

---

Y. Takeuchi · Y. Iwasa  
K. Sato (Eds.)

# Mathematics for Ecology and Environmental Sciences

 Springer

---

BIOLOGICAL AND MEDICAL PHYSICS  
BIOMEDICAL ENGINEERING

Prof. Yasuhiro Takeuchi  
Shizuoka University  
Faculty of Engineering  
Department of Systems Engineering  
Hamamatsu 3-5-1  
432-8561 Shizuoka  
Japan  
email: takeuchi@sys.eng.shizuoka.ac.jp

Prof. Yoh Iwasa  
Kyushu University  
Department of Biology  
812-8581 Fukuoka  
Japan  
e-mail: yiwasscb@mbox.nc.kyushu-u.ac.jp

Dr. Kazunori Sato  
Shizuoka University  
Faculty of Engineering  
Department of Systems Engineering  
Hamamatsu 3-5-1  
432-8561 Shizuoka  
Japan  
email: sato@sys.eng.shizuoka.ac.jp

Library of Congress Cataloging in Publication Data: 2006931399

ISSN 1618-7210

ISBN-10 3-540-34427-6 Springer Berlin Heidelberg New York

ISBN-13 978-3-540-34427-8 Springer Berlin Heidelberg New York

This work is subject to copyright. All rights are reserved, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilm or in any other way, and storage in data banks. Duplication of this publication or parts thereof is permitted only under the provisions of the German Copyright Law of September 9, 1965, in its current version, and permission for use must always be obtained from Springer. Violations are liable to prosecution under the German Copyright Law.

Springer is a part of Springer Science+Business Media

springer.com

© Springer-Verlag Berlin Heidelberg 2007

The use of general descriptive names, registered names, trademarks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.

Cover concept by eStudio Calamar Steinen

Cover production: WMXDesign GmbH, Heidelberg

Production: LE-TeX Jelonek, Schmidt, Vöckler GbR, Leipzig

Printed on acid-free paper      SPIN 10995792      57/3141/NN - 5 4 3 2 1 0

# Nonlinearity and Stochasticity in Population Dynamics

J. M. Cushing

**Summary.** Theoretical studies of population dynamics and ecological interactions tend to focus on asymptotic attractors of mathematical models. Modeling and experimental studies show, however, that even in controlled laboratory conditions the attractors of mathematical models are likely to be insufficient to explain observed temporal patterns in data. Instead, one is more likely to see a collage of many patterns that resemble various dynamics predicted by a deterministic model that arise during randomly occurring temporal episodes. These deterministic “signals” might include patterns characteristic of a model attractor (or several model attractors – even from possibly different deterministic models), transients both near and far from attractors, and/or unstable invariant sets and their stable manifolds. This paper discusses several examples taken from experimental projects in population dynamics that illustrate these and other tenets.

## 7.1 Introduction

During the last century mathematicians and theoretical ecologists developed a plethora of deterministic models for the dynamics of biological populations and ecological systems. The mathematical analysis of these models, most of which are based on differential or difference equations, is overwhelmingly focussed on the asymptotic dynamics of model solutions. The standard procedure is to locate equilibrium states and perform a linearization stability analysis. In some cases a global analysis of asymptotic dynamics is possible (using Lyapunov functions, Poincaré-Bendixson theory, etc.). Periodic solutions play an important role in some models and their existence and asymptotic stability often preoccupies the mathematician. In more recent years, considerable interest has arisen in more complicated asymptotic dynamics and attractors (such as chaotic attractors), although their study has been mostly by means of computer simulations.

With all the historical and current attention paid to the attractors of deterministic models, one would naturally assume that they must play an

important role in our understanding of biological ecosystems and in the description and explanation of observed patterns in population data. Yet, it is widely recognized that there is a serious gap between theoretical models and ecologically data (for example, see (Aber 1997)). Few examples exist of models that provide quantitatively accurate descriptions of population time series data, and even less that provide quantitatively accurate and reliable predictions of population and ecosystem dynamics. Of what use, then, to the ecological sciences – particularly the applied ecological sciences – is the vast literature on mathematical models whose asymptotic dynamics we mathematicians spend so much time and effort analyzing?

What should one expect to see when examining ecological time series data? Should one look for temporal patterns that are explainable by the attractors of deterministic models? Given that “noise” is inevitable in ecological time series data, should one look for “fuzzy versions” of attractors? Something of the sort is usually uttered when noise is mentioned in model studies (although when noise is considered it is usually not carefully modeled). In addition, the (rather obvious) caveat is usually mentioned that too much noise will completely obliterate deterministic attractors (in which case, of course, their role is not clear). To relate a model to data one has to think carefully about the source of the “noise” in the data (i. e., the inevitable deviations of data from model predictions). Are these “errors” due primarily to inaccurate measurements? If so, then of course too much noise will likely obliterate any deterministic trends (attractors or other), and the problem of connecting model to data is more concerned with the problem of obtaining accurate data. Even if data is highly accurate (even exact) there will be deviations of data from model predictions because no model can capture all of the mechanisms that determine the dynamics of a biological population. External forces and internal processes not a part of the model result in “environmental” and “demographic” noise. Another possibility is, then, that one might come to find in an ecological data set that transient dynamics predominate (relative to a given model) and take precedence over model predicted asymptotic attractors. Perhaps it is even the case that ecological data typically exhibit repeated episodes of transients as they are continuously buffeted by stochastic perturbations and, as a result, asymptotic attractors play only a small role or even no role at all.

The answers to these questions can determine what one looks for in data and what tools one uses to analyze data; in other words, they can determine what one actually “observes” in data and hence one’s judgement about the “validity” of a model and the accompanying theory.

For ecology to become a more precise science and to raise its principles above qualitative descriptions and general verbal metaphors, it is necessary to make stronger connections between models and data. This involves not just new deterministic model equations and their mathematical analysis, but methods to deal with model parameterization/validation and stochasticity (the inevitable deviation of data from model predictions). A time tested pro-

cedure used in science to connect theory and models to data is to isolate phenomena, under controlled and replicated experimental conditions, and to manipulate and perturb a system in order to observe its responses. The understanding resulting from such experimental and modeling procedures form a basis for the study of larger scale systems. To quote E. O. Wilson (2002):

“When observation and theory collide, scientists turn to carefully designed experiments for resolution. Their motivation is especially high in the case of biological systems, which are typically far too complex to be grasped by observation and theory alone. The best procedure, as in the rest of science is first to simplify the system, then to hold it more or less constant while varying the important parameters one or two at a time to see what happens.”

