MATH 2208: ORDINARY DIFFERENTIAL EQUATIONS

Project 1: An Application from Ecology: Modelling the Spruce Budworm Outbreak

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§A. The Spruce Budworm

This project concerns the outbreak of an insect pest known as the North American Spruce Budworm (Choristoneura fumiferana) in Canada. The Canadians observed that the spruce budworm population underwent irruptions approximately every 40 years. For unknown reasons the budworm population would explode, devastating the forests, 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.

As is often the case in real world modeling, the models became simpler as the researchers learned which processes were critical to the dynamics of the system and which could be removed from the model without seriously affecting it usefulness.

For the rest of this project we will try to answer the question why an outbreak can happen using a mathematical model by Ludwig. Note that an outbreak means there is a sudden jump in the population of the insect.

§B. Ludwig's Model

In the paper [1], Ludwig proposes an elegant model of the spruce budworm population as follows. A key factor in determining the spruce budworm population is the available amount of foliage. Since the budworm population evolves much faster (they can increase their density 5 fold in one year) than the surrounding forest (balsam fir tree has a life span of 100 - 150 years); it is reasonable to assume that any parameter of our model that is associated to the foliage change very slowly. Indeed, for our analysis, we begin with a logistic growth model with intrinsic growth rate k and carrying capacity N where we consider these foliage parameters as constants.

Next we modify the model to account for predation by birds. We introduce a harvesting function $\eta(P)$ to get the model

$$\frac{d\mathbf{P}}{dt} = k\mathbf{P}\left(1 - \frac{\mathbf{P}}{\mathbf{N}}\right) - \eta(\mathbf{P}) \tag{1}$$

Let's see if we would can derive a plausible model for the harvesting function $\eta(P)$. The following assumptions were made in [1] based on practical observation:

(A) If the budworm density **P** reaches a critical value (which is called the saturation point) then the predation starts to level off (birds are eating as fast as they can, so it doesn't matter if there is more food available to them).

- (B) We assume there is very little predation if the budworm population **P** is small (birds don't bother looking for them and find other sources of food instead. For example, if birds decide that beetles are abundant, they will congregate around tree trunks and branches where beetles can be found, leaving the spruce budworms unmolested.)
- (C) Once the budworm population increases by a noticeable amount (but still smaller than the saturation point) the birds learn of the newer easier prey (the budworms) and then actively hunt for them!

■ Question 1 (2 points).

On your piece of paper, sketch what a graph of $\eta(P)$ should look like so that assumptions (A)-(C) are satisfied.

Solution. **Note:** Ideally your graph should look like that in the next problem. However, with the limited information from A-C, we can't guarantee that. As long as your graph of $\eta(P)$ vs. **P** is almost flat initially (B) and finally (A), and is increasing inbetween (C), you get full score.

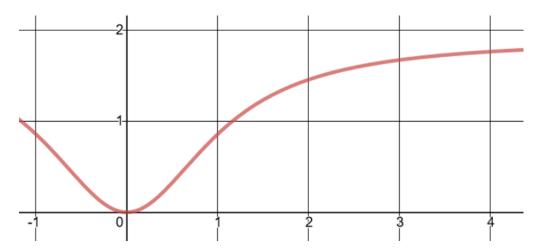
■ Question 2 (2 points).

Consider the following predation term (known as a Holling Type III predation function)

$$\eta(\mathbf{P}) = \beta \frac{\mathbf{P}^2}{\alpha^2 + \mathbf{P}^2}$$

Graph this function in Desmos (www.desmos.com). You will have the option to add a slider for each parameter, which you should do. Slide the various sliders to get a feeling for how the parameters α and β change the function. Make sure to restrict your attention to positive **P** values only. Is this function consistent with your sketch? What is different?

Solution. **Note:** As mentioned in the last problem, the desmos picture may or may not look exactly like what you had drawn before. Your answer doesn't have to be "Yes it is consistent". If it is not consistent, you should point out the difference.



■ Question 3 (2 points).

The parameters α and β are called the predation parameters. One is a measure of predation efficiency, that corresponds to the number of successful attacks by the birds and the other is known as the switching value, indicates the population at which predators begin showing increased interest in harvesting budworms. Which parameter (α or β) controls which aspect of the predation?

Solution. α controls the switching value. β controls the predation efficiency.

§C. Numerical Exploration of Solutions

For the remainder of this project, we will assume that $\beta = \alpha = 1$ and N = 10. We'll explore the behavior of our model as we change the foliage parameter k. You will need to print and attach your Matlab/Octave graph at the end of this project. So make sure to provide meaningful labels and titles in the graph. You can use separate colors for separate curves if you have access to a color printer.

\blacksquare Question 4 (2 points).

With the foliage parameter k=0.5, suppose the system is in a 'happy' or refuge state. Meaning the population is in a balance with its environment. There is no concern the budworms will destroy the entire forest. Use the 0DE45 function to approximate the solution of equation (1) with the initial value P(0) = 0.1 for $0 \le t \le 200$ and use time step size of $\Delta t = 0.1$. Use solid black lines for the plot. Refer to the 0DE45_example.m on Blackboard for a reminder how to use 0DE45.

