



PERSPECTIVES

Nonlinear Population Dynamics: Models, Experiments and Data

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Understanding observed temporal fluctuations in population abundance is a central goal of population biology. The hypothesis that complex fluctuations are a result of deterministic nonlinear effects, as predicted by simple nonlinear mathematical models, has proved both controversial and elusive to test. Nonlinear theory suggests many possibilities for complex fluctuations, such as chaotic and strange attractors, quasi-periodicity and invariant loops, fractal basins, of attraction, and so on. However, convincing evidence for the occurrence of such exotic phenomena in biological populations is meager. There are many reasons for this. Among them are the difficulties in gathering adequate and appropriate data; the impracticality, if not impossibility, of experimental manipulation and replication of ecological systems; the scarcity of validated and predictive mathematical models; inadequate connections between data and models for purposes of their parameterization and validation; and the ever present factor of noise in biological data. Nevertheless, a great deal of interest surrounds the possibility of using nonlinear mathematical models to describe,

explain and even predict the dynamics of biological populations. In particular, there has been special interest in some of the more exotic features of nonlinearity such as chaos (claims of which, however, have been held in skepticism by many empirical ecologists).

Mathematical models often are used for discussing theoretical principles in population dynamics and for drawing conclusions concerning “qualitative” or “phenomenological” properties of the dynamics. They have been less successful in providing accurate quantitative descriptions and predictions that can serve as testable hypotheses to be rigorously confronted with data. This is not surprising, given the difficulties mentioned above and the weaknesses of many modeling methodologies.

What are the components necessary for a convincing mathematical model? In our opinion a modeling exercise in population biology should contain at least the following basic ingredients. First, the deterministic “skeleton” of the model should not be *ad hoc*, but instead should be based upon biological principles and, as much as possible, upon the specific mechanisms judged important by biologists with regard to the dynamics of the specific population of interest

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(under the circumstances of interest). As in all sciences that are successfully integrated with mathematical models, an authoritative model must be built on such a foundation. Of course, there is always a relentless tradeoff between model detail and mathematical tractability. Simplifications must be made by ignoring mechanisms considered of less importance. By identifying and isolating the dominant mechanisms one can aim to build a simpler model with fewer parameters. An ecological model with an over abundance of parameters and state variables (relative to the amount of data available) is not statistically testable.

Second, due to the prevalence of noise in biological data, a stochastic version of the model must be constructed in order to account for inevitable deviations from the predictions of the deterministic model. The nature of the stochasticity and the form that it takes in the model should again be based upon the biological circumstances, that is to say upon what is judged to be the source of the noise in the situation under study. The stochastic model becomes a testable hypothesis for the statistical explanation of data. It provides the means for a strong connection between a model and data.

Third, parameter estimation (or model "calibration") and model validation from data should be distinct procedures. Some model parameters can be estimated separately from the time series data; some parameters might even be controlled by an investigator. However, other parameters must be statistically estimated (with confidence intervals) from the time series data by some method, e.g. by maximum likelihood or conditioned least squares methods. However, the data used for parameter estimation should not be used to evaluate the accuracy of the model. In a sense, models that are only parameterized (calibrated) cannot go wrong, since by design they "fit" or "interpolate" the data in some optimal manner. A model that cannot fail provides little information. This is particularly serious if the number of estimated parameters far exceeds the number of data points. *Independent* data, i.e. data not used to estimate parameters, should be utilized in the evaluation of the model's descriptive accuracy and predictive capabilities. This requires reserving some of the

available data (or obtaining new data) for this purpose. It also involves devising some rigorous statistical tests to evaluate the parameterized model against this independent data.

A strong case for a model is made if its parameterization is validated against independent data sets. An even stronger case for the model is made if its parameterization provides predictions, perhaps unexpected and unintuitive predictions, which can be subsequently documented by means of observations and controlled experiments.

