This argument is suspect because it is basically a group-selectionist argument. Individual selection, by contrast, is expected to favor high intrinsic rates of increase, thus promoting the possibility of limit cycles and chaos.

The danger of extinction in chaotic populations is more apparent than real, especially for populations of abundant organisms (such as insects that are characterized by high average population densities). In many population models chaotic fluctuations can have a relatively low amplitude of fluctuation, e.g. two orders of magnitude. Populations of real insects typically fluctuate with much higher amplitudes: 10 out of the 13 insects in Table 1 undergo fluctuations with amplitude of 3 orders of magnitude or higher. One of these populations, the larch budmoth, oscillates with more than 5 orders of magnitude! Nevertheless, despite such extreme fluctuations,

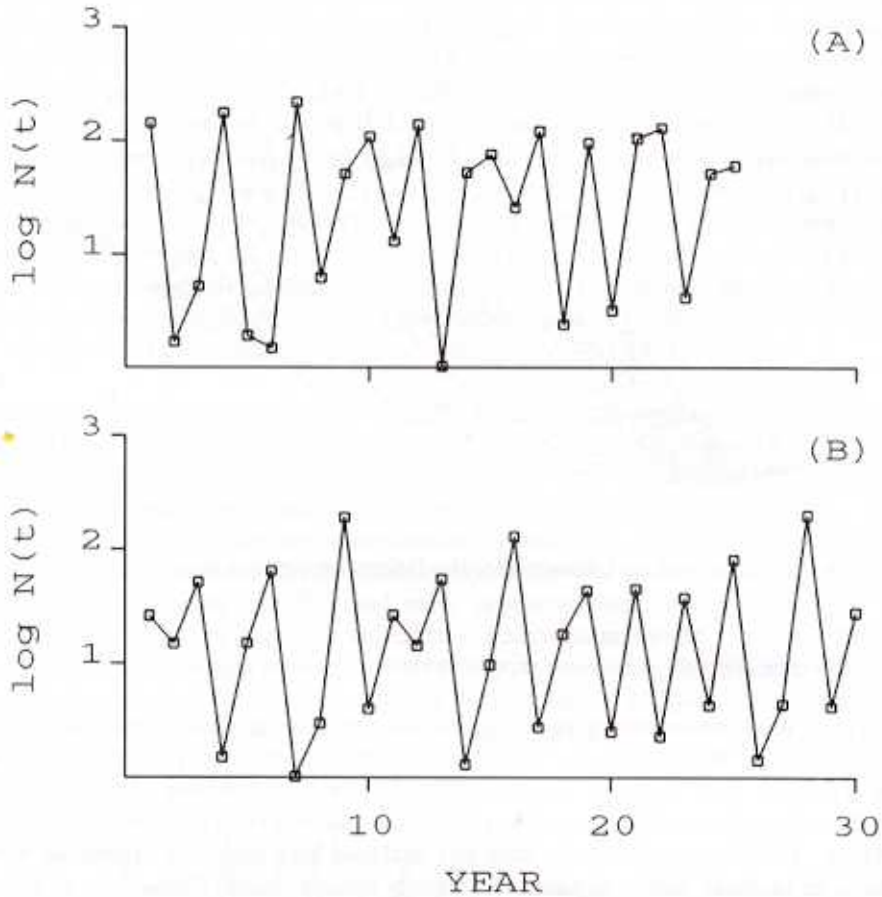

Figure 11. (a) Annual cases reports for measles in Baltimore from 1928 to 1952 (observed time series). (b) A sample trajectory generated by the model (1) without noise; parameters estimated by fitting Baltimore measles data.

and the prayers of Swiss foresters, the larch budmoth exhibits no signs of going extinct. Moreover, under certain circumstances chaos may actually reduce the probability of extinction, rather than increase it. Recent results in metapopulation theory indicate that persistence at the metapopulation level is promoted by asynchrony among the subpopulations (Reeve 1988). Sensitive dependence on initial conditions means that two subpopulations starting from almost identical initial conditions will diverge very rapidly. Thus chaos promotes asynchrony, and therefore metapopulation persistence. This idea was recently investigated with metapopulation models in which global climate patterns cause synchronization among subpopulation fluctuations, and it was shown that probability of persistence is enhanced when local populations fluctuate chaotically (Jon Allen, pers. comm.).

Table 3. Fitting response surfaces to the measles data. (Columns as in Table 1.)

Source of data	Length	$\lvert\lambda\rvert$	Dynamics[1]	Λ
Aberdeen	20 y	0.86	OS	-0.19
Baltimore Co.	27 y	0.57	OS	-0.23
Baltimore	25 y	2.69	Chaos	0.42
Bornholm 1	21 y	1.10	LC	0.13
Bornholm 2	22 y	0.60	OS	-0.12
Copenhagen 1	20 y	1.37	LC	0.05
Copenhagen 2	20 y	2.34	LC	0.25
Detroit 1	22 y	1.53	Chaos	0.14
Detroit 2	21 y	1.99	LC	0.34
Milwaukee 1	27 y	1.27	LC	0.23
Milwaukee 2	27 y	0.78	OS	-0.03
New York	36 y	1.14	LC	-0.13
St. Louis	20 y	0.77	OS	-0.09

[1] Dynamics obtained by iterating model (1) without noise.

I have argued in this paper that applied ecologists and, in particular, forest managers should seriously consider the possibility of complex dynamical behaviors in natural populations. It is easy to blame weather for insect outbreaks, but the reality may be that populations of many forest insect pests fluctuate in response to density-dependent factors, such as interactions with resources or natural enemies. This is not a pessimistic conclusion. On the contrary, if outbreaks of a forest pest are caused by climatic fluctuations, little can be done about preventing them until we learn to regulate weather. On the other hand, if outbreaks are driven, for example, by a cyclical interaction with predators, then a judicious program of biocontrol might help keep the pest in check.

Acknowledgments

I am grateful to A. Berryman, J. Hayes, J. Reeve, G. Simmons, and A. Taylor for reading and commenting on the manuscript. I also thank S. Ellner for many helpful discussions, and in particular for pointing out that the definition of the Lyapunov exponent can be generalized for noisy systems.

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Detecting Low-Dimensional Chaos in Population Dynamics Data: a Critical Review

Stephen Ellner[1]

Introduction

Methods of analyzing time series data for evidence of chaotic dynamics have been extensively developed and applied over the last ten years, and as a result chaos is now recognized as a frequently occurring phenomenon in physical, chemical, and physiological systems (for surveys see, e.g., Olsen and Degn 1985, Mayer-Kress 1986, Schuster 1988, Glass and Mackey 1988, Krasner 1990). These methods have been applied to data on the dynamics of natural populations, with the conclusion that there is evidence for low-dimensional chaotic dynamics (Schaffer 1984; Schaffer and Kot 1985a, b,1986; Kot et al. 1988; Schaffer et al. 1990; Olsen et al. 1988; Sugihara and May 1990), but the validity of these analyses remains controversial (May 1987a, b; Pool 1989a, b; Berryman and Millstein 1989; Kot et al. 1988).

In this paper, my goal is to show by example that many of the features that have been presented as evidence for chaos in population dynamics can also be observed in simulated data from non-chaotic, stochastic population models. I also identify the qualitative properties that create the spurious impression of chaos. In brief, population fluctuations with a constant period (e.g., one outbreak each year) but variations in amplitude (some outbreaks larger than others) can easily have features that have been interpreted as evidence for chaos, even in cases where chaos is not actually present.

These results leave moot the question of whether or not the populations are actually chaotic. Their implication is simply that methods of "detecting" chaos imported from other disciplines should not be accepted uncritically, without examining their ability to tell the difference between true chaos, and plausible alternative explanations. What is plausible depends on the system under study, so a method that is perfectly reliable when treating chemical reactions or fluid dynamics in the laboratory, may be unreliable when applied to the dynamics of natural populations in the field. Population dynamics may be expected to exhibit unambiguous temporal structure for reasons unrelated to the presence or absence of chaos -- e.g., overlapping generations, limits to rates of increase or decrease, seasonality and other gradual trends in environmental conditions -- and it is necessary to determine if a method for detecting chaos can be fooled by these other sources of regularity. My contention here is that some methods that have been, and are currently, in use are unreliable for exactly this reason: the non-random structure they reveal is genuinely present, but it may not be a sign of chaos. I also review more careful uses of current methods, and describe methods now in development whose assumptions are more realistic for applications to population dynamics.

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Reconstructing Chaotic Attractors

Much of the evidence for chaos in population dynamics is based on graphical attractor reconstruction in time-delay co-ordinates, originally suggested by Ruelle (Packard et al. 1980) and first applied to population dynamics by Schaffer and Kot (Schaffer 1984, Schaffer and Kot 1985a, b). To illustrate this method and its potential effectiveness in unmasking chaos, Fig. 1 shows its application to the Rössler differential equations, a standard example of chaos in a simple nonlinear system (Schuster 1988). The Rössler equations are the three-variable system

$$\frac{dx}{dt} = -z-y, \quad \frac{dy}{dt} = x+0.15y, \quad \frac{dz}{dt} = 0.2+z(x-10),$$

but the simulated "data set" consists of only $x(t)$, to mimic a situation in which data are available on only one species out of a multi-species community. To obtain a chaotic attractor with the visual appearance of population outbreaks, the values of $x(t)$ were exponentially transformed ($x \rightarrow \exp(a+bx)$), but the transformation has no effect on the qualitative properties used as evidence of chaos (Eckmann and Ruelle 1985).

When the data are plotted as "population" abundance $x(t)$ versus t (Fig. 1a), there is a clear periodicity in the timing of outbreaks but no regular pattern in their magnitudes, and one might easily conclude that the fluctuations in outbreak magnitude are random. However, attractor reconstruction demonstrates that the fluctuations are entirely deterministic. (Here "random" means that future outbreak magnitudes cannot be predicted based on events up to the present, such as past outbreak magnitudes or past values of exogenous variables affecting the system; a "deterministic" process is one which in principle can be predicted in advance, given sufficient information about events up to the present). For reconstruction in 3-dimensional space, the data values $\{x(t), t=1, \ldots N\}$ are used to construct the points $X(t) = (x(t), x(t+L), x(t+2L))$; L is called the *lag* or *time-delay*. These points are connected in temporal sequence by a smooth curve (here, a cubic spline interpolation) to draw the "reconstructed" trajectory in 3-space (Fig. 1b). This trajectory is clearly not just wandering at random, but instead traces out a low-dimensional object (the *attractor*) that appears to lie within a 2-dimensional surface.

This visual impression is strengthened by taking a slice through the attractor (called a *Poincaré section*, shown in Fig. 1b as a vertical plane) and looking head-on at the points where the trajectory crosses the section (Fig. 1c). The points all lie in a thin band, indicating a one-dimensional intersection between the attractor and the Poincaré section. A truly one-dimensional intersection with zero thickness would imply that the attractor is contained in a two-dimensional surface (in fact the fractal dimension of this attractor is slightly above 2, but an accurate determination of the dimension requires more data than are shown here).

Finally, graphing the relationship between successive points on the section (called the *Poincaré map*, Fig. 1d) generates points that lie on a single curve. The significance of finding such a simple Poincaré map, rather than a haphazard scatter of points, is that it reveals an underlying deterministic rule for the dynamics: given exact knowledge of the population's abundance in the past, future changes in abundance can be predicted with perfect accuracy. The essential last step is the conclusion that these same properties hold in the full multi-variable

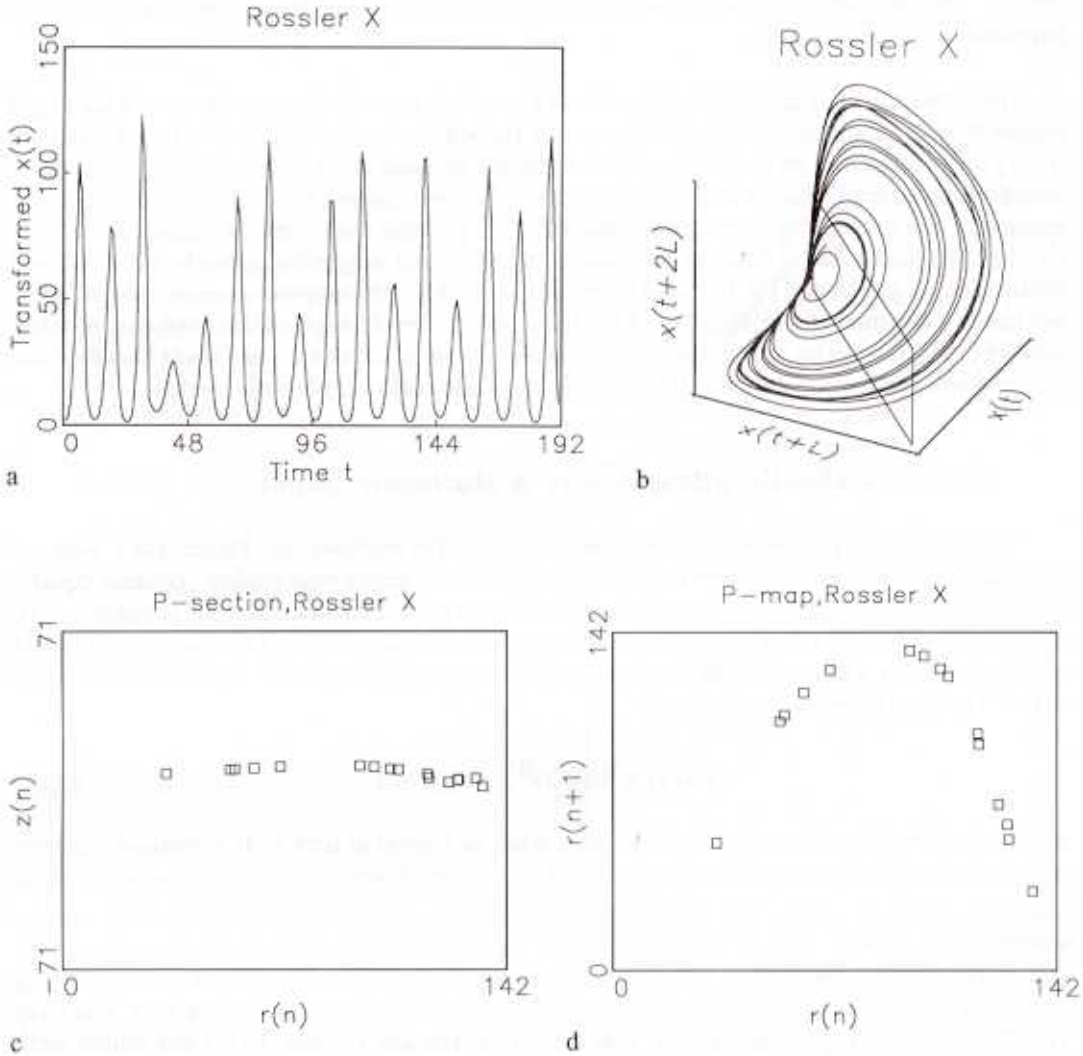

Figure 1. Attractor reconstruction for data produced by the Rössler equations. (a) The simulated "data", $N = 200$ values of a single variable $x(t)$. (b) The reconstructed attractor in 3-space with $L = 1$ time unit. (c) A Poincaré section. This is a head-on view of the vertical plane outlined in Fig. 1b, showing the locations where the trajectories cross from behind the plane to in front of it. r_n is the radius (horizontal distance from the left edge of the plane) at the nth crossing, and z_n is the vertical coordinate (i.e., z_n is the value of $x(t+2L)$ at the nth crossing time). (d) The corresponding Poincaré map, which is the graph of r_{n+1} vs. r_n for the section-crossing points shown in Fig. 1c. The numerical solutions of the Rössler equations were obtained by fourth-order Runge-Kutta with variable stepsize (Press et al. 1989), for $t = 0$ to 200 with initial values $(x_0, y_0, z_0) = (10, 0, 0)$; the values of $x(t)$ at $t = 100.5, 101, 101.5, \cdots 200$ were recorded.

system. Takens' Theorem (Takens 1981, Schuster 1988) asserts that this is true, if a sufficiently large number of lags are used.

