Explaining and predicting patterns in stochastic population systems

Shandelle M. Henson[1*], **Aaron A. King**[2], **R. F. Costantino**[3], **J. M. Cushing**[4], **Brian Dennis**[5] **and Robert A. Desharnais**[6]

[1]*Department of Mathematics, Andrews University, Berrien Springs, MI 49104, USA*
[2]*Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996, USA*
[3]*Department of Ecology and Evolutionary Biology, and* [4]*Department of Mathematics and Interdisciplinary Program in Applied Mathematics, University of Arizona, Tucson, AZ 85721, USA*
[5]*Department of Fish and Wildlife Resources and Division of Statistics, University of Idaho, Moscow, ID 83844, USA*
[6]*Department of Biological Sciences, California State University, Los Angeles, CA 90032, USA*

Lattice effects in ecological time-series are patterns that arise because of the inherent discreteness of animal numbers. In this paper, we suggest a systematic approach for predicting lattice effects. We also show that an explanation of all the patterns in a population time-series may require more than one deterministic model, especially when the dynamics are complex.

Keywords: population dynamics; stochasticity; lattice effects; deterministic skeleton; chaos

1. INTRODUCTION

Animal population systems, with their pervasive noise yet identifiable dynamic patterns, afford special opportunities to study the interplay between stochasticity and low-dimensional deterministic trends (Bjørnstad & Grenfell 2001). For nearly a century, the hypothesis that some population fluctuations are shaped largely by low-dimensional deterministic forces has caused considerable controversy. During the last decade, however, careful studies involving mathematical models, controlled laboratory population experiments and statistical techniques have unequivocally identified many low-dimensional deterministic nonlinear phenomena in population data. These phenomena include equilibria, cycles, transitions between dynamic regimes (bifurcations), multiple attractors, resonance, basins of attraction, saddle influences, stable and unstable manifolds, transient phenomena and chaos (e.g. Costantino *et al.* 1995, 1997; Benoît *et al.* 1998; Cushing *et al.* 1998, 2003; McCauley *et al.* 1999; Fussmann *et al.* 2000; Benton *et al.* 2001; Bjørnstad & Grenfell 2001; Dennis *et al.* 2001; Nelson *et al.* 2001).

A powerful paradigm for analysing the mix of noise and order in population time-series is the 'deterministic skeleton' (Tong 1993, 1995; Chan & Tong 2001). The deterministic skeleton is what would remain of the system if one could tune the unexplained stochastic variability down to zero. The skeleton is a deterministic model that can be analysed with the tools of dynamical systems theory; it fixes the geometry of state space, providing a stage for the dance of stochasticity. Chance events allow the system to visit (and re-visit) the various deterministic entities on the stage, including unstable invariant sets, which under strict deterministic theory would have little or no impact on population time-series. Thus ecological time-series can display a stochastic mix of many of the dynamic features of the skeleton, including multiple attractors, transients, unstable invariant sets, such as saddles, and stable or unstable manifolds (Schaffer *et al.* 1993; Cushing *et al.* 1998; Henson *et al.* 1999).

Recently, 'lattice effects' joined the list of nonlinear phenomena discovered in laboratory population data (Henson *et al.* 2001; King *et al.* 2002, 2003). Lattice effects in population time-series are recurrent patterns that arise because of the inherent discreteness of animal numbers. Most deterministic skeletons

$$x_t = f(x_{t-1})$$

allow a continuum of system states x_t, where x_t is the number (or vector of numbers) of animals at time t; such models cannot predict lattice effects. Thus far, lattice effects have been modelled in an *ad hoc* fashion (Henson *et al.* 2001; King *et al.* 2002, 2003) by simply rounding off the state variables of continuous-state models to produce integer-valued states:

$$x_t = \text{round}[f(x_{t-1})].$$

In this paper, we suggest a systematic approach for predicting lattice effects. We also illustrate that an explanation of all the patterns in a stochastic population system may require more than one deterministic model, especially when the dynamics are complex.

