



Spruce Budworm Population Model in ODE

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Abstract

The objective of this paper is to examine the model of the population growth and decline of the spruce budworm in the Northeastern region of the United States and Canada. The model, as indicated in the 1978 paper, by Ludwig, Jones, and Holling, observes the growth rate of the budworm with regards to the effects of predation and carrying capacity.

Introduction

The spruce budworm is a very destructive insect that feeds on coniferous forest, particularly the balsam fir. There are about a dozen species of the budworm, most of which are capable of destroying entire forests. Therefore, outbreaks of the insect play a very detrimental role in the flourishing of these forests.

Outbreaks have been modeled by mathematicians and ecologists by use of the cusp-catastrophe theory, which exhibits a dramatic variance in their population from inconsiderable to outstanding.

Outbreak Model

Initially disregarding any predation occurring, Ludwig et al. begins with the basic logistic model for the spruce budworm population N , given by

$$\frac{dN}{dt} = r_B N \left(1 - \frac{N}{K_B} \right),$$

where r_B represents the intrinsic birth rate of the budworm. K_B is the carrying capacity which is directly dependent upon the density of the foliage.

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As avian predators are introduced, our basic logistic model is then modified by subtracting the predation rate $p(N)$ chosen by Ludwig et al.

$$\frac{dN}{dt} = r_B N \left(1 - \frac{N}{K_B} \right) - p(N)$$

The predation rate is defined as

$$p(N) = \frac{BN^2}{A^2 + N^2},$$

where A and B are constants.

As a result, we have the Model as

$$\frac{dN}{dt} = r_B N \left(1 - \frac{N}{K_B} \right) - \frac{BN^2}{A^2 + N^2} \quad (1)$$

As predation occurs, the budworm population naturally decreases. If the consumption of prey by avian predators increases, as a result the budworm population decreases. However, the amount of predation is limited by a level of saturation. Therefore, we assume that the predation will approach an upper limit.

$$\lim_{N \rightarrow \infty} p(N) = \lim_{N \rightarrow \infty} \frac{BN^2}{A^2 + N^2} = \lim_{N \rightarrow \infty} \frac{\frac{d}{dN}(BN^2)}{\frac{d}{dN}(A^2 + N^2)} = \lim_{N \rightarrow \infty} \frac{2BN}{2N} = B$$

By using L'Hospital's Rule, we get the upper limit B . Next, we take the first derivative of $p(N)$.

$$p'(N) = \frac{d}{dN} \left(\frac{BN^2}{A^2 + N^2} \right)$$

By using Quotient Rule, we then differentiate the equation.

$$p'(N) = \frac{(A^2 + N^2)2BN - BN^2(2N)}{(A^2 + N^2)^2}$$

After some algebra, we get

$$p'(N) = \frac{2A^2BN}{(A^2 + N^2)^2}.$$



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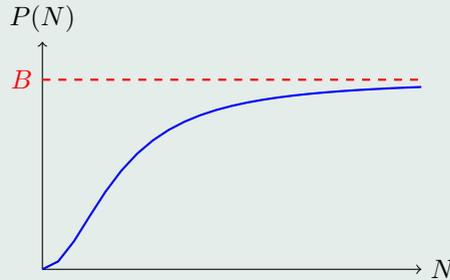


Figure 1: Graph of $p(N) = (BN^2)/(A^2 + N^2)$.

Because both A and B are constants, $p'(N)$ is positive. Therefore, the function $p(N)$ is always increasing, which is shown in Figure 1. Next, we check for concavity and find an inflection point in order to obtain a critical value.

We first use Quotient Rule to take the second derivative.

$$p''(N) = \frac{(A^2 + N^2)^2(2A^2B) - 2A^2BN [2(A^2 + N^2)2N]}{(A^2 + N^2)^4}$$

We can simplify further.

$$p''(N) = \frac{2A^2B(A^2 - 3N^2)}{(A^2 + N^2)^3}$$

We then take $A^2 - 3N^2$ and set it equal to 0 in order to find the inflection point of $p(N)$.

$$\begin{aligned} A^2 - 3N^2 &= 0 \\ N &= \pm \sqrt{\frac{1}{3}A^2} \end{aligned}$$

Because populations can only be positive, the negative value of N can be ignored. Therefore,

$$N = \sqrt{\frac{A}{3}}.$$



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This inflection point acts as a switch that determines the point at which the predation rate either increases or decreases. For values less than $\sqrt{A/3}$, the predation rate is increasing faster. For values greater than $\sqrt{A/3}$, predation rate is slower as it continues to increase toward the upper limit B .

