

## Can noise induce chaos?

Brian Dennis, Robert A. Desharnais, J. M. Cushing, Shandelle M. Henson and R. F. Costantino

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An important component of the mathematical definition of chaos is sensitivity to initial conditions. Sensitivity to initial conditions is usually measured in a deterministic model by the dominant Lyapunov exponent (LE), with chaos indicated by a positive LE. The sensitivity measure has been extended to stochastic models; however, it is possible for the stochastic Lyapunov exponent (SLE) to be positive when the LE of the underlying deterministic model is negative, and vice versa. This occurs because the LE is a long-term average over the deterministic attractor while the SLE is the long-term average over the stationary probability distribution. The property of sensitivity to initial conditions, uniquely associated with chaotic dynamics in deterministic systems, is widespread in stochastic systems because of time spent near repelling invariant sets (such as unstable equilibria and unstable cycles). Such sensitivity is due to a mechanism fundamentally different from deterministic chaos. Positive SLE's should therefore not be viewed as a hallmark of chaos. We develop examples of ecological population models in which contradictory LE and SLE values lead to confusion about whether or not the population fluctuations are primarily the result of chaotic dynamics. We suggest that "chaos" should retain its deterministic definition in light of the origins and spirit of the topic in ecology. While a stochastic system cannot then strictly be chaotic, chaotic dynamics can be revealed in stochastic systems through the strong influence of underlying deterministic chaotic invariant sets.

*B. Dennis, Dept of Fish and Wildlife Resources and Division of Statistics, Univ. of Idaho, Moscow, ID 83844, USA (brian@uidaho.edu). – R. A. Desharnais, Dept of Biological Sciences, California State Univ., Los Angeles, CA 90032, USA. – J. M. Cushing, Interdisciplinary Program in Applied Mathematics, Univ. of Arizona, Tucson, AZ 85721, USA. – S. M. Henson, Dept of Mathematics, Andrews Univ., Berrien Springs, MI 49104, USA. – R. F. Costantino, Dept of Ecology and Evolutionary Biology, Univ. of Arizona, Tucson, AZ 85721, USA.*

The search for a definition of chaos has been guided by attempts to describe carefully the basic properties and patterns that are possible in certain deterministic dynamic systems. The definition proposed by Alligood et al. (1997) is indicative: "an orbit is chaotic if it is bounded, not asymptotically periodic and has a positive Lyapunov exponent."

Ecological time series data represent a mixture of deterministic and stochastic forces, and can be modeled as stochastic perturbations around a deterministic dynamic model (the "skeleton," Tong 1990). A central question becomes: can the deterministic skeleton of a complex nonlinear system be experi-

mentally identified as equilibrium, periodic, or chaotic?

The definition of the Lyapunov exponent (LE) was extended to stochastic systems (Crutchfield et al. 1982, McCaffery et al. 1992) and in recent years this extension has been treated as an indicator of chaos in ecological populations (Turchin 1993, 1995, 2003, Ellner and Turchin 1995, Perry et al. 1997, Turchin and Ellner 2000). However, the LE and its extension, the stochastic Lyapunov exponent (SLE) are different. The deterministic LE is an average over the deterministic attractor, whereas the stochastic Lyapunov exponent (SLE) is an average over the steady-state probability distribution.

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In this paper, we develop two examples in population ecology of situations in which the LE and the SLE are discordant. The first example is theoretical: we give a simple paper-and-pencil derivation of the LE and the SLE for a stochastic version of the logistic model of population growth. The second example is empirical: we describe experimental results in which a model fitted to population data provided estimates of the LE and the SLE with widely disparate values. The second example involves the larva-pupa-adult (LPA) model for the flour beetle *Tribolium*. The two examples provide insight into how a system with a negative LE in the absence of noise can have a positive SLE when noise is introduced. The phenomenon can occur even when the deterministic system has a single, critically-damped stable equilibrium, a situation that would not normally be regarded as chaos by empirical ecologists (Poole 1989a, b). We subsequently discuss the historical reasons for our view that taking a positive SLE as a hallmark of chaos confuses the issues and is not consistent with the spirit and impetus of the chaos hypothesis in ecology.

### Deterministic and stochastic Lyapunov exponents

Here we briefly outline the definitions of the LE and SLE. It is the nature of the topic that one can quickly get bogged down with mathematical technicalities and exceptions, especially in a stochastic setting. Our attempt here is to give a mostly verbal account of the features germane to the issues we raise and to the types of models commonly seen in population ecology.

The LE is a quantitative measure that characterizes the dynamic properties of trajectories on deterministic attractors. It is the long-run average rate of divergence of nearby trajectories, and is often referred to as the dominant LE. The LE is defined using the Jacobian matrix of partial derivatives of the system equations. For a continuous-time system, denoted by

$$\frac{dN_t}{dt} = f(N_t) \quad (1)$$

or a discrete-time system in the form

$$N_{t+1} = f(N_t) \quad (2)$$

where  $N_t$  is a vector of state variables and  $f(\cdot)$  is a vector of functions, the Jacobian matrix depends on its location point  $N$  in phase space. The Jacobian matrix  $J(N)$  at a point  $N$  is

