Experimentally induced transitions in the dynamic behaviour of insect populations

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SIMPLE nonlinear models can generate fixed points, periodic cycles and aperiodic oscillations in population abundance without any external environmental variation. Another familiar theoretical result is that shifts in demographic parameters (such as survival or fecundity) can move a population from one of these behaviours to another[1–4]. Unfortunately, empirical evidence to support these theoretical possibilities is scarce[5–15]. We report here a joint theoretical and experimental study to test the hypothesis that changes in demographic parameters cause predictable changes in the nature of population fluctuations. Specifically, we developed a simple

model describing population growth in the flour beetle *Tribolium*[16]. We then predicted, using standard mathematical techniques to analyse the model, that changes in adult mortality would produce substantial shifts in population dynamic behaviour. Finally, by experimentally manipulating the adult mortality rate we observed changes in the dynamics from stable fixed points to periodic cycles to aperiodic oscillations that corresponded to the transitions forecast by the mathematical model.

We modelled the relationship linking larval, pupal and adult numbers at time $t+1$ to the number of animals at time t in the flour beetle (see ref. 9). The model is a system of three difference equations:

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

Here, L_t is the number of feeding larvae, P_t is the number of non-feeding larvae, and pupae and callow adults, and A_t is the number of mature adults, at time t; the unit of time (2 weeks) 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 adult. The quantity $b>0$ 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. The fraction $\exp(-c_{pa}A_t)$ is the survival probability of a pupa in the presence of A_t adults.

For fitting to time-series data, the model was converted to a stochastic model with noise added on a logarithmic scale:

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

Here E_{1t}, E_{2t} and E_{3t} are random noise variables assumed to have a joint multivariate normal distribution with means of zero.

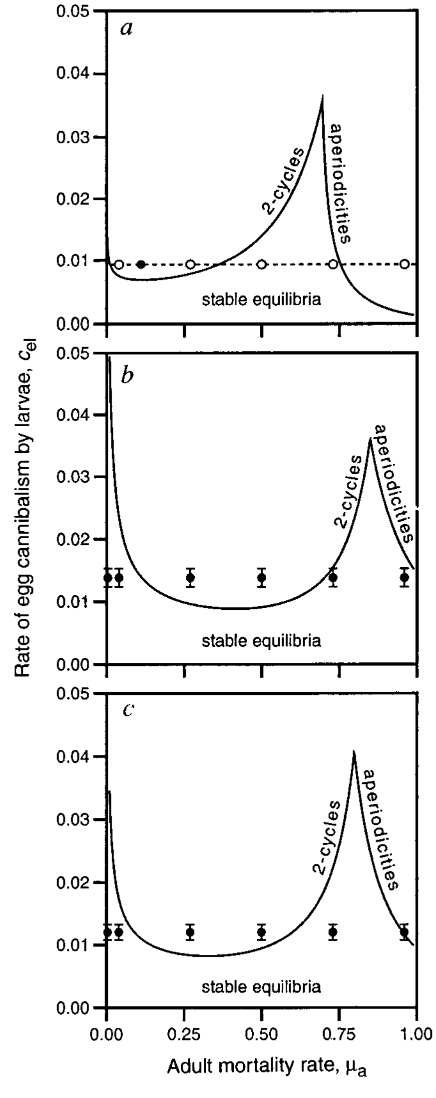

FIG. 1 Stability boundaries for the deterministic model (1) for three experiments. *a*, Sensitive strain[16] with $b=11.68$, $c_{ea}=0.011$, $c_{pa}=0.017$, $\mu_l=0.513$. The filled circle locates the population in parameter space. The broken line and open circles indicate the extrapolated predicted dynamic behaviour as a function of adult mortality. *b*, RR strain with $b=7.88$, $c_{ea}=0.011$, $c_{pa}=0.004$, $\mu_l=0.161$. *c*, SS strain with $b=7.48$, $c_{ea}=0.009$, $c_{pa}=0.004$, $\mu_l=0.267$. The filled circles locate the experimental populations in parameter space. In *b* and *c* the bar represents a 95% confidence interval for c_{el} based on the profile likelihood.

