Session 10: The Spruce Budworm

The spruce budworm is a moth whose larvae eat the leaves of coniferous trees. It is a major pest in Canada and North America. For much of the time it persists at low numbers and does not cause much damage, but every now and then the populations become very large for a few years, and the forests are decimated. It would be useful to know how the spruce budworm alternates from one abundance to another and then persists at that abundance for some time without any apparent change in external influences.

The budworm suffer predation by birds. The birds don’t tend to search for budworms when they are scarce, but just eat those they come across. As the budworms become abundant, the birds start to actively search for them. This means that the rate at which budworms get eaten is low if budworm numbers are low, increases sharply at some point, then stabilises at a high value, once all the birds are eating their fill. Ludwig et al (1978)\(^1\) suggested a Holling’s type III equation for predation rate, \(p(X)\):

\[
p(X) = \frac{BX^2}{A^2 + X^2}.
\]

where \(B\) is the maximum predation rate and \(A\) is the number of budworms at which the predation rate is half its maximum rate.

We will assume that, without predation, the budworm population could be modelled by a logistic equation, so that we have the model:

\[
\frac{dX}{dt} = F(X) = rX \left(1 - \frac{X}{K}\right) - \frac{BX^2}{A^2 + X^2} = \left[r \left(1 - \frac{X}{K}\right) - \frac{BX}{A^2 + X^2}\right]X. \tag{1}
\]

1. Set \(X = 0 \ldots 5000\). Calculate \(p(X)\) for \(B = 200\) and \(A = 1000\), using one line of code. Plot \(p(X)\) against \(X\).

2. Add \(p(X)\) to your graph for \(A = 500\) and \(A = 2000\). What is the maximum value of \(p(X)\)? What effect does the parameter \(A\) have on \(p(X)\)?

3. Write a function, `budworm_grad`, to calculate \(F(X)\) given arguments \(X\), \(t\) and \(p\), in that order. Test it with a simple calculation.

4. Use `ode` to run the model for \(t = 0 \ldots 150\) with initial condition \(X_0 = 100\) and parameter values \(r = 0.05\), \(K = 9000\), \(A = 1000\) and \(B = 200\). Plot the result.

5. Now run the model 6 times with the same parameter values as above, but varying \(X_0\) as follows: \(X_0 = 100, 1000, 2000, 4000, 7000, 10000\). Plot the results all on the same graph. You could try to use a for-loop to do this, first setting up a vector of \(X_0\)s, and using a different value each time.

6. Repeat the above, setting \(r = 0.2\).

7. Repeat the above, setting \(r = 0.09\).

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8. Make a note of your results. If you are not sure what is happening, try some more runs of the model. Try setting $X_0 = 3000$ with $r = 0.09$.

9. We have a model which has either one or three equilibria, depending on the parameter values. When we have one equilibrium, it appears to be stable. When we have three, the middle one appears to be unstable. Let’s now have a look at the maths.

At equilibrium, $F(X^*) = 0$, so from (1), either $X^* = 0$, giving an extinct equilibrium, or

$$\left\{ r \left(1 - \frac{X^*}{K}\right) - \frac{BX^*}{A^2 + X^*^2}\right\} = 0$$

This is not a nice equation to solve, since it is cubic in $X^*$. However, we can investigate the solution graphically, by finding where the line $y = r(1 - X/K)$ cuts the curve $z = BX/(A^2 + X^2)$.

Using similar commands to those in part 1, plot $y$ and $z$ on the same graph for $X = 0 \ldots 10000$, with $r = 0.05$, $K = 9000$, $A = 1000$ and $B = 200$.

10. Add the lines for $r = 0.09$ and $r = 0.2$ in different colours.

You can see that for small values of $r$, the line and curve intersect once, i.e. we have one equilibrium at low abundance. As we increase $r$, we obtain three equilibrium points, then, if we increase $r$ further, we end up with one equilibrium again, this time at high abundance.

11. Repeat the process with $r = 0.11$ and $K = 2000$, 9000, 20000. You will need to set $X = 0 \ldots 20000$. What is the affect of changing $K$ while holding $r$ constant?

12. $F(X)$ is just the difference between the line and the curve multiplied by $X$. Since $X$ is positive, $F$ is positive when the line is above the curve, and negative otherwise. We know that for an equilibrium to be stable, we require $dF/dX\bigg|_{X^*}$, the gradient of $F$ wrt $X$ at the equilibrium, to be negative (see Handout #5, Stability Analysis for Continuous Models), so that the rate of change of $X$ is getting smaller.

Use `budworm.grad` to calculate $F(X)$ for $X = 0 \ldots 10000$, $r = 0.1$, $K = 9000$, $B = 200$ and $A = 1000$. Use `abline` to add a horizontal line along $F = 0$. We can see from this graph that the gradient is positive for the extinct equilibrium, negative for the first and third viable equilibria and positive for the middle one. Thus the model has two stable equilibria, one at small $X$ and one at large $X$.

13. Check the behaviour of the single equilibrium, i.e. set $r = 0.05$ and $r = 0.2$.

14. Parameter estimates for the real budworm population give rise to two stable equilibria. In other words, the same ecological conditions can support two different population levels. So this model can reproduce what happens in reality, although that in itself does not prove that this is the “right” model.

The model suggests that to control budworm populations in the long term we need to push the population parameters into the region where only a single low equilibrium is stable. One way to do this would be to spray the leaves with pesticide. Would this affect $r$ or $K$? How else could you control the population and what effect would this have on the parameters in the model?
15. Suppose on day 0 the population was at 2900 budworms, with $r = 0.09$ and $K = 9000$, with $A$ and $B$ as before. This set of parameter values results in two stable equilibria. Run the model to see how the population changes, and make a note of its value after 500 days.

16. Suppose we arrive on day 500 to spray the trees. If we reduce $r$ to 0.08, we would be in the parameter space with only one equilibrium, and the population could not explode while $r$ remains at 0.08. This would also reduce the equilibrium slightly. Run the model with $r = 0.08$ and initial condition the value on day 500 from part 15.

17. Now suppose that on day 0, the population was 3100 budworms. Repeat parts 15 and 16. Because the population went up to the higher equilibrium, it took much longer for the population to get down to its single equilibrium after spraying. This effect is known as hysteresis. The same effect can be obtained by varying $K$.

See also Murray (1989)\(^2\)