

An interdisciplinary approach to understanding nonlinear ecological dynamics

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Abstract

We describe a research program which covers a spectrum of activities essential to testing nonlinear population theory: from the translation of the biology into the formal language of mathematics, to the analysis of mathematical models, to the development and application of statistical techniques for the analysis of data, to the design and implementation of biological experiments. The statistical analyses, mathematics, and biology are thoroughly integrated. We review several aspects of our current research effort that demonstrate this integration.

Keywords: Bifurcation; Chaos; Insects; Nonlinear dynamics; Stability; Statistical models

1. Interdisciplinary approach

Nonlinear population theory remains controversial 20 years after its modern revival, primarily because experimental evidence for dynamic behaviors such as periodic cycles, aperiodic orbits, multiple attractors, unstable equilibria with stable and unstable manifolds, chaos, and strange attractors is meager (May, 1974; Strong, 1986; Kareiva, 1989; Bartlett, 1990; Logan and Hain, 1991; Costantino and Desharnais, 1991; Logan and Allen, 1992; Hastings et al., 1993). There is a need for new experiments. Our approach is an interdisciplinary research program that spans the activities that are essential to testing nonlinear population theory: from the initial transla-

tion of the biology into the formal language of mathematics, to the analysis of mathematical models, to the development and application of statistical techniques for the analysis of data and model evaluation, to the design and implementation of biological experiments. We begin with a brief description of each part of the program.

Empirical ecologists are continuously refining field and laboratory systems into effective tools of discovery (Hairston, 1989). One such laboratory system, with a long tradition of successful collaboration between experimentalists and theoreticians, is the flour beetle *Tribolium* (Costantino and Desharnais, 1991). Building on existing biological information (Neyman et al., 1956; King and Dawson, 1972; Mertz, 1972; Sokoloff, 1972, 1974, 1977; Bell, 1982), we can write mathematical models for the dynamics of populations with discrete or overlapping genera-

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tions. The larval–pupal–adult (overlapping generations) model of population growth includes three nonlinear intraspecific density-regulating interactions. Cannibalism is the key nonlinear biological process (Chapman, 1928; Park et al., 1970, p. 183). Whatever model is chosen, the translation of the biology into the mathematics must be meaningful; the model must work.

Mathematical ecologists are proficient at formulating growth models and deducing their dynamic behaviors (Freedman, 1980; Guckenheimer and Holmes, 1983; Cushing, 1988). Our approach continues in this tradition, but with a slight modification. We derive demographic dynamical models which are based on the biology of a laboratory animal model with identified intraspecific density-regulating mechanisms. The dynamics of these models are examined mathematically and numerically. This involves an analysis of equilibrium states and their stability, a study of cycles, including periodic cycles, Hopf bifurcations to invariant loops, and an investigation of chaotic dynamics and strange attractors. Knowledge of the kinds of bifurcations that can occur as a function of experimentally controlled model parameters joins the model with the conduct of the biological experiments.

Statistically, the problem of interfacing model with data amounts to specifying a likelihood function. This function gives the probability, under some proposed stochastic mechanism, that the random outcome would be the observed time series. With a likelihood function in hand, development of statistical inference methods (parameter estimation, hypothesis testing, model evaluation, forecasting) is in theory a straightforward, though possibly computationally intensive, process (Stuart and Ord, 1991). The model must include a probabilistic portion that specifies how the variability in the data arose. Converting the deterministic equations to stochastic equations provides an explicit likelihood function.

Experiments provide the data necessary for a rigorous test of the theory. The time series for a particular population is a stochastic realization and as such can be used in the statistical procedures for parameter estimation, hypothesis testing, and model evaluation. While mundane, the well-established *Tribolium* laboratory procedures for culture conditions, media preparation, animal censusing, etc. all con-

tribute to a flexible experimental system which permits a wide array of ecological manipulations.

2. Transitions in dynamic behavior

One of our objectives is to document experimentally transitions between qualitatively different dynamical behaviors as predicted by the deterministic model. The idea is to manipulate biological parameters such as the rates of reproduction and adult and larval mortalities in order to move populations across stability boundaries in parameter space and hence from one dynamic behavior to another, for example, from stable equilibria, to periodic cycles, to chaos. We proceed in two phases.