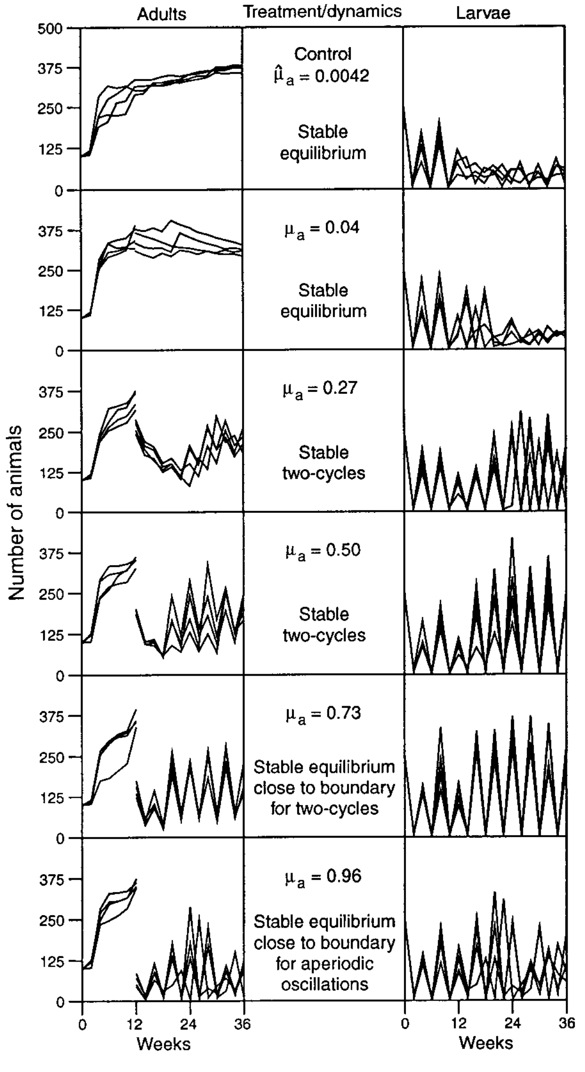

FIG. 2 Time-series data for individual replicates of the RR strain. At week 12 the experimental manipulation of adult mortality rate began. The centre column lists the imposed adult mortality rates and the location of the cultures in parameter space.

The noise variables represent the unpredictable departures of the observations from the deterministic model (1) due to environmental and other causes. Maximum-likelihood estimates of model parameters were calculated under the assumptions that the noise variables are correlated with each other but uncorrelated through time[16]. These assumptions were evaluated for all the data sets by standard diagnostic analyses of time-series residuals[17].

In the study reported here we experimentally set adult mortality rates at values suggested by the analysis of historical time-series data[16] (Fig. 1*a*) to place the experimental cultures in regions of different asymptotic dynamics: $\mu_a = 0.04$, 0.27, 0.50, 0.73 and 0.96. There were also control cultures which were not manipulated. Cultures of *T. castaneum* (24 for each of two genetic strains, RR and SS) were initiated with 100 young adults, 5 pupae and 250 small larvae. Each population was contained in a half-pint (237 ml) milk bottle with 20 g of standard media and kept in a dark incubator at 31 °C. Every two weeks the L_t, P_t, and A_t stages were censused and returned to fresh media. This procedure was continued for 36 weeks. At week 12, four populations of each genetic strain were randomly assigned to each of the six treatments, and the imposition of adult mortalities began. Adult mortality was manipulated by removing or adding adults at the time of a census to make the total number of adults that died during the interval consistent with the treatment value of μ_a. To counter the possibility of genetic changes in life-history characteristics, beginning at week 12 and continuing every month thereafter, the adults returned to the populations after the census were obtained from separate stock cultures maintained under standard laboratory conditions.

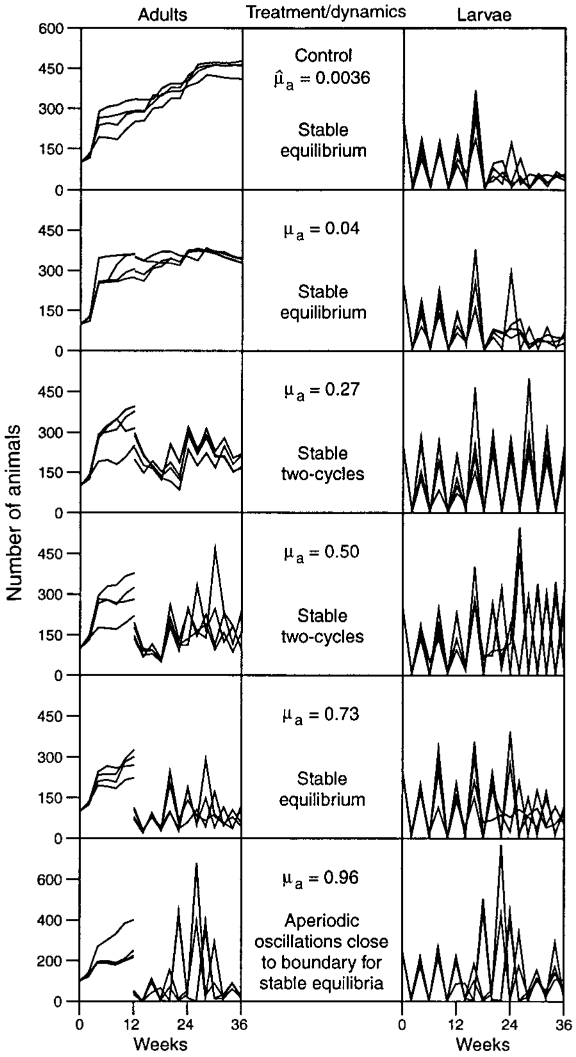

FIG. 3 Time-series data for individual replicates of the SS strain. At week 12 the experimental manipulation of adult mortality began. The centre column lists the imposed adult mortality rates and the location of the cultures in parameter space.