It was in this spirit that I began a collaboration nearly fifteen years ago with a team of mathematicians, statisticians and biologists (R. F. Costantino, R. A. Desharnais, B. Dennis and more recently including S. M. Henson, and A. King). This team’s collaborations has had two broad goals. First, we wanted to derive and validate a successful model for the dynamics of an experimental population (in this case, species of *Tribolium*). We sought a model that makes quantitatively accurate descriptions of observed data and that we could show makes accurate predictions, under a wide variety of circumstances – predictions that could be corroborated by means of controlled experiments. Second, we would then use our model/experimental system to conduct studies of a wide range of nonlinear phenomena. Initially our fundamental focus was on the asymptotic dynamics predicted by a deterministic model (although we developed stochastic versions of the model to explain the deviations of data from model predictions in order to validate the model and to conduct simulations). To date, we have successfully used our system (and several adaptations and modifications) to study a long list of dynamic phenomena, including equilibria and periodic cycles, stability and destabilization, bifurcations, quasi-periodic motion, routes-to-chaos, temporal patterns on chaotic attractors, sensitivity to initial conditions, the control of chaos, temporal phase shifting, periodicity due to environmental forcing, nonlinear resonance, multiple attractors, lattice effects, the role of spatial scale on dynamics, the effect of genetic adaptation on population dynamics, and competition between two species. See the books (Caswell 2001) and (Cushing et al. 2003) (and the references cited therein) for expositions of our methods and for many of our results.

The final chapter of the book (Cushing et al. 2003) contains a list of general conclusions concerning the modeling of biological populations and various nonlinear phenomena that we have studied. The purpose of this paper is to elaborate on one of the main conclusions in that list: “full explanation of a ecological times series data is unlikely to be found by analyses that rely solely on deterministic model attractors.” Instead, it is suggested that

what one is more likely to see in time series data is a mixture – a temporal collage – of many patterns that resemble various deterministic dynamics predicted by a model that arise, perhaps only in part, during randomly occurring temporal episodes. These deterministic “signals” might include one or several attractors, transients both near and far from attractors, and unstable invariant sets and their stable manifolds. Moreover, we found in some of our projects that these deterministic patterns might arise from more than one deterministic model! In this paper, I present several examples taken from our experimental projects that are selected to illustrate these tenets.

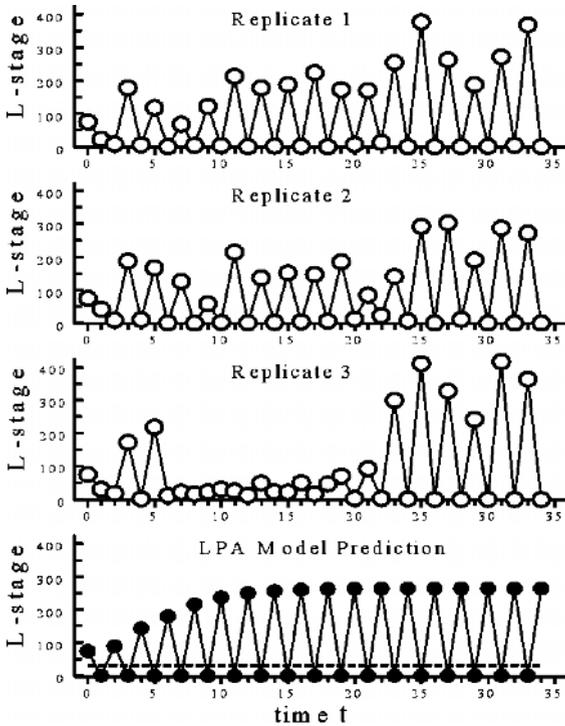
## 7.2 Saddles flybys

In 1980, David Jillson (1980) reported an experiment with *Tribolium castaneum* in which a nonlinear resonance phenomenon was observed in a habitat of periodically fluctuating volume (Henson et al. 1997). Our first example comes from Jillson’s control treatments in which the habitat was of constant volume. Figure 7.1 shows plots of the larval stages in the three replicate cultures. Also shown is the model predicted orbit of the LPA model

$$\begin{aligned} L_{t+1} &= bA_t \exp(-c_{el}L_t - c_{ea}A_t) \\ P_{t+1} &= (1 - \mu_l) L_t \\ A_{t+1} &= P_t \exp(-c_{pa}A_t) + (1 - \mu_a) A_t \end{aligned} \tag{1}$$

with parameter estimates obtain from the data (using maximum likelihood methods and a stochastic version of the model (Dennis et al. 1995; Cushing et al. 1998)). The time unit in this model is two weeks and the generation time is four weeks. The predicted (global) attractor is a 2-cycle. There is also a (unique) positive equilibrium which is a saddle. After a short period of time, two of the three replicate plots of the larval stage resemble the crash-boom cycles predicted by the 2-cycle attractor.

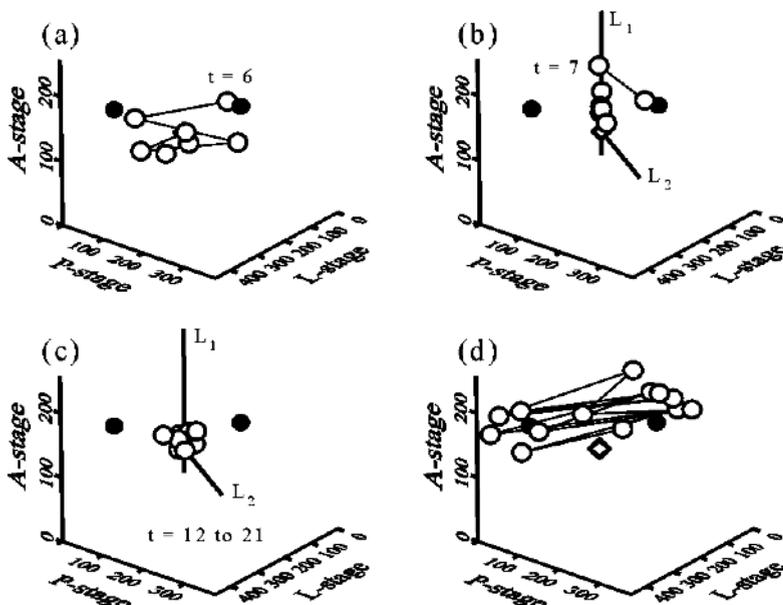
The third replicate is strikingly different, however. Initially it also approaches the 2-cycle attractor, but the approach is interrupted by a long period of subdued oscillation (from  $t = 6$  to about  $t = 20$  or  $21$ , or in other words over seven generations). Figure 7.1 indicates that the larval stage, during this period, is close to the unstable equilibrium predicted by the model. Figure 7.2 shows the data plotted in three dimensional phase space. The initial approach to the 2-cycle attractor was interrupted by a random event that placed the orbit near the (one dimensional) stable manifold of the saddle equilibrium. The data then closely followed the model predicted stable manifold, until it arrived near the saddle where it lingered for 13 time steps. Subsequently this replicate made an oscillatory departure from the saddle (as predicted by the one dimensional unstable manifold) until it too finally arrived near the 2-cycle attractor.



**Fig. 7.1.** The first three plots show the larval stage of three replicate control cultures from an experiment of Jillson (1980). The fourth plot is that of the LPA model predicted time series of the larval stage with the parameter values  $b = 4.44$ ,  $\mu_1 = 0.479$ ,  $\mu_a = 0.154$ ,  $c_{el} = 0.0584$ ,  $c_{ea} = 0.00580$ ,  $c_{pa} = 0.0105$ . The attractor is a periodic 2-cycle. The dashed line shows the larval component of the model predicted saddle equilibrium

To explain the observed time series in the third replicate of Jillson’s controls we see that it is necessary to include not just the model predicted 2-cycle attractor, but also the saddle equilibrium and the geometry of its stable and unstable manifolds. This “unusual” replicate should not be discarded as anomalous (or averaged with the other replicates). Indeed it is valuable. The “saddle flyby” provides more model validation than we would get from time series data that did not visit the saddle (i. e., data orbits like the other two replicates), because it confirms the model predicted dynamics away from the attractor and near the saddle. Stochastic perturbations allow visitation of a wider range of phase space and deepen our understanding of the populations dynamics. (For the same reason they also improve our parameter estimates, since the parameterization procedure is based on the residuals of one-step predictions from each datum point which then have a wider range in phase space (Cushing et al. 2003).)

