

1970s. If you like watching fights, have a look at Zahler and Sussman (1977) and Kolata (1977).

Bead on a Tilted Wire

As a simple example of imperfect bifurcation and catastrophe, consider the following mechanical system (Figure 3.6.7).

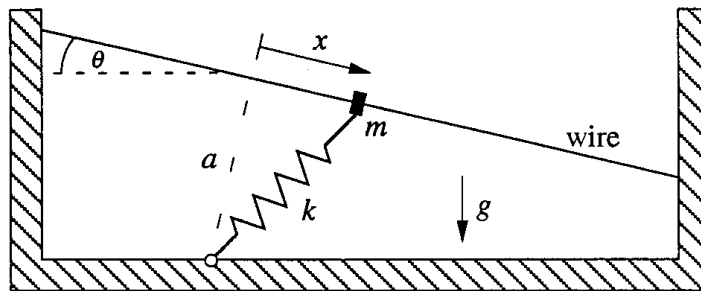


Figure 3.6.7

A bead of mass m is constrained to slide along a straight wire inclined at an angle θ with respect to the horizontal. The mass is attached to a spring of stiffness k and relaxed length L_0 , and is also acted on by gravity. We choose coordinates along the wire so that $x = 0$ occurs at the point closest to the support point of the spring; let a be the distance between this support point and the wire.

In Exercises 3.5.4 and 3.6.5, you are asked to analyze the equilibrium positions of the bead. But first let's get some physical intuition. When the wire is horizontal ($\theta = 0$), there is perfect symmetry between the left and right sides of the wire, and $x = 0$ is always an equilibrium position. The stability of this equilibrium depends on the relative sizes of L_0 and a : if $L_0 < a$, the spring is in tension and so the equilibrium should be stable. But if $L_0 > a$, the spring is compressed and so we expect an *unstable* equilibrium at $x = 0$ and a pair of stable equilibria to either side of it. Exercise 3.5.4 deals with this simple case.

The problem becomes more interesting when we tilt the wire ($\theta \neq 0$). For small tilting, we expect that there are still three equilibria if $L_0 > a$. However if the tilt becomes too steep, perhaps you can see intuitively that the uphill equilibrium might suddenly disappear, causing the bead to jump catastrophically to the downhill equilibrium. You might even want to build this mechanical system and try it. Exercise 3.6.5 asks you to work through the mathematical details.

3.7 Insect Outbreak

For a biological example of bifurcation and catastrophe, we turn now to a model for the sudden outbreak of an insect called the spruce budworm. This insect is a se-

rious pest in eastern Canada, where it attacks the leaves of the balsam fir tree. When an outbreak occurs, the budworms can defoliate and kill most of the fir trees in the forest in about four years.

Ludwig et al. (1978) proposed and analyzed an elegant model of the interaction between budworms and the forest. They simplified the problem by exploiting a separation of time scales: the budworm population evolves on a *fast* time scale (they can increase their density fivefold in a year, so they have a characteristic time scale of months), whereas the trees grow and die on a *slow* time scale (they can completely replace their foliage in about 7–10 years, and their life span in the absence of budworms is 100–150 years.) Thus, as far as the budworm dynamics are concerned, the forest variables may be treated as constants. At the end of the analysis, we will allow the forest variables to drift very slowly—this drift ultimately triggers an outbreak.

Model

The proposed model for the budworm population dynamics is

$$\dot{N} = RN \left(1 - \frac{N}{K} \right) - p(N).$$

In the absence of predators, the budworm population $N(t)$ is assumed to grow logistically with growth rate R and carrying capacity K . The carrying capacity depends

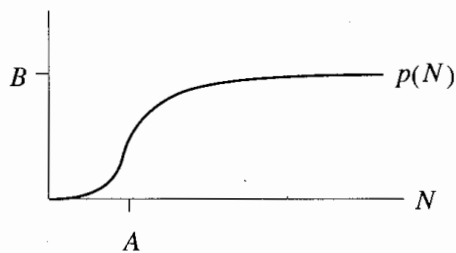


Figure 3.7.1

on the amount of foliage left on the trees, and so it is a slowly drifting parameter; at this stage we treat it as fixed. The term $p(N)$ represents the death rate due to *predation*, chiefly by birds, and is assumed to have the shape shown in Figure 3.7.1. There is almost no predation when budworms are scarce; the birds seek food elsewhere. However, once the population exceeds a certain critical level $N = A$, the predation turns on sharply and then saturates (the birds are eating as fast as they can). Ludwig et al. (1978) assumed the specific form

$$p(N) = \frac{BN^2}{A^2 + N^2}$$

where $A, B > 0$. Thus the full model is

$$\dot{N} = RN \left(1 - \frac{N}{K} \right) - \frac{BN^2}{A^2 + N^2} \quad (1)$$

