Ecology Letters, (2001) **4**: 229–235

REPORT

Chaos and population control of insect outbreaks

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Abstract

We used small perturbations in adult numbers to control large fluctuations in the chaotic demographic dynamics of laboratory populations of the flour beetle *Tribolium castaneum*. A nonlinear mathematical model was used to identify a sensitive region of phase space where the addition of a few adult insects would result in a dampening of the life stage fluctuations. Three experimental treatments were applied: one in which perturbations were made whenever the populations were inside the sensitive region ("in-box treatment"), another where perturbations were made whenever the populations were outside the sensitive region ("out-box treatment"), and an unperturbed control. The in-box treatment caused a stabilization of insect densities at numbers well below the peak values exhibited by the out-box and control populations. This study demonstrates how small perturbations can be used to influence the chaotic dynamics of an ecological system.

Keywords

Chaos, nonlinear population dynamics, population control, phase space, population perturbations, ecological sensitivity, flour beetles, *Tribolium*.

Ecology Letters (2001) 4: 229–235

INTRODUCTION

Sensitivity to initial conditions is a key characteristic of chaos. This has led to suggestions on how small perturbations might be used to influence the dynamics of chaotic systems (e.g. Shinbrot *et al.* 1993; Ott *et al.* 1994; Kapitaniak 1996). One idea is to "nudge" the parameters or state variables at points in the trajectory where the system is sensitive to changes, producing a large desired effect from small perturbations. This approach has been demonstrated in a variety of physical and chemical systems (Ditto *et al.* 1990; Hunt 1991; Singer *et al.* 1991; Gills *et al.* 1992; Petrov *et al.* 1993) and *in vitro* experiments on myocardial (Garfinkel *et al.* 1992) and brain tissues (Schiff *et al.* 1994). There have been discussions about using this method for population control in ecology (Doebeli 1993; Hawkins & Cornell 1999; Shulenburger *et al.* 1999; Solé *et al.* 1999), but no test of the procedures. In the present study, we apply this technique to laboratory populations of the flour beetle *Tribolium castaneum*, and show how small demographic perturbations can be used to dampen large chaotic fluctuations in the densities of the life stages.

MATHEMATICAL MODEL

Previous work (Dennis *et al.* 1995, 1997, 2001; Costantino *et al.* 1995, 1997; Cushing *et al.* 1996, 1998) has shown that changes in the densities of flour beetle life stages in laboratory cultures can be predicted accurately using a system of three deterministic difference equations known as the "LPA" model. The numbers of animals at time t are related to the number of animals at time $t-1$ using

$$
\begin{aligned}
L_t &= b\,A_{t-1}\exp(-c_{\mathrm{EL}}\,L_{t-1}-c_{\mathrm{EA}}\,A_{t-1}),\\
P_t &= L_{t-1}\,(1-\mu_{\mathrm{L}}),\\
A_t &= P_{t-1}\exp(-c_{\mathrm{PA}}\,A_{t-1})+A_{t-1}\,(1-\mu_{\mathrm{A}}),
\end{aligned}
\tag{1}
$$

where L_t is the number of feeding larvae, P_t is the number of large nonfeeding larvae, pupae and callow adults, and A_t is the number of sexually mature adults at time t. The unit of time is two weeks and is, approximately, the amount of time spent in the feeding larval stage under our experimental conditions. The unit of time is also, approximately, the duration of the P-stage. The quantity b 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 rates of mortality in one time unit. The exponential nonlinearities account for the cannibalism of eggs by both larvae and adults and the cannibalism of pupae by adults. The fractions $\exp(-c_{\mathrm{EL}}\ L_{t-1})$ and $\exp(-c_{\mathrm{EA}}\ A_{t-1})$ are the probabilities that an egg is not eaten in the presence of L_{t-1} larvae and A_{t-1} adults in one time unit. The fraction $\exp(-c_{\mathrm{PA}}\ A_{t-1})$ is the survival probability of a pupa in the presence of A_{t-1} adults in one time unit.

For a range of parameter values that are attainable through flour beetle husbandry techniques, the model (1) predicts a variety of dynamical behaviours from stable equilibria, to "quasiperiodic" oscillations, to chaotic oscillations, to periodic cycles. These behaviours have been demonstrated experimentally (Costantino *et al.* 1997). In particular, populations have been shown to exhibit fluctuations around a chaotic attractor (Costantino *et al.* 1997; Dennis *et al.* in press; Cushing *et al.* 2001).