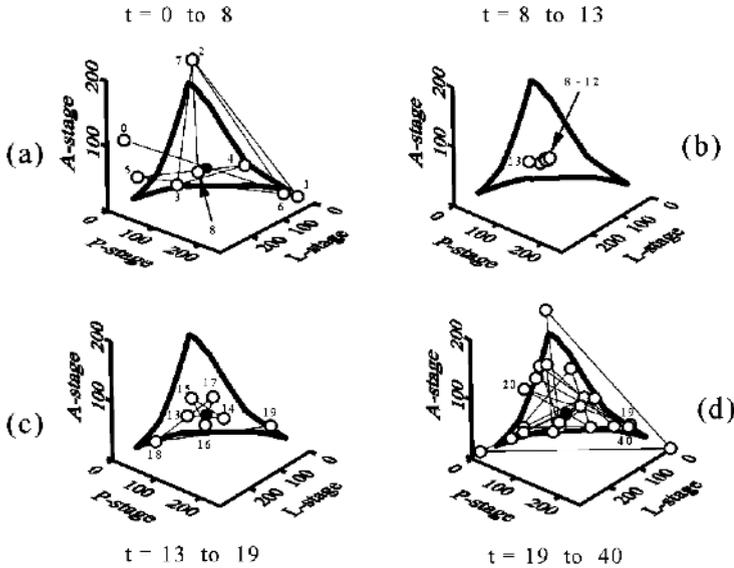
We have seen such saddle flybys in virtually all of our experimental projects (including saddle cycles as well as saddle equilibria). Figure 7.3 shows another example taken from one of the treatments of a route-to-chaos experiment reported in (Costantino et al. 1997; Cushing et al. 2003; Dennis et al. 2001). In this example, the local unstable manifold is two dimensional (instead of one dimensional as in the example of Fig. 7.1) and is associated with



**Fig. 7.2.** The data from Jillson’s replicate 3 produce an orbit in three dimensional phase space. Plots are shown of this orbit over selected temporal subintervals. **a** Initially, from  $t = 0$  to 6 the data orbit approaches the 2-cycle attractor denoted by the solid circles. **b** At time  $t = 7$  a random perturbation placed the data point near the stable manifold of the saddle equilibrium (denoted by the diamond). The vertical lines  $L_1$  and  $L_2$  are tangents to the two dimensional stable manifold at the saddle (as determined from the eigenvectors of the two eigenvalues  $\lambda = 0.80285$  and  $-0.071169$  of the Jacobian matrix respectively). The data orbit from  $t = 7$  to 11 closely follow the tangent line  $L_1$ . **c** From  $t = 12$  to 21 the data orbit lingers near the saddle equilibrium, eventually **d** to return to the 2-cycle attractor

a complex eigenvalue (of magnitude greater than one). The predicted dynamic near the equilibrium is, therefore, quite different from that in Fig. 7.1. The departure of orbits from the unstable equilibrium is expected to be “spiral-like” (with a rotational angle predicted by the argument of the complex eigenvalue). The observed data exhibits this prediction to a remarkable accuracy. This data is from one of three replicates, the other two of which did not undergo such a saddle flyby (Cushing et al. 2003). Notice again that to explain the “anomalous” replicate in Fig. 7.3, as well as the differences between it and the other replicates, we need to include both the attractor and the unstable saddle (and its characteristics) in the analysis.

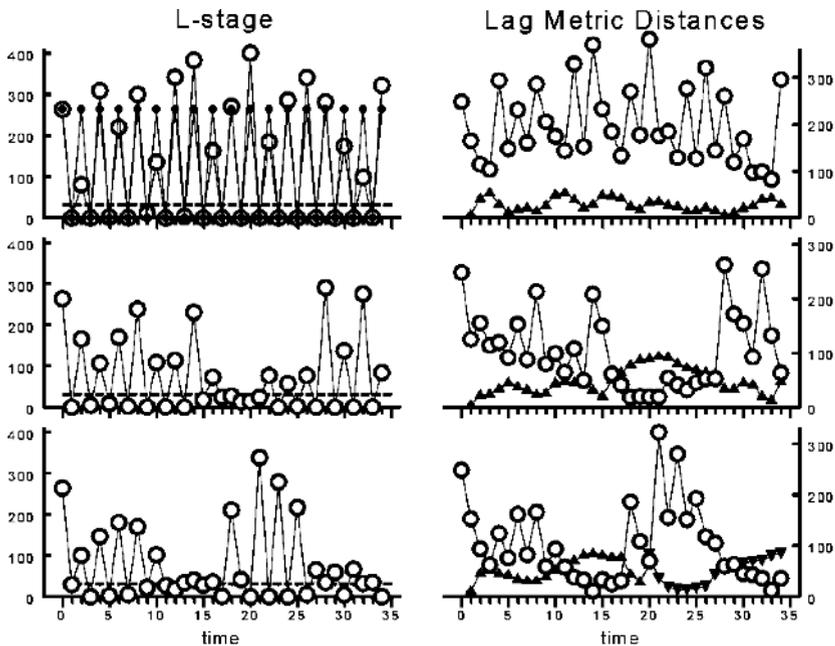
Sometimes a data time series will undergo a saddle flyby after spending considerable time on or near the attractor. For example, a distinctive saddle equilibrium flyby, lasting 38 weeks (over 9 generations), occurred during the 7th year of an 8 year experiment that placed a culture of *Tribolium* on a chaotic attractor (King et al. 2003). In other examples, saddle flybys oc-



**Fig. 7.3.** These four graphs show one replicate from one of the treatments of the route-to-chaos experiment reported in (Costantino et al. 1997; Dennis et al. 2001; Cushing et al. 2003). For the estimated and controlled parameter values ( $b = 10.45$ ,  $\mu_1 = 0.2000$ ,  $\mu_a = 0.9600$ ,  $c_{el} = 0.01731$ ,  $c_{ea} = 0.01310$ ,  $c_{pa} = 0.05000$ ) the LPA model predicts an invariant loop attractor, appearing in the graphs as a triangular shaped loop. The four graphs show the data orbit broken into four temporal segments. The first and fourth segments in graphs **a** and **d**, corresponding to the beginning and the end of the experiment, show a temporal motion around the model predicted invariant loop. A notable perturbation away from the loop attractor occurs when a stochastic event at  $t = 8$  (week 16) placed the data point near a model predicted equilibrium. Graph **b** shows this second segment of the orbit which lingers near the unstable equilibrium for  $t = 8$  to 13 (about 8 weeks or, in other words, two generations). The saddle equilibrium has a two dimensional unstable manifold (the linearization has complex eigenvalues of magnitude greater than one) and therefore the model predicts a rotational departure from the equilibrium with, as it turns out, an rotational angle of approximately 145 degrees. This rotation is clearly seen in the data plotted in **c**

cur more than once in a single time series of data; see (Cushing et al. 2003, p. 142) for an example that occurred in the route-to-chaos experiment.

