MATH 221 - Differential Equations

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

Fall 2020 **Subhadip Chowdhury** **Sep 14-16**

§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 $\mathbf{P}(t)$ is the available amount of foliage. Since the budworm population evolves much faster (they can increase their density $\mathbf{5}$ fold in one year) than the surrounding forest (balsam fir tree has a life span of $\mathbf{100-150}$ years); it is reasonable to assume that any parameter of our model that is associated to the foliage change very slowly. This means that in the time it takes the solution of equation to reach an equilibrium, the intrinsic growth rate k and the carrying capacity $\mathbf{N}$ hardly changes*, and may be considered to be constants for this purpose. Indeed, for our analysis, we begin with a logistic growth model where we consider these foliage parameters as constants.

Next we modify the model to account for predation of the pests by birds. We introduce a **harvesting function $\eta(\mathbf{P})$**† to get the model

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

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

*both of these parameters depends on foliage, why?

†https://en.wikipedia.org/wiki/Greek_alphabet

(A) If the budworm population **P** reaches a critical value (which is called the **saturation point**) then the predation starts to level off (birds are eating as fast as it is physically possible, 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 point

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

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 α and β, 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?

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

Question 3. 2+2 points

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

(b) Calculate $\eta_\infty = \lim_{\mathbf{P}\to\infty} \eta(\mathbf{P})$. For what value of **P** do we have $\eta(\mathbf{P}) = \frac{\eta_\infty}{2}$?

§C. Numerical Exploration of Solutions

We'll explore the behavior of our model as we change the foliage parameter $\boldsymbol{k}$. As we mentioned earlier, for any particular value of $\boldsymbol{k}$, the budworm population reaches an equilibrium point before $\boldsymbol{k}$ can change.

For the remainder of this project, we will assume that $\beta = \alpha = 1$ and $N = 10$.

You will need to save and attach your Python Output pictures at the end of this section. So make sure to provide meaningful labels and titles in the pictures. You can use the `ODEINT_one_parameter_family.ipynb` from Moodle as a reference.

Question 4. **2 points**

With the foliage parameter $k = 0.5$, suppose the system has reached a equilibrium or refuge state, meaning the population is in a balance with its environment. There is no concern the budworms will destroy the entire forest. We would like to find the current Budworm population.

Use `ODEINT` 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 a solid black curve for the plot.

What is the approximate long-term ($t = 200$) budworm population value?

Question 5. **2 points**

Let's suppose the forest canopy grows slightly over a period of years, and now the foliage parameter k is slightly larger. Repeat question (4) with $k = 0.53$. Use a dashed red curve for for this plot. **Draw both plots in the same picture.**

What population is approached at $t = 200$? Was there a significant change in the equilibrium population?

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 $k = 0.55$. Get this new plot to be superimposed with the other two. Use a dotted green curve for this plot.

What population value is approached at $t = 200$? Was there a 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 plot to be superimposed with the other three, but use a dash-dotted blue curve for this plot.

What population value is approached at $t = 200$? Was there a significant change?

Question 8. **0 point**

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 exploded population will go back down to the safe level you had in question (6)? Make a conjecture before moving forward.

Question 9. **2 points**

Set your parameter k back to $k = 0.55$ in your code, and but this time set the initial value $P(0)$ to be the whatever answer you got for $P(200)$ in the $k = 0.58$ case (the budworm population should have exploded to this amount in question (7)). Use a solid black curve again for this plot. All your curves should be in one picture.

What population value is approached at $t = 200$? Did it go back down to the refuge state you had in question (6)?

Question 10. **5 points**

Set the figure size to be **10″** by **6″**, dpi to be **900**. Set the fontsize to be **14**. Give appropriate labels to the axes and the picture overall. Attach and upload your output picture separately or as a page in your project report.

§D. **Equilibrium solutions**

Question 11. **2 point**

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. $\mathbf{P = 0}$. Is it a stable or unstable equilibrium? Explain your reasoning.