2. TRENDS IN STOCHASTIC POPULATION SYSTEMS

We may view a population time-series as the realization of a stochastic process in which the number of animals N_t is a discrete random variable. Suppose N_t has unimodal conditional distribution

$$N_t \sim P(n_{t-1}), \tag{2.1}$$

given the observation of $N_{t-1} = n_{t-1}$ animals at time $t-1$, where the symbol '$\sim$' means 'is distributed as'. If the

time-series is univariate, then the population size N_t has values on the discrete set or 'lattice' of system states $X = \{0,1,2,3,\ldots\}$. If the time-series is multivariate, then N_t is a vector whose entries have values in X. We denote the expected value of N_t given $N_{t-1} = n_{t-1}$ by

$$E[N_t | N_{t-1} = n_{t-1}] = \mu(n_{t-1}).$$

One way to construct a deterministic skeleton for the stochastic process (2.1) is by iterating the conditional expectation as a deterministic map:

$$x_t = \mu(x_{t-1})$$
$$x_0 = n_0. \qquad (2.2)$$

That is, the population size x_t at time t is predicted to be the expected value of the distribution $P(x_{t-1})$, where x_{t-1} was the prediction at time $t - 1$. The system states x_t of the 'mean map' (2.2), being expectations, are not confined to the lattice X; that is, model (2.2) allows a continuum of states. Thus, the mean map (2.2) cannot account for patterns that arise because of the discreteness of animal numbers.

We can construct a skeleton with integer-valued system states by using a different measure of central tendency—one that is confined to the lattice. Given that we observe n_{t-1} animals at time $t - 1$, the most probable next system state on the lattice is

$$\text{mode}[N_t | N_{t-1} = n_{t-1}] = \lambda(n_{t-1}).$$

A deterministic 'mode map' iterates the conditional mode:

$$x_t = \lambda(x_{t-1})$$
$$x_0 = n_0. \qquad (2.3)$$

(If the mode is not unique, we can construct more than one mode map.) The system states x_t of the mode map (2.3) are integer valued.

The mean map (2.2) and the mode map (2.3) together may explain more of the low-dimensional patterns in the stochastic system (2.1) than either map could explain alone. Patterns in the stochastic realizations of (2.1) that are predicted by the mode map but not by the mean map are the result of lattice effects.

(a) Ricker-model example

For example, consider the stochastic Ricker model

$$N_t \sim \text{Poisson}[bn_{t-1}\exp(-cn_{t-1})], \qquad (2.4)$$

where $b,c > 0$. The (deterministic) mean map is the familiar Ricker model

$$x_t = bx_{t-1}\exp(-cx_{t-1}). \qquad (2.5)$$

To construct a mode map for equation (2.4), we must calculate the mode of a Poisson distribution. The mode of $\text{Poisson}[\mu]$ for non-integer μ is the greatest integer less than or equal to μ, that is, $\text{floor}[\mu]$. (If μ is an integer, then the mode of $\text{Poisson}[\mu]$ is non-unique, being equal to both μ and $\mu - 1$. However, for almost all values of b and c, there is no positive integer n_{t-1} for which this happens.) Thus, a (deterministic) mode map is given by

$$x_t = \text{floor}[bx_{t-1}\exp(-cx_{t-1})]. \qquad (2.6)$$

When $b = 23$, $c = 1/43$ and $x_0 = 10$, the mean map predicts a three-cycle while the mode map predicts a five-

cycle. Simulations of the stochastic process (2.4) show episodes of both three-cycles and five-cycles (figure 1). The episodes of five-cycles in the stochastic simulations are lattice effects.