For nearly a decade the authors have been collaborating on interdisciplinary projects in which these modeling principles are applied to the investigation of nonlinear phenomena in population biology. A fundamental goal of the research is to demonstrate that a mathematical model can be a valuable tool in explaining and predicting the dynamics of a biological population and to do so under carefully controlled (and replicated) experimental conditions. Another goal is to document the occurrence of specific, model predicted nonlinear phenomena such as chaos, bifurcation sequences, stable and unstable manifolds, resonances and so on. We are interested in showing how a mathematical model can provide previously unavailable explanations for patterns, even for unexpectedly subtle patterns, in a population's dynamics.

To carry out these projects we utilize laboratory cultures of flour beetles (sp. *Tribolium*). This animal provides the necessary ingredients for our modeling studies. Flour beetles are easy to culture and manipulate in a controlled laboratory setting. Their biology is well understood and their life cycle is sufficiently complicated that the dynamical possibilities are rich. Census counts are accurate and can be taken over many reproductive cycles in a relatively short period of time. Although we use this particular animal, our studies are not designed primarily to further understanding of flour beetle dynamics. Instead, the flour beetle is used to accomplish our goals in studying the role of nonlinearity in population dynamics.

One of several major projects concerns a question that has been of interest since the well-known work of R. M. May and others in the 1970s: will the dynamics of a population undergo

the sequence of dynamical changes (bifurcations) predicted by a mathematical model when a parameter is changed? The capability to predict the consequences of, for example, environmental and/or physiological perturbations is clearly of ecological importance. The ability of mathematical models to do this in a natural setting is certainly in doubt if they cannot do so in a highly controlled laboratory setting. This particular long term project was designed to demonstrate the ability of a relatively simple mathematical model to make such predictions for laboratory cultures of flour beetles and to document the predicted dynamics in controlled and replicated experiments. In its details the project also includes other interesting questions, not the least of which is: will a population follow a specific bifurcation route to chaos and, in particular, can a biological population exhibit chaotic dynamics? The study utilizes the modeling principles outlined above and provides what we feel are the most convincing answers to these questions yet obtained.

As a first step in this project mathematical equations were derived for the deterministic prediction of measurable state variables from one census time to the next. The state variables were chosen to be the numbers of larvae L , pupae P and adult beetles A placed in a 20 g medium of flour which are counted at two week intervals (after which they are returned to a fresh 20 g medium of flour). Many species of *Tribolium* are cannibalistic (Park *et al.*, 1965) and this is the case for the species *Tribolium castaneum* (Herbst) used in this project. The model is built on the assumption that the driving mechanism of the dynamics for this species, under the experimental conditions of this project, are the (nonlinear) interactions among these life cycle stages caused by cannibalism. Specifically, the three discrete recursion formulas for the triple (L, P, A) of state variables, together called the "LPA model", given by the formulas

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

include Ricker-type exponential terms derivable from an assumption that cannibalistic acts result

from random encounters with victims (which is strongly supported by existing knowledge of the behavioral characteristics of the beetles). Stochastic terms are then included in order to account for random deviations from the life stage numbers predicted by these deterministic equations. One "stochastic LPA model" is given by the formulas

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

which have noise added on the logarithmic scale. This is appropriate for the high numbers of individuals typically present in the experimental cultures and the resulting dominance of environmental stochasticity over demographic stochasticity (Dennis *et al.*, 1991). In this model the three terms E_{it} denote normally distributed random variables (uncorrelated in time) with mean 0 and a variance/covariance to be determined as part of the model parameterization.

Parameterization and validation of the models (1) and (2) were initially performed using available historical time series data sets. To do this half the data was used to derive estimates for the model parameters and the other half was used for a validation of the resulting parameterized model. The validation procedure involved detailed statistical analyses of one-step residuals (normality tests, Q-Q plots, hypotheses tests, etc.) computed using the parameterized model prediction from each census triple and the subsequent census triple. Parameter estimates (with confidence intervals) and other details are given in Dennis *et al.* (1995). This initial step resulted in a parameterized and validated model for laboratory cultures of *Tribolium castaneum*. [The model (1) was not the first model investigated. Simpler models, however, failed statistically to pass validation tests.]