HOT REGION OF THE ATTRACTOR

The chaotic strange attractor predicted by the LPA model using previously derived parameter estimates (Dennis *et al.* in press) has regions of differing sensitivities to initial conditions (Fig. 1a). For each of 2000 points on the attractor we computed the three eigenvalues of the Jacobian matrix of the deterministic LPA model. Each point was coloured according to λ_t, the logarithm of largest modulus of the three eigenvalues: blue for negative values, orange for moderate positive values, and red for large positive values. These numbers, which ranged from -1.03 to 3.92, are the "local Liapunov exponents" for one step in the orbit (Bailey *et al.* 1997). They measure the effect of small perturbations on the population trajectory. Values of $\lambda_t > 0$ indicate regions of phase space where nearby trajectories diverge in the next time step; values of $\lambda_t < 0$ are regions where nearby trajectories converge. The red colour indicates a "hot" region of the attractor where larval and adult numbers are small and numbers of pupae are large. Small perturbations in this region can have a large effect on the population.

We followed closely orbits of simulated populations and noticed that differences of a few adults in the "hot region" of the attractor led to widely divergent trajectories. This led to the identification of two rules which we subsequently used as the experimental protocol. The first or "in-box" rule, which forecasts a reduction in larval numbers with small perturbations in the number of adult beetles, is as follows. If the life stage vector $[L_t, P_t, A_t]$ is such that $L_t \leqslant 150$ and $A_t \leqslant 3$ then three adults are added to the culture; otherwise no perturbation is made. We developed a second or "out-box" rule to demonstrate that it is the dynamics associated with the "hot spots" on the