(b) Experimental-system example

A stochastic model for the population dynamics of the flour beetle *Tribolium* is (Dennis *et al.* 2001)

$$\begin{cases} L_t \sim \text{Poisson}\left[ba_{t-1}\exp\left(-\dfrac{c_{\text{ea}}}{V}a_{t-1} - \dfrac{c_{\text{el}}}{V}l_{t-1}\right)\right], \\ P_t \sim \text{binomial}[l_{t-1},(1 - \mu_{\text{l}})], \\ R_t \sim \text{binomial}\left[p_{t-1},\exp\left(-\dfrac{c_{\text{pa}}}{V}a_{t-1}\right)\right], \\ S_t \sim \text{binomial}[a_{t-1},(1 - \mu_{\text{a}})], \\ a_{t-1} \equiv r_{t-1} + s_{t-1}, \end{cases} \qquad (2.7)$$

where L_t is the number of feeding larvae, P_t is the number of non-feeding larvae, pupae and callow adults, R_t is the number of sexually mature adult recruits, S_t is the number of surviving mature adults and l_{t-1}, p_{t-1}, r_{t-1} and s_{t-1} are the respective abundances observed at time $t - 1$. The total number of mature adults is given by $R_t + S_t$, and $a_{t-1} = r_{t-1} + s_{t-1}$ is the total number of mature adults observed at time $t - 1$. The unit of time is two weeks, which is the approximate amount of time spent in each of the L and P classes under experimental conditions, $b > 0$ is the average number of larvae recruited per adult per unit time in the absence of cannibalism and the fractions μ_{a} and μ_{l} are the adult and larval probabilities, respectively, of dying from causes other than cannibalism in one time-unit. The exponentials represent the fractions of individuals surviving cannibalism in each unit of time, with 'cannibalism coefficients' c_{ea}/V, c_{el}/V, $c_{\text{pa}}/V > 0$. Habitat size V has units equal to the volume occupied by 20 g of flour, the amount of medium routinely used in our laboratory.

The (deterministic) mean map of (2.7) is equivalent to

$$\begin{cases} L_t = bA_{t-1}\exp\left(-\dfrac{c_{\text{ea}}}{V}A_{t-1} - \dfrac{c_{\text{el}}}{V}L_{t-1}\right), \\ P_t = (1 - \mu_{\text{l}})L_{t-1}, \\ A_t = P_{t-1}\exp\left(-\dfrac{c_{\text{pa}}}{V}A_{t-1}\right) + (1 - \mu_{\text{a}})A_{t-1}, \end{cases} \qquad (2.8)$$

where the total number A_t of mature adults is given by a single expression. Equation (2.8) is known as the 'LPA model'. It is a well-validated deterministic skeleton for *Tribolium* dynamics and has successfully predicted a wide variety of nonlinear phenomena, including chaos, in laboratory populations (Cushing *et al.* 2003).