A stochastic version of a deterministic model provides a means by which to study such randomly occurring saddle flybys. We can view simulations of a stochastic model as possible outcomes of an experiment (and repeated simulations as replicates of the experiment). Such a model should not be derive in a cavalier fashion. It is not always appropriate, for example, simply to add noise to the right hand side of the equations in a dynamic model, as is often done. Instead one should place random variables of an appropriate



**Fig. 7.4.** The graphs in the left column show three simulations of a demographic stochasticity version of the LPA model (1) with parameter values as in Fig. 7.1. Noise was added to each of the three equations in the LPA model on the square root scale (uncorrelated normal random variables with variances 10, 1 and 1 respectively) (Dennis et al.1995; Cushing et al. 2003). Simulations were started near the 2-cycle attractor, plotted as the solid circles in the upper graph. The open circles graphs show the L-stage component of the simulations and the dashed line that of the saddle equilibrium. The upper graph show no saddle flyby, while that in the middle graph shows one and the bottom graph shows two flybys. The open circles in the right column graphs show Euclidean distance to the saddle of the simulated orbits at each point in time. The solid triangles show the average of the Euclidean distances of the orbit point and its immediate predecessor from the two points on the 2-cycle attractor. (The triangles pointing up are distances to the phase of the 2-cycle shown in the upper graph in the left column, while the triangles point down are the distances to its phase shift)

kind in appropriate terms, so as to describe the type of stochasticity present in the biological system of interest. Figure 7.4 shows three realizations of a version of the LPA model that approximates demographic stochasticity<sup>1</sup>,

<sup>1</sup> This model adds a normal random variable of mean zero to each of the three equations in the LPA model on a square root scale. These random variables are uncorrelated in time. In these simulations covariances among them are assumed equal to zero. This kind of stochastic model is one way to describe demographic stochasticity. See (Dennis et al. 1995; Cushing et al. 2003).

with parameter values from Jillson’s experiment in Fig. 7.1, that were selected to illustrate saddle flybys. Using a stochastic model, one can study what the model predicts will likely be observed in experimental or observational data (the frequency of flybys, transient characteristics due to the geometry of the saddle in phase space, the relative roles of transients and the attractors, etc.).

While the sorting out of the transient and attractor aspects of time series data not might be difficult in some examples, such as that in Figs. 7.1 and 7.4, in other cases it can be fraught with difficulties and pitfalls. If, in an investigation of a data set, one focuses only on attractors and uses diagnostic methods designed for attractors, in a situation when transients are abundant, then obviously it is possible that erroneous conclusions will be drawn. This is particularly true when the attractor is complicated and complex. For example, if stochastically produced transients cause orbits to often revisit the neighborhood of a saddle (or even a repeller), then a large portion of time is spent in regions of phase space where there is exponential separation of orbits. Lyapunov exponents are diagnostic quantities for chaos based on an asymptotic average taken over the attractor. Applying this diagnostic to an orbit that spends enough time near a saddle or repeller can result in the erroneous conclusion that chaos is present. A specific example is given in (Desharnais et al. 1997b), using a stochastic version of the famous Ricker map, in which a “noisy equilibrium” is erroneously diagnosed as chaos by using Lyapunov exponents. Also see (Dennis et al. 2003).

### 7.3 Basin hopping

Saddles and their stable manifolds also occur as boundaries between basins of attraction in models with multiple attractors. While a deterministic model with multiple attractors makes clear-cut predictions about the asymptotic dynamics of orbits (depending on the initial conditions), when noise is present the dynamics can become complicated, and saddles on the basin boundaries of attraction can play an important role in what dynamic patterns are predicted to be observed in experimental (or simulation) data.

A striking example of this occurs in one of our experiments designed to observe a model predicted, two attractor scenario in a modification of the Jillson experiments (Jillson 1980). Jillson investigated the dynamics of *T. castaneum* in a periodically varying habitat by alternating the volume of flour medium in which populations are cultured. Our analysis of Jillson’s data utilizes the LPA model (1) in which habitat volume  $V$  is explicitly introduced:

$$\begin{aligned} L_{t+1} &= bA_t \exp\left(-\frac{c_{el}}{V}L_t - \frac{c_{ea}}{V}A_t\right) \\ P_{t+1} &= (1 - \mu_l) L_t \\ A_{t+1} &= P_t \exp\left(-\frac{c_{pa}}{V}A_t\right) + (1 - \mu_a) A_t . \end{aligned} \tag{2}$$

The hypothesis that the interaction (cannibalism) coefficients are inversely proportional to habitat size has been experimentally confirmed (Costantino et al. 1998). In a temporally varying habitat,  $V = V(t)$  is a function of  $t$ ; in a periodically varying habitat  $V(t)$  is a periodic function of  $t$ .

In our multiple attractor experiment the habitat volume was varied periodically with period two and selected amplitudes (Henson et al. 1999). So, in (2) we have  $V(t) = 1 + \alpha(-1)^t$  where  $\alpha$  is an amplitude and  $c_{el}$ ,  $c_{ea}$ , and  $c_{pa}$  are the coefficients in a standardized unit of volume (in our experiments, the volume occupied by 20 grams of flour medium) under constant habitat conditions ( $\alpha = 0$ ).

For parameter values estimated for *T. castaneum* in a constant habitat ( $\alpha = 0$ ) (Costantino et al. 1997) the LPA model (2) predicts a stable 2-cycle attractor. In a periodically varying habitat ( $\alpha > 0$ ) the model predicts two different 2-cycle attractors that perturbed from the two phases of this 2-cycle. (This is true, in fact, in a rather general setting (Henson 2000).) These 2-cycles, while out-of-phase, are not phase shifts of one another and have distinctively different amplitudes; a large amplitude 2-cycle is called the “resonance” cycle and a small amplitude 2-cycle is called the “attenuant” 2-cycle (Costantino et al. 1998). An unstable (saddle) equilibrium present when  $\alpha = 0$  perturbs to a saddle 2-cycle that sits on the basin boundary separating to the regions of attraction for the resonance and attenuant 2-cycles. This multi-attractor scenario occurs for  $0 < \alpha < 0.42$ . At  $\alpha = 0.42$  the attenuant and saddle 2-cycles annihilate one another in a saddle-node bifurcation, leaving a single 2-cycle – the stable resonant cycle.

The experiments reported in (Henson et al. 1999) verified the occurrence of the LPA model’s multiple attractor predictions by growing cultures for appropriately selected amplitudes  $\alpha$  of flour volume oscillations between 0 and 1. In particular, the presence of the two 2-cycle attractors – resonant and attenuant – was observed in the experimental data at  $\alpha = 0.4$ . (One reason this is interesting is because the attenuant oscillation was counter-intuitive biologically and seemed not to be a possible dynamic for the beetles.)