How does reconstruction fare with real-world population data? Apparently, quite well. Fig. 2 repeats Schaffer and Kot's (1985b, 1986) attractor reconstruction for Davidson and Andrewartha's (1948) frequently-cited study of outbreaks of the apple blossom thrips *Thrips imaginis*. Using the monthly census data (shown in Fig. 2a) as $x(t)$ and reconstructing in 3-dimensional space, an apparently low-dimensional attractor is obtained (Fig. 2b), that resembles the Rössler attractor in Fig. 1a. The points on the Poincaré sections lie in a thin band, suggesting a nearly 1-dimensional intersection (Fig. 2c), and the Poincaré map for *Thrips* (Fig. 2b) suggests a single smooth curve and hence a deterministic explanation of the fluctuations. On the basis of this evidence, Schaffer and Kot (1986) list *Thrips* among "apparent examples of real-world chaos," and reject Davidson and Andrewartha's earlier conclusion that the magnitude of outbreaks is essentially random.

Spurious chaotic attractors in a stochastic population model

The results in Fig. 2 reveal some regular structure in the outbreaks of *Thrips*; but it does not necessarily follow that the outbreak magnitudes are chaotic rather than random, because equally convincing "evidence" for chaos can be generated by non-chaotic models for this population. To illustrate this claim, I use a simple stochastic population model inspired by Bulmer (1974), in which seasonality and bounded rates of change produce temporal structure that mimic features of chaos. The specific model is

$$x(t+1) = \lambda(t)x(t)^{\beta}, \quad 0 < \beta < 1, \tag{1}$$

where $x(t)$ is the population density (# of individuals or #/area) at time t. If λ remains constant over time, then (1) is a conventional-type model for density-dependent population growth, whose solutions converge to the stable equilibrium $x = \lambda^{1/(1-\beta)}$. The fluctuations in λ represent two sources of variation in the population's vital rates: periodic (e.g. seasonal) variations, and year-to-year environmental variability. These are not *ad hoc* assumptions for the sake of mimicking chaos, but have been recognized by other modelers for populations on which long-term data were available (Bulmer 1974, London and Yorke 1973, Yorke and London 1973) and which were subsequently analyzed for evidence of chaos (Schaffer 1984; Schaffer and Kot 1985a, b,1986; Schaffer et al. 1990; Sugihara and May 1990). For example, models of infectious diseases in human populations often include seasonally varying contact rates; and Bulmer (1974), applying model (1) to Canadian wildlife, invoked periodic variations in prey abundance to explain the periodic component in predator growth rate. However, like many "strategic" models in population biology, model (1) is used here as a heuristic device to help elucidate general properties of more complicated systems, without claiming that it is quantitatively accurate for any specific population.

Following Bulmer (1974), I used the log-additive form

$$\ln \lambda(t) = \mu + p(t) + \sigma Z(t) \tag{2}$$

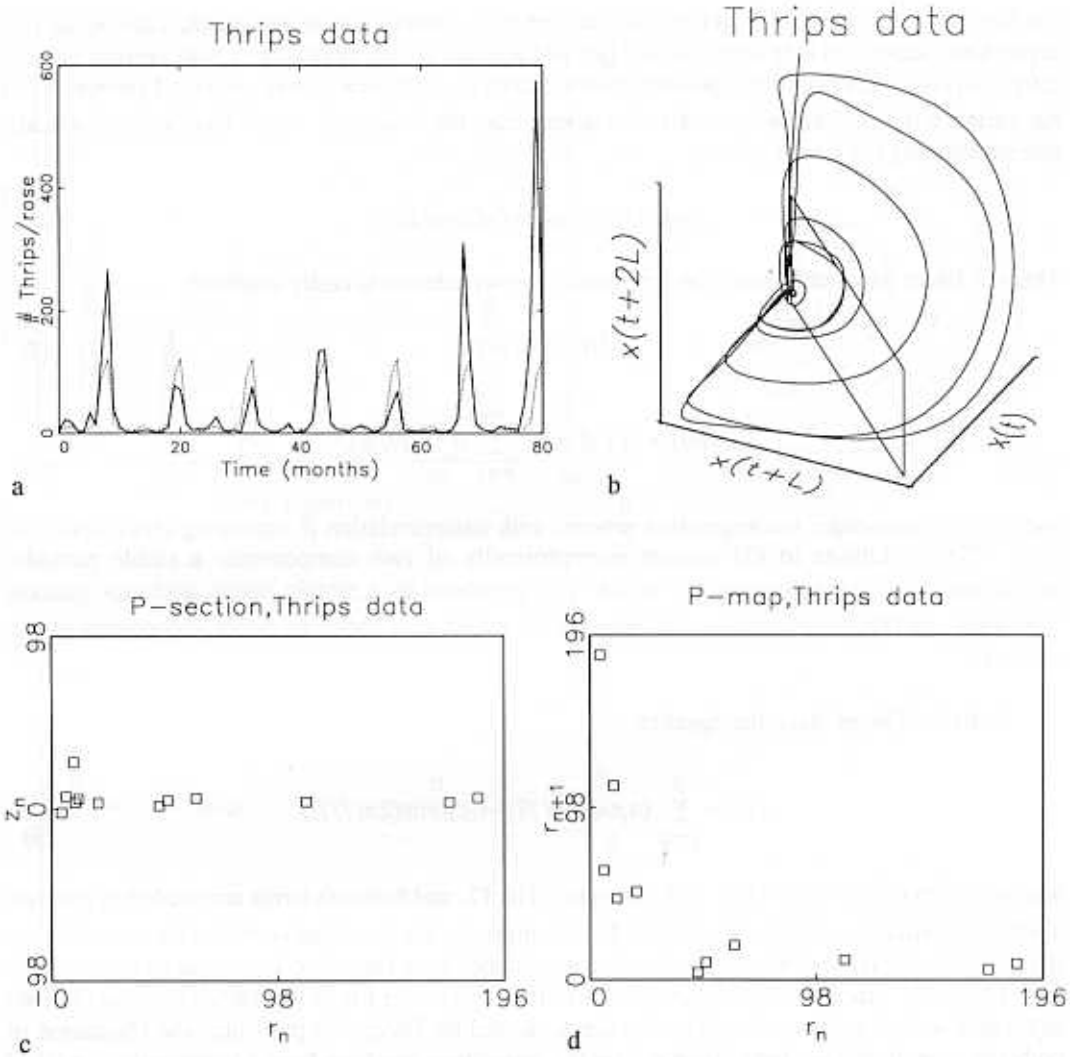

Figure 2. Attractor reconstruction for monthly census data on *Thrips imaginis* (Davidson and Andrewartha 1948). (a) The monthly census data [solid], N = 81 monthly values, and the estimated periodic component $x(t) = \exp(y_p(t))$ [dots]. (b) The reconstructed attractor in 3-space with L = 2 months. (c) Poincaré section and (d) Poincaré map for the *Thrips* census data. Following Schaffer and Kot's (1985a, b;1986) procedures, the data were smoothed by taking a 3-point running average prior to reconstruction, and a cubic spline interpolation was used to draw the trajectory in (b) and to determine the section-crossing points.

for the input function $\lambda(t)$. $\mu+p(t)$ is the periodic component of the input, consisting (on logarithmic scale) of a long-term average (μ), and periodic trends in vital rates with average value 0 ($p(t)$). $Z(t)$ is a sequence of independent random variables with mean 0 and variance 1 (hence $\sigma Z(t)$ has variance σ^2), representing random deviations from the "seasonal" trend. Defining $y(t) = \ln x(t)$ and substituting (2) into (1), gives

$$y(t+1) = \mu+p(t)+\beta y(t)+\sigma Z(t). \tag{3}$$

This is a linear equation; hence, the asymptotic ($t\rightarrow\infty$) solution is easily obtained:

$$y(t) = y_p(t)+\varepsilon(t), \tag{4}$$

where

$$y_p(t) = \mu(1-\beta)^{-1} + \sum_{k=1}^{\infty} \beta^{k-1} p(t-k), \tag{5}$$

and $\varepsilon(t)$ is a first-order autoregressive process with autocorrelation β, satisfying $\varepsilon(t+1)=\beta\varepsilon(t)+\sigma Z(t)$. Thus solutions to (3) consist asymptotically of two components: a stable periodic oscillation $y_p(t)$, and superimposed "noise" $\varepsilon(t)$ generated by a simple linear stochastic process. The solutions are never chaotic, and there is no underlying chaos in either component of the solution.

To fit the *Thrips* data, the equation

$$p(t) = \sum_{i=1}^{3} (a_i \sin(2\pi t/T_i) + b_i(\cos(2\pi t/T_i)) \tag{6}$$

was used with periods T_i = 12, 6, and 3 months. The 12- and 6-month terms are needed to generate alternating outbreak amplitudes; the third term improves the quantitative fit but has no effect on the qualitative results. Parameter values were estimated by a two-stage least squares method (see Fig. 3 legend). Since these parameters are strictly *a posteriori* fits to the *Thrips* data, similarities to the data are not evidence that (1) is the correct model for *Thrips*. In particular, the alternation of outbreak magnitudes has been "built in" via (6), rather than resulting from a mechanistic model of population regulation subject only to annual forcing. Such a model would be preferable, but the information needed to build it (e.g., density responses, interactions with other organisms, ...) is lacking. The point of using (6) with parameters estimated from the data is that spurious evidence of low-dimensional chaos is not found only at biologically implausible or carefully hand-picked parameter values.

Fig. 3 shows reconstruction applied to a typical simulation of model (1) with estimated parameters for *Thrips* (Fig. 3a), duplicating the analysis of the real census data in Fig. 2. With similar length time-series, the model produces an equally convincing visual impression of a low-dimensional attractor (Fig. 3b), even though it does not have a finite-dimensional attractor. In fact with a suitable choice of time-delay L, very similar "attractors" are easily obtained from virtually any data $x(t)$ in which (i) there are large outbreaks that are similar in shape and duration but have

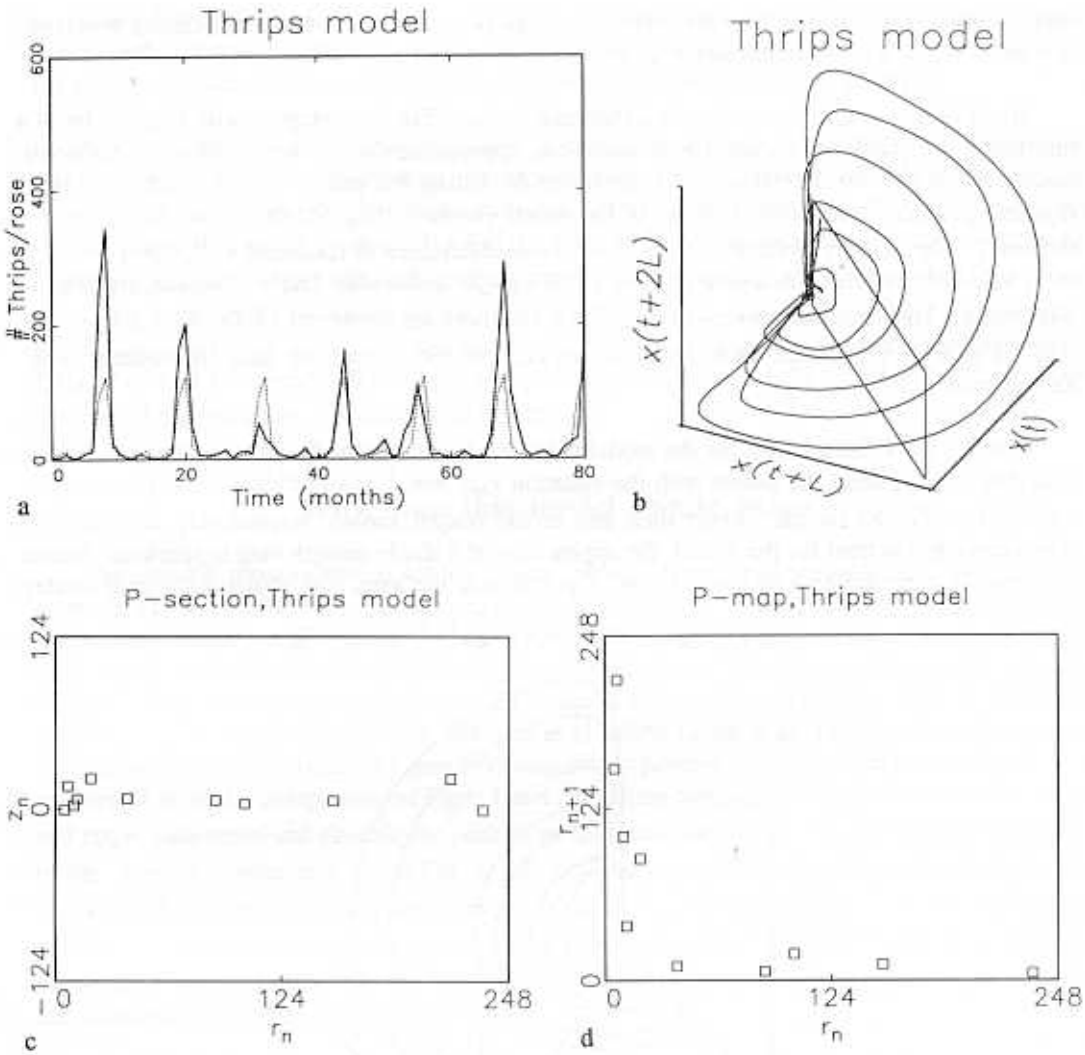

Figure 3. Application of equation (1) to *Thrips imaginis*. (a) A set of simulated census "data" [solid], N = 81 monthly values, and the periodic component $x_p(t) = \exp(y_p(t))$ [dots]. (b) Reconstructed attractor for the simulated data in 3-space with $L = 2$ months. (c) Poincaré section and (d) Poincaré map for the simulated census data. The parameter values for the simulation were $a_1 = -0.85$, $a_2 = 1.11$, $a_3 = -0.16$, $b_1 = -0.87$, $b_2 = 0.02$, $b_3 = 0.34$, $\sigma = 0.77$, $\mu = 2.36$, $\beta = 0.52$. The a_i, b_i, and μ were chosen to minimize $\Sigma\varepsilon(t)^2$ for $y(t)$ = observed values of ln(*Thrips* abundance), and then β and σ were estimated by fitting an AR(1) model to $\varepsilon(t)$. In both stages the model is linear in the parameters, so estimates were obtained by ordinary least squares. Maximum likelihood parameter estimates assuming Gaussian $Z(t)$'s (proc AUTOREG in GAUSS) were nearly identical. The simulated data were smoothed and interpolated as in Fig. 2.

varying amplitudes; and (ii) there are extended periods of time between outbreaks, during which $x(t)$ is small compared to the outbreaks (e.g., Fig. 4).