$$J(N) = \frac{\partial f(N)}{\partial N} \quad (3)$$

Trajectories of the model originating in a neighborhood of the point  $N$  tend to converge toward or diverge from each other depending on the eigenvalues of  $J(N)$ . In a continuous-time model, “almost all” trajectories near  $N$  diverge if one or more of the eigenvalues has a positive real part (there might be trajectories on a set of measure zero, i.e. a reduced-dimension set in phase space, that converge). In a discrete-time model, almost all trajectories near  $N$  diverge if one or more of the eigenvalues lies outside of a unit circle centered at the origin in the complex plane. The convergence and divergence of trajectories basically follows from Taylor series linear approximation of the model equations (1, 2) near  $N$ . For a continuous-time system, let  $\lambda(N)$  denote the largest real part among the eigenvalues of  $J(N)$ . For a discrete-time system, let  $\lambda(N)$  denote the largest of the logarithms of the absolute values of the eigenvalues. The quantity  $\lambda(N)$  is known as the local LE, and its value can vary considerably from point to point throughout phase space. The (dominant) LE,  $\lambda$ , is the long-term average value of  $\lambda(N_t)$  along a trajectory  $N_t$  followed through time. The LE is

$$\lambda = \lim_{t \rightarrow \infty} \frac{1}{t} \int_0^t \lambda(N_u) du \quad (4)$$

in a continuous-time system, or

$$\lambda = \lim_{t \rightarrow \infty} \frac{1}{t} \sum_{j=0}^t \lambda(N_j) \quad (5)$$

in a discrete-time system, provided the limits exist. For practical purposes, existence of the limits requires existence of a bounded attractor, such as a stable point, stable cycle, invariant loop, torus, or strange attractor. When the model trajectory settles down onto an attractor, the relative contribution of the early transient part of the trajectory to the average (4, 5) becomes vanishingly small as time becomes large. Thus, the time-average (4, 5) is effectively the average value of  $\lambda(N)$  on an attractor. If there are multiple attractors, each attractor has its own  $\lambda$  value which corresponds to starting the trajectory anywhere within the basin of attraction for that attractor.

A positive LE is an indication of a chaotic attractor; small differences in initial conditions are, on average, magnified on the attractor. A negative LE indicates that trajectories differing by tiny changes in initial conditions tend in the long run to converge, as is the case with a stable point equilibrium or a stable periodic cycle.

For data analysis, a common practice is to fit a model and then follow a model trajectory through time. At each time step, the model-estimated Jacobian matrix is evaluated. The long-run average dominant eigenvalue is then found using one of various methods (one common method is to calculate the ongoing product of the

Jacobian matrices, similar to multiplying a Leslie projection matrix repeatedly to get the eigenvalue representing the long-term population growth rate; see Dennis et al. 2001 for details).

In the stochastic setting, we consider  $f(N_t)$  to represent some underlying deterministic tendency influencing the vector of state variables  $N_t$ . The state variables in addition are assumed to be influenced by stochastic forces (noise). Many types of stochastic models have the structure of a noise model superimposed on an underlying deterministic model (the skeleton). Examples are the continuous time diffusion processes (Karlin and Taylor 1981, Gardiner 1983), and discrete time stochastic difference equations (Tong 1990).

Like the LE, the definition of the SLE revolves around the Jacobian matrix (3). If an average like (4) or (5) is calculated by following a stochastic model trajectory through time, the quantity may or may not converge, depending on the properties of the model. If the stochastic model is ergodic, meaning that it settles down into a long-run statistical equilibrium (or more technically, that neighborhoods of the state space are revisited in finite time with probability 1), then long-run averages such as (4) or (5) usually converge. An ergodic stochastic model typically has a long-run probability distribution, known as a stationary distribution, that is independent of time and initial conditions. The limit involved in (4) or (5) is equivalent to the expected value of the local LE with respect to the stationary distribution of the stochastic model.

To summarize, the LE and the SLE concepts both start from the idea that trajectories originating near a point  $N$  tend to converge to or diverge. The dominant eigenvalue in the linearization of the model near  $N$  provides a measure of the rate of convergence or divergence (if  $N$  is an equilibrium point of a deterministic system, then that eigenvalue provides the familiar test of the local stability of the equilibrium; May 1974a). The LE and the SLE arise as averages by following a model trajectory through time and calculating the resulting eigenvalues at all states visited by the system. If a deterministic system has an attractor, then the averaging process used to construct the LE will converge to the average on the attractor. The SLE average, however, converges to the average with respect to the stationary distribution of the stochastic model. Usually, a deterministic attractor is a set of dimension much reduced from the dimension of the state space. By contrast, a stochastic model with a stationary distribution typically produces trajectories that visit and revisit all portions of the state space, even though the underlying skeleton has a reduced dimension attractor. Thus, in a stochastic model, the LE of the skeleton and the SLE are substantially different concepts. The differences are noteworthy in the following two examples.

## Continuous-time logistic model

The following analytical demonstration illustrates how the SLE can be positive even when the underlying deterministic model has a point equilibrium that is stable for all positive initial population sizes.

### (a) Deterministic model

A continuous-time model of the growth of a single population is

$$\frac{dN_t}{dt} = f(N_t) \quad (6)$$

where  $f(\cdot)$  is a function specifying any dependence of the population growth rate,  $dN_t/dt$ , on population abundance,  $N_t$ . A well-known example is the logistic model, in which the function  $f(\cdot)$  is quadratic (Gotelli 1995, Hastings 1997):

$$\frac{dN_t}{dt} = aN_t - bN_t^2 \quad (7)$$

When the constants  $a$  and  $b$  are both positive, the logistic model (7) has a positive equilibrium at  $N_\infty = a/b$  that is stable and is the attractor for all positive initial population sizes. The origin under such circumstances is an unstable equilibrium.

