

BRINGING LIFE (SCIENCE) TO CALCULUS THROUGH COMPUTER LABORATORY PROJECTS

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Introduction

Reports including *Bio 2010: Transforming Undergraduate Education for Future Research Biologists* [2] and *Math and Bio 2010* [5] emphasize that aspects of biological research are becoming more quantitative and that there is a need to introduce future life science researchers to a greater array of mathematical and computational techniques and more sophisticated mathematical reasoning. Moreover, one of the themes discussed at the Biology CRAFTY Curriculum Foundations Project was that “Creating and analyzing computer simulations of biological systems provides a link between biological understanding and mathematical theory,” [3], and the Bio 2010 report asserts the importance for biologists to be able to use computers as tool: “Computer use is a fact of life of all modern life scientists. Exposure during the early years of their undergraduate careers will help life science students use current computer methods and learn how to exploit emerging computer technologies as they arise,” [2].

Creative solutions can be employed to achieve the desired integration of mathematical, computational, and biological content without radically changing major requirements or requiring additional credit hours of course work. Additionally, presenting quantitative approaches to biological problems to all biology majors, not just those who intend to pursue research careers, in their introductory college mathematics courses provides these students with a wider range of tools and can better motivate the mathematics. This paper focuses on one example an activity that is used in the Biocalculus II course at Benedictine University. The mathematical content of this project is the dynamical behavior of a single ordinary differential equation. The mathematics included in this rich activity include the stability analysis of equilibria, bifurcation diagrams, and parametric representations. The biology addresses the behavior of a spruce budworm population in a balsam fir forest [4]. Other sample activities are available on the author’s web site:

<http://www.ben.edu/faculty/tcomar/>

Analyzing the Spruce Budworm Model

We now present a project used in the second semester biocalculus course that analyzing a model for spruce budworm infestations due to Ludwig, Jones, and Holling [4]. The spruce budworm is an insect pest which consumes the needles of balsam fir trees. The trees ultimately die due to the removal of these needles. Typically spruce budworm population densities are low, but in an outbreak year, spruce budworms may cause significant devastation by killing up to 80% of the mature trees in a forest [1, 6]. We first describe the model and then outline the computer activity.

There are three variable quantities in this model. The first is the budworm density, N , measured in large budworm larvae/acre of land. The second, S is the number of ten square feet units of branch surface area/acre, and the third, E is a measure of food energy reserves available to the budworm. As the last two quantities change much more slowly with respect to time than the budworm density, we will consider a simplified version of the model in which S and E are assume to be constant. The budworm density is modeled by the differential equation:

$$\frac{dN}{dt} = RN \left(1 - \frac{N}{K}\right) - \beta \frac{N^2}{\alpha^2 + N^2}, \quad (1)$$

where R is the intrinsic growth rate, K is the carrying capacity, and α and β are positive parameters characterizing the predation. The first term of the right-hand side of the equation provides for logistic growth in absence of a predator. The second term is a Holling Type III functional response for predation. Specifically, when the budworm density is low, predation is low; as the budworm density increases, predation increases but only up to maximal rate of β . To make the model easier to analyze, we transform the equation into a nondimensional form via the following substitutions:

$$x = \frac{N}{\alpha}, \quad s = \frac{\beta t}{\alpha}, \quad r = \frac{R\alpha}{\beta}, \quad k = \frac{K}{\alpha}$$

The nondimensional form of Equation (1) is

$$\frac{dx}{ds} = x \left[r \left(1 - \frac{x}{k}\right) - \frac{x}{1 + x^2} \right]. \quad (2)$$

We now proceed with the activity.