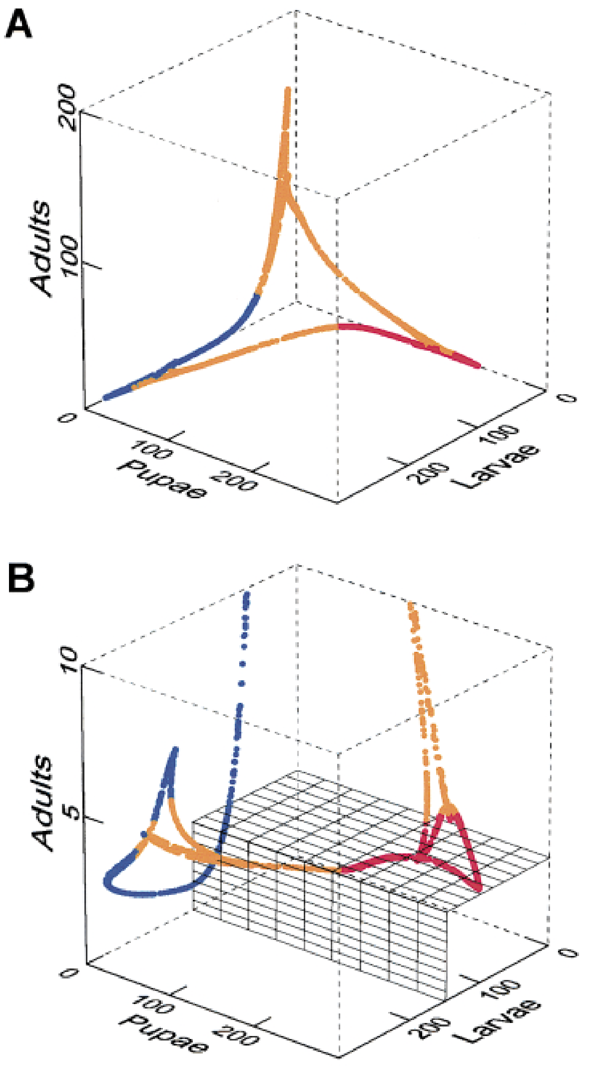

Figure 1 Chaotic attractor of the deterministic LPA model in phase space. The pictures were generated from 2000 iterations of the LPA model after the initial transients disappeared. The attractor is coloured according to λ_t, the logarithm of largest moduli of the three eigenvalues of the Jacobian matrix of the LPA model (1) evaluated at the point (L_t, P_t, A_t) using the following conditional least squares parameter estimates (Dennis *et al.* 2001): $b = 10.45$, $c_{\mathrm{EL}} = 0.01731$, $c_{\mathrm{EA}} = 0.01310$, $\mu_{\mathrm{L}} = 0.2000$, with $\mu_{\mathrm{A}} = 0.96$ and $c_{\mathrm{PA}} = 0.35$ both set experimentally. The colours range from blue for negative values ($\lambda_t < 0$), to orange for moderate values ($0 \leqslant \lambda_t \leqslant 3$), to red for large positive values ($\lambda_t > 3$). (A) The full attractor has "hot regions" (red) where the trajectories show strong divergence and "cold regions" (blue) where trajectories converge. (B) The axis scale for adult numbers is changed to magnify the base of the attractor. The grids show the boundary of the "in-box" and "out-box" regions used in the experimental design described in the text. The "hot spots" of the attractor fall mostly within this box.

chaotic attractor that are responsible for the reduction in larval numbers and not simply the fact that adults were added to the culture. Under this rule, if the life stage vector $[L_t, P_t, A_t]$ is such that $L_t > 150$ *or* $A_t > 3$ then three adults are added to the culture; otherwise no manipulation is made. The regions where the in-box and out-box perturbations are applied are represented in Fig. 1(B).

MATERIALS AND METHODS

We conducted an experimental evaluation of the predicted perturbation responses by establishing nine laboratory populations of the *RR* strain of the flour beetle *T. castaneum.* As in a previous study designed to demonstrate chaotic population dynamics (Costantino *et al.* 1997; Dennis *et al.* in press), we experimentally set the adult mortality rate at $\mu_A = 0.96$ and manipulated the adult recruitment rate so that it would equal $P_{t-1}\exp(-c_{PA}A_{t-1})$ with $c_{PA} = 0.35$. Each population was maintained in a half-pint (237 mL) milk bottle with 20 g of standard media and kept in a dark incubator at 32 °C. Every two weeks the larval, pupal and adult stages were counted and returned to fresh media, and dead adults were counted and removed. Adult mortality was set by removing or adding adults at the time of a census to make the fraction of adults that died during the interval equal to 0.96. Recruitment rates into the adult stage were manipulated by removing or adding young adults at the time of a census to make the number of new adult recruits consistent with the value of $c_{PA} = 0.35$. To counter the possibility of genetic changes in life-history characteristics, at every other census the adults returned to the population after the census were obtained from separate stock cultures maintained under standard laboratory conditions. Three of the populations formed an experimental control treatment where no perturbations were applied for the duration of the experiment. For the six remaining cultures, the above procedure was continued for 132 weeks; however, at week 134 and thereafter, in addition to manipulating μ_A and c_{PA}, we applied the in-box perturbation rule to three populations and the out-box rule to three populations until the termination of the experiment at week 210.

STOCHASTIC SIMULATIONS

Since noise is common to all ecological systems, even in the laboratory, the model-predicted time series were obtained using a stochastic LPA model. Realizations representing demographic stochasticity were obtained by adding random noise on a square root scale (Dennis *et al.* in press). Applying the square root transformation to equations (1–3) and adding noise, yields

$$\sqrt{L_t} = \sqrt{bA_{t-1}\exp(-c_{EL}L_{t-1} - c_{EA}A_{t-1})} + E_{1t}$$

$$\sqrt{P_t} = \sqrt{L_{t-1}(1-\mu_L)} + E_{2t}$$

$$\sqrt{A_t} = \sqrt{P_{t-1}\exp(-c_{PA}A_{t-1}) + A_{t-1}(1-\mu_A)} + E_{3t} \quad (2)$$

The terms $\mathbf{E}_t = [E_{1t}, E_{2t}, E_{3t}]'$ constitute a random noise vector assumed to have a joint normal probability distribution with a mean vector of zeros and a variance–covariance matrix denoted by Σ. The deterministic skeleton of the model (1) is obtained by setting $\Sigma = \mathbf{0}$, or equivalently, by letting E_{1t}, E_{2t}, and E_{3t} equal zero. The demographic nature of the stochasticity would stipulate that the noise variables are uncorrelated with each other within a time unit (off-diagonal elements of the matrix are zero) as well as uncorrelated through time. In a previous study using different data (Dennis *et al.* in press), the first two diagonal elements of Σ were estimated as $\sigma_{11} = 2.332$ and $\sigma_{22} = 0.2374$. We used these estimates in our simulations. Since both c_{PA} and μ_A were fixed experimentally, adult numbers followed (1); therefore, we set $E_{3t} = 0$. In rare cases when one of the equations gave a negative value in a simulation, the value for that life stage was set equal to zero.