However, an interesting and unexpected phenomenon occurred in the multi-attractor experiment. Each replicate culture whose initial conditions were placed in the attenuant 2-cycle’s basin of attraction, while clearly exhibiting the features (quantitatively and qualitatively) of the model predicted attenuant 2-cycle early in the experiment, ultimately moved to the basin of the resonant 2-cycle and assumed that attractor’s characteristics. No culture in the experiment made the reverse basin migration. The analysis of the experiment presented in (Henson et al. 1999) showed how the saddle cycle and its stable (two dimensional) manifold exhibited a strong influence on the dynamics. Because of stochastic perturbations, the data orbits underwent flybys of the saddle 2-cycle that caused a lingering near that saddle and the basin boundary, which ultimately resulted in a stochastic jump to the resonant 2-cycle basin. These phenomena are in fact predicted by simulations

of a stochastic version of the periodic LPA model (2). (Why reverse basin jumps never occur in this case remains an open question.)

The multi-attractor experiment, and the stochastic model used to explain it, show that the predictions of a deterministic model can be altered by noise in important, but predictable and observable ways. In this experiment (and in the stochastic model) one of the two deterministic attractors becomes, in effect, a transient. While the deterministic model helps to explain the results of the experiment, the stochastic version of the model “corrects” (or modifies) the deterministic predictions and provides deeper understanding and insight into the biological system.

Jillson’s experiments also included periodic forcing of the habitat volume with other periods. An analysis of the temporal patterns observed in his data, based on the periodically forced LPA model of period 4 and on attractor basin switching and basin boundary saddles, appears in (Henson et al. 2002). In this case, multiple basin switches (back and forth) are observed in some individual time series.

Stochastic attractor basin hopping has also been used as a means to explain phase shifts in oscillatory data time series in non-fluctuating habitats. See (Henson et al. 1998, 2003).

## 7.4 Lattice effects

The most ambitious experimental project undertaken by our research team during the last decade involved the investigation of a route-to-chaos. This experiment is reported in (Costantino et al. 1997; Dennis et al. 2001) and summarized in our book (Cushing et al. 2003). An analysis of the “chaos” treatment in this experiment not only illustrates the issues described above – the stochastic “dance” of attractors, saddles, and transients – but uncovered some other interesting modeling issues and dynamic phenomena.

In the eight year (96 generations) time series data from the treatment that was designed to corroborate the chaotic attractor predicted by the deterministic LPA model, one can observe a distinctive recursive temporal pattern – a near 11-cycle. An explanation for this dynamic pattern was found when we discovered that there exists an 11-cycle lying on the chaotic attractor that, although a (unstable) saddle cycle, highly influences motion on the attractor. It was surprising to us that such a subtle pattern is discernible in real population data, especially in the presence of chaos and noise<sup>2</sup>.

---

<sup>2</sup> Others have also noted transient periodicity in data. Lathrop and Kostelich (1989) found evidence for saddle cycles in a long series of data from the Belousov–Zhabotinskii reaction. So et al. (1998) found evidence for saddle cycles in neuronal electrophysiological recordings. Kendall et al. (1993) and Schaffer et al. (1993) observed similarities between saddle cycles on a chaotic attractor predicted by an epidemiological model and historical measles case-report data.

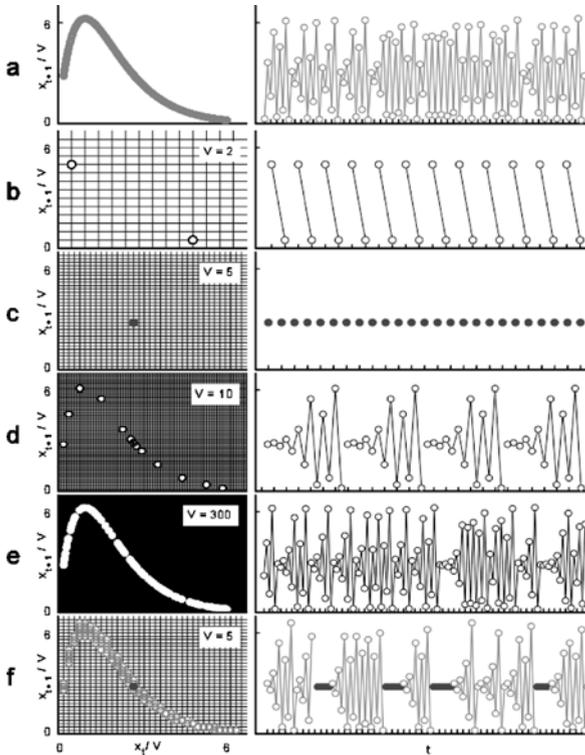
Furthermore, one finds an even more prominent cyclic pattern – a near 6-cycle pattern – in the times series data. However, it turns out that there is no 6-cycle on the chaotic attractor (or anywhere else in phase space). There is seemingly no explanation possible for this pattern based on the deterministic LPA model. This mystery was solved when, after thinking about the details of the manipulations performed in the experimental protocol, we investigated various “integerized” version of the LPA model. (The experimental data comes in whole numbers, of course, as do individuals in all life stages of the beetle populations.) See for example the model described by Eqs. (4) below. This and other “lattice” models predict, for the initial conditions of the chaos treatment, that the final state of the orbit should be a 6-cycle that is remarkably similar to the pattern observed in the data (Henson et al. 2001)!

On the other hand, a deterministic lattice model cannot predict chaos, since bounded orbits necessarily reach, in finite time, a periodic cycle. Moreover, there are usually more than one “lattice” attractor in such a model. This is true in the lattice LPA model used for the chaos experiment and, as a result, numerous other cyclic patterns might be observable in the data. But what then becomes of chaos? More generally, what roles do the continuous state LPA model and its asymptotic attractors play?

When noise is added to the lattice LPA model we get a stochastic model that predicts the dynamics of the integer value experimental data. Stochasticity continually produces transients on the lattice and these transients, it turns out, resemble the underlying continuous state space attractor (chaotic, in this case). Thus, simulations of a stochastic integerized model predict an episodic interplay of deterministic patterns – attractor, saddles, and transients – from both the deterministic lattice and the deterministic continuous state space model. This phenomenon is illustrated using simpler “toy” models in (Henson et al. 2001; Cushing et al. 2003) and such an example appears in Fig. 7.5. An analysis of the chaos experiment using these notions appears in (King et al. 2003).

Whereas the experiment was designed to put a population into chaotic dynamics – as predicted by the deterministic, continuous state space LPA model – other deterministic patterns are predicted by the lattice LPA model. Specifically the lattice LPA model identified several cycles of various periods as important on the lattice. Stochastic simulations of the lattice LPA model predicted the observed data should contain (randomly occurring) episodes of all these deterministic patterns – and even occasional flybys of the saddle equilibrium (of the deterministic continuous state space model). Indeed, our analysis of the data showed this to be the case; see Fig. 7.6.