2.1. Model identification and parameter estimation

The initial research phase for the study of transitions is two-fold: model identification and parameter estimation. Explicit connections between biologically meaningful models and carefully collected data are critical. To locate reliably populations in parameter space, statistical methods for point and interval estimation of parameters, as well as for model evaluation, are essential. With the model and parameter estimates in hand, we can calculate a map of parameter space which delimits regions whose boundaries indicate changes in dynamic behavior. We can also compute a bifurcation diagram.

2.2. Documenting transitions experimentally

A bifurcation diagram summarizes the transitions in the dynamical behavior of a model as a function of its parameter values. The qualitative changes or bifurcations that occur in a mathematical model are the guide posts in the design of the biological experiments: laboratory protocol corresponds to the bifurcation diagram. The values of the experimentally controlled parameters are determined by the model and are chosen to place the populations in regions of equilibria, cycles, invariant loops, and chaos. We then compare the observed dynamic behavior of the experimental populations (time series data) under the various values of the controlled parameters to that predicted by the theoretical model.

We look at two types of life histories to do this comparative population dynamic research: discrete and overlapping generations. Different models are appropriate for these biological circumstances; nevertheless, each involves model identification and parameter estimation as a first step before attempting to document transitions in dynamic behavior experimentally.

3. Discrete generation experiments

The simplest mathematical models used for the dynamics of populations with discrete generations utilize difference equations of the form $N_{t+1} = bN_t f(N_t)$. This equation determines how the density N_t of, say, adults in one generation determines the density N_{t+1} of adults in the next generation. The so called 'density regulation factor' $f(N)$ must be prescribed in such a way as to reflect the basic biology (fertility, mortality, and growth rates) of the particular species being described.

3.1. Model identification

A large number of functional forms for $f(N)$ have been used in the literature (e.g., May and Oster, 1976). This is true even for models attempting to describe *Tribolium* dynamics (Costantino and Desharnais, 1991). Generally speaking, it is widely accepted that, at least for large densities, the function $f(N)$ should be a decreasing function of N , expressing the fact that density regulation implies that an increase in the current generation should result in a decrease in the next generation. For low densities, however, a population may experience the opposite effect, in which $f(N)$ increases with N . There is evidence that populations of *Tribolium* can exhibit this so called 'Allee effect' (Allee, 1931; for a recent discussion see Dennis, 1989).

A commonly used density function is $f(N) = \exp(-cN)$, $c > 0$ (Ricker, 1954). In this interpretation b is the net reproductive rate, i.e., the number of adult offspring produced per parent per unit time, and c is a measure of density-dependent regulation (e.g., cannibalism, intraspecific interactions, etc.).

The modification $f(N) = \gamma N^{\alpha-1} \exp(-cN)$ allows for an Allee effect when $\alpha > 1$. For models like this,

$$N_{t+1} = \beta N_t^\alpha \exp(-cN_t) \quad (1)$$

($\beta = b\gamma$) in which the graph of the right hand side $bNf(N)$ has 'one hump,' there is a great deal known about the asymptotic dynamics. Typically there is a period doubling cascade to chaos as b is increased, with bifurcations occurring at calculable critical points.

One stochastic version of the difference equation model is particularly promising. At the population sizes typical of flour beetle cultures, we expect the variability component due to environmental fluctuations to outweigh the component due to demographic fluctuations (Costantino and Desharnais, 1981; Dennis and Patil, 1984; Dennis and Costantino, 1988; Desharnais et al., 1990). One characteristic of models with environmental variability seems to be that noise is additive on a logarithmic scale (Dennis et al., 1991). Applying this notion to the above model we write

$$N_{t+1} = \beta N_t^\alpha \exp(-cN_t + E_t) \quad (2)$$

where E_t has a normal $(0, \sigma^2)$ distribution, and E_0, E_1, E_2, \dots are uncorrelated. This construction preserves the deterministic model as the conditional mean of $\ln N_{t+1}$ given a particular value of N_t .

3.2. Parameter estimation

Beetles are cultured so as to mimic a species with a fixed breeding interval and nonoverlapping generations. Adults are placed in fresh flour media and allowed to oviposit for a fixed period of time which we call the breeding interval. At the end of the breeding interval adults are removed and the media with eggs returned to vials. After 6 weeks the flour is sifted and the next generation of adults is counted. The immatures which do not reach adulthood are discarded. The new adults are placed in fresh flour to initiate another generation.