Dimensionless Variables

To simplify our model, we introduce dimensionless variables. This is sometimes convenient when working with complicated systems. By scaling these variables, we can avoid the inclusion of units, which will further simplify our process.

There are four parameters in the Model, namely r_B , K_B , B and A . If we let

$$u = \frac{N}{A} = \frac{\text{density}}{\text{density}}, \quad \text{and} \quad \tau = \frac{Bt}{A} = \frac{(\text{density/time})(\text{time})}{\text{density}}$$

The fact that the dimensions cancel leaves us with variables without units. If we use the chain rule, we can reduce the terms in order to lessen the amount of parameters used.

By the chain rule, we get

$$\frac{dN}{dt} = \frac{dN}{du} \cdot \frac{du}{d\tau} \cdot \frac{d\tau}{dt}$$

We then simplify it

$$\frac{dN}{dt} = A \cdot \frac{du}{d\tau} \cdot \frac{B}{A}$$

Canceling the A 's, we have

$$\frac{dN}{dt} = B \cdot \frac{du}{d\tau}$$



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We then replace dN/dt with $B(du/d\tau)$ and with Au , we get

$$B \cdot \frac{du}{d\tau} = r_B \cdot Au \left(1 - \frac{Au}{K_B} \right) - \frac{BA^2u^2}{A^2 + A^2u^2}.$$

Multiply both sides by $1/B$ and cancel A^2 in predation term.

$$\frac{du}{d\tau} = \frac{Ar_B}{B} \cdot u \left(1 - \frac{Au}{K_B} \right) - \frac{u^2}{1 + u^2}$$

Notice that the equation still contains the two parameters r_B and K_B . If we let

$$r = \frac{Ar_B}{B} \quad \text{and} \quad q = \frac{K_B}{A},$$

we get

$$\frac{du}{d\tau} = ru \left(1 - \frac{u}{q} \right) - \frac{u^2}{1 + u^2}.$$

In this reformulation, u , τ , r and q are dimensionless variables, making our equation much more manageable. In this equation, the parameters in equation (1), namely r_B , K_B , B , and A have now been reduced to two parameters r and q .

Steady States

In this section, we will find the equilibrium points of the equation and use MATLAB and **dfield** to plot our results.

To find the equilibrium points, we set $du/d\tau = 0$.

$$ru \left(1 - \frac{u}{q} \right) - \frac{u^2}{1 + u^2} = 0,$$



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which is equivalent to

$$ru \left(1 - \frac{u}{q}\right) = \frac{u^2}{1 + u^2}.$$

We can see that $u = 0$ is always a solution, and the other solutions must satisfy

$$r \left(1 - \frac{u}{q}\right) = \frac{u}{1 + u^2}, \quad (2)$$

where the left hand side of the equation is the growth rate *per capita*, and the right hand side is the death rate *per capita* due to predation, both in scaled variables. See Figures 2, 3, 4, 5, and 6.

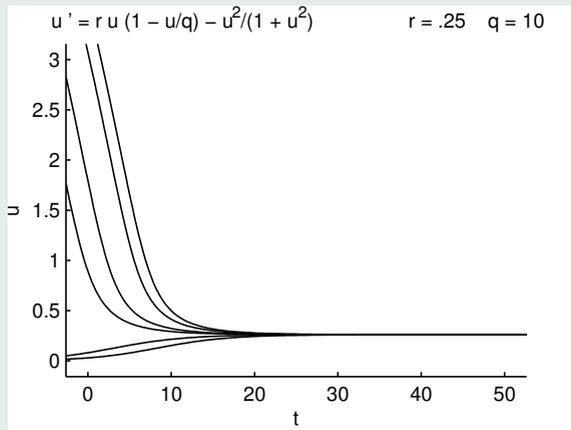
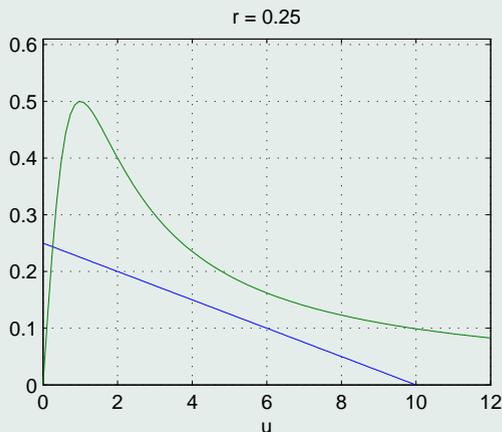