RESULTS

Predicted and observed time series for larval numbers are shown in Fig. 2. The panels on the left side of the figure show realizations from the stochastic version of the LPA model (2) with parameters estimated from a previous study (Dennis *et al.* in press). The panels on the right side are for one representative replicate population from each of the three experimental treatments. Both the simulated and observed populations in the unperturbed control treatment (Fig. 2a,b) show large chaotic fluctuations in larval numbers similar to those observed in previous studies with flour beetles (Costantino *et al.* 1997; Dennis *et al.* in press). The in-box perturbations, which were designed to decrease the amplitude of the fluctuations in insect numbers, had the desired effect. The model and experimental populations in the in-box treatment exhibit large amplitude fluctuations prior to the in-box perturbations (blue symbols in Fig. 2c,d), but these oscillations dampened dramatically after the in-box perturbations were applied (red symbols in Fig. 2c,d). On the other hand, as predicted by the model, the out-box populations continued to exhibit large amplitude fluctuations in larval numbers before and after the out-box perturbations were applied (Fig. 2e,f). This was despite the fact that, in accordance with experimental protocol, the out-box perturbations were

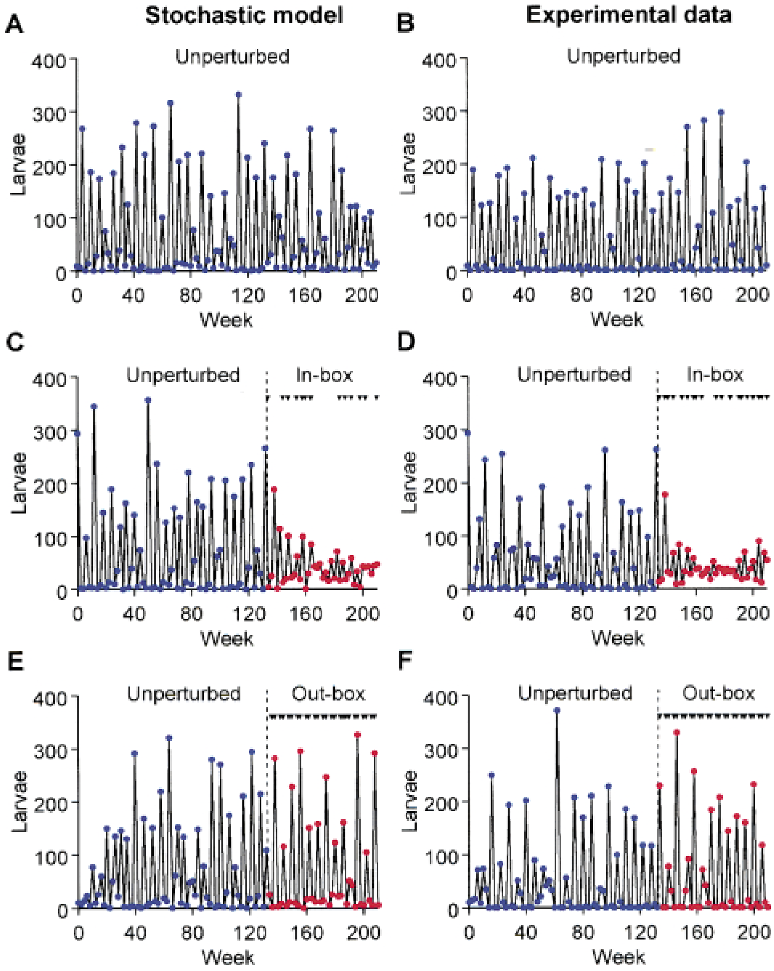

Figure 2 Time series plots of numbers of larvae for the stochastic model and experimental data. The simulations are from the stochastic LPA model (2) with the experimental initial conditions and the same parameter values as Fig. 1. The blue symbols are for the unperturbed populations; the red symbols are for data collected after the perturbation protocols were started at week 134 (dashed lines). The small inverted triangles indicate when the actual perturbations were applied. (A) A realization of the stochastic LPA model. (B) One of the replicate experimental populations from the control treatment group. (C) A realization of the stochastic LPA model using the in-box perturbation protocol. (D) One of the replicate experimental populations from the in-box treatment group. (E) A realization of the stochastic LPA model using the out-box perturbation protocol. (F) One of the replicate experimental populations from the out-box treatment group.

applied more often than the in-box perturbations (small triangles in Fig. 2). This demonstrates that the dampening effect of the in-box treatment was due to the timing of the perturbations to coincide with the occurrence of life stage numbers in a sensitive region of phase space (box in Fig. 1b).