The other **non-extinction equilibrium** solution(s) can be calculated by setting the remaining factor equal to zero as follows

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

Let's use `Desmos` to estimate the root(s) (i.e. equilibrium solutions) of above equation. 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

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

separately in `Desmos`. Add the slider for k and set the max and min value of k to be $\mathbf{0 \le k \le 1}$. 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.

Question 12. **3+1+1 points**

Set the value $k = \mathbf{0.5}$. 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 $\mathbf{P(0) = 0.1}$ what is the long term behavior of $\mathbf{P}(t)$**?**

How does this fit with your observation in question **4**?

Question 13. **3+1+1 points**

Set the value $k = \mathbf{0.55}$. 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 $\mathbf{P(0) = 0.1}$ what is the long term behavior of $\mathbf{P}(t)$**?**

How does this fit with your observation in question **6**?

Question 14. **3+1+1 points**

Set the value $k = \mathbf{0.58}$. 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 $\mathbf{P(0) = 0.1}$ what is the long term behavior of $\mathbf{P}(t)$**?**

How does this fit with your observation in question **7**?

■ Question 15. 1+1 points

Refer again to your phase line in question **13**, i.e. $k = 0.55$. If $P(0)$ is the long-term value of $P(t)$ from question (14), what is the long term behavior of $P(t)$**?**

How does this fit with your observation in question **9**?

■ Question 16. Bonus 5 points

Once you have finished answering the questions in this section, you should turn the information garnered about the equilibrium points in above questions into information about the population of budworms. To be precise, can you answer the following questions?

- Is it possible for the population to die out?
- Is it possible for the 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 k and N 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.

§E. Bifurcation Diagram

In the last section, you probably noticed that sometimes, as you increase k, a new equilibrium point suddenly appears and then divides into two, or two equilibrium points coalesce into one and then disappear. The points (k, P) for which this occurs are the bifurcation points.

■ Question 17. 5+2 points

On your piece of paper, draw axes for the population P (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).

§F. Hysteresis

This system has a bifurcation diagram containing what is known as a **hysteresis loop**. As the forest matures, foliage parameter k increases over time, the equilibrium value of budworm population increases gradually until k moves beyond the bifurcation point. Then we suddenly have an outbreak. 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 foliation parameter k now begins 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 refuge state due to a death wave. At this point, the cycle restarts and the loop continues.

■ **Question 18.** **4+2 points**

Read the above paragraph and demonstrate how the dynamical phenomenon of hysteresis loop can be understood in terms of your bifurcation diagram. Exactly how much would you have to reduce the parameter $\boldsymbol{k}$ in order to get out of the outbreak state.

Note: what we're asking here is for you to **translate** these sentences about "behavior" to sentences about the bifurcation diagram. In other words, to translate from a more "science" way of stating and understanding the observations to a more "math" way of stating and understanding them. It's an essential skill for applying math!

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.