What density (population) value is approached in t = 200?

Solution.

P(200) = 0.68338

■ Question 5 (2 points).

Let's suppose the forest canopy grows slightly, and now the foliage parameter k is slightly larger. Repeat question 4 with k = 0.53, but before you hit run read the following:

Use the 'hold on' command so that your old graph is not erased (that way you can compare the graphs). Recall that the command 'clf' will clear the figure, so make sure that command is NOT in your code. Use dashed lines for this curve.

What density (population) value is approached at t = 200? Was there a significant change?

Solution.

P(200) = 0.79891

Not a very significant change.

■ Question 6 (2 points).

Let's suppose the forest canopy grows again slightly, and now the foliage parameter k is slightly larger. Repeat question 4 with k = 0.55, but before you hit run read the following:

Get this new graph to be superimposed with the other two. Use dotted lines for this graph.

What density (population) value is approached? Was there a significant change?

Solution.

$$P(200) = 0.93175$$

Not a very significant change.

■ Question 7 (2 points).

Let's suppose the forest canopy grows again slightly, and now the foliage parameter k is slightly larger. Repeat question 4 with k = 0.58.

Again, try to get this new graph to be superimposed with the other three, but use dash-dotted lines for this graph).

What density (population) value is approached? Was there a significant change?

Solution.

$$P(200) = 7.8346$$

Yes, there is a very significant change.

■ Question 8 (1 points).

Oh no! It looks like there was an outbreak! However, you remember that k = .55 led to happy state, so you call the local forester to reduce the canopy so that the foliage is reduced. Consequently, the foliage parameter goes back to k = 0.55. Do you think the population will go back down to the safe level you had in question 6?

Solution. **Note:** Although it's a Yes/No question, either answer is acceptable. We will know for sure in the next part.

■ Question 9 (2 points).

Set your parameter k back to k = 0.55 in your code, and set the initial value to P(0) = 7.8346 (your population should have exploded to this amount in problem 7). Use the solid lines again for your plot. Then run your code.

What density (population) value is approached? Did it go back to the 'happy' state you had in question 6?

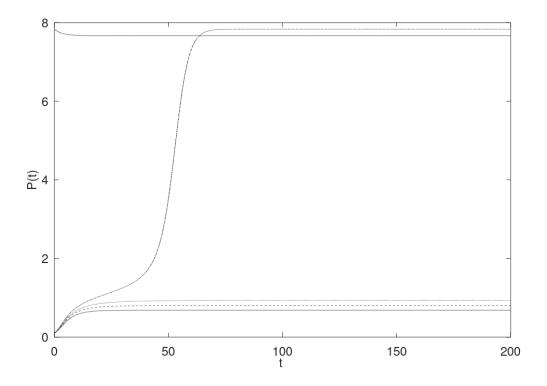
Solution.

$$P(200) = 7.6687$$

It did NOT go back to the happy state.

■ Question 10 (5 points).

Print and attach your Matlab/Octave graph.



Solution.

§D. Equilibrium solutions

■ Question 11 (1 points).

To try to make sense of all this craziness, we will use a qualitative analysis, starting with phase lines. One equilibrium solution of this model corresponds to extinction i.e. P = 0. Show that the other non-extinction equilibrium solution(s) satisfies,

$$k\left(1 - \frac{P}{10}\right) - \frac{P}{1 + P^2} = 0$$

(remember, we set N = 10).

Solution. Equilibrium solution can be obtained by solving the equation $\frac{dP}{dt} = 0$, which implies

$$kP\left(1-\frac{P}{10}\right)-\frac{P^2}{1+P^2}=0$$

Since we do not care about the extinction solution, we can get rid of the P=0 solution. Dividing both sides of above equation by P gives the required equation.

Let's use Desmos to estimate the roots (i.e. equilibrium solutions). Since only one of the terms in above equation depends on k, it would be more informative for us if we graph the two functions

$$f(x) = k\left(1 - \frac{x}{10}\right)$$
 and $g(x) = \frac{x}{1 + x^2}$

separately in Desmos. Add the slider for k and set the max and min value of k to be $0 \le k \le 1$. The solutions are the points where the two graphs intersect. You can then hover over those points in Desmos to see the approximate coordinate values.

For the next three problems you will be asked to draw phase lines. Please put them next to each other on your piece of paper.

\blacksquare Question 11 (3+1+1 points).

Set the value k = 0.5. Use the Desmos graph to estimate the equilibrium solutions and their stability. Then draw the phase line on your piece of paper. Label the equilibria with approximate numerical values.

According to your phase line, if P(0) = 0.1 what is the long term behavior of P(t)?

How does this fit with your observation in question 4?

Solution. According to the phase line P(t) goes to the equilibrium at **0.683** in the long term. This is consistent with our previous observation.

\blacksquare Question 12 (3+1+1 points).

Set the value k = 0.55. Use the Desmos graph to estimate the equilibrium solutions and their stability. Then draw the phase line on your piece of paper. Label the equilibria with approximate numerical values.