As in Figs. 1 and 2, the points on a Poincaré section (Fig. 3c; compare with Fig. 2c) lie in a thin band. A quantitative measure of thickness, appropriate for the nearly linear relationship among the points on the section, was obtained by fitting the points with a quadratic curve, regressing z_n (the vertical co-ordinate of the points shown in Fig. 3c) on r_n (the horizontal co-ordinate). The measure of thickness was θ = (standard deviation of residuals) ÷ (standard deviation of r_n values). In 250 simulations of model (1), $\log_{10}\theta$ had a very nearly Gaussian distribution with mean −1.15, standard deviation 0.33. The thickness for the actual *Thrips* data, $\log_{10}\theta = -0.98$, is entirely consistent with these values; i.e., the model and the data are equally "low-dimensional".

Finally, the Poincaré map for the model (Fig. 3d) is essentially the same as that seen in the data (Fig. 2d). Fitting the points with the equation $r_{n+1} = a r_n^b$ is significant in both cases ($P < .001$, $R^2 = .77, .83$ for the *Thrips* data and model output shown, respectively, in a log-log regression), but at least for the model, the appearance of a single smooth map is spurious. Model (1) actually generates two separate clouds of points near the axes, one showing the relationship

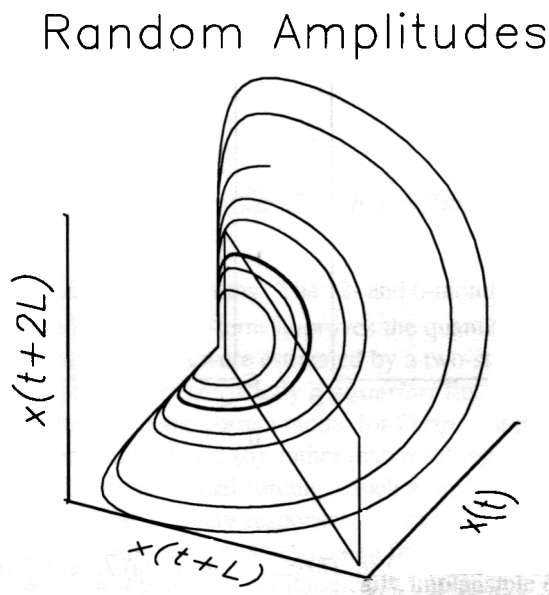

Figure 4. The reconstructed "attractor" in 3-space for a model with "white-noise" outbreak amplitudes, $N = 200$ values for $0 \le t \le 40$, $L = 0.4$. The data were generated by the equation

$$x(t) = \sum_{j=1}^{10} \exp(a_j - 20(t-4j)^2),$$

which produces outbreaks of duration ≈ 1, at times $t = 4, 8, 12, \ldots 40$. The amplitudes a_j were independent random draws from a normal distribution with mean 0, variance 0.25.

between a Fall outbreak and the following Spring outbreak, the other the relationship between a Spring outbreak and the following Fall outbreak. The elongated shape of the clouds results from the greater variation in the amplitude of large outbreaks compared to small outbreaks.

Model (1)'s ability to generate data with features of low-dimensional chaos is not limited to short data-sets. When the simulations are extended from 7 to 70 years of monthly values (Fig. 5), there still appears to be a low-dimensional attractor. In 500 simulations, the Poincaré section remained thin [$\log_{10}\theta = -1.00 \pm 0.17$(SD)], and the fit of the apparent Poincaré map by the equation $r_{n+1} = a\, r_n^b$ was still highly significant [$P < .001$ in all cases for a log-log fit; average $R^2 = .31 \pm .067$(SD) for all crossings, $0.53 \pm .061$(SD) for crossings n+1 and n less than 9 months apart: see Fig. 5 legend]. Simulations extended to 200 years gave nearly identical results [$\log_{10}\theta = -0.97 \pm 0.13$(SD); $R^2 = .31 \pm .041$(SD) for all crossings, $0.53 \pm .036$(SD) for crossings less than 9 months apart, $P < .001$ in all cases].

Why does this model mimic chaos?

The example shown above is not just a fluke, because there are identifiable qualitative features of model (1) which allow it to produce spurious signs of chaos. The apparent one-dimensionality of the Poincaré section points in Figs. 3 and 5 is a consequence of the specific choice of Poincaré section and of the time-lag L used in plotting the attractor. The Poincaré section is typically chosen to be the vertical plane defined by the equation $x(t)$-$x(t+L) = 0$ (Schaffer 1984; Schaffer and Kot 1985a, b,1986; Kot et al. 1988; Schaffer et al. 1990; Olsen et al. 1988). Intersection points are recorded whenever $x(t)$-$x(t+L)$ goes from negative to positive (crossing from behind the plane to in front of it, in the perspective of Figs. 3 and 5). These crossings occur at times t_n when $x(t_n)$ and $x(t_n+L)$ are equal and straddle the peak of an outbreak (Fig. 6a, b). Thus the radial coordinate of the point of intersection (r_n in Fig. 3c, d) is roughly proportional to the outbreak amplitude. The vertical coordinate of the intersection point (z_n in Fig. 3c), is $x(t_n+2L)$. For the value of L used in this reconstruction, z_n sits very near to the next trough between outbreaks. As a result, z_n shows little variation relative to the outbreak amplitudes, and all points of intersection lie near the one-dimensional curve $z_n = 0$ on the section.

This bias toward a low-dimensional appearance is most pronounced if z_n sits exactly at the bottom of the trough between outbreaks. If outbreaks are symmetric about their peaks, with troughs occurring halfway between peaks, then the choice of L that achieves this is $L^* = T/3$ where T is the time between peaks. Reconstructions of population dynamics (and many other systems: e.g. Roux et al. 1983, Mpitsos et al. 1988) have often used values of L near $T/3$, based on the generalization (Schaffer 1984, Schaffer and Kot 1985a) that values between $T/5$ and $T/2$ usually give the best results. For example $L^* = 2$ months for *Thrips* ($L = 2$ months used here and by Schaffer and Kot 1985b,1986), $L^* \cong 3.2$ years for the Canadian lynx cycle ($L = 3$ years used by Schaffer 1984, Schaffer and Kot 1986). Reconstructions of measles and other childhood disease data ($T = 12$ months, $L^* = 4$ months) are often cited as examples of low-dimensional attractors (e.g. Olsen and Degn 1985,1988, May 1987a, Stewart 1989, Schaffer et al. 1990, Sugihara and May 1990). In these studies usually L = 2-3 months has been used; consequently $x(t_n+2L)$ precedes the trough, but it is still negligibly small compared to the outbreaks on an arithmetic

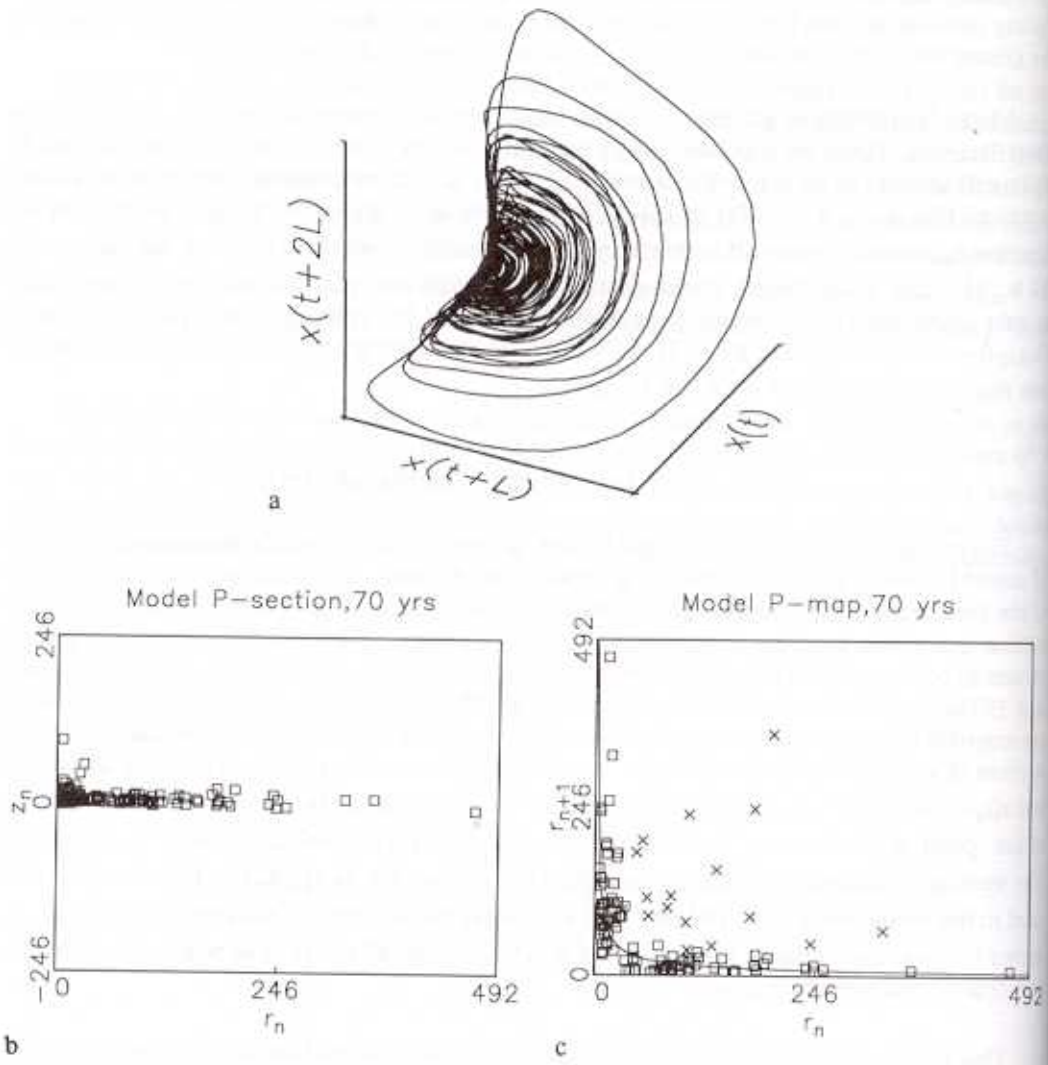

Figure 5. Simulations of Equation (1) for 70 years of monthly values, with parameters as in Fig. 3. (a) The reconstructed "attractor" in 3-space with $L = 2$ months. (b) Poincaré section as in Fig. 3; the thickness of this section is $\log_{10}\theta = -0.85$. (c) The Poincaré map as in Fig. 3. The x's indicate (r_n, r_{n+1}) pairs for which the successive crossings of the Poincaré section occur more than 9 months apart, rather than at the usual 6-month interval, due to exceptional patterns of environmental variation that eliminate the small outbreak in some years. The solid line is the equation $r_{n+1} = 584.9 r_n^{-0.756}$, fit by log-log regression with the exceptional (x) crossings excluded ($R^2 = .58$, $P < .001$); the fit remains significant if exceptional crossings are not excluded ($r_{n+1} = 310.8 r_n^{-0.558}$, $R^2 = .31$, $P < .001$). The simulated data were smoothed and interpolated as in Figs. 2 and 3.

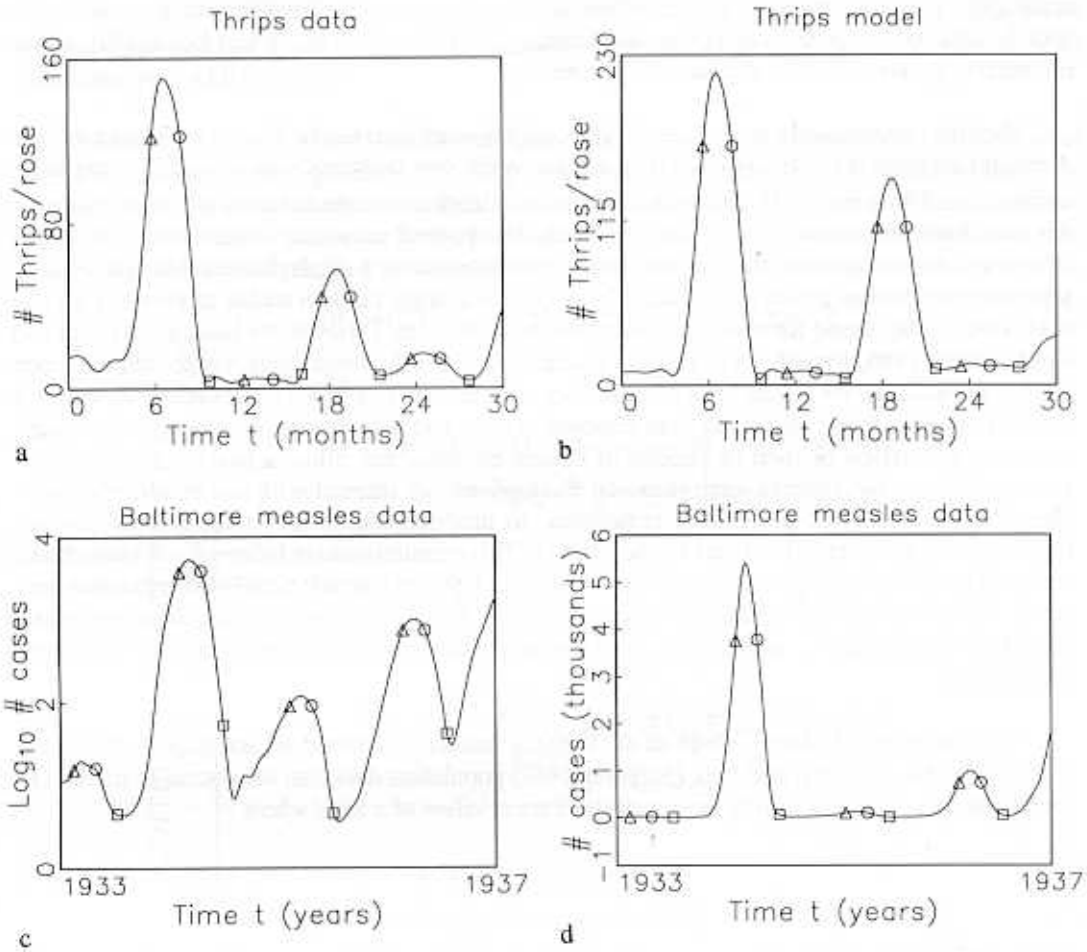

Figure 6. Locations of Poincaré section crossings in reconstructed population trajectories $X(t)$, with smoothing and interpolation as in Figs. 2 and 3. Values of $x(t_n)$, $x(t_n+L)$ and $x(t_n+2L)$ are shown by a triangle, circle, and box, respectively; $x(t_n+2L)$ is the vertical co-ordinate of crossing points on the Poincaré sections used in Figs. 2 and 3. (a) *Thrips* monthly census data, $L = 2$ months. (b) Model (1) with *Thrips* parameters, $L = 2$ months. (c) Measles incidence in Baltimore on logarithmic scale, $L = 2.4$ months. (d) Measles incidence in Baltimore on arithmetic scale, $L = 2.4$ months. Measles incidence data were taken from Yorke and London (1973).

scale (Fig. 6c, d). Thus, the one-dimensional appearance of the Poincaré sections does not "confirm the approximately two-dimensional nature of the flows" (Schaffer and Kot 1985a), and is not reliable evidence for low-dimensional dynamics.