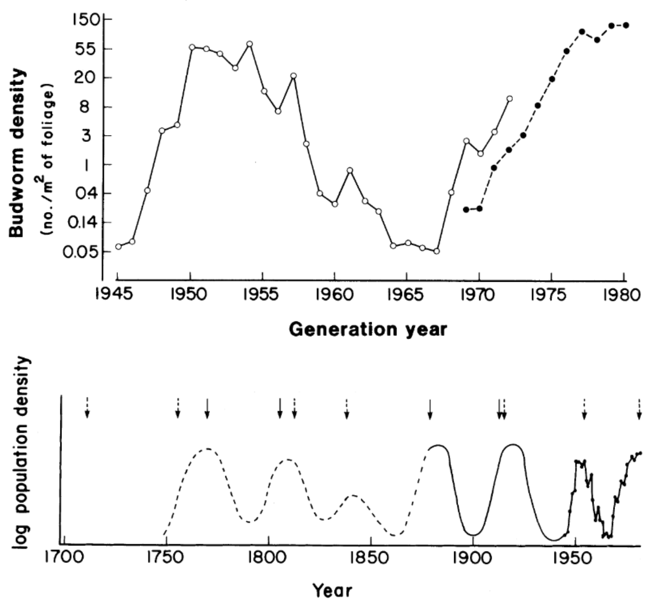

Figure 1: Picture Courtesy: T. Royama

§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

[Optional] Project 1 Extra Material: The Cusp Catastrophe

Note: This part of the project requires ideas from a Multivariable Calculus course. This is not a Bonus project. You will get no extra points for completing this part. It is only included here in case you are interested in learning more about this topic.

§G. Cusp Catastrophe

Recall that the original population model was given by

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

What if instead of fixing the value of N, we allow both k and N to vary? In this section, we will try to understand how the dependent variable P behaves as it responds to two independent control parameters k and N.

■ Question 19.

Observe that the ODE is still autonomous. Explain why the equilibrium solutions of this ODE would form a surface over the kN−plane. What is the equation of the surface?

■ Question 20.

Try graphing this surface on the computer so that you can rotate it. Set the bounds on k and N to be $0 \leq k \leq 2, 0.01 \leq N \leq 25$ and bounds of P to be $0 \leq P \leq 40$.

Use a software or website of your choice to plot the 3D picture. The following website might be helpful: https://matplotlib.org/mpl_toolkits/mplot3d/tutorial.html

■ Question 21.

Draw the plane $N = 10$ and look at the intersection of the plane with the surface. It should look like the bifurcation diagram you had obtained in your project.

■ Question 22.

Now let's find the bifurcation set of points (k, N) for our two-parameter family of ODE. It is a set of points instead of values because we have two parameters. We can do this analytically, just like we do for a one-parameter family.

(a) What are the analytic conditions for a bifurcation to occur?

(b) We would like to use above analytic conditions to find an equation for the bifurcation set in the (k, N) parameter plane. Note that we can ignore the extinction solution $P = 0$ for the purpose of finding the roots.

Check that

$$N = \frac{2P^3}{P^2 - 1}, \quad k = \frac{2P^3}{(1+P^2)^2}$$

satisfies the analytic conditions. Note that this gives a parametrized curve in kN−plane.

■ **Question 23.** □

Use your favorite software to plot the paramterized curve above. This is the bifurcation set! Is it what you expected? Explain how it relates to the full equilibrium surface in **3D**, and what it tells us about the number of equilibrium points of **P** for different values of $\boldsymbol{k}$ and **N**.

■ **Question 24.** □

Sketch the rough shape of the bifurcation diagram in following cases using pen and paper. You don't need to give the exact coordinate. Use the 3D bifurcation diagram for reference.

1. $\mathbf{N} = 2$ but $\boldsymbol{k}$ varies
2. $\boldsymbol{k} = \mathbf{0.2}$ but **N** varies
3. $\boldsymbol{k} = \mathbf{0.56}$ but **N** varies (recall that this was one the bifurcation points when $\mathbf{N} = \mathbf{10}$ and $\boldsymbol{k}$ varied)

■ **Question 25.** □

The bifurcation surface you obtained above is called a **cusp catastrophe**. Catastrophe theory is a branch of bifurcation theory. The five dynamical properties that occur together at a **cusp catastrophe** are:

(i) The behaviour is bimodal for some values of the control factors.

(ii) Abrupt catastrophic changes are observed between one mode of behaviour and another.

(iii) There is hysteresis, that is, the abrupt change from one mode of behaviour to another takes place at different values of the control factors depending on the direction of change.

(iv) There is an inaccessible zone of behaviour for some values of the control factors.

(v) Similar paths in the control space can lead to divergent behavior.

Describe how each of these dynamical properties can be understood in terms of equilibria of our two-parameter family of ODEs.