In the next step of this project the asymptotic dynamics of the parameterized deterministic LPA model were investigated, analytically and numerically, and predictions were formulated concerning the effects of changes in one of the model parameters, namely the adult death rate μ_a . The model, it turns out, predicts a very particular sequence of bifurcations as μ_a is

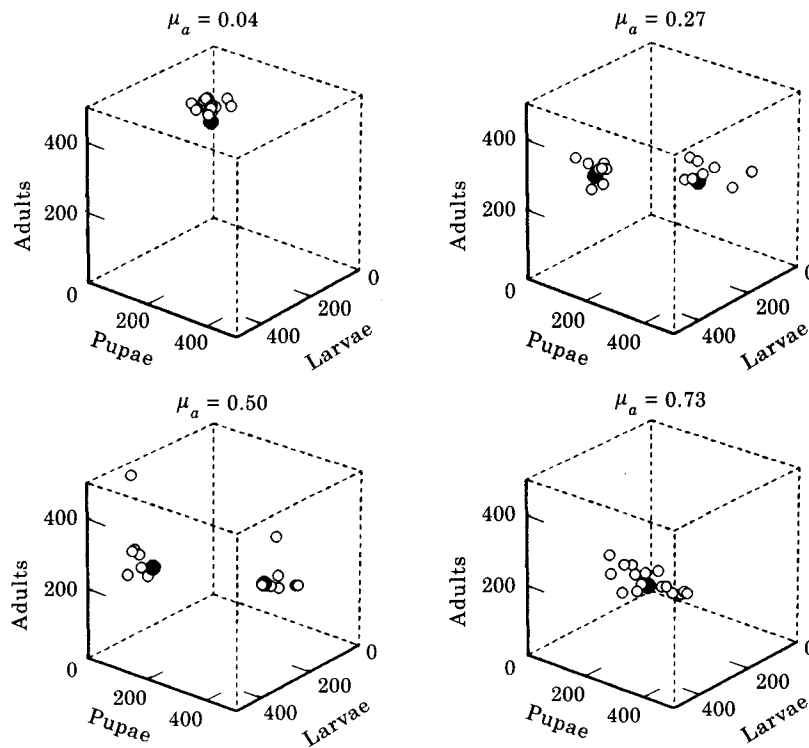


FIG. 1. In one experiment μ_a (the fraction of adults dying per 2 week time unit) was manipulated to the value shown. The resulting data triples of life-stage numbers are plotted as open circles (after initial transients are eliminated). The deterministic model (1) predicts stable equilibria for $\mu_a = 0.04$ and 0.73 (shown as a single solid circle) and stable periodic two-cycles for $\mu_a = 0.27$ and 0.50 (shown as two solid circles).