The spurious appearance of a one-dimensional Poincaré map results from the presence of two dominant frequencies in the periodic component $y_p(t)$: one outbreak each 6 months, one large outbreak each 12 months. As explained above, the alternation of outbreak magnitudes produces the two clouds of points in Figs. 3 and 5, which the eye (and statistical curve fitting) can easily interpret as a smooth curve plus random errors. For data having a single dominant frequency with superimposed random noise, the Poincaré "map" is just a single random scatter of points (e.g., Kot et al. 1988). The reason for alternating outbreak magnitudes in *Thrips* is not known. Schaffer and Kot's (1985b, 1986) hypothesis of chaotic interactions with other organisms is a possibility, since models of multispecies interactions can oscillate with several frequency components. However a second frequency might also result from seasonality (e.g., two periods each year when temperature, moisture, abundance of food or paucity of natural enemies, etc. allow a period of population growth). Moreover, random environmental fluctuations can interact with age-structure or non-chaotic mechanisms of population regulation, to produce oscillations with several distinct frequency components (Nisbet and Gurney 1982). This counterintuitive behavior – a nonperiodic perturbation producing a periodic response – can occur because intrinsic population regulation may act as a "filter" on the environmental "noise," amplifying some frequencies while damping others. Thus there are plausible alternatives to chaos as an explanation for the alternating outbreak magnitudes.

"Stretching and folding" (Roux et al. 1983), a feature of chaotic attractors seen in disease (Schaffer and Kot 1985a) and lynx (Schaffer 1984) population data, can also occur in model (1). Stretching (divergence of nearby trajectories) occurs at values of x and t where

$$\frac{d}{dx}\{\lambda(t)x^{\beta}\} = \beta\,\lambda(t)/x^{1-\beta}$$

is > 1, while folding (convergence of trajectories) will tend to occur if the same expression is < 1. Since $1-\beta > 0$, (1) will have both stretching and folding if parameters are such that outbreaks are sufficiently large and rapid: stretching during the increase (x small, $\lambda(t)$ large) and folding during the decrease (x large, $\lambda(t)$ small).

Nonlinear forecasting methods

Sugihara and May (1990) have recently suggested a graphical approach based on nonlinear forecasting for identifying chaos in short, noisy time-series. Their method is based on the sensitive dependence on initial conditions that characterizes chaotic systems: trajectories that start near to each other diverge exponentially. Hence attempts to predict future values become less and less accurate as one tries to predict further into the future. Sugihara and May (1990) suggest using this property to test for chaos, by using the first half of the data to construct a series of nonparametric time-series models for predictions $T_p = 1, 2, 3, \ldots$ time-units ahead, and determining the models' accuracy when applied to the second half of the data. According to

Sugihara and May (1990), a decrease in prediction accuracy as T_p increases is "a signature of chaotic dynamics as distinct from uncorrelated additive noise," while a constant prediction accuracy "indicates pure additive noise."

Sugihara and May's (1990) method has been extended by Wolpert and Miall (1990) to other prediction models, and Sugihara et al. (1990) present applications to measles incidence data. An example of the method is shown in Fig. 7. Following Sugihara and May (1990) I used first-differencing to reduce first-order linear correlations, a nonparametric model based on averaging nearest neighbors as the predictor, and the correlation coefficient ρ between observed and predicted

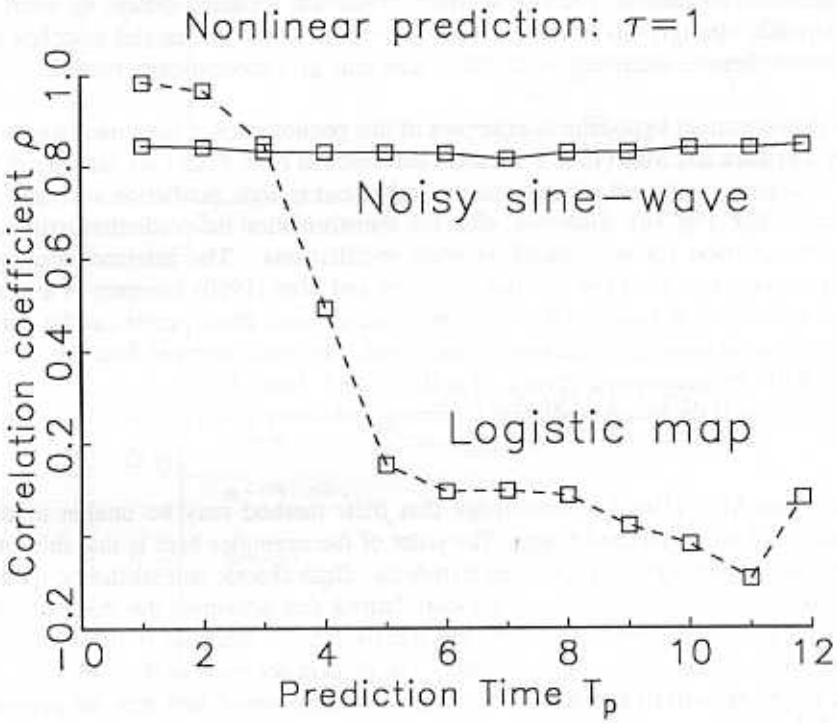

Figure 7. Sugihara and May's (1990) nonlinear forecasting method for distinguishing between chaos and measurement errors. Solid: a noisy sine-wave $x_t = \sin(2\pi t/10)+U_t$, $t = 1, 2, 3, \ldots$ with U_t independent random draws from a uniform distribution on the interval [-0.25, 0.25]. Dash: the chaotic logistic map $x_{t+1} = 4x_t(1-x_t)$. The graphs show the prediction accuracy (correlation coefficient ρ between observed and predicted values) as a function of the prediction interval T_p. For example, $\rho(3)$ is the correlation between observed and predicted values 3 time-steps into the future. $N = 1000$ data values were used for each, with the first 500 values used to define the model and the remainder used to determine the prediction accuracy. The time-delay for both was $L = 1$; the number of lags was $d = 3$ for the logistic, $d = 5$ for the sine-wave. For the logistic I followed Sugihara and May's (1990) recommendation, choosing d to maximize the one-step-ahead prediction accuracy. For the sine-wave this procedure was not possible, as the accuracy continued to increase as additional lags were added, but for $d \geq 5$ the values of ρ remained nearly unchanged up to $d = 10$, the largest value examined.

values as the measure of prediction accuracy. The prediction-accuracy criterion clearly differentiates between chaotic data (from the logistic map) and noisy periodic data (a sine-wave with additive noise).

However, chaos versus "uncorrelated additive noise" is an unrealistically narrow range of alternatives to consider for population dynamics. Once nonlinear stochastic models are admitted as alternatives, the property used as the sign of chaos – declining prediction accuracy with increasing prediction interval – is not at all unique to chaotic systems. Many finite-order Markov processes have the "mixing" property, that present and future values are asymptotically independent as the temporal separation increases. The rate at which prediction accuracy decays for such processes therefore depends strongly on how well the short-term prediction model matches the actual dynamics; hence alternate treatments of the same data may give contradictory results.

Rather than construct hypothetical examples of this phenomenon, I have used some of the data analyzed by Sugihara and May (1990). Measles incidence in New York City satisfies the criterion for chaotic behavior: prediction accuracy one month ahead is high, prediction accuracy 6 or more months ahead is low (Fig. 8a). However, after log-transformation the prediction error is constant, satisfying the criterion for nonchaotic periodic oscillations. The intermediate square-root transformation gives results of the sort that Sugihara and May (1990) interpret as a mix of chaos and random measurement errors. Of course only one of these descriptions can be correct. The same can be done in reverse to chickenpox incidence: the untransformed data are interpreted as nonchaotic with measurement errors (Sugihara and May 1990), but after exponential transformation there is declining prediction accuracy, indicating a mix of chaos and random errors (Fig. 8b).

Sugihara and May (1990) acknowledge that their method may be unable to distinguish between chaos and autocorrelated noise. The point of the examples here is that this *caveat* may often be fatal for applications to population dynamics. Both chaotic and stochastic dynamics can have autocorrelations, and the short-term autocorrelations that determine the shape of an outbreak are affected by data transformations; e.g., log transformation converts multiplicative noise to additive noise, and rounds off "spiky" outbreaks. The relative accuracy of short-term vs. long-term predictions, therefore, will be sensitive to the scale of measurement, and may not provide a clear indication of chaos.

More quantitative approaches to detecting chaos

Quantitative methods for characterizing chaotic-looking data have been developed over the last decade by theoretical physicists (e.g., Eckmann and Ruelle 1985, Schuster 1988). The methods most commonly used in applications (Krasner 1990) are based on calculating a few key quantities that characterize a system's dynamics – primarily the Lyapunov exponents (defined below) and the dimension of the attractor (Eckmann and Ruelle 1985). Accessible surveys of the available methods and their limitations can be found in the physics literature (Mayer-Kress 1986, Albano et al. 1987, Abraham et al. 1989, Theiler 1990), and their uses for analyzing population dynamics data are examined by Godfray and Blythe (1990).

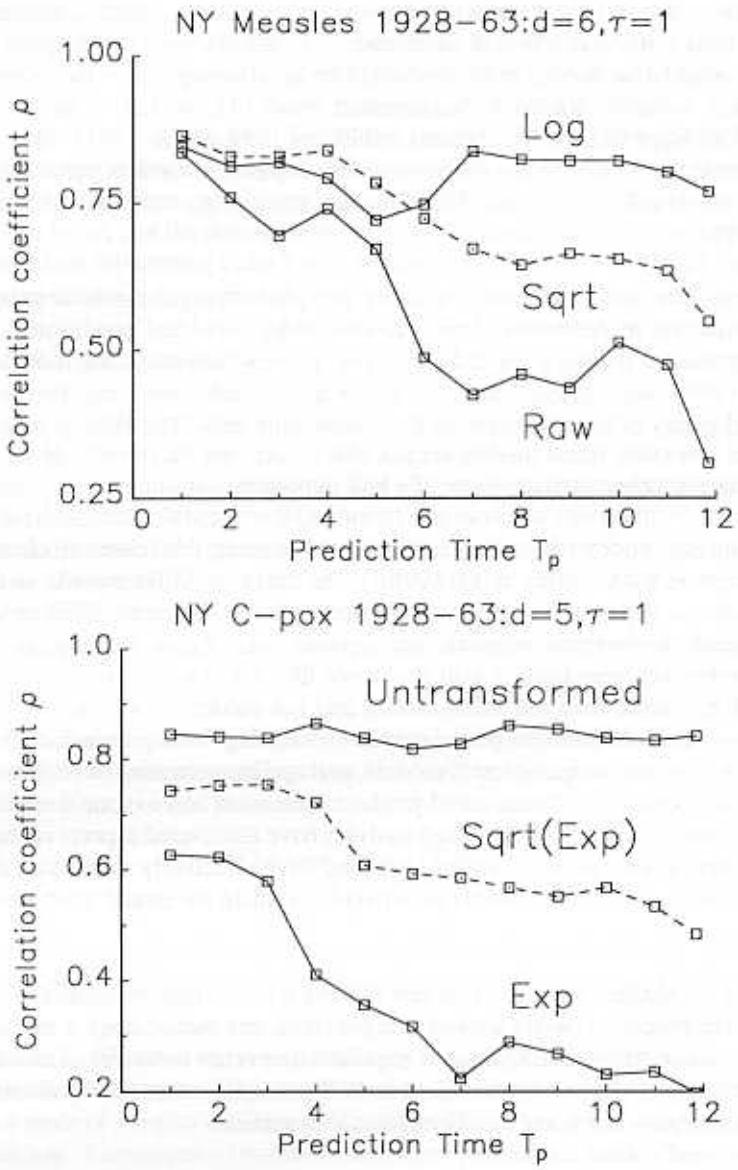

Figure 8. Effects of data-transformation on prediction accuracy in the nonlinear forecasting method. (a) Monthly reported cases of measles in New York City, 1928-1963: untransformed data vs. square-root and logarithmic transformations. (b) Monthly reported cases of chicken-pox in New York City, 1928-1963: untransformed data vs. an exponential transformation ($x \rightarrow \exp(4.3+.0024*x)$) and its square root ($x \rightarrow \exp(2.15+.0012*x)$). The values of L and d are those used by Sugihara and May (1990). The incidence data were taken from Yorke and London (1973).

These methods are reliable if the data are abundant (10^3 - 10^5 values), if measurement error is nil, and if the data really come from a deterministic system (Mayer-Kress 1986, Abraham et al. 1989). With careful fine-tuning some methods can be also applied to moderate-size data sets (several hundred values) with small measurement errors (e.g. Albano et al. 1987, Ellner 1988, Grassberger 1988, Rapp et al. 1988, Havstad and Ehlers 1989, Smith 1991). However, if data are sparse, have limited accuracy, or come from a system exposed to random perturbations, the results may be ambigous or simply incorrect if taken at face value (e.g., Ramsay and Yuan 1989, Ruelle 1990, Smith 1991).

Nonetheless, the option remains of using the physicists' methods anyway, paired with extensive simulations to determine their behavior under non-ideal conditions. This option is critically dependent on having a limited "universe" of credible competing models to use as trial cases. Sayers (1990) summarizes econometricians' use of tools from chaos theory in this way, to evaluate the adequacy of linear models for macroeconomic data. The definite results are modest – in several cases low-order linear models are not able to account for features of the data – but they are as reliable as any other statistical test of a null hypothesis.

Schaffer and co-workers have taken this line in arguing the "case for chaos in childhood diseases" (reviewed by Schaffer et al. 1990). The class of SEIR models is the universe of alternatives, and simulations of chaotic vs. noise-perturbed non-chaotic SEIR models are used to establish a baseline for interpreting results on empirical data. Again, this approach means that the definite conclusions are more modest than one would like: for example, measles incidence data are consistent with a chaotic seasonal SEIR model, and not consistent with a non-chaotic seasonal SEIR model with additive Gaussian perturbations representing finite-population effects. Therefore there is a possibility that other stochastic models, perhaps incorporating environmental variability rather than finite-population effects, could produce dimension and exponent estimates consistent with the data. Nonetheless, the chaos-based analyses have discovered aspects of the data that were not apparent using more traditional approaches, and have effectively eliminated from contention earlier hypotheses invoking finite-population effects to explain the erratic timing and magnitude of outbreaks.

For population studies, however, it is rare to have the information needed to define a limited class of plausible models. To get around this problem, one would need a statistical theory for estimates of attractor dimension, Lyapunov exponents, or other measures of chaos, one which is valid over a very broad class of models (Sayers 1990). In particular, the universe of alternatives must include both noise-driven and chaotic nonlinear dynamics.

A surprising finding in recent years is that statistical methods of time-series modeling can be successful at identifying the "rules" (i.e., the equations of motion) governing a deterministic chaotic system (e.g. Farmer and Sidorowich 1987, 1988a, b; Casdagli 1989; Abarbanel et al. 1990; Abraham et al. 1989). The "moral" of chaos is that apparently complicated dynamics can be produced by simple rules, such as the density dependence described by the logistic map. In such cases, often more can be learned from limited data by estimating the rules, rather than by estimating quantities indicative of chaos directly from the data.

Motivated by these findings, I and several colleagues have been developing statistical theory for estimates of Lyapunov exponents based on nonlinear time-series models (McCaffrey et al. 1991, Ellner et al. 1991). Lyapunov exponents quantify the sensitive dependence on initial conditions that is the defining feature of chaos: a system with bounded fluctuations is chaotic if its largest Lyapunov exponent λ is positive. Lyapunov exponents are defined at any level of noise (Kifer 1986) and therefore provide a very general criterion for identifying chaos when a stochastic component may be present. However the predominant method for estimating λ from data (Wolf et al. 1985) assumes *a priori* that the data were generated by a deterministic system, as does Wales's (1991) method based on forecasting (which uses relationships between λ, entropy, and prediction errors that break down if noise is present).