The Jacobian of the logistic model for any particular population size  $N$  is the derivative of  $f(\cdot)$  evaluated at  $N$ :

$$f'(N) = a - 2bN \quad (8)$$

In one dimension, the Jacobian is its own eigenvalue. This eigenvalue (8) separates the state space of abundances into two regions. The eigenvalue is positive for values of  $N$  lying below one half of the stable equilibrium ( $N < a/(2b) = N_\infty/2$ ). Two initial conditions in this lower abundance region, separated by a small distance, would have model trajectories that diverge from each other for a short time period. Indeed, the logistic model trajectories initiated at low abundances resemble exponential growth. In other words, the region of abundance near zero in the logistic model has the property of temporary sensitivity to initial conditions. Of course, if enough time elapses, the distance between any two trajectories in this low region will eventually decrease as the trajectories approach  $N_\infty$ .

The eigenvalue (8) is negative for values of  $N$  greater than  $N_\infty/2$ . All trajectories initiated at positive abundances eventually enter this high abundance region containing the stable point equilibrium,  $N_\infty$ . In this region, nearby trajectories converge, rather than diverge. Trajectories in the high abundance region do not have the property of sensitivity to initial conditions.

The LE for the model is the long-run average value of the eigenvalue on the attractor. In this case, the LE is the Jacobian evaluated at the stable point equilibrium,  $N_\infty$ :

$$\lambda = f'(N_\infty) = f'(a/b) = -a \quad (9)$$

The negative sign of  $\lambda$  confirms the absence of deterministic chaos in this model. It is well-known, in fact, that a one-dimensional autonomous differential equation cannot have chaotic solutions (Drazin 1992).

### (b) Stochastic model

The following continuous-time stochastic version of the logistic model has been frequently studied (Dennis and Patil 1984). Let  $N_t$  be a diffusion process (Karlin and Taylor 1981, Gardiner 1983) with infinitesimal mean function  $m(n) = an - bn^2$  and infinitesimal variance function  $v(n) = \sigma^2 n^2$  ( $\sigma^2 > 0$ ). This is identical to assuming that  $N_t$  is governed by an Ito stochastic differential equation of the form

$$dN_t = (aN_t - bN_t^2)dt + \sigma N_t dW_t \quad (10)$$

where  $dW_t$  has a normal distribution with mean 0 and variance  $dt$  (Weiner process increment). The model has

been proposed to represent a population growing logistically but subjected to environmental noise fluctuations (Leigh 1968, Dennis and Patil 1984). The parameter  $\sigma^2$  scales the intensity of the noise fluctuations.

The statistical distribution for  $N_t$  governed by (10) converges to a long-term stationary distribution, provided the noise intensity is not too large. The stationary distribution is a gamma distribution (Dennis and Patil 1984), with probability density function given by

$$p(n) = \frac{\beta^\alpha}{\Gamma(\alpha)} n^{\alpha-1} e^{-\beta n}, \quad (11)$$

in which  $\alpha = (2a/\sigma^2) - 1$  and  $\beta = 2b/\sigma^2$  (Fig. 1). The condition for the existence of the stationary distribution is  $\alpha > 0$  (or  $\sigma^2 < 2a$ ). The stationary gamma model has had extraordinary success in describing equilibrial dynamics of single species populations (Costantino and Desharnais 1981, Dennis and Costantino 1988, Desharnais et al. 1990, Kemp and Dennis 1993).

For the stochastic logistic model (10), the SLE is the Jacobian (8) averaged over the long-run stationary distribution. Noting that the expected value of a gamma variate is (Rice 1995)

