PROJECT # 1
THE SPRUCE BUDWORM

The spruce budworm is an insect which is a serious threat to forests. This is especially true in eastern Canada, where it attacks the leaves of the balsam fir tree. The insect is always present. It is usually held at bay by birds which feed off the insect, but sometimes there is a relatively sudden outbreak of the pest that can result in the entire destruction of a forest over a period of about four years.

We are dealing with rather complicated interactions between trees, budworms, and birds. Here are some of the pertinent features of the system.

- The leaves of the trees provide food for the budworms.
- The leaves of the trees also provide coverage for the budworms, essentially hiding them from the birds.
- The birds feed on the budworms if they can find them. If the budworms are in large supply the birds will make short work of them. However, the birds have plenty of other sources of food, so they are not critically dependent on the budworms. This means that we can consider the population of birds to be constant.
- There are different time scales for the growth pattern of the population of budworms and the growth of trees and forests. The budworm population operates on a fast time scale. For example, they can multiply five-fold in one year. On the other hand, trees grow relatively slowly. Typically a balsam fir will replace its foliage completely in about seven years, and a typical tree lives for about 100 years.

The project. The first project this semester will be concerned with the problem of modelling spruce budworm populations. This is described in our textbook starting on p.158. However, this description will supersede what is asked for there.

Project #1 is due by noon, Friday, **March 4, 2005.**

In this description you will be given a number of tasks. In your write up you should perform all of the tasks but the organization of your paper is up to you. You do not have to follow the order of the tasks. You should organize your paper to communicate the results in the most intelligible way.

The purpose of your paper is to describe how the mathematics developed in Tasks 1–6 can be used in Tasks 7 and 8 to explain what happens in a forest before, during, and after a budworm outbreak. Therefore Tasks 7 and 8 will count for a disproportionate part of the grade on the project.

The model. In 1978, Ludwig, Jones, and Holling published a paper in which they proposed an ingenious model of the interaction of the insects, the trees, and the predatory birds. They proposed that the budworm population B obeys a logistic model modified by a predation rate,

$$\frac{dB}{dt} = r_B B\left(1 - \frac{B}{K_B}\right) - p(B) \tag{1}$$

where r_B is the intrinsic growth rate of the budworm and K_B is the carrying capacity, which is assumed to depend upon the amount of foliage available. The predation rate $p(B)$ was chosen by Ludwig, et al, to take into account the observed facts about spruce budworms and their predators.

- First, if there are few budworms they tend not to be observed by birds, and the birds feed on other, more readily available food sources. Thus the predation rate is **extremely small** if the budworm population is small.

- When the budworm population increases to a certain point, they are observed by the birds and the predation rate increases rapidly.

- Finally, if there are a lot of budworms, the birds feed to capacity on them, become sated, and eat no more budworms.

Task 1. Explain how the form of the predation rate chosen by Ludwig, et al,

$$p(B) = \frac{\beta B^2}{\alpha^2 + B^2}, \tag{2}$$

where α and β are constants, incorporates these facts. Include a graph of the predation rate. (Use $\alpha = \beta = 1$.) Compute $p_\infty = \lim_{B\to\infty} p(B)$. For what value of B do we have $p(B) = p_\infty/2$? Compare $p(B)$ to B/α as $B \to 0$ and explain what **extremely small** means in this case.

Introduction of dimensionless variables. It is often convenient to change variables when analyzing models. In this case, the model equation

$$\frac{dB}{dt} = r_B B\left(1 - \frac{B}{K_B}\right) - \frac{\beta B^2}{\alpha^2 + B^2} \tag{3}$$

contains four parameters. When we introduce the new variables

$$\mu = \frac{B}{\alpha} \text{and} \tau = \frac{\beta}{\alpha} t,$$

and the "lumped constants"

$$R = \frac{\alpha r_B}{\beta} \text{and} Q = \frac{K_B}{\alpha}$$

into equation (3), it simplifies to

$$\frac{d\mu}{d\tau} = \mu\left[R\left(1 - \frac{\mu}{Q}\right) - \frac{\mu}{1 + \mu^2}\right]. \tag{4}$$

You are not required to show this, but you might want to do the computation anyway.