A pilot study reveals the potential of this discrete-generation protocol for studying nonlinear dynamics. A fixed number of adults of the sooty strain of *T. castaneum* was placed into 120 ml glass vials containing 20 g of media. Adult densities ranged from 4, 8, 12, ..., 100 for a total of 25 treatments.

Each initial adult density was replicated twice. After a breeding interval of 7 days, adults were removed and the offspring allowed to develop for an additional 5 weeks.

The data (Fig. 1a) are the experimental equivalent of a one-dimensional map of the adult population in two consecutive generations. These results suggest a one-humped curve as discussed above. To locate this experimental system in the continuum of dynamical behaviors, we fit the model to the data by calculating maximum likelihood (ML) estimates for the parameters in Eq. 2. The ML parameter estimates are $\beta = 10.76$, $\alpha = 1.684$, and $c = 0.07636$. These estimates are represented by the smooth curve in Fig. 1a.

3.3. Documenting transitions experimentally

Using β as a bifurcation parameter and fixing the parameters α and c at their estimated values we constructed the bifurcation diagram in Fig. 1b. The estimated value of $\beta = 10.76$ places the population well into the range of the model's chaotic behavior. We are now ready to put the experimental system to the test.

By experimentally manipulating the breeding interval we have a way to alter the rate of reproduction per generation which is the bifurcation parameter β . Short breeding intervals lead to lower values of β . Since the pilot study described above with a breeding interval of 7 days predicts chaotic dynamics, shorter breeding intervals are forecast to cover the entire sequence of dynamical behavior from stable

equilibria, through period-doublings, to chaos. Such experiments are currently underway in our laboratories.

Long-term time series data on populations placed experimentally where the model predicts different dynamic behaviors provides the test of the model-predicted dynamics. To minimize transient behavior, initial conditions are set near a predicted attractor. The rigorous statistical verification of the experimentally designed shifts in dynamical behavior is the evidence for the role of nonlinear mathematics in population biology.

4. Overlapping generation experiments

In order to account adequately for the population dynamics in the case of overlapping generations, 'structured' models are required, i.e., models that include the dynamics of different life cycle stages (or groupings of stages). The methodology for developing such models in discrete time using systems of coupled nonlinear difference equations (or nonlinear matrix equations) is now well developed (Cushing, 1988; Caswell, 1989).

4.1. Model identification

Since we have information about the biology of flour beetle population growth, we can deduce the form of the functional relationship linking the values of larval, pupal and adult numbers at time $t + 1$ to

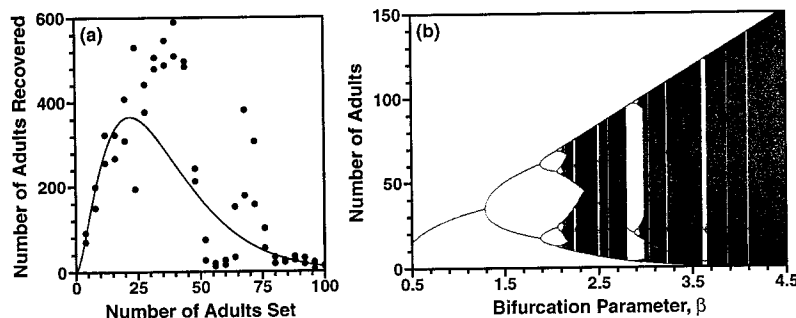


Fig. 1. Results for the pilot study of the discrete generation model. In panel (a) the number of *Tribolium* adults recovered are plotted against the number of adults set. The smooth curve is the Eq. (1) fit by the methods of nonlinear least squares. Panel (b) is a bifurcation diagram for populations based on Eq. (1) with β as the bifurcation parameter. The remaining parameters were set equal to their estimated values. The estimated value of $\beta = 10.76$ places the populations well into the chaotic region.