$$E(N) = \int_0^\infty np(n) dn = \alpha/\beta \quad (12)$$

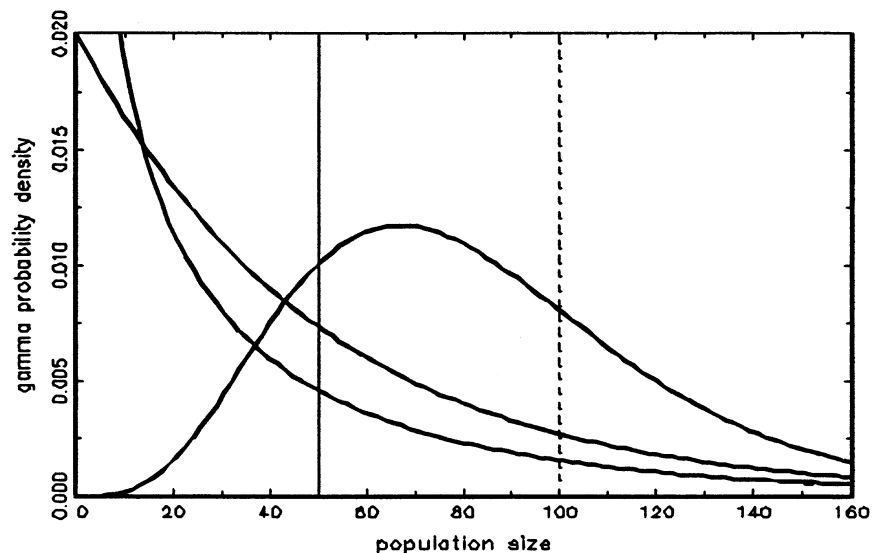


Fig. 1. Solid curves: three gamma probability distributions of equilibrium population abundance. The gamma density curves are given by  $p(n) = \beta^\alpha n^{\alpha-1} e^{-\beta n} / \Gamma(\alpha)$ , where  $\alpha = (2a/\sigma^2) - 1$ ,  $\beta = 2b/\sigma^2$ , and  $n$  is population size, and are plotted using  $a = 0.06$ ,  $b = 0.0006$ , and three different values of  $\sigma^2$ . The mound-shaped curve corresponds to  $\sigma^2 = 0.02$  ( $\alpha = 5$ ). The decreasing J-shaped curve intersecting the vertical axis at 0.02 is the exponential distribution, a special case of the gamma distribution corresponding to  $\sigma^2 = 0.06$  ( $\alpha = 1.0$ ). The decreasing J-shaped curve with a pole at zero corresponds to  $\sigma^2 = 0.08$  ( $\alpha = 0.5$ ). Vertical dashed line: deterministic equilibrium abundance level (carrying capacity)  $N_\infty = a/b = 100$ . Vertical solid line: abundance level  $N_\infty/2 = 50$  below which the Jacobian of the deterministic logistic model is positive. The J-shaped gamma distribution with a pole produces a positive stochastic Lyapunov exponent, while the stochastic Lyapunov exponent for the mound-shaped gamma distribution is negative. The exponential distribution case produces a stochastic Lyapunov exponent of zero.

we have

$$\lambda_s = E[f'(N)] = E(a - 2bN) = a - 2bE(N) = \sigma^2 - a \quad (13)$$

If  $\sigma^2 > a$ , the SLE is positive, indicating overall sensitivity, on average, to initial conditions. Appending the condition for existence of the stationary distribution, we find the conditions for a positive SLE to be  $a < \sigma^2 < 2a$ .

Thus, the average sensitivity to initial conditions in the stochastic logistic model (10) is determined by the noise intensity. If  $\sigma^2 < a$ , the noise intensity is low compared to the strength of the deterministic forces ( $a = |-a| = |\lambda|$  is the magnitude of the eigenvalue measuring the stability of the deterministic point equilibrium). The LE and SLE are in concert: neither indicate chaos (Fig. 1). If  $a < \sigma^2 < 2a$ , the SLE is positive and the LE remains negative. The two measures are then not accord. What happens is that the gamma stationary distribution becomes J-shaped, with the largest portion of probability near the origin (Fig. 1). The population spends the bulk of its time in the abundance region between 0 and  $N_\infty/2$ , in which the Jacobian (8) is positive. For  $2a < \sigma^2$ , there is no stationary distribution. The time-dependent probability distribution of  $N_t$  piles up over an arbitrarily small interval near zero as  $t \rightarrow \infty$ . The stochastic population undergoes a “noise-induced transition” (Horsthemke and Lefever 1984) from long-run equilibrium to certain extinction. Enroute to extinction, trajectories will display sensitivity to initial conditions.

This behavior of the SLE is not peculiar to the diffusion process version of the logistic. In the familiar deterministic, discrete-time versions of the logistic, such as the quadratic map and the Ricker map, chaos occurs when density dependence becomes so overcompensatory that it continually knocks the population to levels near zero, a repelling set (Berryman and Millstein 1989, Berryman 1991). If the discrete-time models are converted to stochastic models, noise alone can cause a positive SLE by perturbing the population to levels near zero, even when the underlying map is not overcompensatory but rather predicts just a critically damped stable point (Desharnais et al. 1997).

## LE and SLE estimated from experimental data

Here we display an empirical example in which a population model, fitted to an experimental data set, provides point estimates and confidence intervals for the LE and SLE. The confidence intervals for the LE and SLE yield the conclusion that the LE and the SLE have opposite signs.

In a recently reported experiment, demographic parameters of laboratory cultures of flour beetles (*Tribolium castaneum*) were manipulated to test a series of bifurcations predicted by a mathematical population model (Dennis et al. 2001). The model, the “LPA model” (larvae–pupae–adult), is a stage structured, discrete time, non-linear population model with three state variables (Dennis et al. 1995). It has successfully explained and predicted a variety of non-linear phenomena, including transitions between dynamic regimes (such as equilibria, two-cycles, three-cycles, invariant loops, and chaos), multiple attractors, saddle influences, sensitivity to initial conditions, and lattice effects (Costantino et al. 1995, 1997, 1998, Cushing et al. 1996, 1998a, b, 2001, Dennis et al. 1995, 1997, 2001, Henson et al. 1999, 2001, Desharnais et al. 2001). In all of these studies, consideration of stochasticity has played a key role in statistical analysis and interpretation of the actual dynamic behaviors displayed by the populations. Our current working hypothesis is that the bulk of departures of data from model are explained by stochastic fluctuations of the “demographic” type: the independent random contributions of births and deaths by individual population members (Dennis et al. 2001).

