A model for spruce budworm and its analysis

I. *The model*

The spruce budworm feeds on conifers and is a major pest in the US and Canada. Budworms harm trees by feeding on the needles, and periodic outbreaks of them occur that can devastate forests. To explore the dynamics of spruce budworm populations Canadian and US biologists have developed several models. We discuss here a single species model proposed by Ludwig, Jones, and Holling, Qualitative analysis of insect outbreak systems: the spruce budworm and forest, *J. Anim. Ecol.*, 47:315-332, 1978.

Let N denote the size of the spruce budworm population. In the absence of predation, an appropriate model for N might be a logistic model, with conifers playing the role of limiting resource. However, many birds eat spruce budworms. Thus we should subract a term from the logistic equation that represents the rate D at which birds consume budworms. As a first guess, it is reasonable to assume that the rate D depends on N and the size P of the population of birds: thus $D = D(P, N)$. The form of the model for N is thus

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - D(P, N). \tag{1}$$

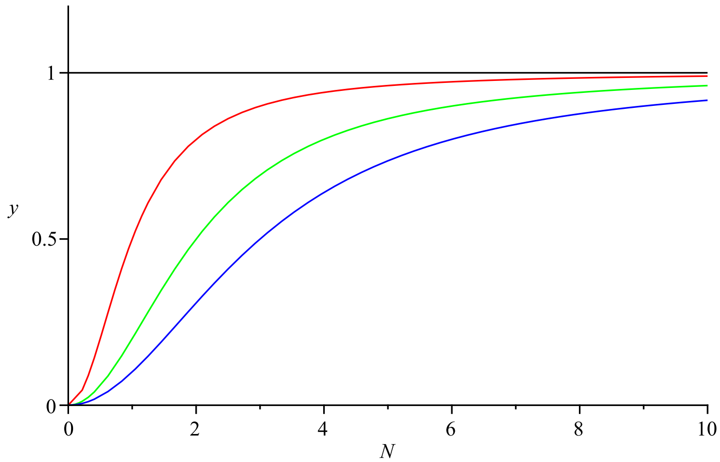
As it stands, this is not complete because we must specify the evolution of P. If an increase or decrease in the spruce budworm population tended to increase or decrease P, we would need to add a differential equation to model P. However, we will assume that the spruce budworm population does not appreciably affect P. This might be the case if the spruce budworm is not a dominant food source of a major species. Hence we will assume P is essentially constant and that D is a function $D(N)$ of N only. Whether this simplifying assumption is a useful approximation must be decided by testing the model against data. It can only be an approximation. At least as far one can trust the Wikipedia article I read, which unfortunately contained no references, the spruce budworm is a preferred food of some species and field data do appear to show the budworm and bird populations are correlated. The virtue of assuming $D = D(N)$ is that we get a single species model.

The model of Ludwig, et al, proposes a specific functional form for D. The idea is that one should expect the properties: (i) $D(0) = 0$; (ii) $D(N)$ is increasing in N; (iii) $B = \lim_{N\to\infty} D(N)$ is finite; and, (iv) $D'(0) = 0$. The first two properties are self-explanatory. As for the third, if the bird population does not increase, the rate of predation can never climb above some maximum amount. The fourth property is imposed so that the rate of increase of $D(N)$ is small for small N. Birds forage in an energy efficient way. If the budworms are few in number and thus hard to find, birds will seek other food and so they will respond only slowly to an increase in budworm populations when N is close to 0. A particular function that satisfies properties (i)-(iv) is

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

The student should verify that $D'(N) = \dfrac{2BA^2N}{(A^2 + N^2)^2}$, and $\lim_{N\to\infty} D(N) = B$, and hence that (i)-(iv) are all true.

Plots of the graph of $D(N) = N^2/(A^2 + N^2)$ are shown in the next figure for $A = 1, 2, 3$. Since $D(N)$ decreases as A increases, the graph with $A = 1$ is the leftmost curve, that with $A = 3$ the rightmost. Thus, decreasing A causes the curve to approach the limit 1 more rapidly.



By inserting this functional form of D, we arrive at the following spruce budworm model.

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \frac{BN^2}{A^2 + N^2}. \tag{2}$$

There are four parameters here, r, K, B, and A. However the qualitative behavior of solutions will be determined by two parameters which are combinations of these, as the following exercise shows.

Exercise 1. Show that if $N^* = N/A$ and $t^* = Bt/A$, then

$$\frac{dN^*}{dt^*} = \rho N^*(1 - \frac{N^*}{q}) - \frac{(N^*)^2}{1 + (N^*)^2}, \tag{3}$$

where $\rho = Ar/B$ and $q = K/A$.