A (deterministic) mode map is equivalent to

$$\begin{cases} L_t = \text{floor}\left[bA_{t-1}\exp\left(-\dfrac{c_{\text{ea}}}{V}A_{t-1} - \dfrac{c_{\text{el}}}{V}L_{t-1}\right)\right], \\ P_t = \text{floor}[(1 - \mu_{\text{l}})(L_{t-1} + 1)], \\ A_t = \text{floor}\left[(P_{t-1} + 1)\exp\left(-\dfrac{c_{\text{pa}}}{V}A_{t-1}\right)\right] \\ \qquad + \text{floor}[(1 - \mu_{\text{a}})(A_{t-1} + 1)]. \end{cases} \qquad (2.9)$$
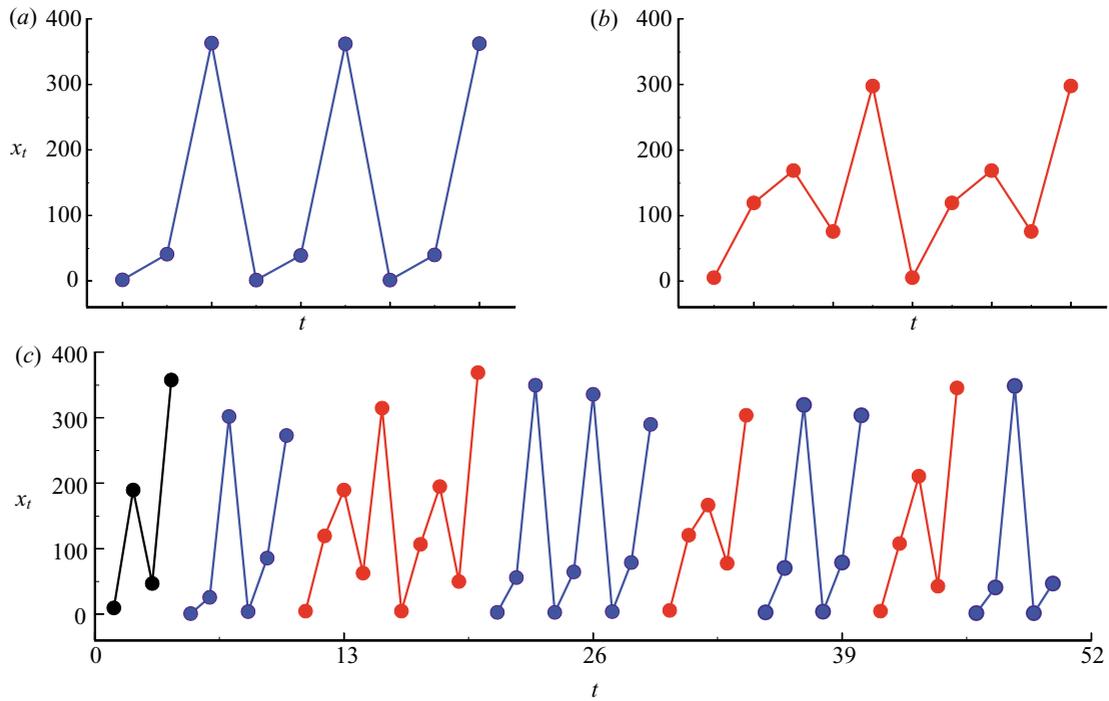
Figure 1. Ricker-model dynamics with $b = 23$, $c = 1/43$ and an initial condition of 10 animals. (*a*) The mean map predicts a three-cycle (blue); (*b*) the mode map predicts a five-cycle (red). (*c*) Simulations of the Poisson model show recurrent episodes of both the three-cycle and the five-cycle.
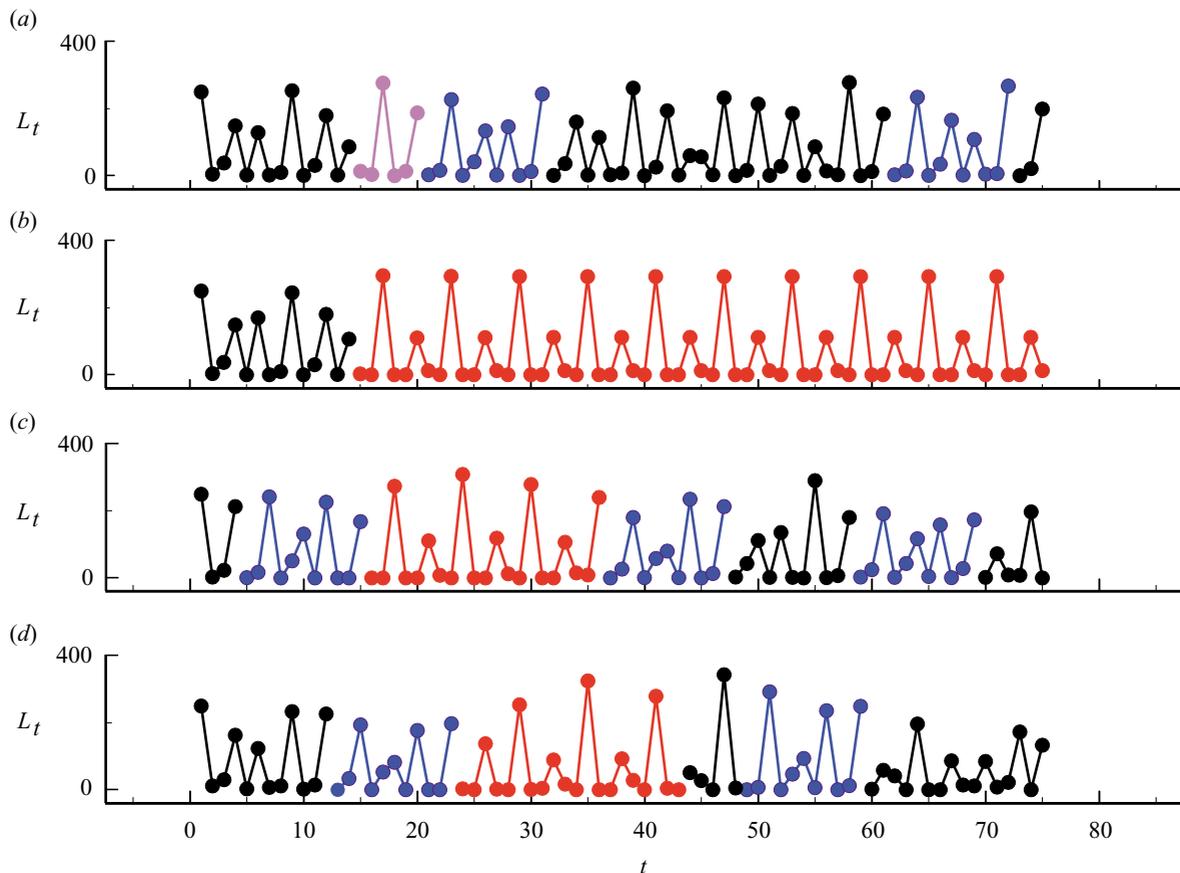