A demographic stochastic version of the LPA model (Dennis et al. 2001) for the flour beetle is given by the following equations:

$$\begin{aligned} L_{t+1} &= (\sqrt{bA_t \exp(-c_{el}L_t - c_{ea}A_t)} + E_{1t})^2 \\ P_{t+1} &= (\sqrt{L_t(1 - \mu_l)} + E_{2t})^2 \\ A_{t+1} &= (\sqrt{P_t \exp(-c_{pa}A_t) + A_t(1 - \mu_a)} + E_{3t})^2 \end{aligned} \quad (14)$$

where  $L_t$  denotes the number of feeding larvae (the L-stage),  $P_t$  denotes the number of non-feeding larvae, pupae, and callow adults (the P-stage), and  $A_t$  denotes the number of adults (the A-stage). The discrete time interval is two weeks. The coefficient  $b > 0$  denotes the average number of larvae recruited per adult per unit of time in the absence of cannibalism,  $\mu_a$  and  $\mu_l$  are the adult and larval probabilities of dying from causes other than cannibalism ( $0 < \mu_a, \mu_l < 1$ ), and the exponentials  $\exp(-c_{ea}A_t - c_{el}L_t)$  and  $\exp(-c_{pa}A_t)$  represent the probabilities that individuals survive cannibalism in one unit of time, with cannibalism coefficients  $c_{el}, c_{ea}, c_{pa} > 0$ . Also,  $E_{1t}, E_{2t}, E_{3t}$  are noise terms assumed to have a joint trivariate normal distribution with mean vector of 0 and a variance–covariance matrix of  $\Sigma$ . In our analyses, covariances among  $E_{1t}, E_{2t}$ , and  $E_{3t}$  at any given time  $t$  were represented by off-diagonal elements of  $\Sigma$ , but they turned out to be negligibly small, consistent with the hypothesis that the noise is largely of the demographic type. We also assumed that the noise terms were uncorrelated through time. The deterministic LPA model is retrieved by setting  $\Sigma = 0$ .

The experiment in question consisted of manipulating adult recruitment so as to fix the parameter  $c_{pa}$  at a set of seven values: 0, 0.05, 0.10, 0.25, 0.35, 0.5, 1.0. Three replicate cultures were maintained at each treatment value of  $c_{pa}$ ; adult mortality in these cultures was manipulated so as to fix the parameter  $\mu_a$  at 0.96. Three unmanipulated control cultures were maintained as well. The set of  $c_{pa}$  values was selected because the LPA model, fitted to an earlier data set, predicted a striking series of transitions in dynamic behavior, the highlight of which was chaos sandwiched in between other presumably more recognizable behaviors (stable point equilibrium, three-cycle, etc.). Complete details of the experiment and the statistical methods can be found in Dennis et al. (2001).

The stochastic LPA model (14) was fitted to data from the experiment using the method of conditional least squares. A bootstrapping method for time series was adapted for obtaining confidence intervals for parameter values. In addition, confidence intervals for functions of parameters, in particular the LE and SLE for each experimental treatment, were obtained with the bootstrapping method. The method also yielded confidence sets for the type of underlying dynamic behavior in the skeleton at each treatment.

We focus here on one treatment in the experiment, in which the contrast between the LE and SLE was especially sharp. For the value  $c_{pa} = 0.5$  (and  $\mu_a = 0.96$ ), the LPA model skeleton under the earlier parameters used to design the experiment had predicted a distinctive three-cycle attractor: the L-stage, for instance, was predicted to display two low abundances followed by a very high abundance. The model, when fitted to the experiment data, indeed produced a point estimate of a three-cycle attractor for the  $c_{pa} = 0.5$  treatment (Fig. 2). Furthermore, in 2000 bootstrap simulations of the experiment and model-fitting process, 100% of the bootstrap data sets had three-cycle behavior as the estimated attractor for  $c_{pa} = 0.5$  (Dennis et al. 2001 gave “pie charts” of the behaviors of the types of bootstrap-estimated attractors for each experimental treatment). The data certainly give the impression of a three-cycle, albeit with some added noise (Fig. 2). Simulations of the stochastic demographic LPA model (14) resemble the data closely (Fig. 2).

The estimated LE for the  $c_{pa} = 0.5$  treatment reinforces the conclusion that a periodic attractor influences dynamics of populations under that treatment. The 95% bootstrap confidence interval for the LE at that treatment was  $(-0.101, -0.080)$ ; the confidence interval spans only negative values. There is no indication that the skeleton for that treatment could plausibly be an aperiodic loop ( $LE = 0$ ) or chaotic ( $LE > 0$ ).