Figure 2: One equilibrium solution when $r = 0.25$.

Bifurcation

The significance of the bifurcation analysis is crucial. It will enable us to further analyze the behavior of the budworm population as the model exhibits several steady states and equilibria. As q remains



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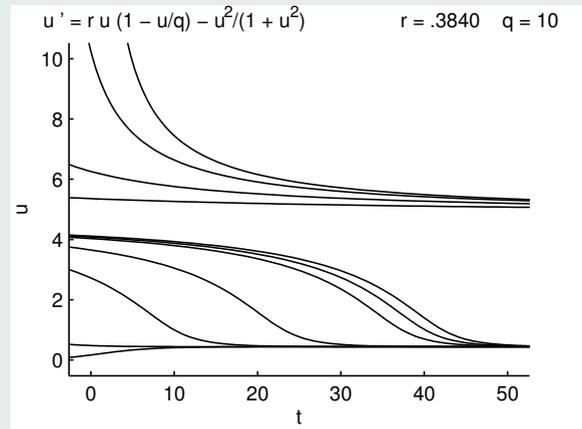
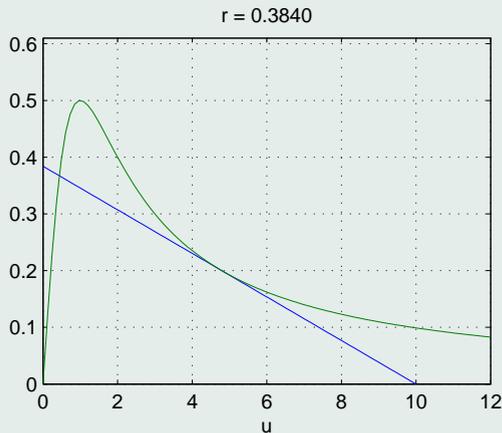


Figure 3: As the reproduction rate increases to $r = 0.38$, we get a stable equilibrium solution and a semi-stable equilibrium solution. The stable equilibrium solution is called the *refuge equilibrium*, and the point tangent to the curve is called the *outbreak equilibrium*.



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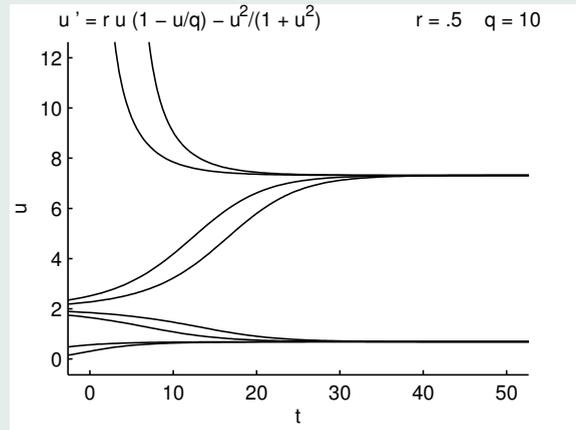
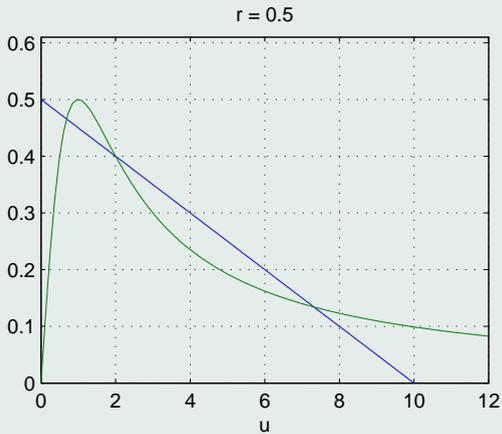


Figure 4: As r continues to increase, there now exists three equilibrium points when $r = 0.5$, two of which are stable and one is unstable.