1. Open up a new Maple worksheet in Worksheet Mode. Enter the command:

with(plots):with(DETools):

2. Show that the equilibrium $\hat{x} = 0$ is unstable.

To perform this step, we need to show that the value of the derivative of the right-hand side of Equation (2) with respect to x evaluated at $x = 0$ is positive. Using Maple, we obtain

$$\frac{d}{dx} \left(x \left(r \left(1 - \frac{x}{k} \right) - \frac{x}{1+x^2} \right) \right) = r \left(1 - \frac{x}{k} \right) - \frac{rx}{k} - \frac{2x}{1+x^2} + \frac{2x^2}{(1+x^2)^2}.$$

Evaluating this expression at $x = 0$, we obtain

$$\left. \frac{d}{dx} \left(x \left(r \left(1 - \frac{x}{k} \right) - \frac{x}{1+x^2} \right) \right) \right|_{x=0} = r > 0.$$

3. Let $R(x) = r \left(1 - \frac{x}{k} \right)$ and $Q(x) = \frac{x}{1+x^2}$. The nonzero equilibria of Equation (2) are the nonzero solutions of

$$R(x) = Q(x). \quad (3)$$

Let c be the value of x for which Q attains maximum value. By experimenting with simultaneous plots of R and Q , find values of k and r as requested.

- (a) Find values of k and r so that Equation (3) has one positive solution less than c .
- (b) Find values of k and r so that Equation (3) has one positive solution greater than c .
- (c) Find values of k and r so that Equation (3) has three positive solutions.

This step can be automated with the following Maple procedure.

```
plotRQ:=proc(k,r,Xmax,Ymax)
  description "This procedure plots the curves R and Q."
  local x, plotQ, plotR:
  plotR := plot(r * (1 - x/k), x = 0..Xmax, y = 0..Ymax, color = red,
    legend = "R");
  plotQ := plot(x/(1+x^2), x = 0..Xmax, y = 0..Ymax, color = green,
    legend = "Q");
  display({plotR, plotQ});
end;
```

We illustrate three plots using this procedure in Figure 1.

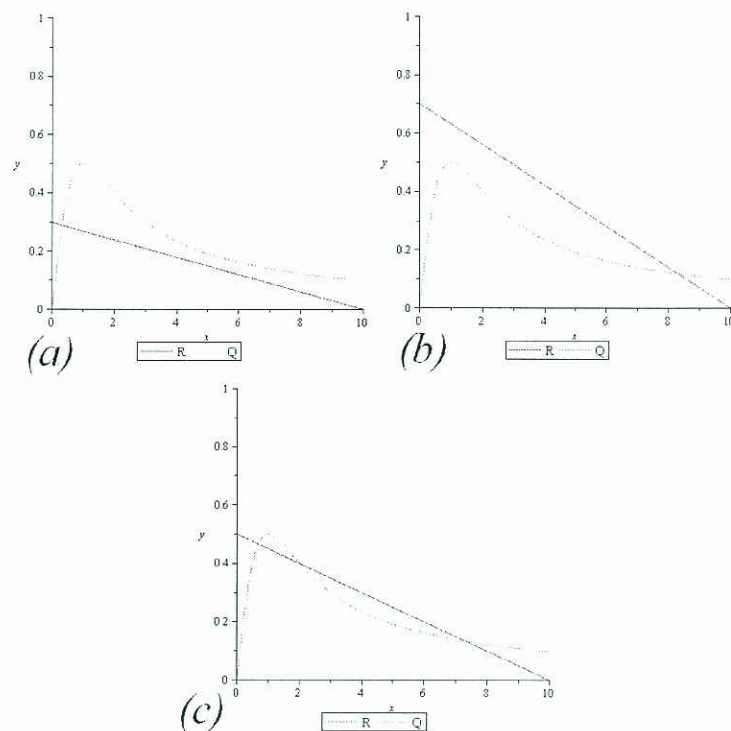


Figure 1: Simultaneous plots of the curves R and Q using the command $\text{plotRQ}(k,r,10,1)$ in the case (a) $k = 10$ and $r = 0.3$, (b) $k = 10$ and $r = 0.7$, and (c) $k = 10$ and $r = 0.5$.

4. Consider the two cases above in which you found one nonzero equilibrium. In both of the cases above, use the values of k and r that you found to plot the phase portrait of Equation (2) in the $x \frac{dx}{ds}$ -plane and use phase line analysis to determine the stability of the equilibrium point.