The basic model we consider is

$$x(t) = f(x(t\text{-}L), x(t\text{-}2L), \ldots, x(t\text{-}dL)) + \sigma\varepsilon(t), \tag{7}$$

where f is an unspecified nonlinear function, and $\varepsilon(t)$ is a sequence of uncorrelated random perturbations to the dynamics. When $\sigma = 0$ (no noise) this model is equivalent to standard attractor reconstruction in d-dimensional space, but our methods allow for $\sigma > 0$, acknowledging the possible importance of random variation in factors affecting the system. Of course (7) has a roster of questionable assumptions (the noise is uncorrelated over time with constant variance; measurement errors are ignored), but it is a first step and certainly more realistic than setting $\sigma = 0$ *a priori*.

Because f is unknown, we are using nonparametric (e.g., spline) or "semi-nonparametric" (SNP) estimates of f. SNP estimates are based on truncated series expansions,

$$\hat{f}(X) = a_0 + \sum_{i=1}^{k} a_i g_i(X;\theta_i) \tag{8}$$

in which X is the state vector $(x(t\text{-}L), x(t\text{-}2L), \ldots x(t\text{-}dL)$, g_i is a specified set of "basis" functions, and θ_i is a set of estimated parameters. SNP shares the advantage of nonparametric methods that one need not choose a specific functional form for $\hat{f}$, which reduces the problem (recently re-emphasized by Morris 1990) that the results of fitting a model to time-series data may be highly dependent on the model chosen. The number of terms in the expansion (k) can be chosen objectively on the basis of the data (Gallant and Tauchen 1990), much like choosing the order of a polynomial regression. Parametric approaches using local polynomial models have been proposed independently by Briggs (1990), and Bryant et al. (1990). Turchin and Taylor (1991; see Turchin, this volume) have proposed a method specifically for population dynamics based on global polynomial models.

Given an estimate of f and the observed values of $X(t)$, estimates of the Lyapunov exponent can be derived from its mathematical definition in terms of the partial derivatives of f (McCaffrey et al. 1991). Under some reasonable qualitative assumptions about (7), we have proved that these estimates are consistent (i.e., the estimates converge to the true value as the sample size increases),

and have derived their asymptotic rate of convergence (McCaffrey et al. 1991, Ellner et al. 1991). These results demonstrate that our methods are applicable to systems with a stochastic component.

In simulation trials, estimates based on (7) have worked quite well when the number of lags (d) and the time-delay (L) are known (McCaffrey et al. 1991, Nychka et al. 1991). For example in 20 trials with $N = 100$ values each from the Henon map ($d = 2, L = 1$) with Gaussian additive measurement errors ($\sigma = .05$), we obtained $\widehat{\lambda} = 0.386 \pm 0.04$ (standard deviation), using a "neural net" SNP model (Gallant and White 1991; McCaffrey et al. 1991). The correct value is $\lambda = 0.418$ (Vastano and Kostelich 1986). To conclude that a system is chaotic, one only needs to know that λ is positive; hence this degree of accuracy is more than adequate. Allowing for noise in the model does not necessarily degrade the performance in noise-free situations. Again, using the Henon system, with local spline estimates of f, we obtained estimated exponents $\widehat{\lambda} = 0.416 \pm 0.0148$ (standard deviation) with $N = 500$ data values, and $\widehat{\lambda} = 0.420 \pm 0.0102$ (standard deviation) with $N = 1000$ ($n = 20$ repetitions in each case). With the standard methods, results with 1024 data values were "poor", and reasonable eimates (within 10%) required several thousand data points (Vastano and Kostelich 1986). Briggs (1990) reports similarly good results using local polynomial models based on 200 – 2000 noise-free data values.

Unfortunately, d and L are generally unknown. The problem of identifying "correct" or "optimal" values of d and L for attractor reconstruction has received considerable attention, but there is no generally accepted solution (Abraham et al. 1989). Early suggestions for choosing d and reducing noise (Broomhead and King 1986) have proved unsuccessful in general (Mees et al. 1987, Fraser 1989). More recent suggestions include Sugihara and May's (1990) prediction accuracy criterion, the BIC Bayesian criterion for identifying the order of time-series models (e.g., Pötscher 1989, Gallant and Tauchen 1990), and information-theoretic criteria based on "mutual information" and "minimal redundancy" (Fraser and Swinney 1986, Fraser 1989, Liebert and Schuster 1989). These all try to quantify the intuitive idea that a good choice of d and L gives maximum ability to predict the system's future from a minimum number of measurements of its past, but they often give different results. For example, the Sugihara-May and mutual information criteria choose $L = 1$ month and $L = 4$ months respectively for the NYC measles data, and $L = 1/24$ and $L = 1/6$ of the time between outbreaks for the Rössler equations (250 x-values with values recorded every 1/24 of the inter-outbreak interval). BIC gives consistent estimates of model order in autoregressions under certain assumptions (Pötscher 1989), but with small data sets it tends to be conservative, choosing a model with slightly too few parameters (Gallant and Tauchen 1990, Nychka et al. 1991).

In theory the true value of λ is the same for all sufficiently large d's, so one can simply increase d until a plateau appears, as is usually done to estimate attractor dimensions when d is unknown. The success of this ploy may depend on the method used to estimate f: local polynomials (Briggs 1990, Brown et al. 1991) and several standard nonlinear regression models including local splines (McCaffrey et al. 1991) often generate spurious exponents when the model includes extraneous lags (model $d >$ true d), while neural nets appear fairly robust to extraneous lags (McCaffrey et al. 1991, Nychka et al. 1991). Thus a value of λ may be estimated roughly when a plateau exists for an increasing number of lags in the model, and is constant over reasonable choices of L.

Figure 9 shows results for a neural net regression model with the time-delay L chosen by several different criteria: mutual information (MI, Fraser and Swinney 1986), BIC with the same time-delay for all values of d, and "local BIC" in which the optimal time-delay is found separately for each value of d. Because BIC is conservative (as noted above), estimates are shown for the BIC-preferred model (solid lines) and also for models with the order [the value of k in equation (8)] increased by 1 (dashed) and by 2 (dots).

The results are cleanest for NYC measles, where all choices of L give a plateau with increasing d and an estimated λ near 0.15/yr. This is roughly half the value estimated by Schaffer et al. (1990), which is understandable given that the methods of Schaffer et al. (1990) will tend to over-estimate λ when $\sigma > 0$. *Thrips* is estimated to be chaotic ($\lambda > 0$) by the MI and BIC criteria, but the local BIC is inconclusive. The large effects of changing the model order suggest that the positive values would not be statistically significant, so while these estimates favor the hypothesis that *Thrips* is chaotic they should not be taken as proof. The results for marten are similar, except that both BIC criteria choose chaotic models while MI is inconclusive.

These results indicate the importance of deriving confidence intervals to attach to the estimated values of λ. Repeated nonlinear function minimizations are required to obtain least-square parameter estimates for each (d, L) examined, so the sort of replication (e.g., bootstrapping) needed for statistical inference, and serious explorations of the method's ability to distinguish between chaos and plausible alternative models, appear to be a job for the supercomputer. Taken pessimistically, these results might suggest that SNP estimation of λ is too data-hungry for use on most population data sets: $n = 432$ is enough (NY measles), but $n \approx 80$ isn't. However much of the variability in current estimates of λ may simply reflect the numerical inaccuracy of nonlinear least-squares for the underlying regression model, and more careful parameter estimation algorithms (now being coded) may give estimates that are less sensitive to changes in the time-delay and model order. The progress to date indicates the potential for developing statistically rigorous estimates of Lyapunov exponents for nonlinear stochastic dynamics, but that potential remains to be realized.

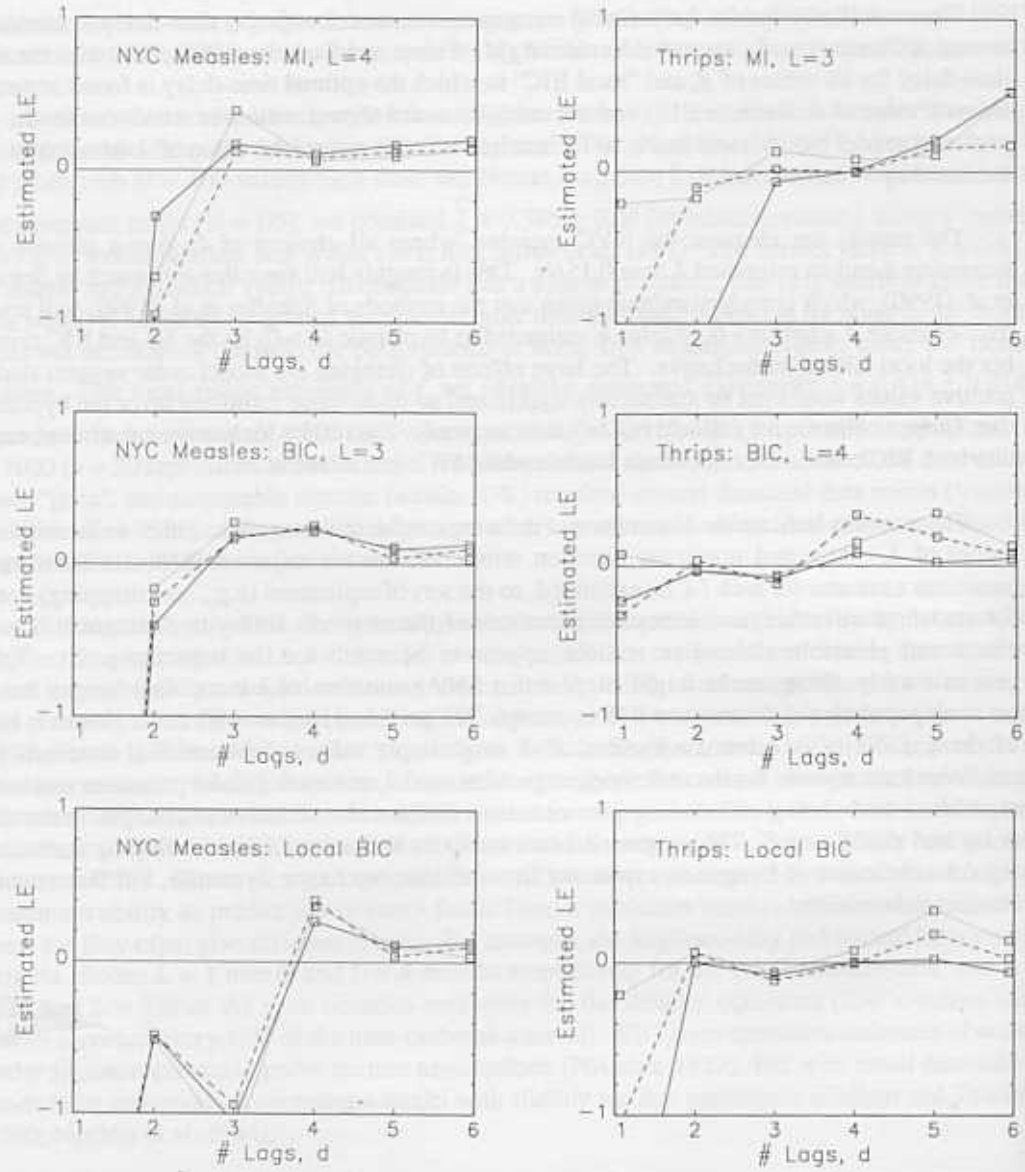

Figure 9. Estimated Lyapunov exponents (in units of yr^{-1}) for New York City measles (same data as in Fig. 8), *Thrips imaginis* (same data as in Fig. 2), and Hudson's Bay Company fur returns for marten 1820-1900 (Jones, 1914). All data series were log-transformed prior to analysis. In the marten series the two pairs of years confounded due to delayed returns (1833/34 and 1836/37; see Jones 1914, p. 202) were averaged. A "neural net" regression model was fitted to equation (7) for all d, L pairs with $1 \leq d, L \leq 6$. The number of units in the network (k in equation (8)) was chosen by the BIC criterion. Assuming that the random perturbations $\varepsilon(t)$ in equation (7) are independent Gaussians with zero mean and constant variance, the criterion is to minimize

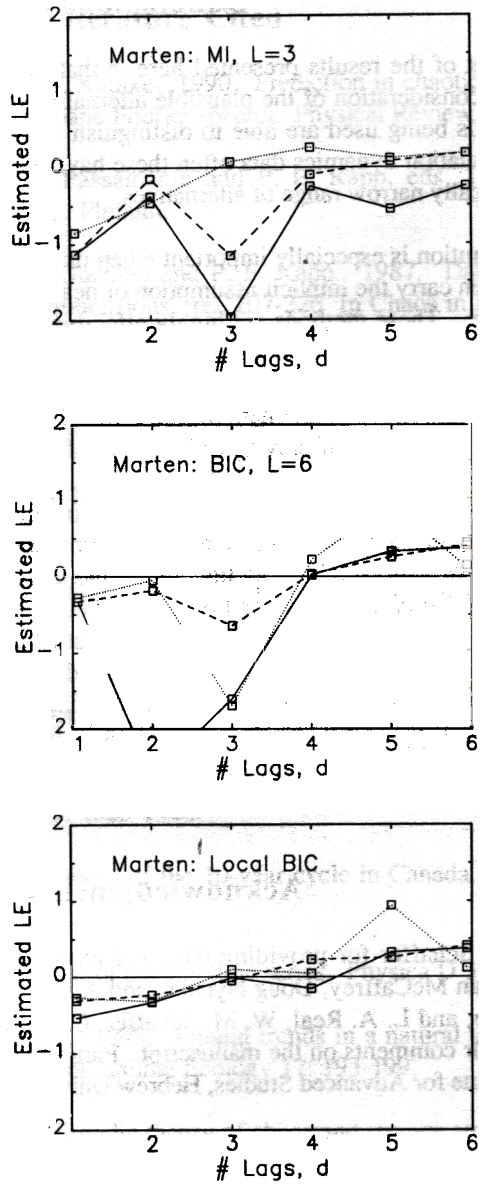

Figure 9. (Continued)

$$\mathrm{BIC} = \frac{1}{2}\{1 + \ln(2\pi) + 2\ln(\mathrm{RMS}) + P\ln(n)/n\}$$

where n is the number of data points, P is the number of parameters in the model, and RMS is the root mean square one-step-ahead prediction error; see Gallant and Tauchen (1990) or Pötscher (1989) for the general form. The solid line shows estimates from the BIC-preferred model; the dashed and dotted lines are for models with 1 and 2 additional units, respectively.

Conclusions

The main point of the results presented here is that claims for evidence of chaos must be accompanied by a consideration of the plausible alternative explanations, and an examination of whether the methods being used are able to distinguish between chaos and the alternatives. In applications to population dynamics data often these have not occurred, or have been carried out within an unrealistically narrow range of alternatives.

This level of caution is especially important when using methods imported from the physical sciences, which often carry the implicit assumption of nearly-perfect measurements on a perfectly deterministic system. These methods are highly effective on accurate data from a deterministic chaotic system--we are far from the situation of 15 years ago, when it appeared that deterministic chaos could never be distinguished from random noise. However, the problem for population biologists is to detect a chaotic component in a real-world population that almost certainly is also subject to random perturbations, if only by the vagaries of climate.

The potential now exists for a second generation of methods that explicitly allow for the stochastic as well as the nonlinear components of population dynamics. Several groups are developing the use of time-series modeling to characterize complex dynamics and estimate Lyapunov exponents (Turchin and Taylor 1991, Bryant et al. 1990, Brown et al. 1991). Attention is being given to dealing with noisy measurements or stochastic dynamics (Möller et al. 1989, Hammel 1990, Kostelich and Yorke 1990, Farmer and Sidorowich 1991, Smith 1991), and though current noise-reduction methods still require abundant data (thousands of values) and very low levels of noise (<< 10%), work in this area is only beginning. The hope for ecological applications is that methods with more realistic assumptions, currently in development, will be applicable over a broader range of situations and harder to fool than the current generation.