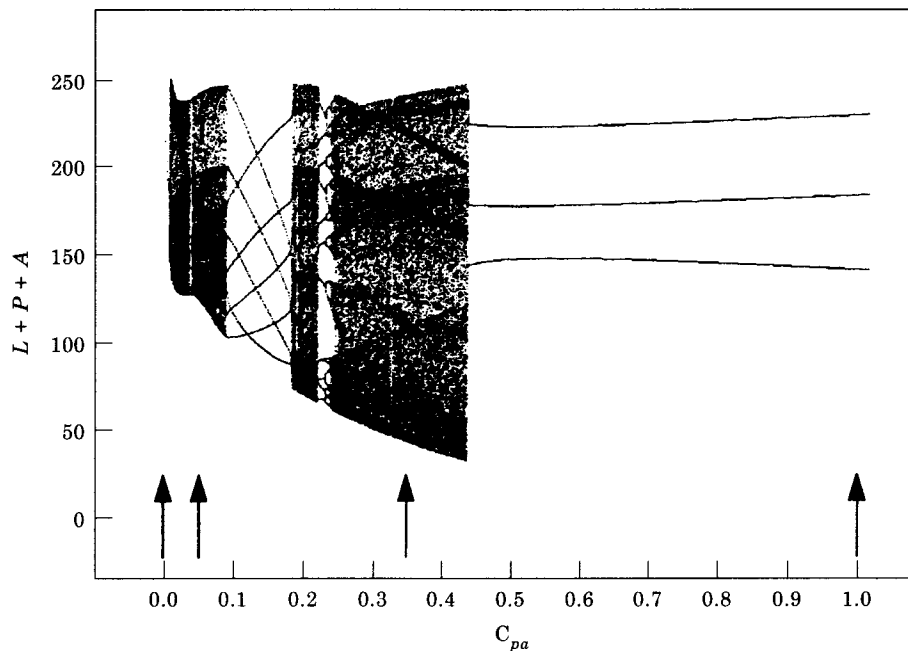


FIG. 2. The bifurcation diagram for the LPA model (1) used to designed experiments by Costantino *et al.* (1997). The arrows mark where four of the manipulated cultures were placed. The phase plane plots of the resulting data for these treatments appear in Fig. 4.

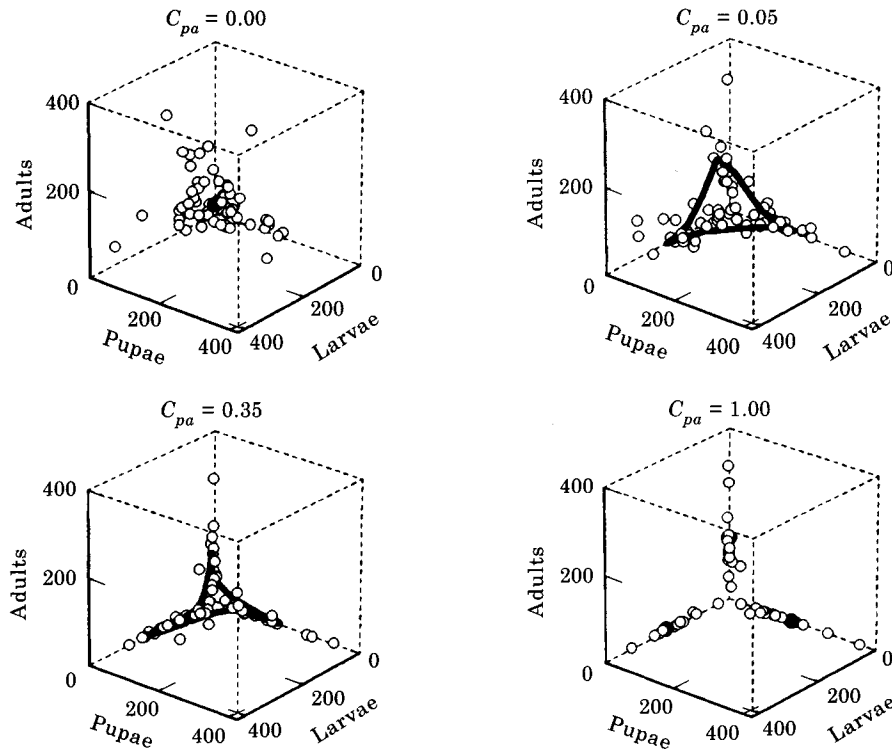


FIG. 3. The deterministic model (1) predicts four different phase space attractors in the experiment indicated in Fig. 4: a stable equilibrium when $c_{pa} = 0.05$; an invariant loop when $c_{pa} = 0.05$; a chaotic strange attractor when $c_{pa} = 0.35$; and a three-cycle when $c_{pa} = 1.00$. These attractors are plotted as dark lines and circles. Open circles show typical orbits of the stochastic model (2). Model parameters, including the variance/covariance matrix for the stochastic model (2), were estimated from data by Dennis *et al.* (1997).