Another perspective on this experiment is provided by viewing the data in phase space. Figure 3 shows plots of the data for all nine experimental populations and nine model populations simulated with the experimental initial conditions and protocols. To eliminate transient changes and emphasize the asymptotic dynamics, the first eight data points from the beginning of the experiment were eliminated for all populations (experimental and simulated), and the first eight data points following the start of the perturbation protocols were excluded for populations (experimental and simulated) in the in-box and out-box treatment groups. The data for the unperturbed experimental populations in the control treatment fill phase space in a pattern that is similar to that predicted by the stochastic LPA model (Fig. 3a,b). This pattern resembles a “fuzzy” version of the chaotic strange attractor predicted by the deterministic LPA model (Fig. 1a). This pattern is also observed in the simulation and experimental data prior to imposition of the in-box and out-box perturbation rules (blue symbols in Fig. 3c–f). However, the in-box perturbations caused the life stage densities to contract towards the origin as predicted by the model (red symbols in Fig. 3c,d). (The deterministic LPA model with the in-box protocol predicts another chaotic attractor with small amplitude fluctuations.) By contrast, the distribution of life stage densities following the out-box perturbations is similar to the distribution before the perturbations were imposed [red vs. blue symbols in Fig. 3e,f).

DISCUSSION

We emphasize that relatively small perturbations were used to obtain the large decrease in the amplitude of the

