Boom, Bust, and Chaos in the Beetle Census

DAMAGE DUE TO flour beetles is a significant cost to the food processing industry. One of the major goals of entomologists is to gain insight into the population dynamics of beetles and other insects, as a way of learning about insect physiology. A commercial application of population studies is the development of strategies for population control.

A group of researchers recently designed a study of population fluctuation in the flour beetle *Tribolium*. The newly hatched larva spends two weeks feeding before entering a pupa stage of about the same length. The beetle exits the pupa stage as an adult. The researchers proposed a discrete map that models the three separate populations. Let the numbers of larvae, pupae, and adults at any given time t be denoted L_t, P_t, and A_t, respectively. The output of the map is three numbers: the three populations L_{t+1}, P_{t+1}, and A_{t+1} one time unit later. It is most convenient to take the time unit to be two weeks. A typical model for the three beetle populations is

$$\begin{aligned} L_{t+1} &= bA_t \\ P_{t+1} &= L_t(1 - \mu_l) \\ A_{t+1} &= P_t(1 - \mu_p) + A_t(1 - \mu_a), \end{aligned} \tag{1.5}$$

where b is the birth rate of the species (the number of new larvae per adult each time unit), and where μ_l, μ_p, and μ_a are the death rates of the larva, pupa, and adult, respectively.

We call a discrete map with three variables a three-dimensional map, since the state of the population at any given time is specified by three numbers L_t, P_t, and A_t. In Chapter 1, we studied one-dimensional maps, and in Chapter 2 we move on to higher dimensional maps, of which the beetle population model is an example.

Tribolium adds an interesting twist to the above model: cannibalism caused by overpopulation stress. Under conditions of overcrowding, adults will eat pupae

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and unhatched eggs (future larvae); larvae will also eat eggs. Incorporating these refinements into the model yields

$$\begin{aligned} L_{t+1} &= bA_t \exp(-c_{ea}A_t - c_{el}L_t) \\ P_{t+1} &= L_t(1 - \mu_l) \\ A_{t+1} &= P_t(1 - \mu_p)\exp(-c_{pa}A_t) + A_t(1 - \mu_a). \end{aligned} \tag{1.6}$$

The parameters $c_{el} = 0.012$, $c_{ea} = 0.009$, $c_{pa} = 0.004$, $\mu_l = 0.267$, $\mu_p = 0$, and $b = 7.48$ were determined from population experiments. The mortality rate of the adult was determined from experiment to be $\mu_a = 0.0036$.

The effect of calling the exterminator can be modeled by artificially changing the adult mortality rate. Figure 1.17 shows a bifurcation diagram from Equations (1.6). The horizontal axis represents the mortality rate μ_a. The asymptotic value of L_t—found by running the model for a long time at a fixed μ_a and recording the resulting larval population—is graphed vertically.

Figure 1.17 suggests that for relatively low mortality rates, the larval population reaches a steady state (a fixed point). For $\mu_a > .1$ (representing a death rate of 10% of the adults over each 2 week period), the model shows oscillation between two widely-different states. This is a "boom-and-bust" cycle, well-known to population biologists. A low population (bust) leads to uncrowded living con-

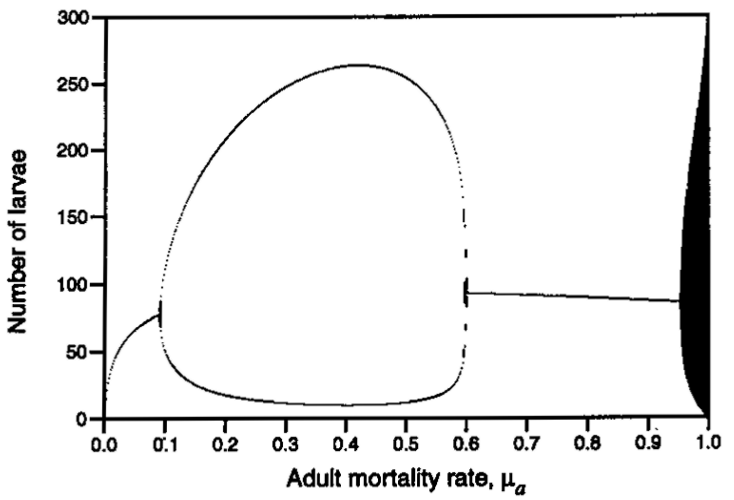

Figure 1.17 Bifurcation diagram for the model equations (1.6).
The bifurcation parameter is μ_a, the adult mortality rate.