This step can be automated using the Maple procedure plotSBWphase below. The figures were exported to Microsoft Paint as bitmaps, and the arrows were created in that program.

```
plotSBWphase:=proc(k,r,Xmax,Ymin,Ymax)
  description "This procedure plots the phase portrait for the spruce
  budworm differential equation in the  $x \frac{dx}{dt}$ -plane.";
  plot( $r \cdot x \cdot \left(1 - \frac{x}{j}\right) - \frac{x^2}{1+x^2}$ ,  $x = 0..Xmax$ ,  $y = Ymin..Ymax$ ,
  labels = ["x", " $\frac{dx}{dt}$ "]); end;
```

From Figure 2, we observe that in both cases, the single nonzero equilibrium is locally stable. Instead of using phase line analysis, we could have numerically

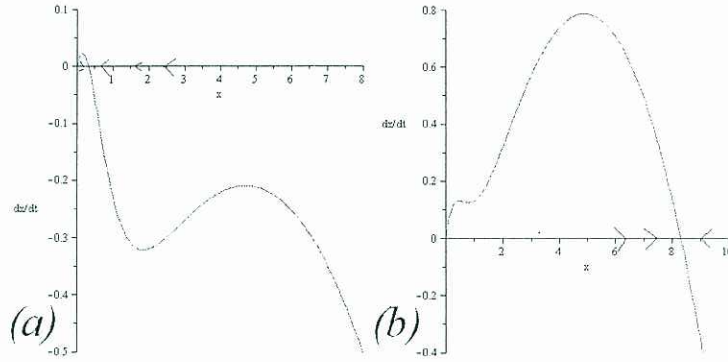


Figure 2: Phase portraits of Equation (2) using the command `plotSBWphase(k, r, Xmax, Ymin, Ymax)` in the case (a) $k = 10$ and $r = 0.3$, $Xmax = 8$, $Ymin = -0.5$, and $Ymax = 0.1$ (b) $k = 10$, $r = 0.7$, $Xmax = 10$, $Ymin = -0.4$, and $Ymax = 0.8$.

solved for the value of the equilibria, substituted the values into the derivative of the right-hand side of Equation (2), and used the stability criterion to determine stability, which is what was demonstrated for the equilibrium $\hat{x} = 0$.

5. Consider the case above in which you found three nonzero equilibria, which we denote by \hat{x}_1 , \hat{x}_2 , and \hat{x}_3 in increasing order. The equilibrium \hat{x}_1 is known as the *refuge level*; \hat{x}_2 is known as the *threshold level*; and \hat{x}_3 is known as the *outbreak level*. Use the values of k and r that you found above to plot the phase portrait of Equation (2) in the $x \frac{dx}{ds}$ -plane and use phase line analysis to determine the stability of each equilibrium point.

The result of using the command `plotSBWphase(10, 0.5, 8, -0.4, 0.4)` is given in Figure 3. Note that the arrows and labels for the equilibria have been added using Microsoft Paint.

From Figure 3, we can conclude that the equilibria \hat{x}_1 and \hat{x}_3 are locally stable and that the equilibrium \hat{x}_2 is unstable.

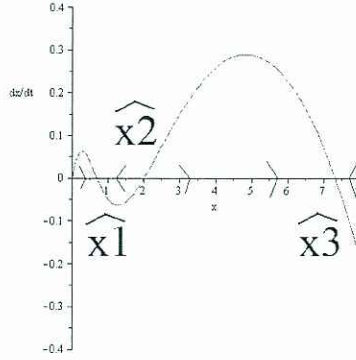


Figure 3: The phase portrait of Equation (2) using the command `plotSBW-phase(10, 0.5, 8, -0.4, 0.4)`.