increased from its minimum of 0 to its maximum of 1: an equilibrium destabilization results in the appearance of a stable two-cycle (i.e. a “period doubling” bifurcation occurs), after which there occurs a restabilization of the equilibrium. Based on this simple model predicted sequence of bifurcations, a series of laboratory experiments were designed and implemented. Replicated cultures of flour beetles were manipulated so as to have adult death rates μ_a corresponding to the different asymptotic dynamics appearing in the bifurcation sequence. The experiment also included unmanipulated controls. That the beetle population data do indeed exhibit the predicted dynamics is visually illustrated by the phase space plots of the data triples (L_t , P_t , A_t) in Fig. 1. The success of the model was also quantified by a repeated model validation using the new laboratory data (see Costantino *et al.*, 1995; Dennis *et al.*, 1997).

Bolstered by the success of this preliminary study, we initiated a long-term experiment whose protocol was based upon an LPA model

predicted sequence of bifurcations involving more exotic dynamics, including chaotic and strange attractors. This sequence occurs in the model when the adult death rate is held high at $\mu_a = 0.96$ and c_{pa} is increased (by manipulating adult recruitment); see Fig. 2. The sequence begins with the destabilization of an equilibrium and an “invariant loop” bifurcation to quasi-periodic oscillations (sometimes called a discrete Hopf or Naimark/Sacker bifurcation) in which orbits move on a closed loop in phase space. With further increases in c_{pa} the predicted dynamics pass through a complicated array of invariant loops and “period locking windows” (where the motion around the loop is exactly periodic) until finally chaotic and strange attractors appear. For sufficiently large values of c_{pa} there is predicted a distinctive cycle of period three. The deterministic LPA model attractors for four selected values of c_{pa} are shown in the phase space plots in Fig. 3, together with typical orbits from the stochastic LPA model (2); these graphically depict the LPA model predictions

based upon the parameterization obtained from the experiments described in Dennis *et al.* (1997).

Based on the predictions in Fig. 3 new experiments were designed and carried out in which replicated flour beetle cultures were manipulated to have $\mu_a = 0.96$ and adult recruitment determined by the selected values of c_{pa} indicated in Figs 2 and 3. The data from these experiments are shown in Fig. 4, together with the predicted attractors (note that these attractors were predicted prior to the experiment and are not fits to the new data!). Once again the visual evidence for the occurrence in the data of the LPA model predicted attractors is striking. See Costantino *et al.* (1997), Desharnais *et al.* (1997) and Dennis *et al.* (1998) for details of these experiments and also experiments at other values of c_{pa} .

The deterministic LPA model (1) also describes well the temporal sequence of data points in phase space (not shown in Fig. 4). In fact, the

model can capture amazing details of the “data orbits”, as the one example shown in Fig. 5 demonstrates. For this particular replicate of the treatment $c_{pa} = 0.05$ the model predicts quasi-periodic motion around the invariant loop in phase space shown in Fig. 4. In Fig. 5 the data orbit is broken into four pieces. The first and fourth pieces, corresponding to the beginning and the end of the experiment, show a temporal motion around the loop as predicted by the model (1) [see Fig. 5(a,d)]. In this replicate, however, a notable perturbation away from the predicted motion on the loop occurs when a stochastic event (at $t = 8$ time units, or week 16) places the data point very near a model predicted equilibrium. This is shown by the second piece of the orbit plotted in Fig. 5(b). During this time interval (from $t = 8$ to 13, i.e. for a period of 10 weeks) the data remains clustered very near this predicted equilibrium. The model predicts, however, that the equilibrium is unstable and

