

Can noise induce chaos?

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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 sta-

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 (λ, μ) to represent some underlying deterministic tendency influencing the vector of state variables \mathbf{x} . 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 tend to converge to or diverge. The dominant eigenvalue in the linearization of the model near provides a measure of the rate of convergence or divergence (if 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

$$\frac{dx}{dt} = f(x) \quad (6)$$

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

$$\frac{dx}{dt} = r x \left(1 - \frac{x}{K} \right) \quad (7)$$

When the constants r and K are both positive, the logistic model (7) has a positive equilibrium at $x_{\infty} = r/K$ 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 x is the derivative of $f(x)$ evaluated at x :

$$f'(x) = r \left(1 - \frac{2x}{K} \right) \quad (8)$$

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 x lying below one half of the stable equilibrium ($x < r/(2K) = x_{\infty}/2$). 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 x_{∞} .

The eigenvalue (8) is negative for values of x greater than $x_{\infty}/2$. All trajectories initiated at positive abundances eventually enter this high abundance region containing the stable point equilibrium, x_{∞} . 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, $\lambda = -r$.

$$\lambda = -r \quad (9)$$

The negative sign of λ 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 X_t be a diffusion process (Karlin and Taylor 1981, Gardiner 1983) with infinitesimal mean function $\mu(x) = r - rx^2$ and infinitesimal variance function $v(x) = \sigma^2 x^2$ ($\sigma^2 > 0$). This is identical to assuming that X_t is governed by an Ito stochastic differential equation of the form

$$dX_t = (r - rX_t^2)dt + \sigma X_t dB_t \quad (10)$$

where B_t has a normal distribution with mean 0 and variance t (Wiener process increment). The model has

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

The statistical distribution for X_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

$$f(x) = \frac{\beta^\alpha}{\Gamma(\alpha)} x^{\alpha-1} e^{-\beta x} \quad (11)$$

in which $\alpha = (2r/\sigma^2) - 1$ and $\beta = 2/\sigma^2$ (Fig. 1). The condition for the existence of the stationary distribution is $\alpha > 0$ (or $\sigma^2 < 2r$). The stationary gamma model has had extraordinary success in describing equilibrium 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 (Ricci 1995)

$$E(X) = \int_0^\infty x f(x) dx = \alpha/\beta \quad (12)$$

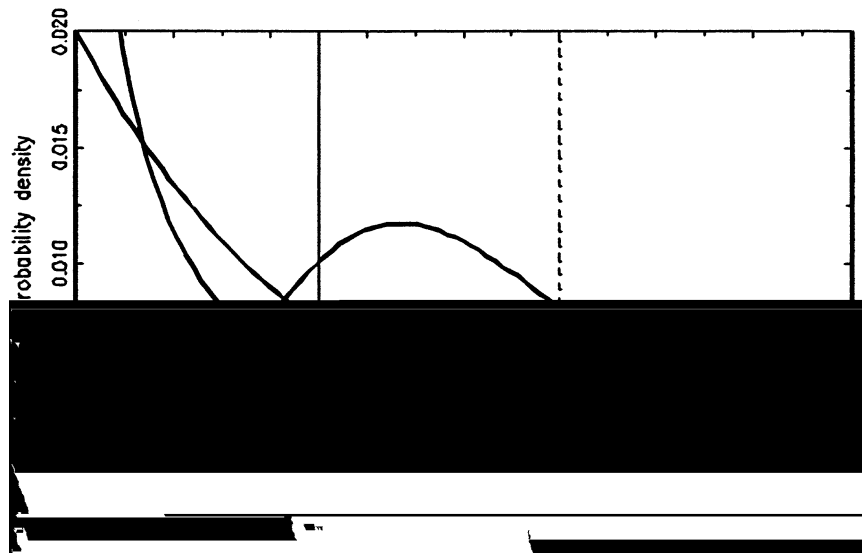


Fig. 1. Solid curves: three gamma probability distributions of equilibrium population abundance. The gamma density curves are given by $f(x) = \beta^\alpha x^{\alpha-1} e^{-\beta x} / \Gamma(\alpha)$, where $\alpha = (2r/\sigma^2) - 1$, $\beta = 2/\sigma^2$, and x is population size, and are plotted using $r = 0.06$, $\sigma^2 = 0.0006$, and three different values of σ^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) $\infty = r/r = 100$. Vertical solid line: abundance level $\infty/2 = 50$ 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 mound-shaped gamma distribution is negative. The exponential distribution case produces a stochastic Lyapunov exponent of zero.

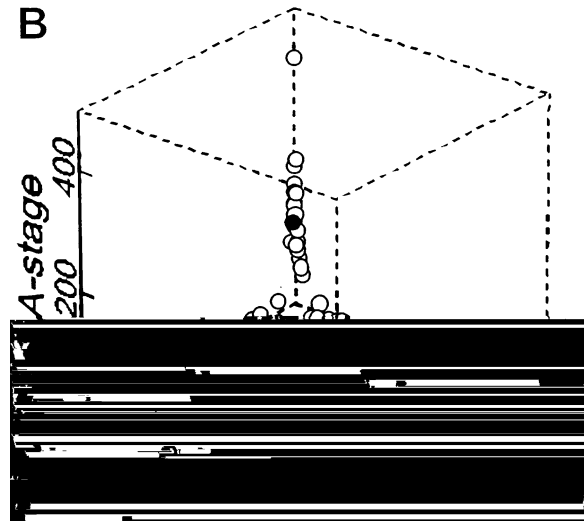
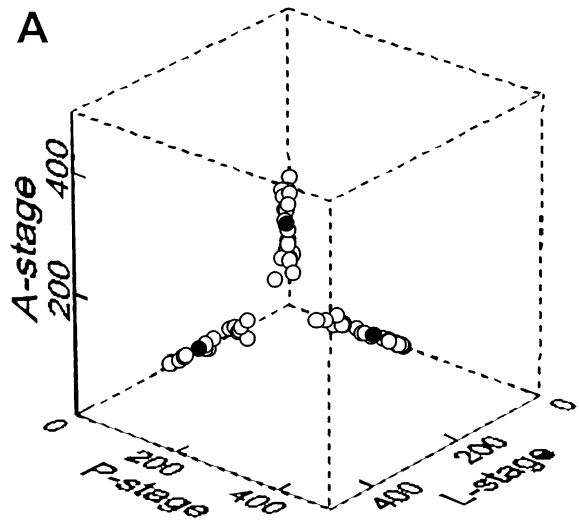
we have

$$\lambda = [\psi'(x)] = (\mu - 2\sigma^2) = \mu - 2\sigma^2 = \sigma^2 - \mu \quad (13)$$

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

Thus, the average sensitivity to initial conditions in the stochastic logistic model (10) is determined by the noise intensity. If $\sigma^2 < \mu$, the noise intensity is low compared to the strength of the deterministic forces ($\mu = |\mu| = |\lambda|$ 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 $\mu < \sigma^2 < 2\mu$, the SLE is positive and the LE remains negative. The two measures are then not accord. What happens is that the

The experiment in question consisted of manipulating adult recruitment so as to fix the parameter ρ_a 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 ρ_a ; adult mortality in these cultures was manipulated so as to fix the parameter μ_a at 0.96. Three unmanipulated control cultures were maintained as well. The set of ρ_a values was selected because the LPA model, fi



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

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description at some level becomes necessary. Impetus

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 analysis represents 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, Grönvall 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

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