We now have several questions to answer. What do we mean by an “outbreak” in the context of this model? The idea must be that, as parameters drift, the bud-

worm population suddenly jumps from a low to a high level. But what do we mean by “low” and “high,” and are there solutions with this character? To answer these questions, it is convenient to recast the model into a dimensionless form, as in Section 3.5.

Dimensionless Formulation

The model (1) has four parameters: R , K , A , and B . As usual, there are various ways to nondimensionalize the system. For example, both A and K have the same dimension as N , and so either N/A or N/K could serve as a dimensionless population level. It often takes some trial and error to find the best choice. In this case, our heuristic will be to scale the equation so that all the dimensionless groups are pushed into the *logistic* part of the dynamics, with none in the *predation* part. This turns out to ease the graphical analysis of the fixed points.

To get rid of the parameters in the predation term, we divide (1) by B and then let

$$x = N/A,$$

which yields

$$\frac{A}{B} \frac{dx}{dt} = \frac{R}{B} Ax \left(1 - \frac{Ax}{K} \right) - \frac{x^2}{1+x^2}. \quad (2)$$

Equation (2) suggests that we should introduce a dimensionless time τ and dimensionless groups r and k , as follows:

$$\tau = \frac{Bt}{A}, \quad r = \frac{RA}{B}, \quad k = \frac{K}{A}.$$

Then (2) becomes,

$$\frac{dx}{d\tau} = rx \left(1 - \frac{x}{k} \right) - \frac{x^2}{1+x^2}, \quad (3)$$

which is our final dimensionless form. Here r and k are the dimensionless growth rate and carrying capacity, respectively.

Analysis of Fixed Points

Equation (3) has a fixed point at $x^* = 0$; it is *always unstable* (Exercise 3.7.1). The intuitive explanation is that the predation is extremely weak for small x , and so the budworm population grows exponentially for x near zero.

The other fixed points of (3) are given by the solutions of

$$r \left(1 - \frac{x}{k} \right) = \frac{x}{1+x^2}. \quad (4)$$

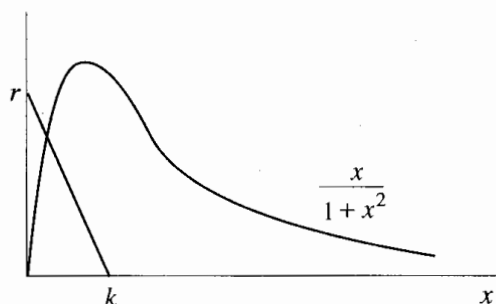


Figure 3.7.2

the curve doesn't—this convenient property is what motivated our choice of nondimensionalization.

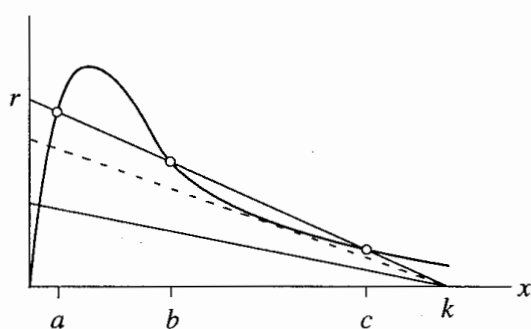


Figure 3.7.3

and eventually coalesce in a *saddle-node bifurcation* when the line intersects the curve *tangentially* (dashed line in Figure 3.7.3). After the bifurcation, the only remaining fixed point is a (in addition to $x^* = 0$, of course). Similarly, a and b can collide and annihilate as r is increased.

To determine the stability of the fixed points, we recall that $x^* = 0$ is unstable, and also observe that the stability type must alternate as we move along the x -axis.