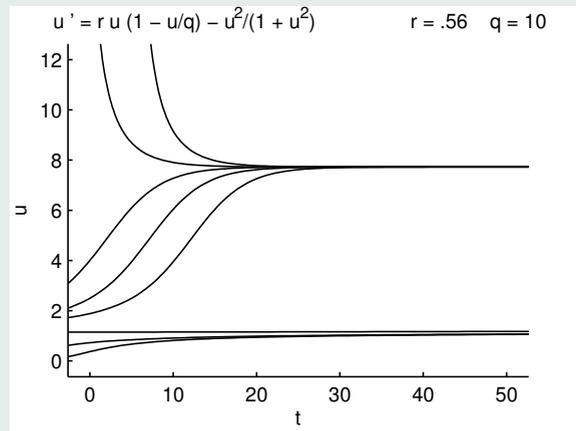
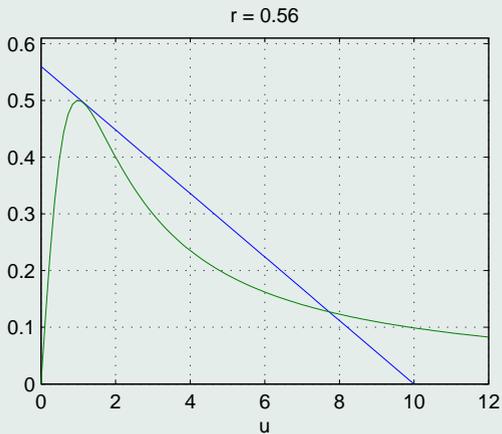


Figure 5: Here, there is a semi-stable equilibrium solution that is tangential to the death rate. This semi-stable equilibrium exhibits a *saddle node* bifurcation.

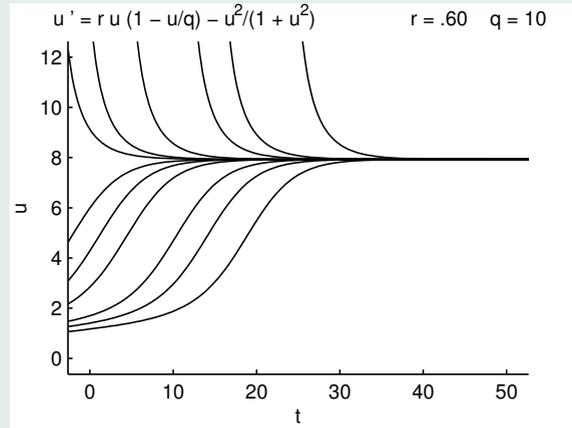
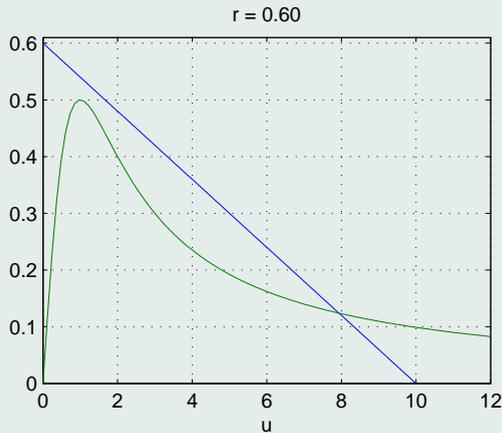


Figure 6: With a fixed value of $q = 10$, for any value of $r > .56$, there will only exist one equilibrium solution. The figure shows one equilibrium solution when $r = 0.60$.

fixed and r increases, the model undergoes several stages where the steady states vary from containing one, two, or three equilibrium solutions. These equilibria will either be stable, unstable, or semi-stable. If we let

$$y_1 = r \left(1 - \frac{u}{q} \right),$$

and

$$y_2 = \frac{u}{1 + u^2}$$

We then set them equal to each other, where

$$y_1 = y_2,$$

we can see all of the solutions will occur where the death rate equals the birth rate (point of intersection).