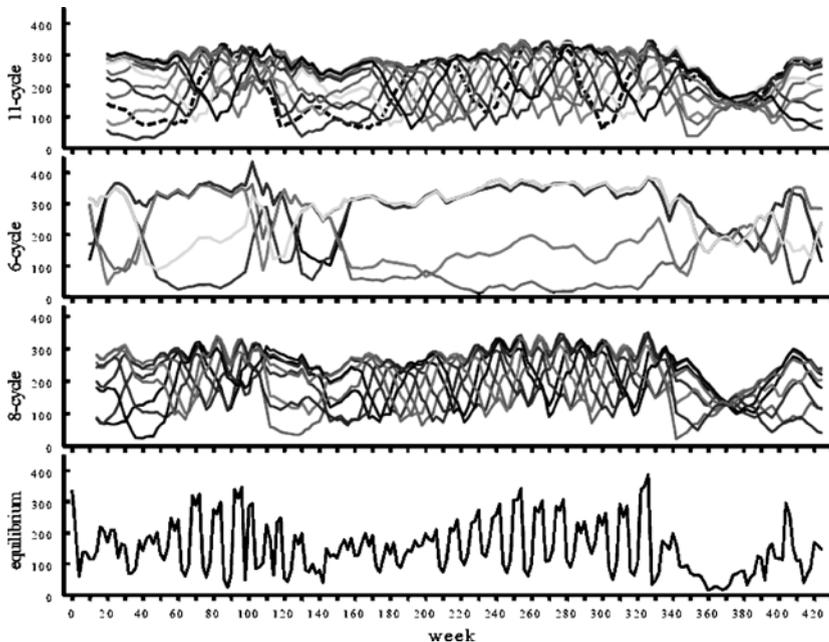
In our analysis of the data obtained from the chaos treatment of our experiment, in order to account for the observed temporal patterns it is not sufficient to consider only the asymptotic (chaotic) attractor predicted by the deterministic, continuous state space LPA model. The chaotic attractor does play a role by contributing observable patterns not predicted by the deterministic lattice model, but conversely so also does the deterministic lattice model



**Fig. 7.5.** **a** With  $b = 17$  and  $c = V = 1$ , the Ricker map  $x_{t+1} = bx_t \exp(-cx_t/V)$  exhibits chaotic dynamics. **b–e** Show periodic lattice attractors of the integerized Ricker map  $x_{t+1} = \text{round}[bx_t \exp(-cx_t/V)]$  with  $b = 17$  and  $c = 1$  for increasing values of  $V$ . Specifically a 2-cycle, 1-cycle (equilibrium), 13-cycle and 117-cycle respectively. In the lagged phase space these attractors (plotted on a density lattice) are seen to increasingly resemble the chaotic attractor. In **f** appears a realization of the (environmental) stochasticity lattice Ricker model  $x_{t+1} = \text{round}[bx_t \exp(-cx_t/V) + \sigma z_t]$  with  $b = 17$  and  $V = c = 1$ . Here  $z_t$  is a standard normal random variable (uncorrelated in time) and  $\sigma$  measures the magnitude of the noise. This realization is to be compared with the continuous state space, chaotic attractor in **a** and the equilibrium lattice attractor in **c**. Noise has “revealed” the underlying continuous state space chaotic attractor. The time series shows intermittent episodes of both the chaotic and the equilibrium dynamics of the continuous and the lattice models

predict patterns that are not predicted the deterministic chaotic attractor. Stochasticity is needed to explain how these patterns manifest themselves (and in this sense stochasticity becomes an aid and not an obstacle, as it is often viewed).

Henson et al. in (Henson et al. 2003b) consider in more generality the modeling methodology that emerged from the chaos experiment. These authors, using the LPA and other models, discuss how recurrent patterns in stochas-



**Fig. 7.6.** One of the treatments of the route-to-chaos experiment reported in (Costantino et al. 1997; Cushing et al. 2003; Dennis et al. 2001) was based on a chaotic attractor predicted by the LPA model (1) with parameter values  $b = 10.45$ ,  $\mu_l = 0.2000$ ,  $\mu_a = 0.9600$ ,  $c_{el} = 0.01731$ ,  $c_{ea} = 0.01310$ ,  $c_{pa} = 0.9600$ . A “signature” of the temporal dynamics on the chaotic attractor is a distinctive 11-cycle. The top graph shows the eleven lag metrics (one for each phase of the 11-cycle) computed using one replicate from the experimental treatment. The lag metric measures the average distance of eleven consecutive data points from the corresponding points on a selected phase of the 11-cycle. A low value indicates that the data was close to the 11-cycle for eleven consecutive time steps. The “unravelled” portions of the lag metric braid indicate time intervals during which the data followed closely this signature of the chaotic attractor. (Recall that one generation is 4 weeks.) The LPA model on an integer lattice predicts the experimental initial conditions (and many others) ultimately arrive at a 6-cycle. The graph second from the top shows the lag metrics for the lattice 6-cycle computed from the data. Unravelled portions indicate intervals during which the data was close to this lattice model “attractor”. The lattice LPA model has several other cycle attractors, one of which is an 8-cycle whose lag metrics appear in the third graph. The bottom graph displays the lag metric computed with respect to the saddle equilibrium. It clearly indicates a saddle flyby late in the experiment. More details of this “anatomy” of the chaotic attractor appear in (King et al. 2003)

tic processes can be predicted by various deterministic models derived from a parent stochastic mode.

For example, a probabilistic model for *Tribolium* dynamics (based on models of demographic stochasticity in life cycle stage specific birth and death

rates) is described by the equations

$$\begin{aligned}
 L_{t+1} &\sim \text{Poisson} \left[ b a_t \exp \left( -\frac{c_{ea}}{V} a_t - \frac{c_{el}}{V} l_t \right) \right] \\
 P_{t+1} &\sim \text{binomial} [l_t, 1 - \mu_l] \\
 R_{t+1} &\sim \text{binomial} \left[ p_t, \exp \left( -\frac{c_{pa}}{V} a_t \right) \right] \\
 S_{t+1} &\sim \text{binomial} [a_t, 1 - \mu_a] \\
 a_{t+1} &= r_t + s_t.
 \end{aligned} \tag{3}$$

Here  $R_t$  is the number of sexually mature adult recruits,  $S_t$  is the number of surviving mature adults, and  $l_t$ ,  $p_t$ ,  $r_t$  and  $s_t$  are the respective numbers observed at time  $t$ . The total number of mature adults is  $A_t = R_t + S_t$  and  $a_t = r_t + s_t$  is the number of mature adults observed at time  $t$ . The symbol ‘ $\sim$ ’ means ‘is distributed as’. This “Poisson/binomial” LPA (or PBLPA) model is integer value and its dynamics occur on a lattice.

One way to construct a deterministic “skeleton” for the PBLPA model is by iterating the conditional expectation (so that the “most likely” data triple  $(L_{t+1}, P_{t+1}, A_{t+1})$  to occur at time  $t + 1$ , given the observed triple  $(l_t, p_t, a_t)$ , is assumed to be the mean of the random variables in the PBLPA model). This results in the continuous state space LPA model (2).