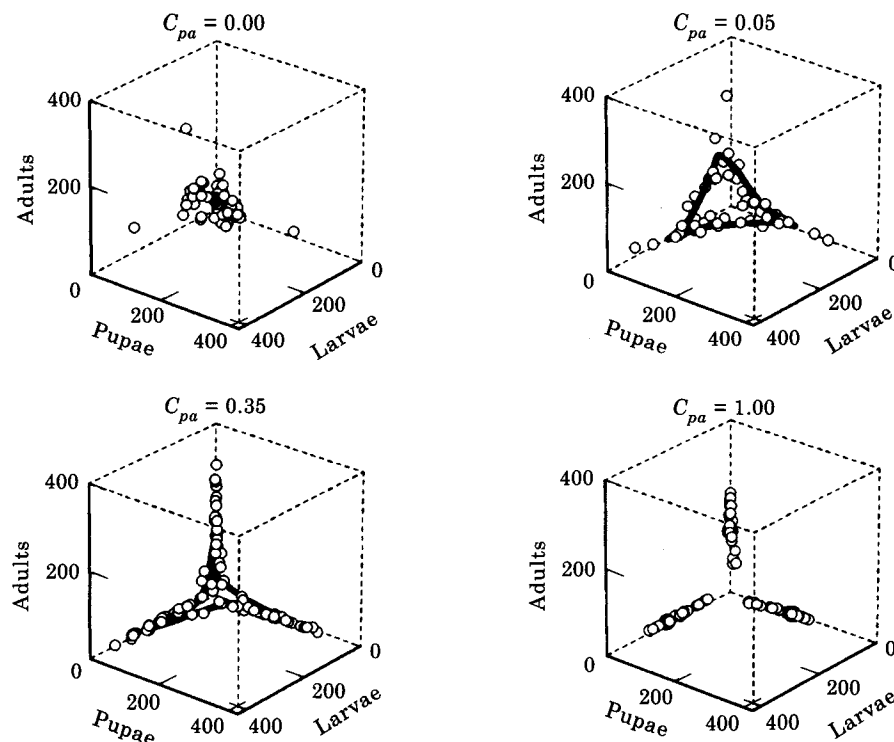


FIG. 4. Data triples of life-stage numbers for the experiments conducted at the four positions shown in Fig. 2 are plotted as open circles (after initial transients are eliminated). The deterministic model predicts a stable equilibria for $c_{pa} = 0.00$; an invariant loop for $c_{pa} = 0.05$; a chaotic strange attractor for $c_{pa} = 0.35$; and a period three cycle for $c_{pa} = 1.00$ (shown as dark lines and circles). It is important to note that the displayed attractors were not obtained from a model parameterization using the displayed data. They were obtained from a parameterization using independent data that was available prior to the experiments (see Dennis *et al.*, 1997). Therefore these attractors constitute a model prediction, not a model “fit”.