For each genetic strain the four replicates of each treatment were randomly assigned into two groups. With half of the data, we fitted model (2) to the time series of the RR (Fig. 2) and SS (Fig. 3) strains. The other half of the data were used for evaluating the model predictions. Analyses of time-series residuals[17] indicated that the stochastic model described the data quite well. Using the model and maximum-likelihood parameter estimates, based on the time series for weeks 12 to 36, we calculated the stability boundaries (Fig. 1*b*, *c*) and bifurcation diagrams (Fig. 4) for each genetic strain.

The parameter estimates placed the control and $\mu_a = 0.04$ treatments in the region of stable equilibria. In the $\mu_a = 0.27$ treatment there was a transition in the dynamics: regular, albeit small, fluctuations were found in the adult data, whereas large and sustained oscillations were noted in larval numbers. These populations were located in the two-cycle zone. At $\mu_a = 0.50$ both strains were in the two-cycle region and displayed sustained oscillations, most noticeably in larval numbers. With $\mu_a = 0.73$ the RR strain was close to the two-cycle boundary but the SS strain underwent another transition and was clearly in the region of stable equilibria. Fluctuations in the RR strain were sustained (Fig. 2) whereas the fluctuations in the SS strain appeared to dampen (Fig. 3).

In the $\mu_a = 0.96$ treatment both strains underwent another transition in the dynamics. The RR strain was in the stable equilibria region and the SS strain was in the region of aperiodic oscillations; however, both were close to the boundary at which a bifurcation to aperiodicities occurs (Fig. 1*b*, *c*). Being close to the aperiodic bifurcation boundary means that the transients of

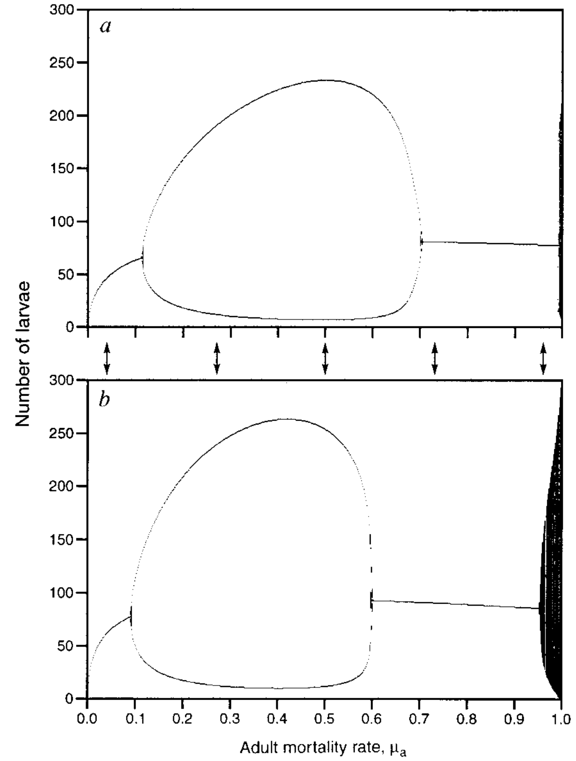

FIG. 4 Bifurcation diagrams for the model equations (1) for parameter values based on the experimental data. *a*, RR strain; *b*, SS strain. The double arrows indicate the adult mortality rate treatments.

the RR strain are expected to appear aperiodic and only slowly decay into the equilibrium. Both genetic strains displayed the expected aperiodic fluctuations (Figs 2 and 3).

Oscillatory approaches to point equilibria, stable periodic oscillations and aperiodic oscillations are difficult to distinguish in short time series with model-free methods. Our model-based parametric approach to classifying dynamic behaviour is statistically more powerful than non-parametric regression methods[18] or parametric flexible-response-surface methods[19]. However, our classifications depend on the adequacy of the model (2). We minimized the risk of error by basing the model on detailed knowledge of a well-studied system[9] and by thorough diagnostic analyses of the resulting time-series residuals[16]. The data (Figs 2 and 3) also give a visual impression of dynamic behaviours consistent with our classifications. Other, less-studied systems require statistical approaches that are more robust to variations in model form[20].

Our joint theoretical and experimental study has documented the transitions in the asymptotic dynamics of laboratory cultures of *Tribolium*. This rigorous verification of the predicted shifts in dynamical behaviour provides convincing evidence for the relevance of nonlinear mathematics in population biology. ☐

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