the number of animals at time t . The model is mechanistic and is to be contrasted to empirical models in which it is assumed that the relationship between animal numbers at times t and $t + 1$ is smooth and can be locally approximated by an interpolation function such as a polynomial. The larval–pupal–adult (LPA) model is a system of three difference equations:

$$L_{t+1} = bA_t \exp(-c_{ca}A_t - c_{el}L_t), \tag{3a}$$

$$P_{t+1} = L_t(1 - \mu_l), \tag{3b}$$

$$A_{t+1} = P_t \exp(-c_{pa}A_t) + A_t(1 - \mu_a). \tag{3c}$$

Here, L_t , P_t , and A_t are the number of feeding larvae, pupae and non-feeding larvae, and adults, respectively, at time t ; the unit of time is taken to be the feeding larval maturation interval so that after one unit of time a larva either dies or survives and pupates. This unit of time is also the cumulative time spent as a non-feeding larva, pupa and callow. The quantity $\beta > 0$ is the number of larval recruits per adult per unit of time in the absence of cannibalism. The fractions μ_l and μ_a are the larval and adult probabilities, respectively, of dying from causes other than cannibalism. The exponential nonlinearities account for the cannibalism of eggs by both larvae and adults and the cannibalism of pupae by adults. The fractions $\exp(-c_{ca}A_t)$ and $\exp(-c_{el}L_t)$ are the probabilities that an egg is not eaten in the presence of A_t adults and L_t larvae. Cannibalism of larvae by adults and of pupae and callows by larvae typically occurs at much reduced rates and is assumed negligible in the model. The fraction $\exp(-c_{pa}A_t)$ is the survival probability of a pupa in the presence of A_t adults. The coefficients c_{ca} , c_{el} , and $c_{pa} > 0$ determine the strength of the cannibalism and are called the ‘cannibalism coefficients.’ It is assumed here that the only significant source of pupal mortality is adult cannibalism.

Adding noise on a logarithmic scale produces the following stochastic model:

$$L_{t+1} = bA_t \exp(-c_{ca}A_t - c_{el}L_t + E_{1t}), \tag{4a}$$

$$P_{t+1} = L_t(1 - \mu_l) \exp(E_{2t}), \tag{4b}$$

$$A_{t+1} = [P_t \exp(-c_{pa}A_t) + A_t(1 - \mu_a)] \exp(E_{3t}) \tag{4c}$$

Here $[E_{1t}, E_{2t}, E_{3t}] = E_t$ is a random vector and is assumed to have a trivariate normal distribution with a mean vector of $\mathbf{0}$ and a variance–covariance matrix of Σ . Covariances among E_{1t} , E_{2t} , and E_{3t} at any given time t are assumed (and represented by off-diagonal elements of Σ), but we expect the covariances between times to be small by comparison. Thus we assume that E_0, E_1, \dots are uncorrelated.

The dynamical properties of the deterministic model are preserved in the stochastic formulation as conditional expected values:

$$E(\ln L_{t+1} | L_t = l_t, P_t = p_t, A_t = a_t) = \ln[ba_t \exp(-c_{ca}a_t - c_{el}l_t)], \tag{5a}$$

$$E(\ln P_{t+1} | L_t = l_t, P_t = p_t, A_t = a_t) = \ln[(1 - \mu_l)l_t]. \tag{5b}$$

$$E(\ln A_{t+1} | L_t = l_t, P_t = p_t, A_t = a_t) = \ln[p_t \exp(-c_{pa}a_t) + (1 - \mu_a)a_t]. \tag{5c}$$

Here is the explicit connection between the mathematical population model and the population time series data: one-step forecasts. Given the number of larvae, pupae, and adults at time t , we can predict the expected number of animals in each life stage at time $t + 1$ (2 weeks later). The working mathematical model is stochastic and the connection between model and data is by one-step forecasts using the deterministic model, not by continued iteration.

4.2. Locating populations in parameter space

The experimental culture conditions are set to mimic overlapping generations. For example, in a study by Desharnais and Costantino (1980) and Desharnais and Liu (1987), cultures of the corn oil sensitive strain of *T. castaneum* were initiated with 64 young adults, 16 pupae, 20 large larvae, and 70 small larvae. Each population was contained in a half-pint milk bottle with 20 g of corn oil media. Every 2 weeks all age-classes, except eggs, were censused and all age-classes, including eggs, were placed in fresh media. This procedure was repeated for 38 weeks.

We fitted the stochastic model (Eqs. 4a, 4b and 4c) to the time series. The maximum likelihood estimates and their 95% confidence intervals are

$b = 11.6772$ (6.2, 22.2), $\mu_a = 0.1108$ (0.07, 0.15), $\mu_1 = 0.5129$ (0.43, 0.58), $c_{ea} = 0.0110$ (0.0040, 0.0180), $c_{el} = 0.0093$ (0.0081, 0.0105), $c_{pa} = 0.0178$ (0.0154, 0.0207). Details of the statistical methods such as the likelihood function, maximum likelihood and conditional least squares estimates, hypothesis testing, confidence intervals, and model evaluation are given in Dennis et al. (1995).