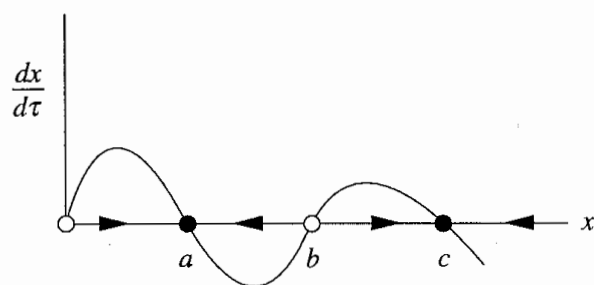


Figure 3.7.4

view of pest control, one would like to keep the population at a and away from c . The fate of the system is determined by the initial condition x_0 ; an outbreak occurs

This equation is easy to analyze graphically—we simply graph the right- and left-hand sides of (4), and look for intersections (Figure 3.7.2). The left-hand side of (4) represents a straight line with x -intercept equal to k and a y -intercept equal to r , and the right-hand side represents a curve that is *independent of the parameters*! Hence, as we vary the parameters r and k , the line moves but the curve doesn't—this convenient property is what motivated our choice of

Figure 3.7.2 shows that if k is sufficiently small, there is exactly one intersection for any $r > 0$. However, for large k , we can have one, two, or three intersections, depending on the value of r (Figure 3.7.3). Let's suppose that there are three intersections a , b , and c . As we decrease r with k fixed, the line rotates counter-clockwise about k . Then the fixed points b and c approach each other

Hence a is stable, b is unstable, and c is stable. Thus, for r and k in the range corresponding to three positive fixed points, the vector field is qualitatively like that shown in Figure 3.7.4. The smaller stable fixed point a is called the *refuge* level of the budworm population, while the larger stable point c is the *outbreak* level. From the point of

if and only if $x_0 > b$. In this sense the unstable equilibrium b plays the role of a *threshold*.

An outbreak can also be triggered by a saddle-node bifurcation. If the parameters r and k drift in such a way that the fixed point a disappears, then the population will jump suddenly to the outbreak level c . The situation is made worse by the hysteresis effect—even if the parameters are restored to their values before the outbreak, the population will not drop back to the refuge level.

Calculating the Bifurcation Curves

Now we compute the curves in (k, r) space where the system undergoes saddle-node bifurcations. The calculation is somewhat harder than that in Section 3.6: we will not be able to write r explicitly as a function of k , for example. Instead, the bifurcation curves will be written in the *parametric form* $(k(x), r(x))$, where x runs through all positive values. (Please don't be confused by this traditional terminology—one would call x the “parameter” in these parametric equations, even though r and k are themselves parameters in a different sense.)

As discussed earlier, the condition for a saddle-node bifurcation is that the line $r(1 - x/k)$ intersects the curve $x/(1 + x^2)$ tangentially. Thus we require *both*

$$r\left(1 - \frac{x}{k}\right) = \frac{x}{1 + x^2} \quad (5)$$

and

$$\frac{d}{dx}\left[r\left(1 - \frac{x}{k}\right)\right] = \frac{d}{dx}\left[\frac{x}{1 + x^2}\right]. \quad (6)$$

After differentiation, (6) reduces to

$$-\frac{r}{k} = \frac{1 - x^2}{(1 + x^2)^2}. \quad (7)$$

We substitute this expression for r/k into (5), which allows us to express r solely in terms of x . The result is

$$r = \frac{2x^3}{(1 + x^2)^2}. \quad (8)$$

Then inserting (8) into (7) yields

$$k = \frac{2x^3}{x^2 - 1}. \quad (9)$$

The condition $k > 0$ implies that x must be restricted to the range $x > 1$.

Together (8) and (9) define the bifurcation curves. For each $x > 1$, we plot the

corresponding point $(k(x), r(x))$ in the (k, r) plane. The resulting curves are shown in Figure 3.7.5. (Exercise 3.7.2 deals with some of the analytical properties of these curves.)