Acknowledgments

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Individual-Level Simulation: New Evidence for Chaos in Population Biology

Nicholas D. Stone[1]

TWO FACTS are readily apparent from the recent debate on chaos in population biology. First, natural systems often exhibit very complex dynamics that, despite their irregularities, appear to contain some order. Second, there is a large class of differential and difference equation models that produce similar dynamics. These mathematical models that produce chaos have been extensively analyzed so that we know how chaotic systems ought to behave: they are deterministic; they are highly sensitive to initial conditions; and they are seemingly random. However, the fundamental question remains: do natural systems display complex dynamics because they are chaotic or merely because of stochastic influences and system complexity? The work described here sheds some new light on this issue.

The finding that initially interested population biologists in chaos was that many of the most basic models of population growth, single-species models like the logistic model, would produce chaotic dynamics over specific ranges of parameter values. However, as many researchers have demonstrated in the last fifteen years (e.g., Hassell et al. 1976, Stubbs 1977, Thomas et al. 1980, Bellows 1981), the required parameter values have almost always proven to be biologically unreasonable. As a result, population biologists as a whole have lost their optimism about finding chaos in natural ecosystems.

Two aspects of this waxing and waning of interest in chaos were unfortunate. First is the focus on single-species models. These models are universally understood to be extreme simplifications. They are useful in a descriptive way; that is, they show the general pattern of population growth expected in populations governed by a density-dependent effect on birth and death rates. However, these models barely begin to approach biological realism. Furthermore, the chaotic behavior of these models is highly irregular and unnatural (see Berryman in this volume, Fig 1), giving the impression that chaos implies wildly fluctuating populations with numbers frequently crashing to levels near zero. In fact, higher order systems can exhibit chaos without biologically unrealistic parameter values or any apparent trend toward self-extinction.

The second regrettable aspect is the focus on the model itself as the item of interest. Most of the attention in studies of chaos in biological systems has been on developing and analyzing difference and differential equation models of low order, specifically to test those models for chaotic dynamics. This emphasis is or ought to be foreign to population biologists. As a rule, their focus should be on accurately identifying and representing the key biological elements and interactions in the system. The type of model chosen should then be dictated by the biology. Research in chaos has been constrained by an *a priori* choice of model form and type.

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The work described here takes a different approach, one that evolved from a project studying the interaction of a parasite, *Campoletis sonorensis*, and one of its hosts, *Helicoverpa virescens*. In that study (Makela et al. 1988), we wanted to simulate the population-level effects of changes in the individual searching behavior of the parasite. Each individual host and parasite adult was simulated individually in an event-driven simulation. Each individual maintained its identity and history and acted as an autonomous entity in the model. Population dynamics were simulated as the sum of individual actions, oviposition, and death. As in nature, population dynamics was an emergent property of the system, not determined by rate equations as in models of the form $dN/dt = f(N, P)$.

The host-parasite model produced dynamics that were extremely complex and apparently realistic. However, because the model included random choices in the selection of individual behaviors, determining the underlying causes of the complexity was inhibited by noise.

The model of predator-prey interaction presented below was constructed specifically to examine the emergent population dynamics of a behavior-driven, individual-level simulation with all random elements removed. The model is therefore unlike most individual-level models or behavior-based models in that the behaviors of individuals are chosen deterministically with if-then rules, rather than through the random choice of behaviors with different probabilities of occurrence.

The model is object-oriented (Stefik and Bobrow 1986), a style of programming that has only recently been applied to model biological systems (Graham 1986; Saarenmaa et al. 1988; Makela et al. 1988; Crosby and Clapham 1990; Sequeira 1990). It was written in an object-oriented programming language, Smalltalk-80[2], in which it is very easy to create computer representations of the individual actors in a complex system.

Understanding the model description requires familiarity with object-oriented programming, so it is reviewed briefly here. More complete discussions abound in the popular and scientific computer-related literature, and excellent summaries can be found in Stefik and Bobrow (1986) and in the introductory chapters of Goldberg and Robson (1983).

Object-Oriented Programming[3]

Traditional procedural computer programming involves defining *data structures* to represent system state and *procedures* to operate on the data structures to reflect changes in system state. Procedures are like mini-programs. They perform operations on a set of arguments passed to them and they can return values to the calling program. For example, to compute the area of a rectangle, one could define a procedure, `calculate–area`, which requires arguments for the lengths of the rectangle's base and height. The area of a square with sides 3 units long would be calculated by the statement, `calculate–area (3, 3)`. Internally, the procedure would multiply the values specified for base and height and return the result.

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[2] Smalltalk-80 is a registered trademark of ParcPlace Systems, Inc.

[3] This section is virtually identical to a similar section in Stone (1990).

In object-oriented programming, one creates structures called *objects* that contain both information on state varibles and procedures for operating on that data. The state of an object (i.e., the values of its state variables) can be accessed or modified only by the procedures defined in that object. Procedures are called *methods* and are invoked by *messages* sent by one object to another or to itself. Methods may return the value of a variable or calculation to the calling object. For example, one could define an object called mySquare with one state variable, sideLength = 3, and a method called calculateArea that computes the length squared and returns the value to the object sending the message. Finding the area of this square would be accomplished by sending the message, mySquare calculateArea. Notice that the message name is the same as the method name and that the message makes no reference to the size of the square.

Classes, Hierarchies, and Inheritance

Objects are specific instances of an object class and object classes are organized into hierarchies. For example, the object, mySquare, would be a particular instance of the class, Square, with sides of length 3. The class definition includes all variable declarations and code for methods. It also includes a special method (called a *class-method*) for creating instances of itself, with appropriate initial values for variables. Creating the object, mySquare, for instance, would be accomplished by the code, mySquare ⇐ Square newWithSide: 3, which sends a message to the Square class, causing the class to create and return a new object with sideLength equal to 3, after which the new object is assigned to the name, mySquare. This process is called *instantiation.*

Object classes may also be subclasses of other classes. Subclasses inherit variable declarations and methods from their parent classes, just as an object inherits from its class. However, subclasses may add variables, add or redefine methods, and specify static class variables. For example, if there were a class, Rectangle, with two variables, base and height, and a method called calculateArea that returns the value of base * height, then the class, Square, could have been created as a subclass of Rectangle. The only coding required would be to redefine the class method for instantiation so that the message, Square newWithSide: X, would return a new instance of Square with both base and height set equal to X.

Despite the semantic conflict, one could also create a class called Triangle as a subclass of Rectangle by modifying the calculateArea method to return 0.5 * base * height. Instances of Triangle would respond appropriately to the same message, calculateArea, as would instances of Square and Rectangle. The sender of the message need not know what the appropriate algorithm is for a particular polygon. This characteristic of object-oriented systems, that different objects can respond in different ways to the same message, is termed *polymorphism.*

Object-Oriented Simulation

Writing an object-oriented simulation involves creating classes to represent the types of actors in the simulation, creating specific instances of those classes with appropriate state variables, and letting them interact by sending messages to one another. The objects in the computer model and

the actors in the natural system are in one-to-one correspondence, and the interactions among actors in the natural system likewise correspond to messages sent among objects in the computer model. In designing an individual-level population dynamics model, the actors clearly include the individual organisms, as well as the physical objects with which they interact.

The Model

The individual-level model of predator-prey interaction was designed to be very simple in that all individuals were created with the same default values for state variables and the environment was likewise completely uniform at the outset, consisting of identical habitat patches. Furthermore, there was no individual variation in the methods used to select behaviors by individuals.

Nevertheless, the simulation was also fairly complex, since many fundamental aspects of each individual's daily life needed to be mimicked. Aging, eating, moving, hiding or hunting, and dying all had to be described in methods, along with behavioral rules to stimulate these actions at appropriate moments.

Object Classes

The class/object hierarchy of the model as well as the relationships among the different object types are shown in Fig. 1. The simulation environment included 225 patches arranged in a 15 x 15 grid, and each patch represented a suitable habitat for the prey. The environment's boundary was closed. Except for the initialization of the model, no migration was allowed.

Each patch was modeled as an instance of the class, Patch. All Patch objects contained their Cartesian coordinate in the grid, but the overall spatial arrangement of the patches was recorded in another object, a single instance of the class, Environment. The Environment object also maintained a list of all the live predators and prey in the simulation. Each day of the simulation consisted of the Environment object sending each actor (instances of the classes: Patch, Predator, and Prey) the message, act. Each object receiving the act message responded as specified by the act method defined in its class. This use of polymorphism allowed the Environment object to treat all the actors identically.

Patches

The state variables in the Patch class included: xyCoord, a pair of integers describing its grid position within the environment; food, an amount of food for the prey; and shelters, a list of refuges in which the prey could escape predators but could not eat. In this analysis, all Patch objects were assigned the same default values, including a single shelter. The Patch class also had variables called prey and predators, which were lists of all prey and predators in that location (Fig. 1).

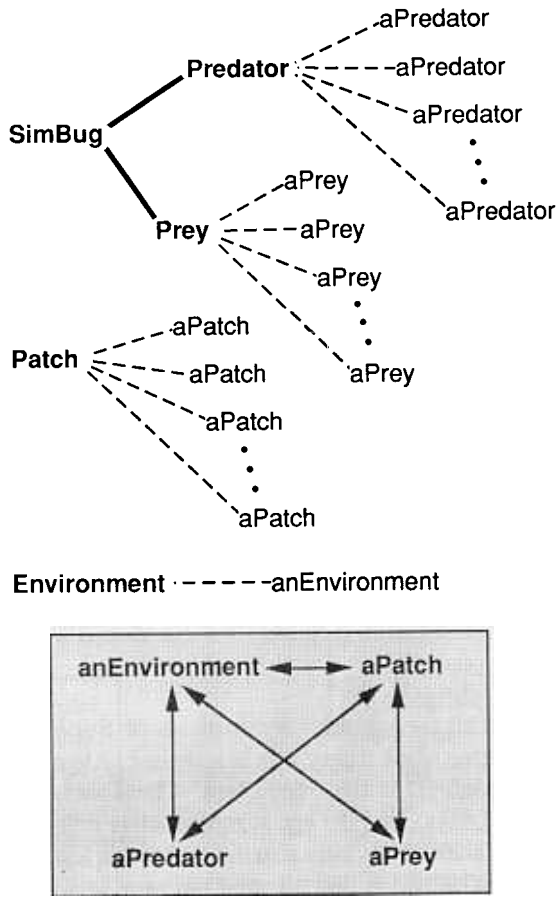

Figure 1. Class-object hierarchy of the predator-prey model and a listing of the linkages among objects in the simulation (box). In the hierarchy, solid lines indicate class-subclass relationships; dashed lines indicate class-object relationships. Class names are shown in bold type on the left. In the box, double-headed arrows indicate that the objects are associated. For example, each predator is associated with one patch and one environment.

Methods defined in the Patch class included: act, which added a constant increment to the amount of food available for the prey up to a maximum value; and removeFood, which decreased the food in a patch and was triggered by a message from Prey objects to simulate eating. Other methods allowed patches to respond to objects requesting information about the patch. An immature prey, for example, sensed the presence of predators within its patch by sending the message, predators size, to its patch. The Patch object responded to this message by returning the length of its list of Predator objects. Finally, there were messages for keeping track of individuals as they entered and left the patch.

Predators and Prey

Because predators and prey shared many aspects of biology and behavior, their object classes were defined as subclasses of an abstract class, SimBug. It had no instances; it was defined for convenience so that shared characteristics of the predators and prey could be coded once and inherited by both subclasses.

Predators and prey were modeled after simple arthropods in their biology. The SimBug class description included variables to hold the name of each individual's Environment and current Patch objects, its age, stomach content (metabolic supply), and the number of eggs ready to oviposit. Males were not included in this simulation. Behaviors implemented in the SimBug class included act and move methods, as well as two messages announcing an individual's arrival in and departure from different patches. The act method (Fig. 2) in turn sent messages like die, eat, and reproduce that were defined differently for each subclass.

The act method was based on the motivational model of animal behavior described by Packard et al. (1990). At each time step, individuals updated their age, chose a motivational mode of behavior (e.g., ingestion, reproduction, escape), and chose an action based on their behavioral mode. Mortality occurred by predation, starvation (defined as going two time steps with exhausted reserves), or by aging past a fixed maximum age. Individuals were always given the opportunity to eat and reproduce if possible. Specific methods for these actions were defined in the subclasses, Prey and Predator.

The Prey class inherited all the variables and methods of SimBug. It also added a variable called inShelter, which was true when a prey was in a shelter. Also, variables that were constant for all Prey instances were defined in the Prey class. These included the metabolic loss rate, maximum age of the prey (20 days), and the age at reproductive maturity (10 days). Methods for choosing motivational modes and actions were also defined at this level in the hierarchy. These are described below. In addition, methods that allowed the prey to act were defined at this level, including methods for eating, ovipositing, dying, and entering and leaving shelters.

Predators were instances of the Predator class, which also inherited variables and methods from SimBug. In addition, all predators shared a maximum age of 30 days and became reproductively mature at 20 days. Predators' metabolic loss rate was also higher than that of prey. Other behaviors and methods were similar to those of the prey.

Eating was more complicated for predators because it involved capturing and consuming a prey. Predators chose prey items from the list of Prey objects recorded in their current Patch object. They had an age-preference for prey that was a function of their own age. Predators chose the first prey in the list that was an acceptable age. Their stomach contents were increased after a kill as a function of the age of the prey they took.

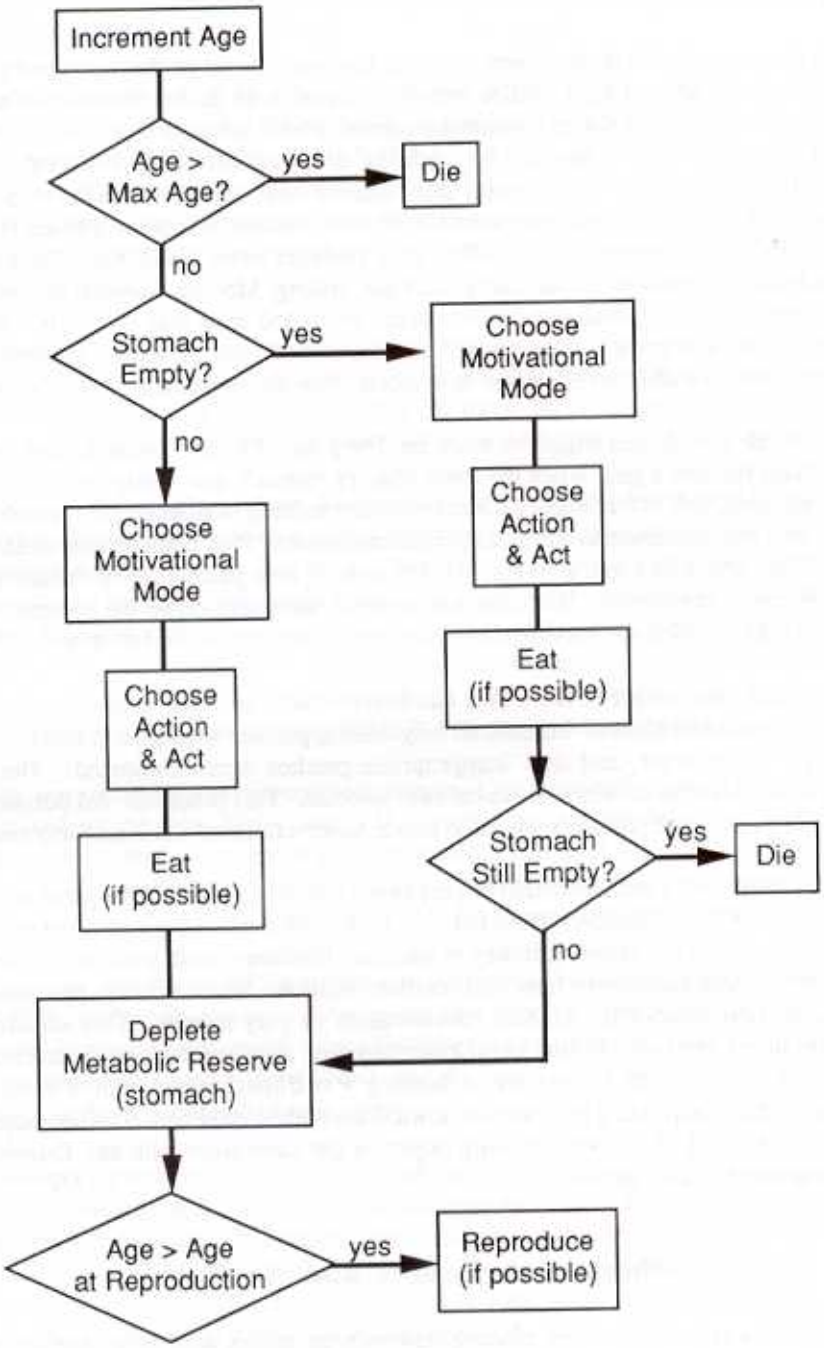

Figure 2. Flow chart representing the act method as implemented for both predators and prey. This method was triggered at each time step of the simulation.