The observed time series for two representative replicates together with the one-step predictions, calculated from Eqs. 5a, 5b and 5c are graphed in Fig. 2 and Fig. 3. In each figure solid lines connect the observed census data (closed circles). Dashed lines connect the observed numbers at time t with the forecast (open circles) at time $t + 1$. The accuracy of a particular forecast can be judged by comparing the predictions at time $t + 1$ with the number of animals actually observed at time $t + 1$. In general, the graphs

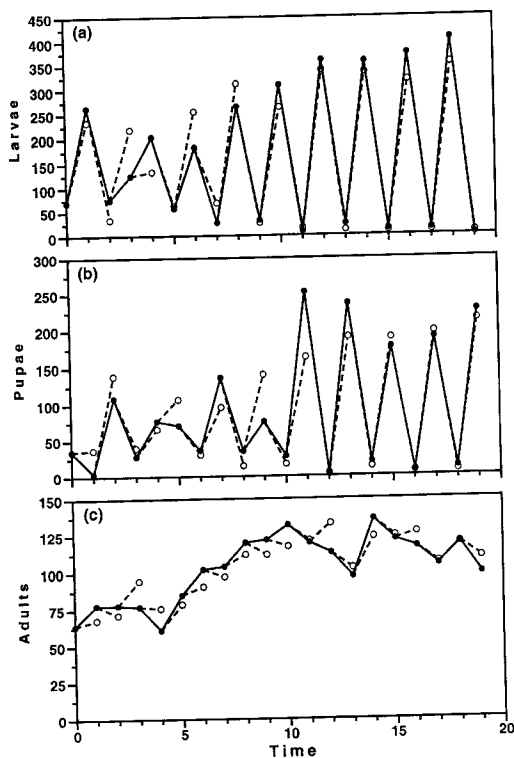


Fig. 2. Time series data (closed circles) and one-step forecasts (open circles) for control replicate A of Desharnais and Costantino (1980). Solid lines connect the observed census data. Dashed lines connect the observed numbers at time t with the forecast at time $t + 1$.

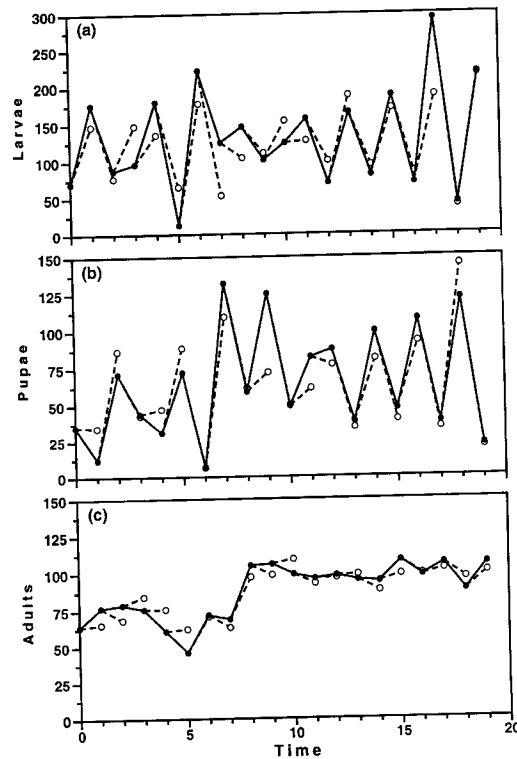


Fig. 3. Time series data (closed circles) and one-step forecasts (open circles) for control replicate C of Desharnais and Costantino (1980). Solid lines connect the observed census data. Dashed lines connect the observed numbers at time t with the forecast at time $t + 1$.

reveal a close association between the one-step forecasts and the census data. The model appears to work.

