

Spruce Budworm in Eastern Canada and Northern Minnesota

Ludwig, Jones and Holling, *Qualitative analysis of insect outbreak systems: the spruce budworm and forest*, Journal of Animal Ecology (1978), **47**, 315-332. (copy available in courseinfo)

Polking, Boggess and Arnold, *Differential Equations*, 158-161.

October 6, 1977 issue of Nature Magazine (Vol. 269, pg. 471)
“The extensive bibliography at the end of the article provides an excellent reading list for those interested in pursuing other realistic examples of mathematical modeling.”

Background:

Spruce budworm (*Choristoneura fumiferana*) is a serious pest in eastern Canada and northern Minnesota. The spruce budworm crawls upon and consumes the leaves of coniferous trees. Excessive consumption can damage and kill the host. The budworms themselves are eaten primarily by birds, who eat many other insects as well. The budworms prefer larger trees. A key factor in determining the spruce budworm population is the leaf surface area per tree. Larger trees have larger leaf surface areas, resulting in larger spruce budworm populations.

The Canadians had observed that the spruce budworm population underwent irruptions approximately every 40 years. For

unknown reasons the budworm population would explode, devastating the pineries, and then return to their previous manageable levels. The loss of timber represented a significant cost to the Canadian wood products industry and various management techniques, pesticide application, for example, were tried without success.

In an effort to understand the cycles of spruce budworm populations, and with an eye toward developing inexpensive and effective management of the problem, several scientists at the University of British Columbia (R. Morris, D. Ludwig, D. Jones and C.S. Holling) studied the problem and produced a series of mathematical models.

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.

Assumptions:

1. In the absence of predation, the population satisfies logistic growth.

$$\frac{dP}{dt} = kP \left(1 - \frac{P}{N} \right) - h(P)$$

2. The effort of predators saturates at high prey densities, *i.e.* there is an upper limit to the rate of budworm mortality due to the predation.

3. If the spruce budworm density is low, birds will opt for some other prey which most likely lives in other parts of the trees (like beetles).

So $\lim_{P \rightarrow \infty} h(P) = a > 0$, $\lim_{P \rightarrow \infty} \frac{h(P)}{P} = 0$ or $h(P) \approx bP^2$ near $P = 0$.

Holling's type III model

$$\frac{dP}{dt} = kP \left(1 - \frac{P}{N} \right) - \frac{DCP^2}{A^2 + P^2}$$

k: the natural growth rate, as in the logistic model;

N: the carrying capacity, as in the logistic model;

D: is a measure of predation efficiency. If birds are good at catching spruce budworms, this number will be larger than if birds often miss the budworm they are attacking.

C: is the bird population, considered a constant in this model;

A: is called the switching value, that is the population at which predators begin showing increased interest in harvesting budworms.

Through observation it had been observed that two of the model parameters, A and N , are directly dependent on the average leaf surface area per tree. Letting S be the average leaf surface area, then $A = 0.5S$, $N = 4S$.

As the finishing touch of the modeling, we denote $B = CD$. Then

$$\frac{dP}{dt} = kP \left(1 - \frac{P}{N} \right) - \frac{BP^2}{A^2 + P^2}$$

Mathematical Analysis:

1. Nondimensionalization: $Q = \frac{P}{A}, s = \frac{Bt}{A}$.

$$\frac{dQ}{ds} = aQ \left(1 - \frac{Q}{b}\right) - \frac{Q^2}{1 + Q^2},$$

where $a = \frac{kA}{B}, b = \frac{N}{A}$.

2. Equilibrium points.

$$aQ \left(1 - \frac{Q}{b}\right) = \frac{Q^2}{1 + Q^2} \Rightarrow Q = 0 \text{ or } a \left(1 - \frac{Q}{b}\right) = \frac{Q}{1 + Q^2}$$

A Real test for your algebra: (a bifurcation problem)

How many times will $f(Q) = a \left(1 - \frac{Q}{b}\right)$ and $g(Q) = \frac{Q}{1 + Q^2}$ intersect?

Three, two, or one. The border line is given by

$$a = \frac{2x^3}{(1+x^2)^2}, b = \frac{2x^3}{1-x^2}$$

Since $a = \frac{kA}{B}$, $b = \frac{N}{A}$, and $A = 0.5S$, $N = 4S$, where S is the average leaf surface area, then $b \approx 8$, and $a \approx \frac{kS}{2B}$.

When $b = 8$, the curve is $a = \frac{8x}{(8-x)(1+x^2)}$.

There are two saddle-node bifurcation points, we call $a_1 (<) a_2$.

Biological interpretation:

1. When the forest is young, so S is small, and $a < a_1$, then there is only one small positive equilibrium point, which is a sink. So the budworm population is controlled by the birds, the equilibrium is kept in a low level, which we call **refuge**.
2. When the forest grows, a passes a_1 , then there are three positive equilibrium points, two of them are sinks, the refuge and a much larger one, which we call **outbreak** level. Outbreak level of budworm is dangerous for the forest. But since when the forest grows, the budworm is kept at refuge level, then it cannot jump to the outbreak level. Thus the forest is still in good shape since budworm is still in low level.

3. But when the forest grows such that a passes a_2 , there is only one equilibrium left, which is the outbreak level. So the budworm population has a sudden increase in a short time. We say an outbreak occurs.

4. When an outbreak occurs, the budworm population is in a high level, then the forest's growth cannot keep up with the budworm, so a in fact decreases. But even a decreases, the budworm population cannot drop back to refuge level, that is called **hysteresis effect**.

5. The fir tree forest are defoliated by budworm, and the forest is taken over by birch trees. But they are less efficient at using nutrients and eventually the fir trees come back, but this recovery will take about 50-100 years.