In this reformulation μ, τ, R, and Q are all dimensionless quantities. μ represents the population, τ the time, R the reproductive rate, and Q the carrying capacity. The advantages of the reformulation in (4) are two-fold. First the number of parameters is reduced from four to two. Secondly, now both parameters appear in the expression $R(1-\mu/Q)$, which is linear in μ, and the more complicated expression $\mu/(1+\mu^2)$ is parameter free.

The equilibrium points. From equation (4) we see that the equilibrium points are defined by the equation

$$\mu\left[R\left(1-\frac{\mu}{Q}\right)-\frac{\mu}{1+\mu^2}\right]=0. \tag{5}$$

Task 2. Is the equilibrium point at $\mu = 0$ stable or unstable? Give a reason for your answer.

The remaining equilibrium points are calculated by setting the remaining factor of equation (5) equal to zero. This eventually leads to a rather intractable solution of a cubic polynomial, so Ludwig, et al, adopted an alternate strategy, that of determining where

$$R\left(1-\frac{\mu}{Q}\right)=\frac{\mu}{1+\mu^2}. \tag{6}$$

The analysis continues by plotting graphs of the left- and right-hand sides of equation (6) versus μ and looking for points of intersection. Figure 1 shows the intersection set for two values of R and one value of Q.

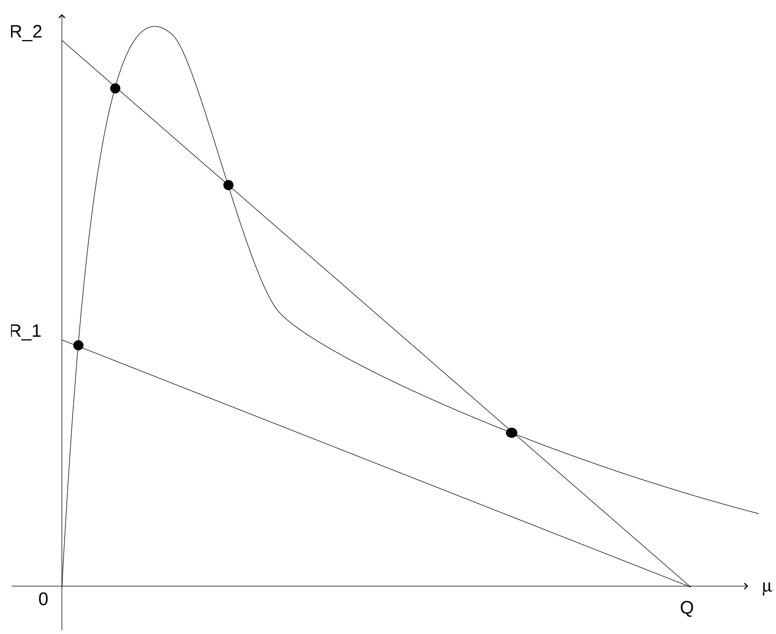

Figure 1. The intersection set for two values of R.

Task 3. Carry out a complete analysis of the different types of intersection sets that can occur between the graphs of the functions

$$R\left(1-\frac{\mu}{Q}\right) \text{ and } \frac{\mu}{1+\mu^2}$$

for all values of R and Q. A type is characterized by the number of points in the intersection, and whether a point is a tangential intersection or not. Your discussion should systematically examine all possibilities. You should end up with a short list of cases, and an explanation of how you know your list is complete. You should also provide a plot like Figure 1, illustrative of each case.

The best way to do the analysis is to examine what can occur for each value of Q as R varies. In other words, fix Q and examine how the intersection of the two curves changes as R increases. A plot of the graphs of $R(1-\mu/Q)$ for a few carefully chosen values of R and a fixed Q superimposed on the graph of $\mu/(1+\mu^2)$ will help to illustrate the changes. Figure 1 shows the intersection set for two values of R.

There are other equally valid ways to do the analysis, but the suggested method will be useful when you address Tasks 7 and 8.

Task 4. For each of the cases you found in the previous step, do a qualitative analysis of the solutions. Notice that since $\mu > 0$, the sign of the right-hand side of the model equation (4) is determined solely by the sign of

$$R\left(1-\frac{\mu}{Q}\right)-\frac{\mu}{1+\mu^2},$$

which in turn is easily determined by noting where the graph of $R(1-\mu/Q)$ lies above or below the graph of $\mu/(1+\mu^2)$.