A numerically calculated stability region is shown in Fig. 4 using the parameter values estimated from the laboratory data. The positive equilibrium destabilization boundaries are of two types. There is a boundary at which a bifurcation to a branch of 2-cycle solutions occurs, and there is a boundary at which a bifurcation to an invariant loop occurs. The maximum likelihood (ML) parameter estimates place the system in a zone of stable 2-cycles (asterisk, Fig. 4). The ML location of the system in parameter space is a point estimate; how much uncertainty is attached to the estimate? Depicted in Fig. 4 is a dashed, cigar-shaped closed curve representing a 95% confidence region for the parameters b and μ_a . The region was calculated with the profile likelihood

method. The dashed curve is a contour indicating where the likelihood ratio test statistic for the two parameters equals 5.992 (the approximate 95th percentile of a chi-squared distribution with two degrees of freedom). Note that most of the confidence region lies within the zone of 2-cycles. However, the tip of the region does extend into the zone of stable point equilibria, in an area where the system undergoes damped oscillations.

4.3. Bifurcation theory leads to new experiments

Using μ_a as a bifurcation parameter we can identify the expected dynamical behaviors as a function of adult mortality (Fig. 5). For very small values of μ_a there is a stable fixed point. The first bifurcation leads to stable 2-cycles. There follows a point equilibrium region that forms a transition between the 2-cycles and the onset of invariant loops.

In an experiment currently in progress, we are systematically varying the value of μ_a in replicate populations by removing/adding adults as necessary at the biweekly census. Each treatment involves a different value of adult mortality; these values are chosen to place populations in different regions of model predicted dynamic behaviors. We are using μ_a values of control (no manipulation), 0.04, 0.27, 0.50, 0.73, and 0.96 with 4 replicates per treatment.

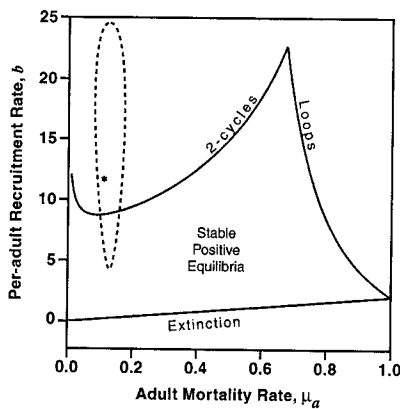


Fig. 4. Stability boundaries for the LPA model for parameter values based on the experimental data (see text). The asterisk locates the estimated values of $b = 11.67$ and $\mu_a = 0.1108$. The elongated closed curve (dashed line) represents a 95% joint confidence region for b and μ_a based on the profile likelihood.

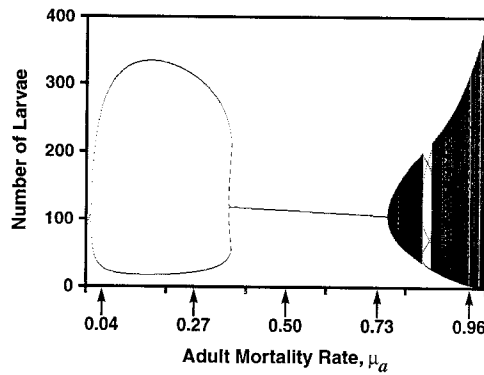


Fig. 5. Bifurcation diagram for the LPA model for parameter values based on the experimental data. There is a bifurcation to a 2-cycle at a small value of $\mu_a = 0.011$. As the bifurcation parameter μ_a increases, the population re-enters the region of parameter space where the positive equilibria are stable (see Fig. 4). However, there is a narrow interval $0.357 < \mu_a < 0.363$ where a stable 2-cycle and a fixed point equilibria coexist, separated by an unstable 2-cycle (dashed lines). For large values of μ_a , the population crosses the equilibrium stability boundary where stable invariant loops bifurcate from the equilibria.

Census data are collected on a biweekly basis for the number of live adults, dead adults, larvae, and pupae for a total of 36 weeks. We classify the dynamical behavior of these populations under the various treatments and compare the observed dynamical behavior to that predicted by theoretical models.

5. Stable and unstable manifolds

In the two experiments described above, we are attempting to manipulate the rate of reproduction and adult mortality in order to move populations across boundaries in parameter space and hence from one dynamic behavior to another. But just as we are using two life histories to test robustly the predictions of bifurcation theory, other subtle dynamic behaviors arise that also may be used to identify the role of nonlinearity in ecology. We now discuss one such example: an unstable equilibrium with stable and unstable manifolds.