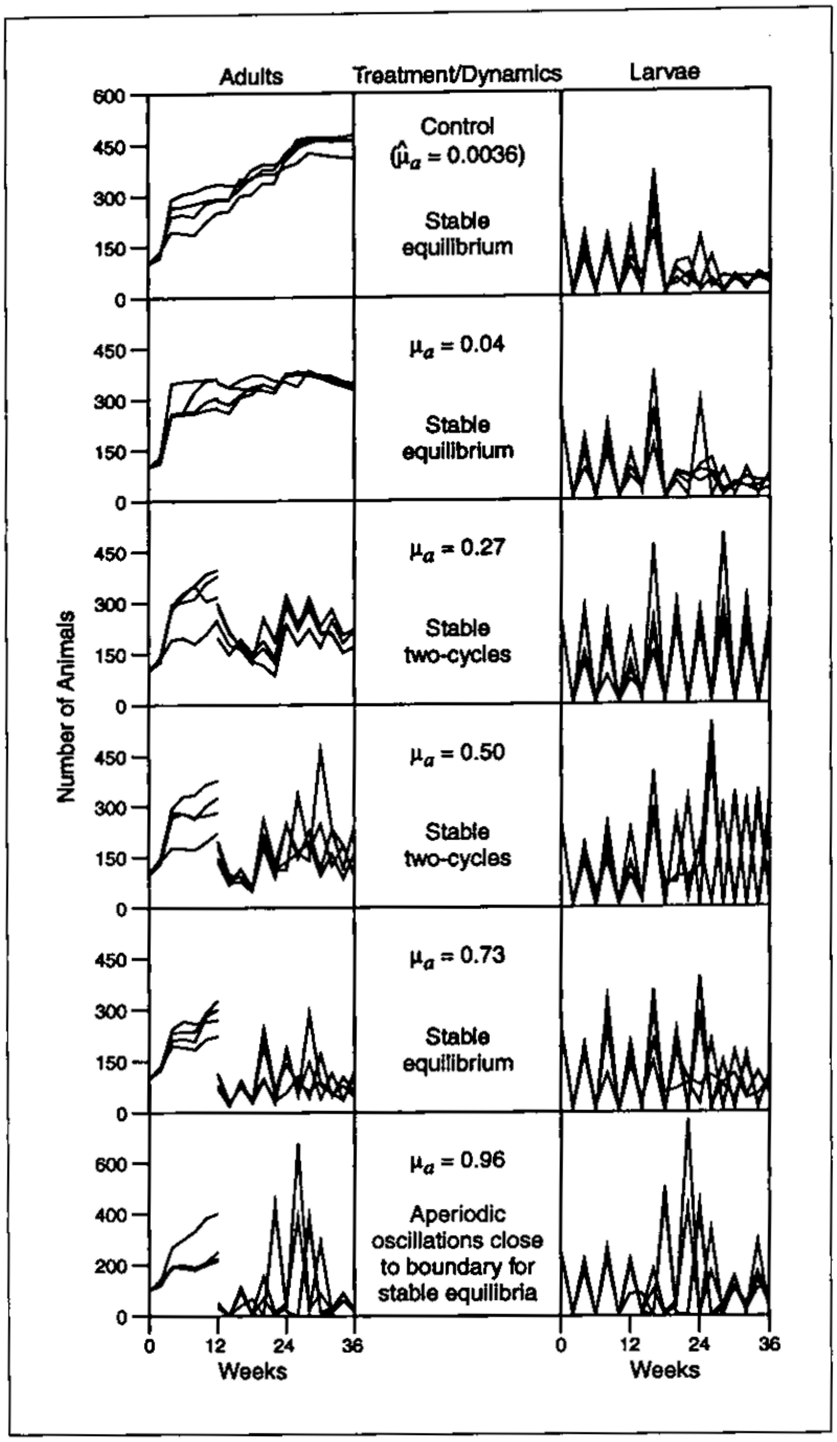

Figure 1.18 Population as a function of time.
Four replicates of the experiment for each of six different adult mortality rates are plotted together.

ditions and runaway growth (boom) at the next generation. At this point the limits to growth (cannibalism, in this system) take over, leading to a catastrophic decline and repeat of the cycle.

The period-doubling bifurcation near $\mu_a = 0.1$ is followed by a period-halving bifurcation at $\mu_a \approx 0.6$. For very high adult mortality rates (near 100%), we see the complicated, nonperiodic behavior.

The age-stratified population model discussed above is an interesting mathematical abstraction. What does it have to do with real beetles? The experimenters put several hundred beetles and 20 grams of food in each of several half-pint milk bottles. They recorded the populations for 18 consecutive two-week periods. Five different adult mortality rates, $\mu_a = 0.0036$ (the natural rate), 0.04, 0.27, 0.50, 0.73, and 0.96 were enforced in different bottles, by periodically removing the requisite number of adult beetles to artificially reach that rate. Each of the five experiments was replicated in four separate bottles.

Figure 1.18 shows the population counts taken from the experiment. Populations of adults from the four separate bottles are graphed together in the boxes on the left. The four curves in the box are the adult population counts for the four bottles as a function of time. The boxes on the right are similar but show the population counts for the larvae. During the first 12 weeks, the populations were undisturbed, so that the natural adult mortality rate applied; after that, the artificial mortality rates were imposed by removing or adding adult beetles as needed.

The population counts from the experiment agree remarkably well with the computer simulations from Figure 1.18. The top two sets of boxes represent $\mu_a = 0.0036$ and 0.04, which appear experimentally to be sinks, or stable equilibria, as predicted by Figure 1.18. The period-two sink predicted also can be seen in the populations for $\mu_a = 0.27$ and 0.50. For $\mu_a = 0.96$, the populations seem to be governed by aperiodic oscillations.