Figure 2. (*a–c*) *L*-stage time-series for *Tribolium* models and (*d*) 148 weeks of experimental data. Parameter values and initial conditions are given in § 2b. (*a*) The mean map predicts chaos, with recurrent fly-bys of a dominant saddle 11-cycle (blue) on the chaotic attractor. (*b*) The mode map predicts a six-cycle (red). The six-cycle pattern appears as a transient of the mean map (pink) and also as part of the saddle 11-cycle. (*c*) The Poisson–binomial model shows episodes of both the 11-cycle and the six-cycle. (*d*) The experimental data also show this effect.

For the experimental parameters and initial condition reported in Dennis *et al.* (2001)—$b = 10.67$, $\mu_1 = 0.1955$, $\mu_a = 0.9600$, $c_{el} = 0.016\ 47$, $c_{ea} = 0.013\ 13$, $c_{pa} = 0.3500$, $V = 1$ and $[L_0, P_0, A_0] = [250, 5, 100]$—the LPA model predicts chaos with a recurring 11-cycle pattern (Cushing *et al.* 2001; King *et al.* 2003), whereas the mode map predicts a six-cycle. The realizations of the stochastic process (2.7) contain episodes of the dynamics of the mean map as well as episodes of the dynamics of the mode map (figure 2).

3. DISCUSSION

We have illustrated how recurrent patterns in stochastic processes may be predicted by various deterministic models derived from the parent stochastic process. The mean and mode maps are examples of two such deterministic models.