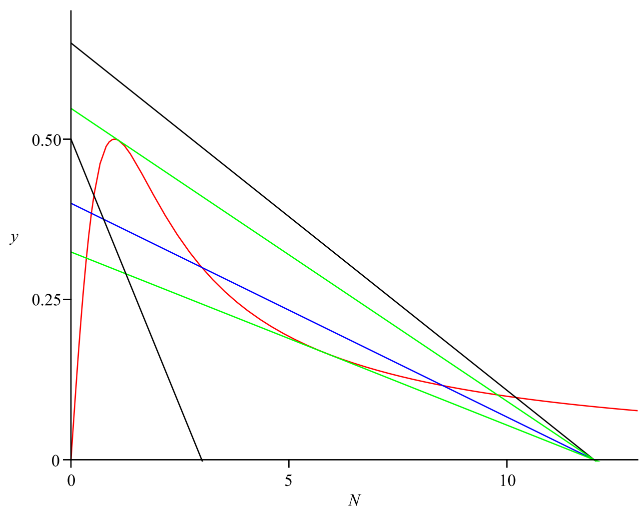
II. *Analysis of the model.*

The object of this section is to analyze how solutions of equation (3) behave and to show how they might explain outbreaks of spruce budworm. To simplify notation, we replace N^* by N and t as t, but we should bear in mind that N and t are dimensionless variables, not the original population size and time scale. Our equation is:

$$\frac{dN}{dt} = \rho N(1 - \frac{N}{q}) - \frac{N^2}{1+N^2} = N\left(\rho(1 - \frac{N}{q}) - \frac{N}{1+N^2}\right), \tag{4}$$

for positive constants ρ and q.

Note that $N = 0$ is always an equilibrium point. From the right-most expression in(3), the *positive* equilibrium points of (4) are the values of N at which the graphs of the linear function $\rho(1 - N/q)$ and the function $N/(1 + N^2)$ intersect. Notice that the y-intercept of $\rho(1 - N/q)$ is ρ and the N-intercept is q. The figure that follows shows the graph of $N/(1 + N^2)$ and graphs of $\rho(1 - N/q)$ for several different values of ρ and q.



As is evident from the figure, the graph of $N/(1+N^2)$ achieves a maximum value of 0.5 at $N = 1$ and falls off monotonically to either side of $N = 1$. This may be confirmed analytically by computing the first derivative of $N/(1+N^2)$. Analysis of the second derivative shows that the graph of $N/(1 + N^2)$ has a unique inflection point, where it changes from concave down to concave up, at $N = \sqrt{3}$. By looking at the figure and using these facts about the shape of the graph of $N/(1+N^2)$ it is clear that there can be either one, two, or three equilibrium points, and no other cases are possible.

It is instructive to analyze how the arrangement and number of positive equilibria depend on ρ and q. If q is small enough, it is clear from the picture that, no matter what ρ is, there will be just one equilibrium point. In fact this is true as long as q is less than or equal to $3\sqrt{3}/2$, which is the x-intercept of the tangent to the graph of $N/(1 + N^2)$ at its inflection point. On the other hand if $q > 3\sqrt{3}/2$, all three cases can occur. This can be seen readily from the figure, remembering that ρ is the y-intercept of the straight line. Imagine increasing ρ starting from 0. Then there will be two values $0 < \rho_1 < \rho_2 < \infty$, such that if $\rho < \rho_1$ or $\rho > \rho_2$, there is one positive equilibrium point, if $\rho_1 < \rho < \rho_2$, there are three positive equilibrium points, and, in the border line cases when $\rho = \rho_1$ or $\rho = \rho_2$, there are two. Notice that when exactly two equilibria occur, at one of them the line $y = \rho(1 - N/q)$ and the graph of $y = N/(1 + N^2)$ are tangent.

Exercise 2. a) In all cases in which there is just one positive equilibrium, $\bar{N}$, show it is asymptotically stable, and, in fact, $\lim_{t\to\infty} N(t) = \bar{N}$ for any positive initial population $N(0) > 0$.

(b) Let $0 < V_1 < V_2 < V_3$ denote the equilibria in increasing order when there are three. Determine which are stable. Sketch how solutions behave for various initial populations.

(c) Repeat (b) when there are two equilibria $0 < V_1 < V_2$. It is necessary here to treat separately the case when the intersection is tangent at V_1 and when it is tangent at V_2.

The parameters ρ and q depend on environmental and biological factors. What happens if they change? We analyze the following simple scenario. The parameter q remains constant but ρ jumps in value occasionally and stays constant between jumps. We will assume that these jumps occur infrequently enough so that between jumps, $N(t)$ has time to approach very closely the stable equilibrium point dictated by the current value of ρ. The following exercise requires a graphing calculator or use of the computer.

Exercise 3. Let $q = 12$.

(a) Let $\rho = z_1 = 0.2$. Show there is a unique equilibrium point N_1 and find its value.

(b) Assume that the population is at the value N_1 and that ρ jumps to $z_2 = 0.4$. Starting from N_1 the population will move to a new equilibrium value N_2. What is it?

(c) Now suppose the population is at N_2 or very close and then ρ jumps to $z_3 = 0.6$. What is the new equilibrium value N_3 the solution move to? You should find that N_3 is very much larger than N_2. This corresponds to an outbreak of the spruce budworm.

(d) Finally, suppose the population is at or near N_3 and ρ jumps back down to $\rho = 0.4$. Find the new equilibrium N_4 that the population moves to. Note that it is **not** the same as N_2? (This phenomenon, in which the parameters of a physical system are changed and then returned to their original values, but the state of the system does not return to its original state, is called *hysteresis*).

(Hint: The figure on the previous page shows lines intersecting at $q = 12$. You can use this figure and a ruler to get approximate values of the equilibria points in (a)–(d) and see visually how they are changing. But you should get precise values also.)

Exercise 4. Can you think of scenarios that would cause ρ or q to change? Remember how they are defined in terms of the original parameters r, K, A, B of the problem.

References. J.D. Murray, Mathematical Biology, Springer-Verlag, 2002, page 7.

J. Istas, Mathematical Modeling for the Life Sciences, Springer-Verlag, 2005, page 15.