6. Two nonzero equilibria occur when the curves R and Q not only intersect but also are tangent at one of the intersection points. Such behavior is an intermediate case between the cases analyzed above. We can determine all ordered pairs (k, r) for which exactly two nonzero equilibria, \hat{x}_1 and \hat{x}_3 occur by solving the system of equations

$$R(x) = Q(x) \tag{4}$$

$$\frac{d}{dx}R(x) = \frac{d}{dx}Q(x). \tag{5}$$

Solve the system for k and r in terms of x .

Using following Maple code

$$\begin{aligned} R &:= x \rightarrow r \cdot \left(1 - \frac{x}{k}\right); \quad Q := x \rightarrow \frac{x}{1+x^2}; \quad eqn1 := R(x) = Q(x); \\ eqn2 &= \frac{d}{dx}R(x) = \frac{d}{dx}Q(x); \quad solve([eqn1, eqn2], [k, r]); \end{aligned}$$

we obtain the solution

$$k = \frac{2x^3}{-1+x^2}, \quad r = \frac{2x^3}{1+2x^2+x^4}.$$

We now have a parametric representation for the cases in which there are exactly two nonzero equilibria. Observe that this parametric representation is defined for $x > 1$.

7. Plot this parametric representation in the kr -plane.

Figure 4 is plotted using the command:

$$\text{plot}\left(\left[\frac{2x^3}{-1+x^2}, \frac{2x^3}{1+2x^2+x^4}, x=1..30\right], k=0..30, r=0..0.8\right);$$

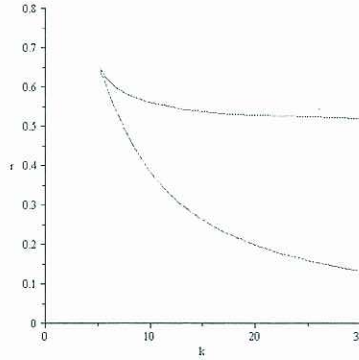


Figure 4: The plot of the parametric representation for the values of the k and r which give rise to two nonzero equilibria.

8. Notice that parametric curve has a cusp. Determine the value of the parameter x at which the cusp occurs.

This can be determined by computing $\frac{dr}{dk} = \frac{dr/dx}{dk/dx}$.

In a simplified form, we have

$$\frac{dr}{dk} = \frac{3(3-x^2)(x^2-1)^2}{2(x^2-3)(1+x^2)^3}. \quad (6)$$

Because the curve is defined only for $x > 1$, the one value of x for which this quantity is not defined is at $x = \sqrt{3}$. Notice that the case in which three nonzero equilibria occur lies inside the cusped region, and the two cases in which one equilibrium occurs lie outside the cusped region.

9. Now that we know the conditions for when two nonzero equilibria appear. Use the values of $x = 1.2$ and $x = 4$ to find the corresponding values of k and r and then plot the curves R and Q and phase portraits as in the previous cases. In both cases, determine the stability of each nonzero equilibrium.

For the case in which $x = 1.2$, we use the Maple code

```
k1 := subs (x = 1.2,  $\frac{2x^3}{-1+x^2}$ ):r1 := subs (x = 1.2,  $\frac{2x^3}{1+2x^2+x^4}$ ):
plotRQ(k1,r1,8,0.6);plotSBWphase(k1,r1,8,-1,0.4);
```

to obtain the results in Figure 5. The first equilibrium $\hat{x}_1 = \hat{x}_2$ is semistable, and the other equilibrium \hat{x}_3 is locally stable.

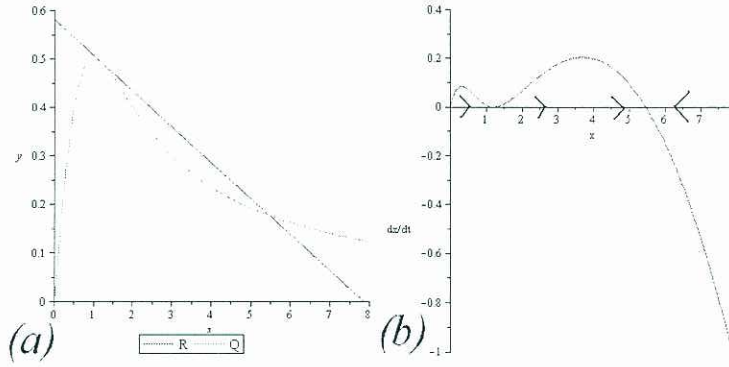


Figure 5: Both plots use the values of k and r for which $x = 1.2$. (a) Simultaneous plots of the curves R and Q . (b) The phase portrait of Equation 2.