For the estimated parameter values, the LPA model equations (Eqs. 3a, 3b and 3c) have a stable 2-cycle given by the (larval, pupal, adult) coordinate points (325, 9, 118) and (18, 158, 106). There is also

a unique positive (unstable) equilibrium $L^* = 125$, $P^* = 61$, $A^* = 97$. In order to understand the model orbits in a neighborhood of this equilibrium we need to evaluate the Jacobian matrix of the map defined by the right hand sides of the model equations at (L^*, P^*, A^*) and compute the eigenvalues and eigenvectors associated with the resulting 3×3 matrix. Leaving the details of these computations aside, we find there exists a two dimensional (adult–pupal) stable manifold and a one dimensional (larval) unstable manifold. By ‘stable’ we mean that if an orbit defined by the nonlinear model equations has a point on this manifold, then it will tend towards the unstable equilibrium (L^*, P^*, A^*) . If an orbit has a point close to this stable manifold, then it will first tend towards the unstable equilibrium before moving away (in an oscillatory manner) in the direction of the unstable manifold.

The identification and characterization of a saddle node in the LPA model (Eqs. 3a, 3b and 3c) adds a new subtlety to the biological interpretation of the time series: there are many routes to the asymptotically stable attractor. Populations may move to the 2-cycle quickly and directly with little hint of the existence of the saddle node. In another approach, populations may move along the 2-dimensional adult–pupal stable manifold toward the unstable equilibrium then move along the 1-dimensional larval unstable manifold to the stable 2-cycle. Are these theoretically possible transitory behaviors recorded in the data?

The time series for replicates A and C are presented in Fig. 2 and Fig. 3. The one-step forecasts clearly show the ability of the model to accommodate both replicates. Statistical tests lead us to accept the hypothesis that the model parameters for these two replicates are the same (Dennis et al., 1995). The saddle node hypothesis suggests that these replicates took different paths to the asymptotic attractor: replicate A moved to the 2-cycle quickly while replicate C was influenced by the stable and unstable manifolds of the unstable equilibrium.

To illustrate the impact of the saddle node on the transitory behavior of the populations we return to the deterministic model. In the simulations (Fig. 6), the initial coordinates of the two examples correspond to the observed animal numbers for replicates A and C at $t = 7$. With $L_0 = 27$, $P_0 = 136$, $A_0 = 104$

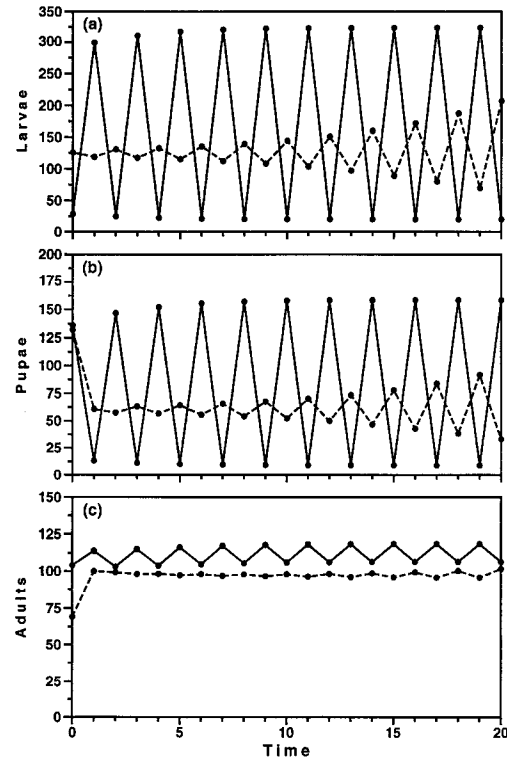


Fig. 6. Deterministic model time series initiated at $L_0 = 27$, $P_0 = 136$, $A_0 = 104$ (solid line) and $L_0 = 125$, $P_0 = 132$, $A_0 = 69$ (broken line) which correspond to the observed coordinates at $t = 7$ for replicates A and C, respectively.

(replicate A at $t = 7$) the orbit moves quickly to the 2-cycle as noted in the data. Setting $L_0 = 125$, $P_0 = 132$, $A_0 = 69$ (replicate C at $t = 7$), the orbit hovers about the unstable equilibrium which is consistent with the data.

6. Concluding remarks

The modern theory of nonlinear dynamics coupled with rigorous statistical methods can guide the conduct of a new phase of population research. Research in which experiments focus on transitions in dynamic behavior, unstable equilibria with stable and unstable manifolds, multiple attractors, chaos or on any number of other properties of nonlinear systems will provide the evidence for the role of nonlinear mathematics in population ecology.

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