On the other hand, we can obtain a deterministic skeleton that remains on the integer lattice (where real data is observed) by using another measure of central tendency, namely, the mode. By iterating the conditional mode we obtain a deterministic lattice mode described, as it turns out (assuming the unlikely event of a non-unique conditional mode), by the equations<sup>3</sup>

$$\begin{aligned}
 L_{t+1} &= \text{floor} \left[ b A_t \exp \left( -\frac{c_{ea}}{V} L_t - \frac{c_{ea}}{V} A_t \right) \right] \\
 P_{t+1} &= \text{floor} [(1 - \mu_l) (L_t + 1)] \\
 A_{t+1} &= \text{floor} \left[ (P_t + 1) \exp \left( -\frac{c_{pa}}{V} A_t \right) \right] + \text{floor} [(1 - \mu_a) (A_t + 1)].
 \end{aligned} \tag{4}$$

---

<sup>3</sup> These equations result from formulas for the mode of a binomial random variable and the mode of a Poisson random variable. The following derivations are due to Michael Trosset and Shandelle Henson (private communication). The pdf for a binomial random variable  $\text{binomial}(n, p)$  is  $f(x) = \frac{n!}{x!(n-x)!} p^x (1-p)^{n-x}$ . If  $x = m$  is the mode, then  $f(m+1) \leq f(m)$  and hence  $p(n+1) - 1 \leq m$ . Also  $f(m-1) \leq f(m)$  implies  $m \leq p(n+1)$ . Since  $m$  is an integer, and since  $p(n+1)$  is almost always an integer, it follows that  $m = \text{floor}[p(n+1)]$ . The pdf for a Poisson random variable  $\text{poisson}(\mu)$  is  $f(x) = \frac{\mu^x e^{-\mu}}{x!}$ . For the mode  $m$ , we see that  $f(m+1) \leq f(m)$  implies  $\mu - 1 \leq m$  and  $f(m-1) \leq f(m)$  implies  $m \leq \mu$ . Since  $\mu$  is almost always not an integer, we have  $m = \text{floor}[\mu]$ . We also point out that the equation for  $A_{t+1}$  is different from that given in (Cushing et al. 2003) because of the nature of the experimental protocol involved in the study discussed in that book.

Examples (in addition to the LPA models and the chaos experiment) given by Henson et al. (2003b) show how temporal patterns from both mean (continuous state space) and mode (lattice state space) models are evident in realizations of a stochastic model.

Notice that from this point of view it is not so appropriate to inquire whether or not a specific time series of ecological data has a particular dynamic predicted by a deterministic model, and thus to identify the time series with some type of asymptotic attractor (equilibrium, limit cycle, chaos, etc.). Instead, one expects to observe intermittent episodes of various kinds of patterns, attractor and transient, from perhaps more than one deterministic skeleton. If one expects to see, and only looks for, deterministic attractor patterns, then the modeling exercise used to study the data might be judged a failure when in fact it is very much a success – a success because it can, using an expanded analysis as described above, successfully explain the observed temporal patterns.

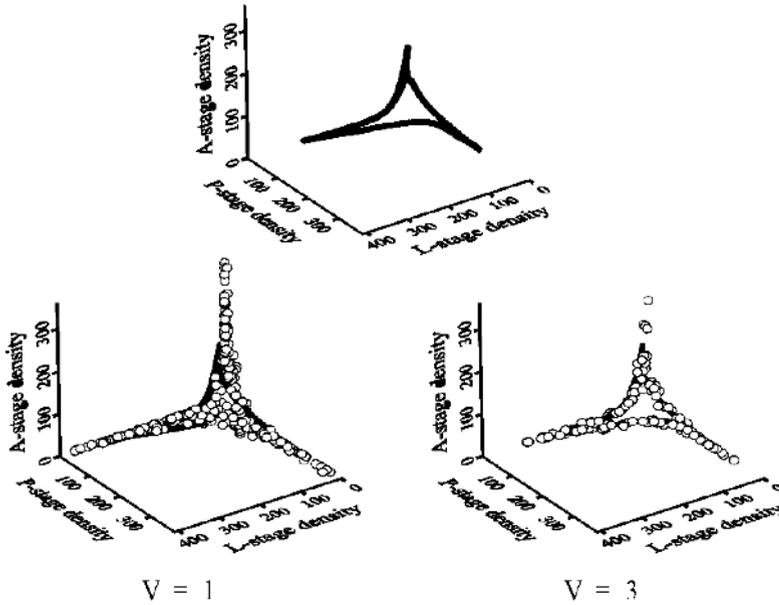
For example, suppose one is looking for evidence of chaotic dynamics in time series data. How reliable are conclusions (pro or con) obtained from techniques and diagnostics (e. g., Lyapunov exponents) that are based on the assumption that the data is on an attractor (with some noise, of course), when, in fact, the dynamics might exhibit a stochastic “dance” of attractors, saddles, and transients (Dennis et al. 2003)? A chaotic attractor could be a role player – in this “dance” – and the fact be overlooked. If we found this to be so in the controlled environment and accurately censused populations cultured in our laboratory, then we would expect it to be so, perhaps even more prominently, in field situations.

## 7.5 Habitat size

Another issue, relating to the important issue of scale in ecology, arose from our route-to-chaos experiment. The predictions of a lattice model can depend significantly on habitat size. This is the case for (3) or (4), whose dynamics change in important ways with the volume  $V$ . This is not the case with the continuous state space LPA model (2) whose dynamics only scale with  $V$ .

For example, with the estimated and controlled parameter values used in the chaos treatment (Fig. 7.3), a change of  $V$  from  $V = 1$  (corresponding to the experimental habitat volume occupied by 20 g of medium) to  $V = 3$  (60 g of medium) changes the lattice model prediction for the experimental initial conditions from the 6-cycle that played such an important role in the dynamics and analysis at  $V = 1$  to a 14-cycle. The 6-cycle is no longer present in the lattice dynamics at the larger habitat volume  $V = 3$ . Thus, a different collage of patterns would have been predicted and utilized in analysis of the data had the experiment been performed in 60 g of medium.

In the state space of densities, the number of lattice points increases with  $V$  (the lattice mesh size decreases) and the dynamics of the deterministic



**Fig. 7.7.** The top graph shows the chaotic attractor, plotted in phase space, predicted by the LPA model in the treatment of the route-to-chaos experiment discussed in the caption of Fig. 7.6. The graph on the lower left shows data points (open circles) from all replicates clustered around the chaotic attractor. This experiment was carried out in a volume occupied by 20 g of standard medium, which corresponds to  $V = 1$  in the LPA model (2). A follow-up experiment was conducted in 60 g, or  $V = 3$ . The results, plotted (as densities) in the lower right hand graph, show a tighter cluster of data points around the chaotic attractor (as predicted by the stochastic lattice model (3))

lattice model converge to the deterministic attractor. This is illustrated for the lattice Ricker model in Fig. 7.5. See Henson et al. (2001, 2003b) for other examples, including the LPA model. Moreover, the stochastic PBLPA model (3) predicts a stronger deterministic (continuous state space) signal as  $V$  increases. This is typical of models with demographic stochasticity (May 2001). We have conducted an experiment that duplicates the chaos treatment, but does so in the larger habitat of 60 g ( $V = 3$ ). Although we have not yet published an analysis of this experiment, one can see in Fig. 7.7 that the prediction of a stronger deterministic signal in a larger habitat is supported by the data.

Conversely, the continuous state space attractor is “lost” from the dynamics of the corresponding lattice model if the habitat size is too small. In other words, the size of the habitat effects the predicted dynamic patterns. In the case of chaos, we know of no studies of chaos in ecological data that consider habitat size as a possible factor.