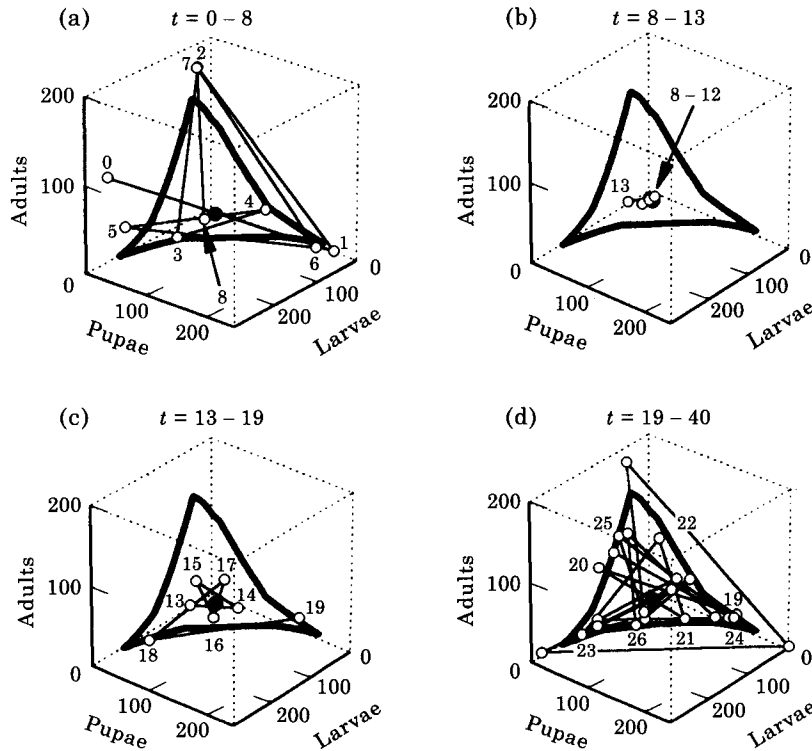


FIG. 5. The model predicted invariant loop and unstable equilibrium (solid circle) for the treatment $c_{pa} = 0.05$ is shown together with the entire data orbit of one replicate (open circles). The data orbit is shown in four sequential pieces: in (a) motion around the loop is interrupted by a stochastic event that places the data near the unstable equilibrium at time $t = 8$; in (b) the data cluster near the unstable equilibrium; in (c) a slow rotational exit from the equilibrium back to the loop occurs; and in (d) a return to motion around the invariant loop is seen.

that the data orbit should therefore return to the invariant loop. Moreover, the model predicts further that this return to the loop should be rotational (with an approximate angle of approximately 145° with respect to the equilibrium). This rotation is clearly seen in the data in Fig. 5(c). This particular replicate (the other replicates for this treatment do not show a stochastic visit near the equilibrium) illustrates two notable points: (1) the relatively simple LPA model can describe subtle details of the data and (2) in the presence of stochasticity and nonlinearity unstable invariant sets must be taken into account.

Parameter estimates come with confidence intervals. It is sometimes the case that the model predicted dynamics, including a stable attractor like an equilibrium or a periodic cycle, are robust within these confidence intervals. In this case one might well conclude that the data time series has the dynamics predicted by the deterministic skeleton (with, of course, accompanying noise).

For example, one might say that a particular data time series is a noisy equilibrium or two-cycle. However, such dynamic robustness is often not present for parameterizations that imply more complicated dynamics such as chaos. In this case it frequently (if not typically) happens that parameter values yielding other types of dynamics and attractors are “densely embedded” within the confidence interval. (For example, see the “periodic locking windows” in Fig. 2.) As parameter values are changed within the confidence intervals, even by arbitrarily small perturbations, qualitatively different types of stable and unstable invariant sets may be encountered: equilibrium, periodic, chaotic, etc. There may also occur multiple attracting sets with complicated fractal or “riddled” basin boundaries. In such cases it is unreasonable to assign characteristics of a specific attractor type (such as chaos) to a specific time series of data. Instead, a more appropriate conclusion is that the data lies in a range of model predicted

dynamic possibilities as found within the parameter confidence intervals (of which chaos is one possibility). In this scenario, especially with the stochastic nature of a data orbit, stable manifolds of unstable invariant sets are relevant, since repeated stochastic events may result in the dominant influence of unstable invariant sets, rather than stable attractors. Long chaotic transients (associated with an unstable chaotic set) in the presence of a model predicted, stable equilibrium or periodic cycle is one example.

We have described one project in which a mathematical model was impressively successful in describing and predicting the dynamics of a biological population and, as a result, in showing convincingly that certain nonlinear phenomena can occur. Some of these experiments are still ongoing (e.g. the chaotic treatment $c_{pa} = 0.35$) and are, at the time of writing, over 180 weeks in length. In addition to this project, the LPA model with appropriate modifications has been applied with equal success in projects involving other nonlinear phenomena.