If P(0) = 0.1 what is the long term behavior of P(t)?

How does this fit with your observation in question 6?

Solution. According to the phase line P(t) goes to the equilibrium at 0.932 in the long term. This is consistent with our previous observation.

\blacksquare Question 13 (3+1+1 points).

Set the value k = 0.58. Use the Desmos graph to estimate the equilibrium solutions and their stability. Then draw the phase line on your piece of paper. Label the equilibria with approximate numerical values.

If P(0) = 0.1 what is the long term behavior of P(t)?

How does this fit with your observation in question 7?

Solution. According to the phase line P(t) goes to the equilibrium at **7.836** in the long term. This is consistent with our previous observation.

\blacksquare Question 14 (1+1 points).

Refer again to your phase line in question 12. If P(0) = 7.8346 what is the long term behavior of P(t)? How does this fit with your observation in question 9?

Solution. According to the phase line P(t) goes to the equilibrium at 7.669 in the long term. This is consistent with our previous observation.

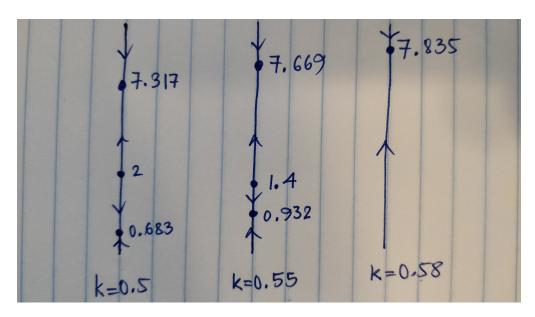


Figure 1: Three Phase Lines

§E. Bifurcation Diagram

\blacksquare Question 15 (4+2 points).

On your piece of paper, draw axes for the equilibrium values p_e (the vertical axis) and the parameter k (on the horizontal axis). Sketch the bifurcation diagram as k increases gradually from (nearly) 0 to 1 (use Desmos). Use dashed lines if the corresponding equilibrium solution branch is unstable (a source) and use a solid line if it is stable (a sink).

Label the bifurcation values in your graph (there should be two) and write down the corresponding numerical values (you can use Desmos to estimate them).

Solution. See figure 2 for the bifurcation diagram. The bifurcation values are **0.385** and **0.5595**.

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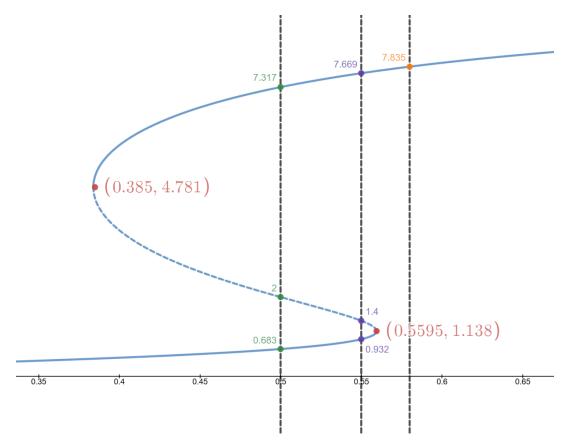


Figure 2: Bifurcation Diagram

§F. Hysteresis

This system has a bifurcation diagram containing what is known as a **hysteresis loop**. As the foliage parameter k increases over time, the equilibrium budworm population increases gradually until k moves beyond the bifurcation point. Then we suddenly have an outbreak and the equilibrium solution makes a jump to the other stable branch. At this point the budworms start to damage the trees, and consequently the foliation parameter k starts to decrease. But the stable population doesn't go back to the previous refuge state. The foliation has to decrease significantly before the budworm population again makes a sudden jump to the previous stable branch due to a death wave. At this point, the cycle restarts and the loop continues.

■ Question 16 (4 points).

Demonstrate the hysteresis loop using your bifurcation diagram. Exactly how much would you have to reduce the parameter k in order to get out of the outbreak state.

Solution. You have to reduce *k* down to **0.385**.

The actual population data [2] collected over northwestern New Brunswick between 1945 and 1980 and estimated population cycles over the past two centuries seem to support the existence of this hysteresis loop.

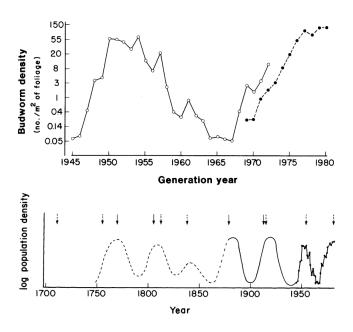


Figure 3: Picture Courtesy: T. Royama

§F. References

- [1] Ludwig, D., D. D. Jones, and C. S. Holling. "Qualitative Analysis of Insect Outbreak Systems: The Spruce Budworm and Forest." Journal of Animal Ecology 47, no. 1 (1978): 315-32. doi:10.2307/3939.
- [2] Population Dynamics of the Spruce Budworm Choristoneura Fumiferana, http://www.jstor.org/stable/1942595