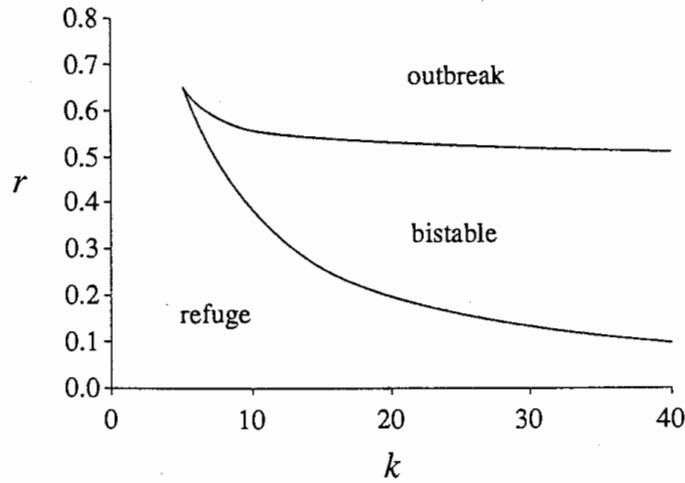


Figure 3.7.5

The different regions in Figure 3.7.5 are labeled according to the stable fixed points that exist. The refuge level a is the only stable state for low r , and the outbreak level c is the only stable state for large r . In the *bistable* region, both stable states exist.

The stability diagram is very similar to Figure 3.6.2. It too can be regarded as the projection of a cusp catastrophe surface, as schematically illustrated in Figure 3.7.6. You are hereby challenged to graph the surface accurately!

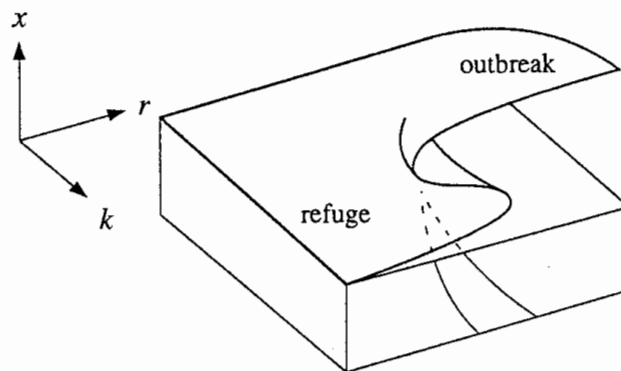


Figure 3.7.6

Comparison with Observations

Now we need to decide on biologically plausible values of the dimensionless groups $r = RA/B$ and $k = K/A$. A complication is that these parameters may drift

slowly as the condition of the forest changes. According to Ludwig et al. (1978), r increases as the forest grows, while k remains fixed.

They reason as follows: let S denote the average size of the trees, interpreted as the total surface area of the branches in a stand. Then the carrying capacity K should be proportional to the available foliage, so $K = K'S$. Similarly, the half-saturation parameter A in the predation term should be proportional to S ; predators such as birds search *units of foliage*, not acres of forest, and so the relevant quantity A' must have the dimensions of budworms per unit of branch area. Hence $A = A'S$ and therefore

$$r = \frac{RA'}{B}S, \quad k = \frac{K'}{A'} \quad (10)$$

The experimental observations suggest that for a young forest, typically $k \approx 300$ and $r < 1/2$ so the parameters lie in the bistable region. The budworm population is kept down by the birds, which find it easy to search the small number of branches per acre. However, as the forest grows, S increases and therefore the point (k, r) drifts upward in parameter space toward the outbreak region of Figure 3.7.5. Ludwig et al. (1978) estimate that $r \approx 1$ for a fully mature forest, which lies dangerously in the outbreak region. After an outbreak occurs, the fir trees die and the forest is taken over by birch trees. But they are less efficient at using nutrients and eventually the fir trees come back—this recovery takes about 50–100 years (Murray 1989).

We conclude by mentioning some of the approximations in the model presented here. The tree dynamics have been neglected; see Ludwig et al. (1978) for a discussion of this longer time-scale behavior. We've also neglected the *spatial* distribution of budworms and their possible dispersal—see Ludwig et al. (1979) and Murray (1989) for treatments of this aspect of the problem.

EXERCISES FOR CHAPTER 3

3.1 Saddle-Node Bifurcation

For each of the following exercises, sketch all the qualitatively different vector fields that occur as r is varied. Show that a saddle-node bifurcation occurs at a critical value of r , to be determined. Finally, sketch the bifurcation diagram of fixed points x^* versus r .

3.1.1 $\dot{x} = 1 + rx + x^2$

3.1.2 $\dot{x} = r - \cosh x$

3.1.3 $\dot{x} = r + x - \ln(1+x)$

3.1.4 $\dot{x} = r + \frac{1}{2}x - x/(1+x)$

3.1.5 (Unusual bifurcations) In discussing the normal form of the saddle-node bi-