For example, using a modification of the LPA model suitable for a periodically fluctuating habitat of flour, a theoretical explanation of an unusual "resonance" phenomenon observed by Jillson (1980) has been obtained (Henson & Cushing, 1997; Costantino *et al.*, 1998). In Jillson's experiment a significant increase in biomass was obtained by periodically alternating the flour medium with an average of 20 g rather than holding the volume constant at 20 g. Moreover, beyond providing a theoretical explanation of this phenomenon, the periodic LPA model makes some (biologically) unexpected predictions related to the existence of two different stable periodic cycles with quite different characteristics (averages, phases, etc.). Based upon these model predictions, laboratory experiments were recently designed and implemented to substantiate the existence of these two cycles. Not only are both model predicted cycles clearly found in the resulting data, but dynamic subtleties in the data correspond beautifully to model predicted effects due to a third and unstable ("saddle") cycle. A report of these results is in preparation (Henson *et al.*, in prep.). Furthermore, the multiple attractors of the periodic LPA model, together with stochas-

ticity, suggest a hitherto unavailable explanation of a well-known, stuttered one-step transition (or "chicken step") which causes a phase shift in the time series oscillations of beetle populations. Experiments to test this hypothesis are underway.

In yet another study, unstable invariant sets were found to play a crucial role. Cushing *et al.* (1998) show how the LPA model (1)–(2) provides an explanation for transient effects in data orbits due to stable manifolds of unstable equilibria (and hence for differences among replicated cultures).

These studies demonstrate that mathematical models, even "simple" mathematical models, are capable of providing accurate descriptions, explanations and predictions for the dynamics of biological populations. To further support this assertion many other investigations are in progress or being planned. These include studies of metapopulations and migration, populations with non-overlapping generations and one-dimensional maps (with the famous period doubling route to chaos), and multi-species competition systems.

The results of our work demonstrate several issues that have general relevance to nonlinear population dynamics. Since all ecological systems are stochastic, the role of nonlinear dynamical theory must be understood in the context of stochasticity. Nonlinearity and stochasticity together have many important implications. One is that a study of stable attractors alone might be insufficient to account for the dynamical possibilities of a population. Random events can frequently and repeatedly produce visits near unstable invariant sets, such as equilibria or cycles, or near their stable manifolds. The result can be a strong influence, even a dominance, of unstable sets on the dynamics of a population. For example, the exponential expulsions that occur near unstable sets lead to a kind of sensitivity to initial conditions that is not related to the deterministic concept of chaos (Desharnais *et al.*, 1997). As another example, unstable sets and their stable manifolds often form the boundaries between basins of attraction of multiple attractors and thus small stochastic perturbations near such an unstable set can result in very different predicted

asymptotic dynamics. Furthermore, if the basin boundary is complicated (fractal or riddled) it may not be reasonable, in a stochastic setting, to assign a particular deterministic attractor type to a data orbit. This does not necessarily mean that the deterministic skeleton of a stochastic model is uninformative, however, since it will often exert a strong influence on stochastic model orbits and thereby provide means for explaining and predicting observed patterns in data orbits.

In addition to stochasticity, another general point that should be taken into account with regard to the effects of nonlinearity is that parameter estimates for models necessarily come with confidence intervals. If a particular dynamical property of a validated model is robust throughout these confidence intervals, then it is not unreasonable to assert that a data orbit has this property. However, in some situations this is not the case and such an assertion becomes problematic. For example, as pointed out above, deterministic model chaotic attractors can be "densely" embedded with other attractor types throughout confidence intervals. In this case it does not seem reasonable to ask whether a particular set of data is or is not chaotic. A data orbit may be greatly influenced by chaotic invariant sets lying within the parameter confidence intervals (even when they are unstable), but they may also be greatly influenced by other non-chaotic types of invariant sets (especially in view of stochasticity).

We are excited by the opportunities provided by nonlinear theory and mathematical modeling in ecology. A stimulating interplay can occur between mathematical modeling and biological experimentation in population biology, an interplay in which mathematical analysis provides not only quantitative descriptions and explanations of observed dynamical phenomena, but suggests new biological hypotheses and experiments. However, more strong interdisciplinary studies are needed in which mathematical models survive experimental challenges as

scientific hypotheses. Successful efforts in this direction will help establish the confidence necessary to make mathematical modeling a serious predictive tool in ecology.

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