Behavior

Behaviors were chosen deterministically by if-then rules based on the individual's current state (e.g., hunger, position, and age). Rules were developed in an *ad-hoc* manner, in an attempt to model as simply as possible the motivational model of animal behavior described by Packard et al. (1990). These rules were coded in two methods, chooseGoal and chooseAction. First a motivational mode or goal was chosen, then actions were chosen to meet those behavioral objectives. This implementation of an animal's decision-making scheme was based on the general model developed by Saarenmaa et al. (1988). Prey goals included: Food, Rest, Escape, Dispersal, and Reproduction; actions included: Eating, Resting, Hiding, Moving, Staying, Reproducing. The behavioral repertory of immature prey was more restricted than that of adults. Adults could disperse or sense the approach of predators. Immatures could not. They sensed predators only in their current patch. Adults also attempted to oviposit when they reached reproductive age.

The goal, Dispersal, was triggered when the Prey object's patch became crowded or low on food, and Food became a goal when the Prey object's stomach was nearly empty. Once a set of goals was decided, the Prey object's chooseAction method was triggered, which selected an action and then sent messages to carry out the actions chosen. Prey could decide to enter a shelter, remain in their current location, or move. If they moved, they picked one of the adjacent patches in the environment to move to. This selection involved narrowing down the potential locations to a subset that best satisfied the Prey object's goals, then selecting the first member of this subset.

Even though there might be more than one suitable patch to move to, patch selection was not implemented as random choice. Instead, all neighboring patches were placed into an ordered list, always in the same order, and then inappropriate patches were eliminated. The first patch remaining in the list after elimination was always selected. This procedure did put some bias into the direction that prey and predators tended to move; however, it also eliminated any randomness.

Predator behavior differed from that of prey in the following ways. Their goals included Food, Rest, Hunting, and Reproduction. They fed only by killing prey. They could not eat the food in patches, and they were not able to kill prey in shelters. Predators could sense the presence of prey in patches up to three steps away from their current location. When hunting, predators moved as directly as possible toward the highest concentration of prey nearby. This sensing ability is analogous to insect predators keying in on kairomones or chemical cues in the environment that relate to prey density. In the model, a hunting Predator object sent a message to the Environment object requesting the direction toward the highest prey concentration nearby. Recall that the Environment object was the only object in the simulation with any knowledge of the spatial arrangement of the patches.

Simulation Results and Analysis.

The model was initialized by placing newborn predators and prey into the simulation environment at one edge of the grid (Fig. 3). Prey were placed first, ten per day for five days after which two predators were added per day for 20 days. Subsequently, no individuals were added except

by individuals giving birth. In each day of the simulation, every location updated its food supply, and each predator or prey was allowed to act.

A time-series from a run of this model is shown in Fig. 4. The system clearly exhibits complex dynamics. The system ran for several thousand days (hundreds of generations) without any indication of repeating or stabilizing. A phase plot (Fig. 5) from the simulation shows a complex or strange attractor in two dimensions. From Fig. 3, one can see also that the dispersion of predators and prey in the environment went from patterns that were easy to follow (a wave of prey spreading out before a wave of predators), to a more complex and jumbled situation after approximately 200 days.

Fig. 6 shows the effects of very small variations in the initialization of the model. By adding 11 prey on the fifth day of the model initialization instead of 10, for a total of 51 instead of 50, the model's trajectory was totally changed so that 50 days later, the two trajectories bore no resemblance, except that in phase space they were constrained within the same attractor.

To summarize, the simulation was deterministic, it produced pseudo-random but bounded population dynamics; and it exhibited extreme sensitivity to initial conditions. This combination of characteristics defines chaotic behavior. There is some chance that the pseudo-random oscillations produced by the model would eventually stabilize to some periodic or quasi-periodic pattern. Still, the output from the model is remarkably realistic; it is unpredictable within a bounded region of phase space; and it is completely deterministic. This is exactly the kind of system behavior that, when observed in nature, sparks arguments about whether it is chaos or the influence of stochastic events that is responsible. In this case, randomness has been eliminated.

To obtain some confirmation of the chaotic nature of the model's dynamics, two analyses were undertaken based on the time series data. However, since the model is not in the form of differential equations, testing for chaos is complicated. The methods used were the same one might use to test whether a time series observed in the field is chaotic. The Lyapunov exponent and fractal dimension of the system were estimated using algorithms from the Dynamical Software program (Schaffer et al. 1988). Calculation of the Lyapunov estimate employed Wolf et al.'s (1985) method, and calculation of the fractal dimension was by the method of Grassberger and Procaccia (1983). Both estimates used a univariate time series of just the total prey numbers over time. Over a wide range of parameter values for sampling interval and delay, the estimate of the Lyapunov exponent was positive (appx. 0.04), and the correlation dimension was approximately 4.7, indicating a fairly high-ordered chaotic system.

If the two-species system was chaotic, one obvious question was whether the single-species model would behave similarly. That is, is the complexity coming from the interaction, or is it driven by the prey dynamics? To examine this question, the model was run with no predators. The results are shown in Fig. 7. At first glance, it seems that no chaos is present. The prey population increased in a sigmoidal pattern and seemingly stabilized at a carrying capacity of about K=1095 individuals. Fitting the Ricker (1954) equation

$$N_{t+1} = N_t e^{r\left(1 - \frac{N_t}{K}\right)}$$

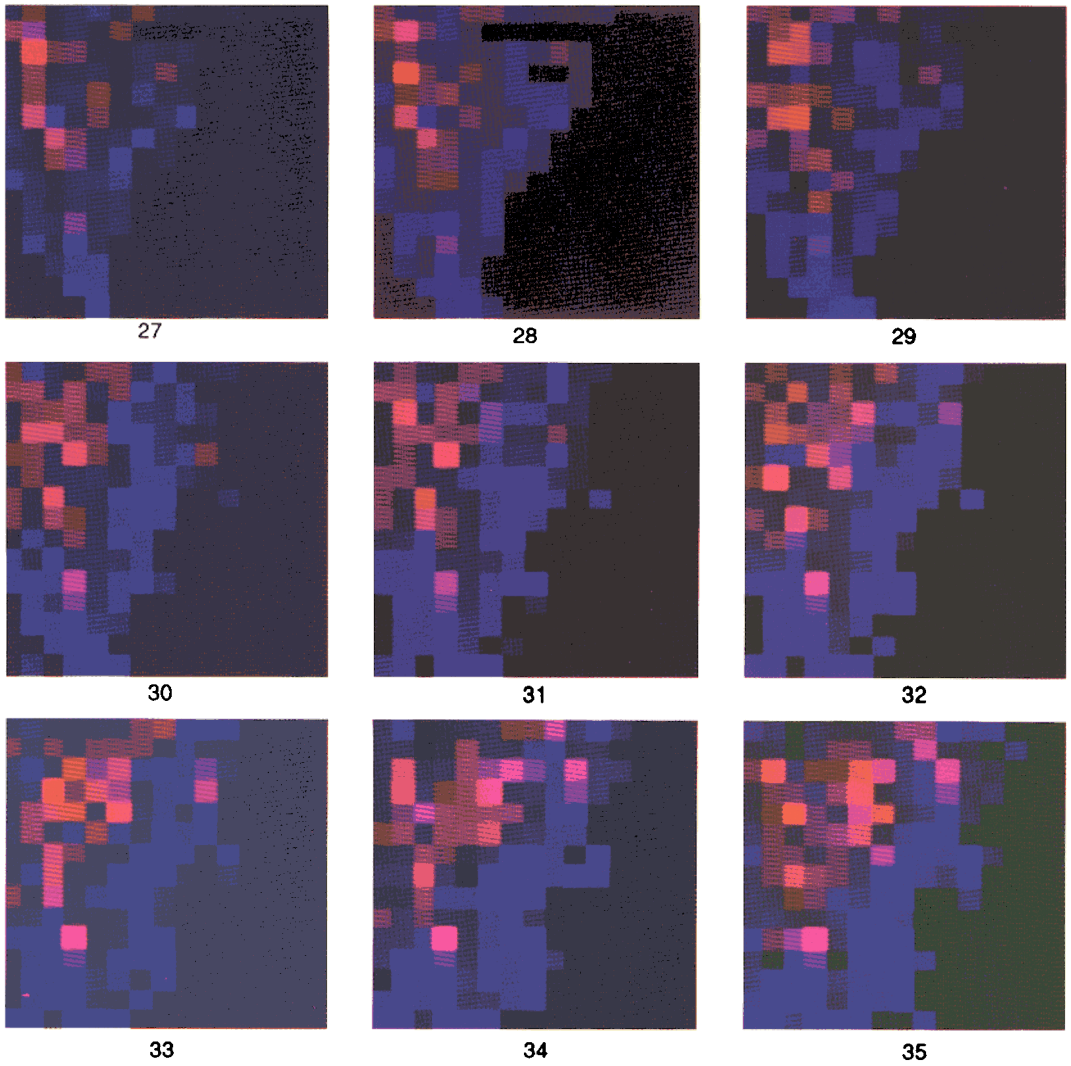

Figure 3. The spatial pattern of predator-prey dynamics is shown in a series of charts. The environment is represented by the 15 x 15 grid. Prey population density in each grid cell or patch is indicated by the intensity of blue color. Predator population density is indicated by the intensity of red color. Thus, a black cell is empty; a bright blue cell contains only prey at a high density;

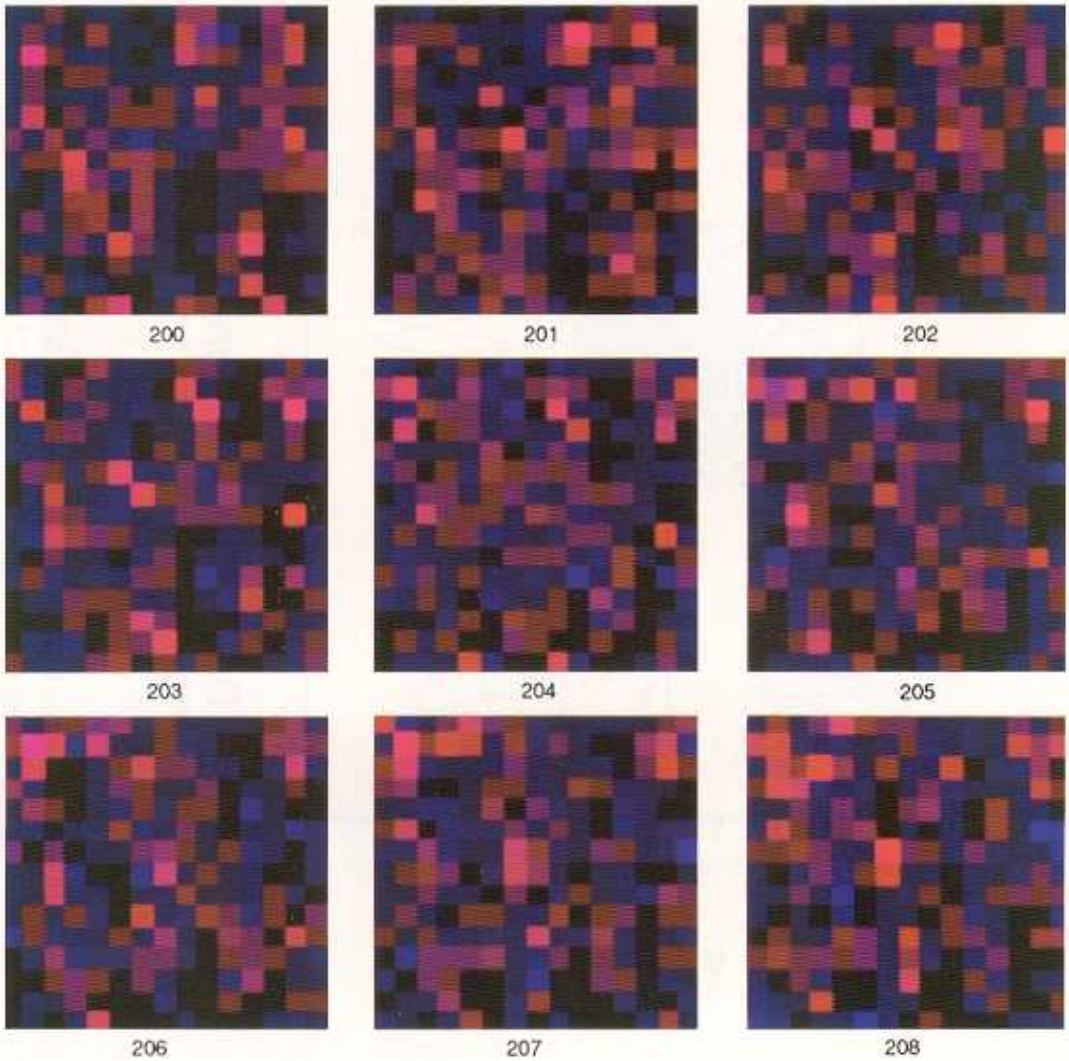

Figure 3. (continued) and a purple or lavender color indicates the presence of both predators and prey. A sequence of 9 days is shown at the beginning of the simulation, and another sequence of 9 days is shown after 200 days of simulation.