The SLE tells a different story. The 95% bootstrap confidence interval for the  $c_{pa} = 0.5$  treatment was  $(0.013, 0.025)$ , spanning entirely positive values. According to some recent authors in population ecology,

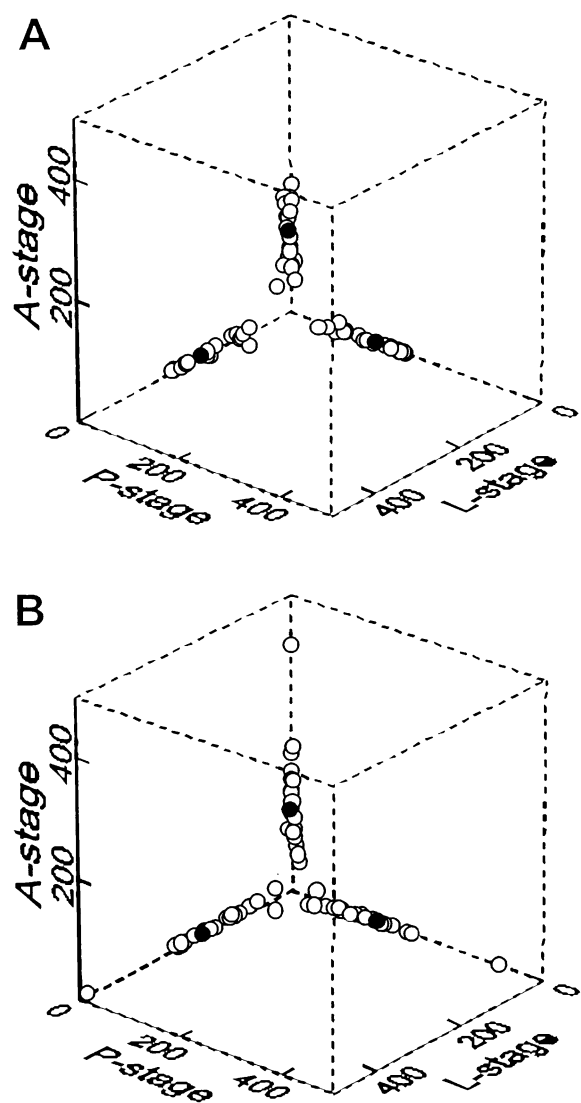


Fig. 2. (A) Population abundance data (open circles) and underlying 3-cycle attractor (solid circles) of the deterministic portion of the fitted stochastic LPA model, plotted in phase space. Data and model are from Dennis et al. (2001). (B) Simulated data from the fitted stochastic LPA model.

this situation, consisting of an underlying, strongly periodic attractor with demographic noise, should be labeled “chaos,” due to the positive SLE. We disagree.

## Discussion

### The hypothesis of chaos in ecology

For evaluating uses of the SLE, it is valuable to keep in mind the historical context of the chaos hypothesis in ecology. The fundamental assertion of mathematical ecology has been, from the beginnings of the discipline, that simple deterministic models can help unlock sub-

stantial gains in understanding population systems (Scudo and Ziegler 1978, Kingsland 1985). The news that simple deterministic models could display exotic, seemingly random behavior (May 1974b) was electrifying, precisely because real population time series often seemed devoid of unambiguous signals. The hypothesis of chaos in ecological populations originally emphasized low-dimensional, non-linear, deterministic forces. According to the hypothesis, if a few non-linear forces such as predation or overcompensating density dependence could be correctly identified, then the seemingly stochastic fluctuations of population abundances might be largely explained in terms of simple deterministic models. May (1976) wrote:

“Quite apart from their intrinsic mathematical interest, the above results raise very awkward biological questions. They show that simple and fully deterministic models, in which all biological parameters are exactly known, can nonetheless (if the non-linearities are sufficiently severe) lead to population dynamics which are in effect indistinguishable from the sample function of a random process. Apparently chaotic population fluctuations need not necessarily be due to random environmental fluctuations, or sampling errors, but may reflect the workings of some deterministic, but strongly density dependent, population model.”

The deterministic, low-dimensional formulations of population models were fully in keeping with the scientific spirit and excitement attending the concept of chaos, as exemplified by May's quote above. After May's discoveries, mathematical ecologists contributed many deterministic population models with potential for chaotic behavior (May and Oster 1976, May 1986, Hastings et al. 1993). However, convincing evidence at that time for actual chaos in an ecological population was not forthcoming. In fact, in an influential study (Hassell et al. 1976), one-dimensional, discrete time models were fitted to data from many populations, and only stable point and stable cyclic dynamics were estimated for all the field populations surveyed. While Schaffer (1985) pointed out that the focus on one-dimensional models was misdirected, and that potential for chaos was nearly ubiquitous in realistic models with three or more state variables, debate about the relevance of chaos for understanding real population fluctuations continued. Mathematical ecologists tended to be enthusiastic and optimistic, but seasoned empirical ecologists were highly skeptical. The leading counter-hypothesis was that population abundances, though undeniably influenced by endogenous forces, were largely buffeted by exogenous forces of an essentially stochastic nature (Berryman and Millstein 1989, Poole 1989a, b, Berryman 1991).

### Randomness and chaos

Are noise and chaos different? The word “indistinguishable” in May's quote above was a tempting challenge

to mathematicians, who responded with hundreds of papers on the properties of non-linear dynamic models. The mathematical properties of deterministic chaos gradually became better understood, and mathematical definitions of chaos emerged. While the technicalities of the chaos definitions vary to this day among textbooks, the property of sensitivity to initial conditions was a nearly universal ingredient.

Sensitivity to initial conditions was not enough, though, according to the definitions. The exponential growth equation, for example, is sensitive to initial conditions when the growth rate is positive, but was not regarded as chaotic. The definitions made clear that chaos was a property of an attractor of a deterministic system. Typical additional requirements for chaos were that the attractor had to be bounded and densely embedded with periodic solutions (Drazin 1992).