## 7.6 Concluding remarks

The examples taken from our experimental projects for inclusion in this paper were chosen to illustrate that non-attractor dynamics can play an important role in explaining dynamic patterns observed in data. This is not to say, of course, that attractors are unimportant. Indeed, we designed virtually all of our experimental projects on the basis of model predicted attractors. Nonetheless, we found that in order to obtain a complete and satisfactory explanation of our data it is necessary to include unstable invariant sets, stable manifolds, and so on. This is true even though our experiments involve (seemingly) low dimensional ecosystems cultured in controlled environments in which population counts are highly accurate and stochasticity is minimized. We can successfully account for the dynamic patterns observed in our data by using deterministic model predicted patterns blended together by stochasticity (in most of our cases, demographic stochasticity). In this setting stochasticity becomes an aid, rather than a hindrance, in that it provides the means by which the collage of observed patterns arise (and, in the process, by which the “validation” of the deterministic skeleton that underlies the model is strengthened).

Biological populations and ecosystems are complex, at all levels of organization, and our experience suggests that the mix of stochasticity and nonlinearity will likely be important in most systems. The “higher dimensions” (internal and external) ignored in models with a relatively few number of state variables produces deviations from model predictions (which is modeled as stochasticity). A good example is the plethora of models in which state variables are total population sizes and which in effect treat all individuals as identical, a gross oversimplification in most biological systems. Mathematicians could contribute more to theoretical and applied ecology by extending their efforts beyond the analysis of asymptotic attractors in deterministic models. The study of attractors is, of course, the first step. However, by including stochasticity (in an appropriate way), one can suggest how the deterministic dynamics are likely to manifest themselves in real data. (As we have seen, one can do better than to say that attractors simply made “fuzzy” by noise.) This will strengthen the connection between data and models, and thereby aid ecologists in attempts to account for observed dynamic patterns.

## References

1. Aber, J. D. (1997), Why don't we believe the models?, *Bulletin of the Ecological Society of America* 78: 232–23
2. Caswell, H. (2001), *Matrix Population Models: Construction, Analysis and Interpretation*, Second edition, Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts
3. Costantino, R. F., R. A. Desharnais, J. M. Cushing and B. Dennis (1997), Chaotic dynamics in an insect population, *Science* 275: 389–391

4. Costantino, R. F., J. M. Cushing, B. Dennis and R. A. Desharnais and S. M. Henson (1998), Resonant population cycles in temporally fluctuating habitats, *Bulletin of Mathematical Biology* 60: 247–275
5. Cushing, J. M., B. Dennis, R. A. Desharnais, R. F. Costantino (1998), Moving toward an unstable equilibrium: saddle nodes in population systems, *Journal of Animal Ecology* 67: 298–306
6. Cushing, J. M., R. F. Costantino, Brian Dennis, R. A. Desharnais, S. M. Henson (2003), *Chaos in Ecology: Experimental Nonlinear Dynamics*, Theoretical Ecology Series, Academic Press/Elsevier, San Diego
7. Cushing, J. M. (2004), The LPA model, *Fields Institute Communications* 43: 29–55
8. Dennis, B., R. A. Desharnais, J. M. Cushing, and R. F. Costantino (1995), Nonlinear demographic dynamics: mathematical, models, statistical methods, and biological experiments, *Ecological Monographs* 65 (3): 261–281
9. Dennis, B., R. A. Desharnais, J. M. Cushing, S. M. Henson and R. F. Costantino (2001), Estimating chaos and complex dynamics in an insect population, *Ecological Monographs* 71, No. 2: 277–303
10. Dennis, B., R. A. Desharnais, J. M. Cushing, S. M. Henson, R. F. Costantino (2003), Can noise induce Chaos?, *Oikos* 102: 329–340
11. Desharnais, R. A., Costantino, R. F., J. M. Cushing and B. Dennis (June 1997), Letter to editor, *Science* 276: 1881–1882
12. Henson, S. M. (2000), Multiple Attractors and Resonance in Periodically Forced Population Models, *Physica D: Nonlinear Phenomena* 140: 33–49
13. Henson, S. M. and J. M. Cushing (1997), The effect of periodic habitat fluctuations on a nonlinear insect population model, *Journal of Mathematical Biology* 36: 201–22
14. Henson, S. M., J. M. Cushing, R. F. Costantino, B. Dennis and R. A. Desharnais (1998), Phase switching in biological population, *Proceedings of the Royal Society* 265: 2229–2234
15. Henson, S. M., R. F. Costantino, J. M. Cushing, B. Dennis and R. A. Desharnais (1999), Multiple attractors, saddles and population dynamics in periodic habitats, *Bulletin of Mathematical Biology* 61: 1121–1149
16. Henson, S. M., R. F. Costantino, J. M. Cushing, R. A. Desharnais, B. Dennis and Aaron A. King (19 Oct 2001), Lattice effects observed in chaotic dynamics of experimental populations, *Science* 294: 602–605
17. Henson, S. M., R. F. Costantino, R. A. Desharnais, J. M. Cushing, and B. Dennis (2002), Basins of attraction: population dynamics with two stable 4-cycles, *Oikos* 98: 17–24
18. Henson, S. M., J. R. Reilly, S. L. Robertson, M. C. Schu, E. W. Davis and J. M. Cushing (2003a), Predicting irregularities in population cycles, *SIAM Journal on Applied Dynamical Systems* 2, No. 2: 238–253
19. Henson, S. M., A. A. King, R. F. Costantino, J. M. Cushing, B. Dennis and R. A. Desharnais (2003b), Explaining and predicting patterns in stochastic population systems, *Proceedings of the Royal Society London B* 270: 1549–1553
20. Jilison, D. (1980), Insect populations respond to fluctuating environments, *Nature* 288: 699–700
21. Kendall, B. E., W. M. Schaffer and C. W. Tidd (1993), Transient periodicity in chaos, *Physics Letters A*. 177: 13–20

22. King, A. A., R. F. Costantino, J. M. Cushing, S. M. Henson, R. A. Desharnais and B. Dennis (2003), Anatomy of a chaotic attractor: subtle model-predicted patterns revealed in population data, *Proceedings of the National Academy of Sciences* 101, No. 1: 408–413
23. Lathrop, D. P. and E. J. Kostelich (1989), Characterization of an experimental strange attractor by periodic orbits, *Physics Reviews A*. 40: 4028–4031
24. May, R. M. (2001), *Stability and Complexity in Model Ecosystems*, Princeton Landmarks in Biology, Princeton University Press, Princeton, New Jersey
25. Schaffer, W. M., B. E. Kendall, C. W. Tidd and J. F. Olsen (1993), Transient periodicity and episodic predictability in biological dynamics, *IMA Journal of Mathematical Applications to Medicine and Biology* 10: 227–247
26. So, P., J. T. Francis, T. I. Netoff, B. J. Gluckman, and S. J. Schiff (1998), Periodic orbits: a new language for neuronal dynamics, *Biophysics Journal*. 74: 2776–2785
27. Wilson, E. O. (2002), *The Future of Life*, Alfred A. Knopf, New York, p.111