The patterns predicted by the mean and mode maps are related. One can imagine that the mode map presses a lattice 'screen' onto the continuum state space of the mean map, requiring that each step be 'rounded' to a nearby lattice node. Thus, when the dynamics of the mean map are simple (for example, a globally attracting cycle of small period), the dynamics of the mode map are typically similar to those of the mean map. When the dynamics of the mean map are complex, however, the mode map may drastically simplify the mean-map dynamics, as a trajectory on a lattice must eventually cycle. In this case, the mode map locks on to a cycle that results from discretizing the geometry of the continuum state space of the mean map. Thus, a mode-map cycle typically reflects some feature of the mean-map dynamics, such as a transient pattern, an unstable cycle, a fragment of an unstable cycle or some attractor that lies 'nearby' in the mean-map parameter space. Lattice effects become important when the cyclic patterns predicted by the mode map occur more frequently in the stochastic system than they do in the mean map. A tool called the 'lag metric comparison' (LMC) can be used to quantify the existence, length and frequency of cycle episodes in stochastic data (King *et al.* 2003).

In the Ricker example (figure 1), the mean map predicts a three-cycle. It seems strange at first glance that the mode map would lock onto a five-cycle rather than something resembling the mean-map three-cycle. The model parameters, however, place the mean map in the big period-locking window of the Ricker bifurcation diagram, where an unstable chaotic set lurks in the background, influencing transients. Thus, it is not surprising that the mode map can lock onto dynamics that are quite different from the mean-map three-cycle—nor is it surprising that the stochastic model (2.4) shows much richer dynamics than a simple noisy three-cycle.

In the LPA example (figure 2), a probable reason that the mode map locks onto the six-cycle is that a similar pattern appears in the mean map as a transient and as part of the recurrent saddle 11-cycle fly-by predicted by the mean map. The mean map also has a six-cycle 'nearby' in parameter space (at $\mu_a = 1$). The six-cycle, however, is not a prediction of the mean map in the sense of being an invariant set on the chaotic attractor of equation (2.8), or in the sense of being predicted by equation (2.8) to occur in episodic runs. Thus, the recurrent six-cycle observed in the stochastic model is a lattice effect.

The theoretical considerations in this paper were, in fact, motivated by episodic cyclic patterns observed in chaotic *Tribolium* data (Cushing *et al.* 2001; Henson *et al.* 2001; King *et al.* 2002, 2003). It is therefore interesting to compare the predictions of models (2.7)–(2.9) with the experimental data reported in Dennis *et al.* (2001), although strictly speaking the stochastic model does not conform to the experimental protocol. (A consequence of the protocol was that adult recruitment and survivorship were made deterministic with respect to process error.) The data, like the simulations of the stochastic model, contain episodes of both the mean-map 11-cycle and the mode-map six-cycle (figure 2). In Henson *et al.* (2001) and King *et al.* (2002, 2003), the six-cycle episodes occurring in the data were hypothesized to be lattice effects.

Discretizing the state variables of a chaotic system generally fragments the chaotic attractor into multiple lattice attractors (Domokos & Scheuring 2002; King *et al.* 2002, 2003); that is to say, the mode map generally predicts multiple cycles, dependent upon the initial condition. Furthermore, the mode-map cycles tend to be 'weakly stable' in the sense that small perturbations on the lattice cause complex transients, as the system attempts to follow the underlying mean tendency of chaos on the continuum. The stochastic discrete-state system is a transient kaleidoscope of all of the cycles predicted by the mean and mode maps. The specific lattice cycles involved depend on the granularity of the lattice, which depends on population size (Henson *et al.* 2001). However, lattice effects can occur even for large population sizes (Jackson 1989) and may possibly hamper the detection of chaos in ecological data. In Dennis *et al.* (2001, 2003) and King *et al.* (2003), we explore what it means for a stochastic discrete-state system to be influenced by chaos, and use the LMC to suggest new ways to detect chaos in population data.

Ecological time-series are stochastic, but contain patterns. To the extent that such patterns can be explained and predicted by low-dimensional deterministic models, the dynamics of the system are amenable to the powerful tools of dynamical-systems theory. A suite of low-dimensional deterministic models, derived from a parent stochastic model, may give a more complete account of the dynamics than any one deterministic model alone.

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