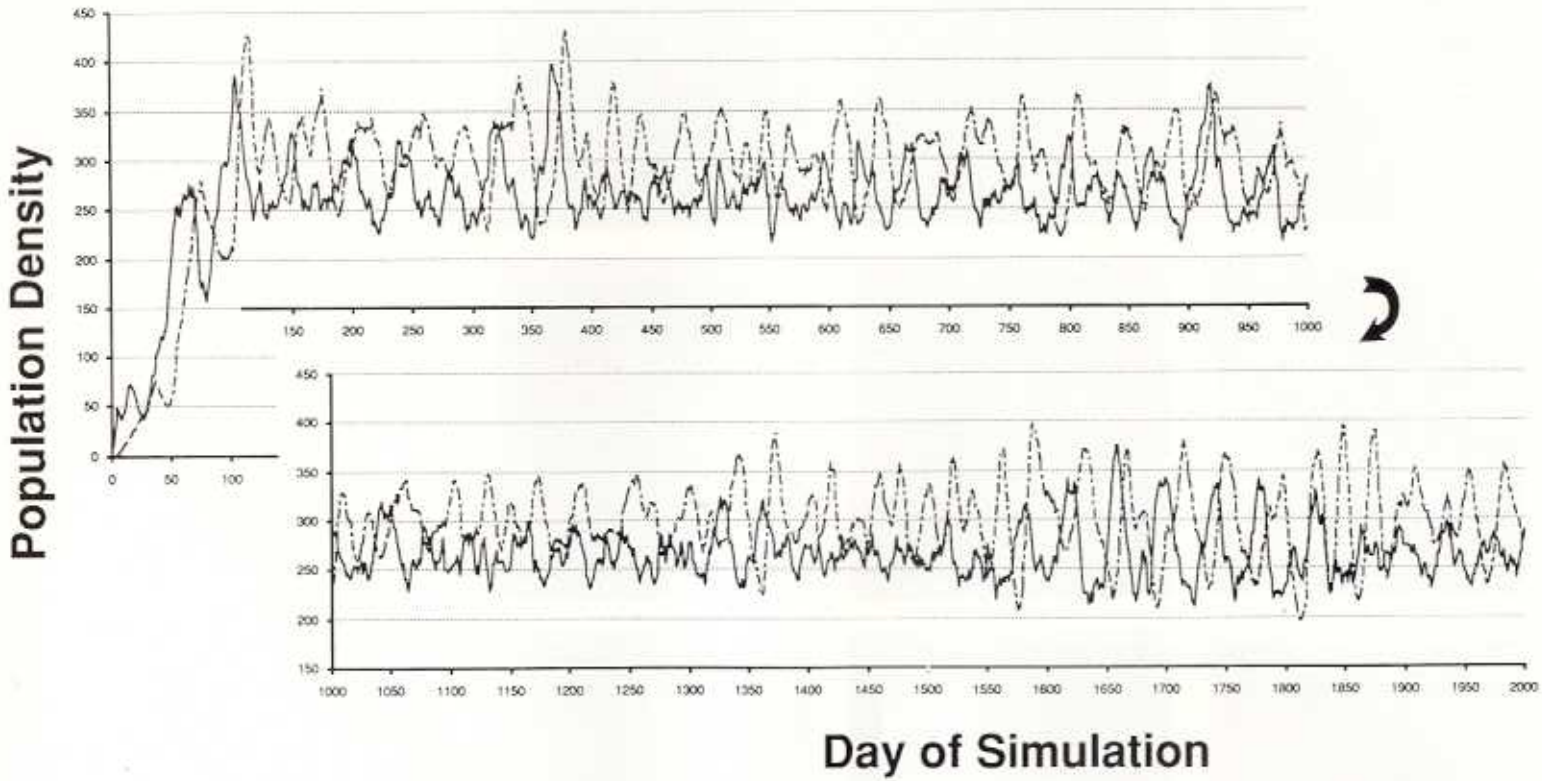

Figure 4. Time series plot of simulated predator (dashed line) and prey (solid line) numbers over time in days. This simulation was initialized with 50 prey and 40 predators over the first 25 days.

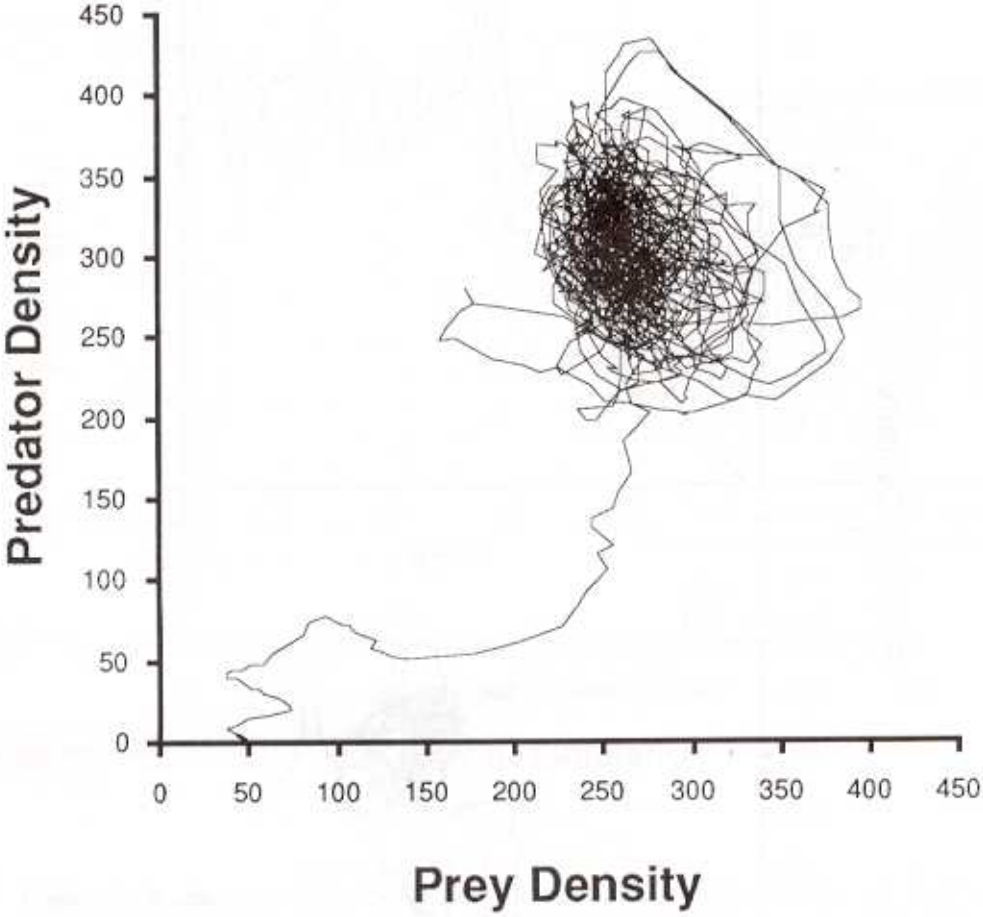

Figure 5. A phase plot of the time series data from Fig. 4. The attractor has a fractal dimension of approximately 4.7.

to these data yielded an estimated intrinsic rate of increase of about r=0.08. This result is well below the values that would produce chaos in the equation ($r > 2.69$). However, a close inspection of the system's dynamics near equilibrium revealed that this single-species system never did settle down (Fig. 7, inset). This effect could not be explained by using a Ricker model constrained to integer values, and the time series data showed a positive Lyapunov exponent and a fractal (correlation) dimension of 4.9. Apparently, the single-species system was also chaotic. In this case, however, the chaos caused only a minor disturbance in an otherwise stable system — the attractor was strange but small.

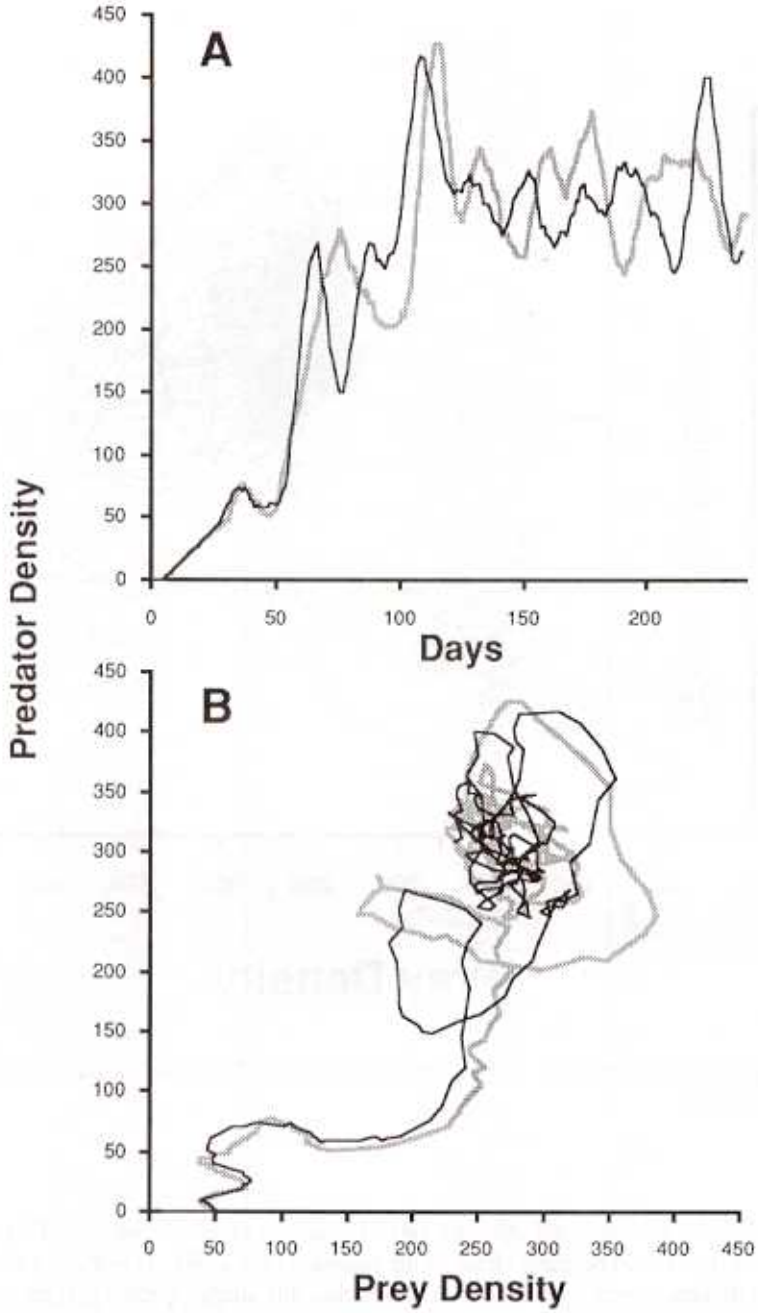

Figure 6. Sensitivity of the model to initial conditions is shown by comparing the first parts of two simulations, identical except for the insertion of one extra prey in the second simulation (solid line). *A* shows a time-series of the predator populations from the two simulations; *B* shows the two phase plots superimposed.

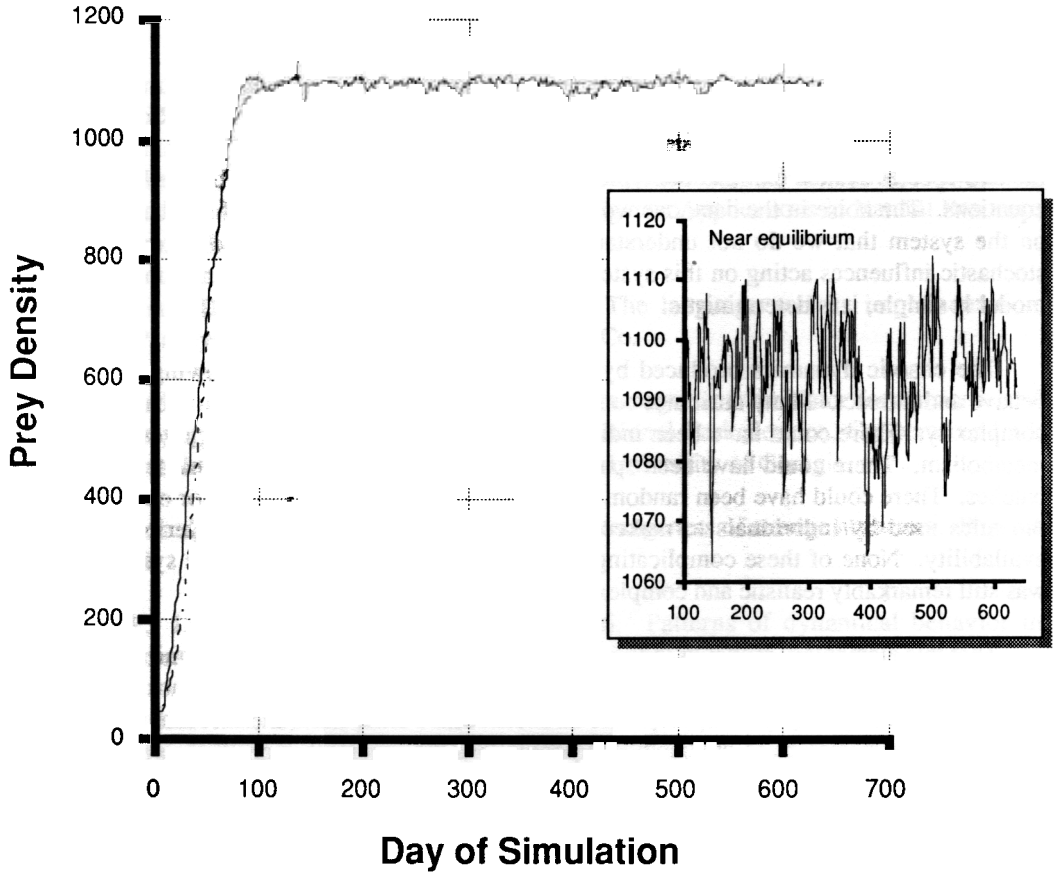

Figure 7. A time-series plot (solid line) of simulated prey population initialized as in the simulation shown in Fig. 1, but with no predators. The dashed line was generated by a simple logistic model with r=0.08 and K=1095 (see text). Inset is a plot of the system dynamics about equilibrium for 500 days after day 100, showing chaotic cycles about K. This system had a fractal dimension of approximately 4.9.

Conclusions

If one were to examine this simulated interaction as though it were a natural system, one would very likely conclude that the single-species system is well modeled by a Ricker or logistic model, that the intrinsic rate of increase in the prey population is in a very normal range, and that the two-species system exhibits the typical limit-cycle dynamics predicted by the Lotka-Volterra equations. The noise in the data, one would argue, is just that—evidence of stochastic influences on the system that we do not understand or cannot measure. In fact, however, there are no stochastic influences acting on this system. There are no forces that we do not understand. The model is simple; it is deterministic.

The chaotic dynamics produced by this model were generated by allowing individuals to behave and interact. Many attributes could have been added to the model to increase the system's complexity. There could have been individual variation in factors like aging rates, fecundity, or metabolism. There could have been spatial heterogeneity, variation in the characteristics of the patches. There could have been random choice involved in decision making or even variation in the rules used by individuals to make decisions. There could have been periodicity in food availability. None of these complicating factors existed in the model, yet the system dynamics was still remarkably realistic and complex.

That this elementary model of individual's interacting produced chaotic dynamics indicates that there is something fundamental about population interactions that results in chaos. Perhaps it is the spatial or compartmental aspect of the environment. Perhaps it is the fact that individuals are affected by the decisions of others so that populations are inherently non-linear systems. In any case, high-order chaos may well be the foundation upon which we study population dynamics.

As we have seen here, even though a system is chaotic, it need not be wildly fluctuating or unpredictable. It may, in fact, be well enough bounded to be modeled effectively by a simple logistic function. However, this work suggests that arguments discounting the role of chaos in population dynamics are premature.

This study also suggests that chaotic population models can be constructed based directly on observation of individual behaviors and actions. Furthermore, such models can be experimentally validated by comparing emergent properties from the models with emergent properties of the natural populations: survivorship and natality functions, functional response relationships, and dispersion patterns, for example. This type of modeling and its relationship to chaotic dynamics warrant further attention.

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