For the case in which $x = 4$, we use the Maple code

```
k2 := subs (x = 4,  $\frac{2x^3}{-1+x^2}$ ):r2 := subs (x = 4,  $\frac{2x^3}{1+2x^2+x^4}$ ):
plotRQ(k2,r2,8,0.6);plotSBWphase(k2,r2,8,-0.6,0.1);
```

to obtain the results in Figure 6. The first equilibrium \hat{x}_1 is locally stable, and the equilibrium $\hat{x}_3 = \hat{x}_2$ is semistable.

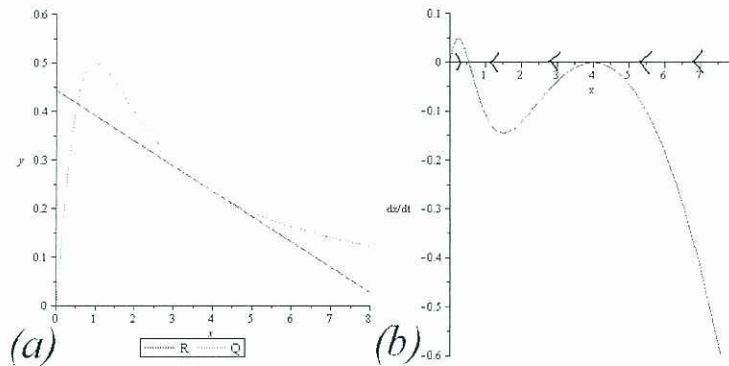


Figure 6: Both plots use the values of k and r for which $x = 4$. (a) Simultaneous plots of the curves R and Q . (b) The phase portrait of Equation 2.

10. Set $k = 10$. Create a bifurcation diagram for Equation (2) in which r is the bifurcation parameter. Observe two nonzero bifurcation values and describe the type of bifurcations that occur at these values.

The bifurcation diagram can be created with the simple Maple code:

```
unassign('r');
implicitplot( $x \left( r \left( 1 - \frac{x}{k} \right) - \frac{x}{1+x^2} \right)$ ,  $r = 0..1$ ,  $x = 0..10$ ,  $gridrefine = 5$ ,
thickness = 3)
```

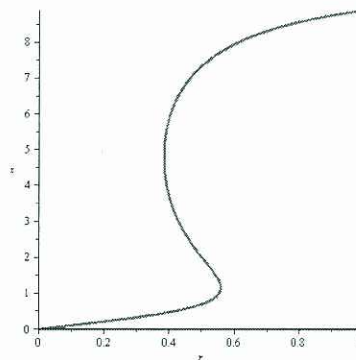


Figure 7: The bifurcation diagram for Equation (2) with $k = 10$ and bifurcation parameter r .

The bifurcations at the nonzero bifurcation values are saddle node bifurcations, which is consistent with our preceding analysis. Note that the portion of the curve connecting the two nonzero bifurcation points represents an unstable equilibrium point. (The branch of the bifurcation diagram along the r -axis also

represents an unstable equilibrium, which was determined at the beginning of the activity.)

11. Interpret the mathematical analysis in biological terms.

We have already mentioned that the equilibrium \hat{x}_1 is the refuge equilibrium and the equilibrium \hat{x}_3 is the outbreak equilibrium. The spruce budworm population remains under control until conditions change for the population to explode past the threshold equilibrium and establish a stable outbreak equilibrium. The question for pest management specialists is to determine methods to keep the population under control in the refuge state. Details on the management of the spruce budworm can be found in [6].

Acknowledgments

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References

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