During the years following the chaos discoveries, attitudes about the nature of stochastic forces changed. Under the emerging view, true randomness did not exist in the macroscopic world (as it does in the world of atomic and subatomic particles). All apparent random behavior would have deterministic causes, but some systems would require unwieldy, high-dimensional models to describe the state variables properly (West 1985). A coin toss, the quintessential example of a random system, could in principle be described adequately, if inconveniently, by Newton's laws (Kolata 1986). Adopting a stochastic model to describe a system became viewed as a matter of convenience: absent a low-dimensional deterministic model of the system, a stochastic model at least might provide the long-run frequency tendencies of the system states. Successful probabilistic description would occur when the stationary probability distribution of the stochastic model closely resembled the invariant measure of the (presumably chaotic) attractor in the deterministic system (Lasota and Mackey 1985). Algorithms for generating “random” numbers with computers exploit such resemblances. Randomness *is* chaos, but calling it “noise” is a strategic modeling decision amounting to an admission that the system fluctuations remain high dimensional and unexplained.

### Noise-induced sensitivity

During the years following the chaos discoveries, stochastic population models also received increased attention. May (1974a) again catalyzed the discussion: “So far, all the models have assumed an unvarying, deterministic environment. But real environments are uncertain. The birth rates, carrying capacities, competition coefficients, and other parameters which characterize natural systems all, to a greater or lesser degree, exhibit random fluctuations.” In other words, real ecological systems might be so complex that probabilistic

description at some level becomes necessary. Impetus for the stochastic approach came from conservation biology (Leigh 1981, Shaffer 1981, Lande and Orzack 1988, Dennis et al. 1991).

Early in the stochastic investigations it became clear that a stochastic model can display behavior considerably different from its deterministic counterpart, especially when non-linear forces are influential. For instance, when stochastic versions are constructed in the form of a deterministic “signal” perturbed multiplicatively by exogenous “noise”, the central tendency measures such as means or modes can bear little resemblance to the deterministic dynamics (for instance, Dennis and Patil 1984). Differences in the dynamic behaviors of deterministic models and their stochastic versions, termed “noise-induced transitions,” were studied intensively in physics (Horsthemke and Lefever 1984).

The mathematical definition of “sensitivity to initial conditions” in terms of the SLE was extended to stochastic systems by mathematical physicists (Mayer-Kress and Haken 1981, Crutchfield et al. 1982). It was noted that for simple models such as the logistic map perturbed by noise, positive SLE’s occurred at far lower values of the control parameter than for positive LE’s. Such dynamic phenomena were referred to as “noise-induced chaos” (Crutchfield et al. 1982), in keeping with the vocabulary of the contemporary investigations of noise-induced transitions (Horsthemke and Lefever 1984). Later, a formal mathematical definition of chaos for stochastic systems was given by Eckmann and Ruelle (1985). They considered a system to be chaotic if it exhibits sensitivity to initial conditions (as determined by a positive SLE) and bounded fluctuations. This definition omitted requirements on the attractor of the underlying deterministic model.

### Unstable chaotic invariant sets

The sensitivity to initial conditions as determined by a positive SLE can indeed arise in “chaos-like” ways. Rand and Wilson (1991) noted that sensitivity to initial conditions in a stochastic system can arise when chaotic invariant, but repelling, sets on stable manifolds are embedded in the underlying deterministic model. Gao et al. (1999), taking issue with Crutchfield et al. (1982), suggested that the term “noise-induced chaos” should refer only to such situations involving chaotic invariants. The idea is that in a noisy system, a trajectory would often leave the deterministic attractor and come under the influence of the manifold of the chaotic set. The trajectory would display a “fly by” (Cushing et al. 1998a) of the unstable chaotic set, and thus would sometimes appear to be under the influence of chaotic dynamics.

However, the SLE by itself cannot distinguish such noise-revealed chaotic invariant sets from other types of initial condition sensitivity. As we have shown here, average sensitivity to initial conditions can occur in stochastic models even without such lurking chaotic repellers. All that is needed is for any kind of repelling region of phase space to be revisited often enough for the SLE average to be positive. Such a region could be an unstable point on a stable manifold (Cushing et al. 1998a). A stable manifold is not even needed; in the stochastic logistic example we described here, the unstable origin did not have an associated stable manifold, but its neighborhood was revisited enough for the SLE to be positive. Noise is indeed pervasive, but the details of the deterministic phase space are important to understanding population fluctuations.

We suggest the term “noise-revealed chaos” for describing the revisitation of chaotic unstable sets when noise is added to a deterministic model. Note that documenting such a situation would require substantial knowledge of the workings of the deterministic aspects of the system. In fact, just establishing that there exists a chaotic-but-unstable invariant set in any deterministic model can be a formidable simulation challenge.