In each case,

- create a phase line below the graph where equilibrium points and direction of flow are indicated, and
- write a description of the ecological significance of the given phase line. Why are some equilibrium points more or less dangerous than others?

You should turn the information garnered about the equilibrium points in Tasks 2–4 into information about a population of budworms modelled by equation (4). To be precise, can you answer the following questions?

- Is it possible for a population to die out?
- Is it possible for a population to grow without bound?
- For a logistic equation the carrying capacity is an asymptotically stable equilibrium point. Is the same true in this case?
- For a given set of parameters R and Q what are the possible limiting populations?

It is not necessary to include the answers to these questions in your report unless you think they will add to the content.

The bifurcations. In carrying out Task 4, you will have seen that sometimes, as you increase R, a new equilibrium point suddenly appears and then divides into two, or two equilibrium points coalesce into one and then disappear. The points (R, Q) for which this occurs are called *bifurcation points.*

At the bifurcation points the graphs of the functions $R(1-\mu/Q)$ and $\mu/(1+\mu^2)$ intersect tangentially. The curves intersecting means that

$$R\left(1-\frac{\mu}{Q}\right) = \frac{\mu}{1+\mu^2}. \tag{7}$$

The fact that the curves have the same tangent means that

$$\frac{d}{d\mu}\left\{R\left(1-\frac{\mu}{Q}\right)\right\} = \frac{d}{d\mu}\left\{\frac{\mu}{1+\mu^2}\right\}. \tag{8}$$

Task 5. Solve equations (7) and (8) for R and Q to get

$$R = \frac{2\mu^3}{(1+\mu^2)^2}, \tag{9}$$

and

$$Q = \frac{2\mu^3}{\mu^2-1}. \tag{10}$$

Plot the *bifurcation curve,* which by definition is the parametric curve defined by (9) and (10). In doing so, you should be sure to capture the important part of the curve. The interesting range for R is between 0 and about 2. The interesting range for Q is from 0 to about 40 or so.

Notice that $Q > 0$, so (10) requires that $\mu > 1$. When you use MATLAB to plot the curve, you will find that you need fairly high resolution in order to get a smooth and accurate curve.

After plotting the curve, indicate on your plot the areas where the intersection set has 1 point, and where it has 3 points. Explain what happens as we cross the bifurcation curve.

Task 6. Pick a pair (R, Q) for which there is only one positive equilibrium point, and pick another pair for which there are three. For each of these enter the differential equation (4) into `dfield6` and plot the solution μ versus τ for various initial population sizes.

The effect of an aging forest. As a forest matures, the total area of all of the leaves increases slowly. Since the leaves are food for the budworms, the carrying capacity K_B is roughly proportional to this area. On the other hand, the increasing area provides more coverage for the insects, and has the effect of lowering the predation rate. Ludwig, et al, assumed that the parameter α is also proportional to the total leaf area. The effect on our lumped parameters is that $Q = K_B/\alpha$ is roughly constant, while $R = \alpha r_b/\beta$ increases as time passes and the forest grows.

As indicated in the introductory paragraphs, R increases much more slowly than the budworm population reacts. This means that in the time it takes the solution of equation (4) to reach an equilibrium, the parameter R hardly changes, and may be considered to be a constant for this purpose. If we look at this in another way, for any particular value of R, the budworm population may be considered to be at an equilibrium point.

Task 7. Use our model to describe what happens to the budworm population as R increases. To make things specific, use $Q = 30$, and let R increase from 0.1 to about 1. Do not do any more computations. Simply use what you have already learned. You might consider that the increase takes place in small discrete steps, where for each new value of R you start the budworm population with the equilibrium value reached in the previous step, and let the population proceed to a new equilibrium. The question is, which equilibrium point and why? A refinement of what you see in Figure 1 might be useful. At some point you should observe an *outbreak* of the budworm population. Be sure to specify (in words) exactly what an outbreak consists of, where it occurs, and why.

After an outbreak the large population of budworms start eating the leaves at a rate sufficient to cause the total leaf area to decrease. As a result the parameter R now begins to decrease.

Task 8. Use our model to describe what happens to the budworm population as R decreases from a high level (≈ 1). At some point you should observe a sudden decrease in the budworm population. Specify exactly where it occurs and why. Do you see the possibility of a long term cycle in the life of a forest infested with budworms?