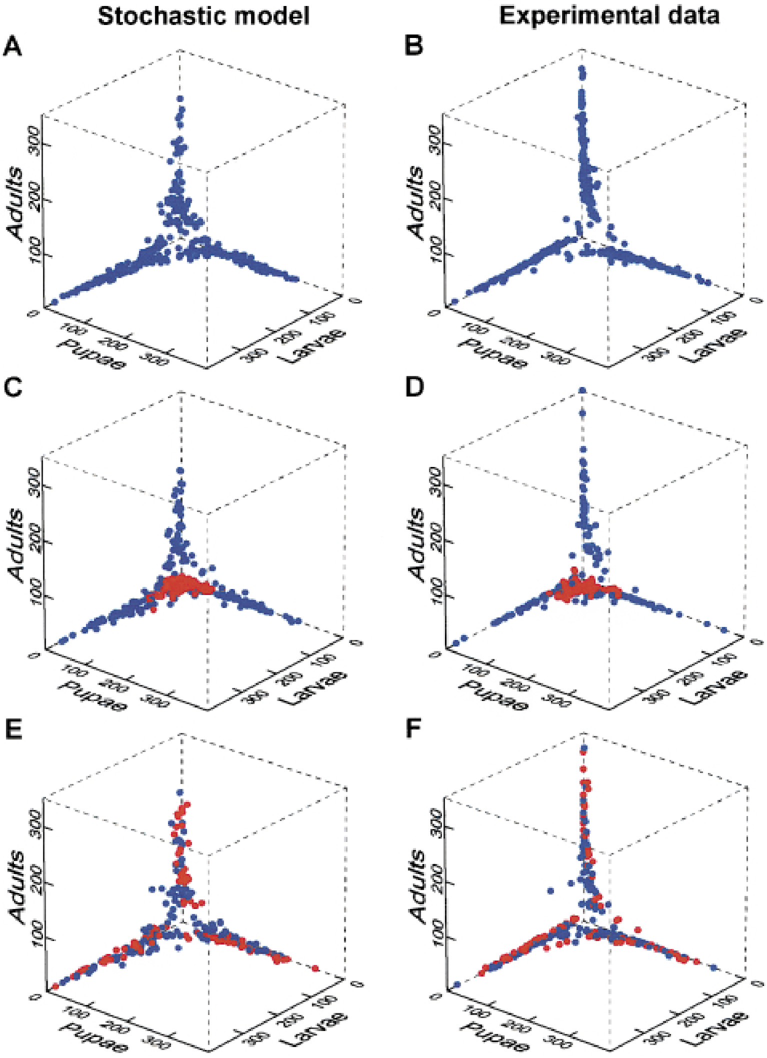

Figure 3 Phase space plots of numbers of larvae, pupae, and adults for the stochastic model and experimental data. The simulations are from the stochastic LPA model (2) with the same initial conditions, number of replicates, and number of census points as the experimental treatments and the same parameter values as Fig. 1. To de-emphasize the effects of transient changes, excluded from the plots are all simulated and observed data for weeks 0–14 and all simulated and observed data for weeks 134–148 in the in-box and out-box treatments. The blue symbols are for the unperturbed populations; the red symbols are for data collected after the perturbation protocols were started at week 134. (A) Data from three independent realizations of the stochastic LPA model. (B) Data from the three replicate experimental populations in the control treatment group. (C) Data from three independent realizations of the stochastic LPA model using the in-box perturbation protocol. (D) Data from the three replicate experimental populations in the in-box treatment group. (E) Data from three independent realizations of the stochastic LPA model using the out-box perturbation protocol. (F) Data from the three replicate experimental populations in the out-box treatment group.

fluctuations seen in the in-box populations. Over the period during which the treatment perturbations were applied (weeks 134–210), a total of 156 adults were added to the three experimental cultures in accordance with the in-box rule. During the same period we counted a total of 6545 adults in the three unperturbed control populations. Thus the perturbations represent only 2.4% of the number of adults we could have expected if the perturbations were not applied. Nevertheless, these in-box perturbations resulted in a 82.7% decrease in the number of adults and a 48.3% decrease in the total number of insects (adults + pupae + larvae) counted during this period relative to the unperturbed controls. By contrast, over the same period, we added a total of 234 adults to the out-box populations and obtained only a 4.3% decrease in the total number of adults and a 3.7% decrease in the total number of insects relative to the unperturbed controls.

The stochastic LPA model (2) was remarkably effective at predicting the dynamical behaviour of the experimental populations. Model simulations exhibited the same amplitude and general pattern of fluctuations as seen in the experimental data (Fig. 2). The model also predicted correctly the response of the experimental cultures to the in-box and out-box perturbations (Figs 2 and 3). This is particularly impressive considering that parameter values used here were obtained from a previous study (Dennis *et al.* in press) and were estimated using separate data; the model was not "fit" to the data from the current experiment.

We were able to use small perturbations of the state variables to influence the dynamics of the insect populations in our experimental study because the life stage numbers repeatedly entered a region of phase space where the dynamics are sensitive to change. According to the LPA model (1), a portion of the asymptotic attractor for this system occupies a sensitive region of phase space (Fig. 1). In general, this will be true if the attractor of a dynamical system is chaotic, since these attractors have a long-term sensitivity to initial conditions. However, a chaotic attractor is not a prerequisite for the use of small perturbations to influence dynamics. Portions of nonchaotic attractors, such as cycles and invariant loops, may also extend into sensitive regions of phase space where small perturbations can have large effects, even though the "averaged" motion on the attractor does not produce long-term sensitivity to initial conditions. By targeting perturbations to coincide with times when the system is in the sensitive region, small inputs can still produce large effects. For example, if we let $c_{PA} = 0.50$ in the deterministic LPA model, the attractor is a cycle of period three with large amplitude fluctuations (Dennis *et al.* in press) and one of the points of the three-cycle lies inside the "box" shown in Fig. 1(B). Numerical studies with the stochastic LPA model (2) suggest that the in-box experimental protocol would be highly effective in reducing the amplitudes of the fluctuations in this nonchaotic case.

Can small perturbations be used to influence the dynamics in real ecosystems? An answer to that question remains ahead of us. Here we have made the step from theoretical possibility to demonstration in the laboratory. The prerequisite for a similar approach to be effective in field populations is a good working model of the dynamics of the system which can be used to make accurate predictions. Such models will come from careful studies of the mechanisms that determine ecological change (Kendall *et al.* 1999; Perry *et al.* 2000; Turchin & Ellner 2000).

ACKNOWLEDGEMENTS

This research was supported, in part, by grants from the U.S. National Science Foundation (DMS 9616205, DMS 9625576, DMS 9973126, DMS 9981374, DMS 9981423, DMS 9981458) and an American Fellowship, American Association of University Women, to S.M.H.

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BIOSKETCH

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Editor, M. Hochberg
Manuscript received 16 November 2000
First decision made 28 December 2000
Manuscript accepted 12 February 2001