### Estimating chaos

It was one thing to define chaos; it was another thing to estimate it. Early work on searching for chaos in ecological data used graphical methods to portray the low-dimensional, deterministic attractors embedded within time series data (Schaffer 1985). In the 1980s, mathematical physicists offered some statistical methods for estimating LE’s and SLE’s, but the data requirements of the methods were too large for general use in ecology (Ellner et al. 1991). Statisticians took up the study of chaos surprisingly late (Bartlett 1990, Berliner 1992). McCaffrey et al. (1992) and Nychka et al. (1992) studied the statistical properties of non-parametric estimates of SLE’s in time series. McCaffrey et al. (1992) accepted Eckmann and Ruelle (1985) definition of chaos as sensitivity to initial conditions, and wrote: “only sensitive dependence on initial conditions distinguishes chaotic systems from non-chaotic systems, and any such system with bounded fluctuations and sensitive dependence on initial conditions is chaotic, whether or not it is purely deterministic.” They used various non-parametric regression methods to estimate the deterministic model (skeleton) and lag time (embedding dimension) underlying a time series. The estimated SLE was obtained from the estimated stochastic model (estimated skeleton plus noise). The approach was non-mechanistic in the sense that the estimated skeleton was merely a highly flexible surface fitted to the data that did not contain any a priori hypothesized relationships among state variables.



The understanding and use of “mechanistic” non-linear stochastic models for analyzing time series data was greatly enhanced by (Tong 1990). In this approach, a non-linear dynamic system model (the skeleton) is used as the core of a statistical time series model, by adding noise to the model in some fashion. Statistical theory then prescribes methods of estimating model parameters (fitting the model to data), testing different model structures, and evaluating the results. Thus, if hypothetical mechanisms explaining a population’s fluctuations could be identified and formulated into a deterministic model, then the model can potentially be connected to time series data, evaluated, and used for predictions. Noteworthy are the cautions that Tong sounded about the complexities of interpreting the SLE in such models (Yao and Tong 1994, Tong 1996).

With the data requirements reduced to ecologically feasible levels, claims of chaos in ecological systems followed. In the early studies, chaos was defined as sensitivity to initial conditions, as indicated by a positive SLE. Turchin and Taylor (1992) used a parametric flexible-surface regression method (response surface methodology) to estimate the skeleton and SLE. Turchin (1993) and Ellner and Turchin (1995), using the parametric and non-parametric frameworks, documented examples of apparently chaotic time series of ecological populations, as indicated by positive SLE estimates. These SLE estimates were not accompanied by estimates of the standard errors (Falck et al. 1995a, b). Moreover, estimates of the LE’s of the underlying skeletons were not reported. Thus, we do not know whether the apparent chaos was due to the influence of underlying low-dimensional chaotic attractors or to stochastic visitation of transient areas in phase space where trajectories tend to diverge.

More recently, Turchin and Ellner (2000) undertook a double-pronged analysis of time series from Fennoscandian vole populations. They combined model-free time series analysis using kernel regression with the fitting of mechanistic predator-prey models. A fascinating latitudinal gradient in stability was documented, with the northernmost populations experiencing “quasi-chaos” (mechanistic model) or “weak chaos” (phenomenological model). Their analyses represent one of the most sophisticated investigations of time series from field populations published to date.

The “global Lyapunov exponent” that Turchin and Ellner (2000) reported is what we here have termed the SLE. The chaos they document is that of “exogenous noise amplified by sensitive dependence on initial conditions.” We suggest that their conclusions about dynamics would be more complete and interpretable if they had reported point estimates and confidence intervals for the LE, along with estimates and confidence sets for the types of dynamic behaviors in the model skeletons.

We point out also that the local LE (see paragraph after (3)) can sometimes aid in the interpretation of

dynamic behavior and deserves more attention (Bailey et al. 1997, Grenfell et al. 2002). Because its value varies across phase space, the local LE can help chart regions of sensitivity to initial conditions. Cushing et al. (2001), for instance, produced a map of a chaotic attractor in the LPA model, color-coded according to values of the local LE. The map of the “hot” and “cold” spots of the attractor served as the basis for the design of an experiment to test the control of chaos with tiny perturbations (Desharnais et al. 2001). As with the LE and SLE, the local LE can be defined differently for stochastic systems, but the interpretation of the differences seems more straightforward.

## Concluding remarks

Defining chaos in terms of a positive SLE confounds both stochasticity and complex non-linear dynamics. It classifies noisy systems as chaotic as well as systems under the influence of low-dimensional, non-linear forces. We have shown that non-linear models with simple deterministic dynamics, such as a stable point equilibrium, can display positive SLE’s in the presence of noise. Furthermore, we have displayed a real example of an experimental population in which a positive SLE was quite uninformative about what kind of dynamics were present. While ecological systems with positive SLE’s possess, on average, “sensitivity to initial conditions,” we do not believe that ecologists would want to label all such systems as chaotic.

From the beginning, our work has emphasized the importance of stochasticity in ecological dynamics. It is a misrepresentation to claim that we “... see the goal of analysis as the characterization of the purely endogenous part [of] underlying fluctuations also known as the ‘deterministic skeleton’” (Turchin 2003). What we take issue with, rather, is the practice of calling a system with a noisy equilibrium “chaotic,” under the SLE classification.

Mathematical chaos is more clearly defined for deterministic systems, and we suggest that the word “chaos” in mathematical modeling be reserved for describing that ever-fascinating deterministic behavior. All ecological systems are subject to “noise,” and so our suggestion would imply that ecological populations cannot be strictly chaotic. The way is open, though, for ecologists to demonstrate that populations are strongly influenced by underlying skeletons with chaotic dynamics or whatever other dynamics (Dennis et al. 2001). Indeed, the provocative challenge issued by mathematical ecologists was the hypothesis that population fluctuations might be largely deterministic, caused by simple non-linear interactions.

Can noise induce chaos? We suggest the answer should be “no”.

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