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However, the semi-stable solutions occur when the reproduction rate reaches a value in which the curves are tangent. In order to determine the values of r and q where the curves are tangent, we take the derivatives of each curve and find out where they are equal.

$$\frac{dy_1}{du} = \frac{dy_2}{du}$$

To differentiate both sides of our equation, we start with

$$\frac{d}{du} \left[r \left(1 - \frac{u}{q} \right) \right] = \frac{d}{du} \left[\frac{u}{1 + u^2} \right],$$

then differentiate both sides with respect to u .

$$-\frac{r}{q} = \frac{1 - u^2}{(1 + u^2)^2}$$

Multiply by $-q$ on both sides and solve for r .

$$r = \frac{q(u^2 - 1)}{(1 + u^2)^2} \quad (3)$$

Now that we have solved for r , we can substitute it back into equation (2) to solve for q .

$$\frac{q(u^2 - 1)}{(1 + u^2)^2} \left(1 - \frac{u}{q} \right) = \frac{u}{1 + u^2}$$

Distribute the q and multiply both sides by $(1 + u^2)^2$.

$$(qu^2 - q) \left(1 - \frac{u}{q} \right) = \frac{u(1 + u^2)^2}{(1 + u^2)}$$

After some algebra, we get

$$qu^2 - u^3 - q + u = u(1 + u^2)$$



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We can simplify further.

$$qu^2 - q = 2u^3$$

Now solve for q .

$$q = \frac{2u^3}{u^2 - 1}$$

Now that we have q , we can substitute it back into the equation (3) and solve for r .

$$r = \left[\frac{2u^3}{u^2 - 1} \right] \cdot \left[\frac{u^2 - 1}{(1 + u^2)^2} \right]$$

Cancel the $u^2 - 1$ terms and get

$$r = \frac{2u^3}{(1 + u^2)^2}$$

Now we are able to sketch a parametric graph in rq -space. This will enable us to get a clear reference to understand the values of r and q that will render one, two or three clear equilibrium solutions. Regions with three equilibrium solutions contain two stable and one unstable equilibria. However, any values of r and q that lie directly on the curves (boundaries) will render one stable and one semi-stable equilibrium solution. These curves indicate where the budworm population drastically changes. See Figure 7.

Cusp Catastrophe

We saw in our bifurcation analysis that the graph of $q = 0$ and $q \neq 0$ displays two very different situations. The graphs in the ru -plane (see Figure 8) can render one, two or three equilibria, and their stability jumps significantly. Notice that as r increases, the solutions remain stable until $r=.3840$. At this point, there suddenly occurs another equilibrium solution. As r increases even further, we experience a third equilibrium solution, where two are stable and one is unstable.

If we compare the graphs from Figure 8 with the graphs of Figures 2-6 we can see how they relate. Notice that when r reaches a value of roughly .56 (as shown in Figure 5), the stable equilibrium dramatically increases in the u -direction at point B to point D. This suggests that the budworm population



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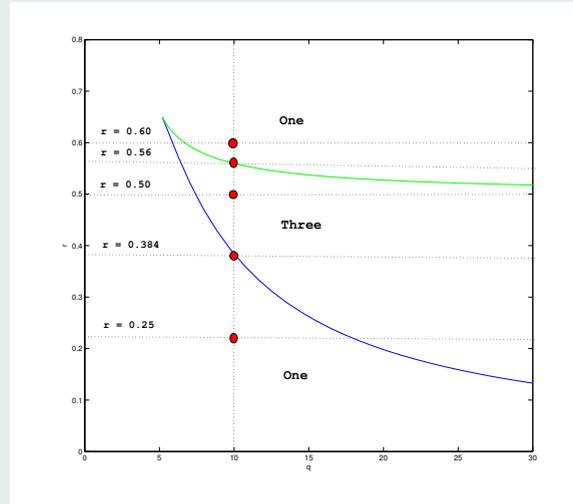
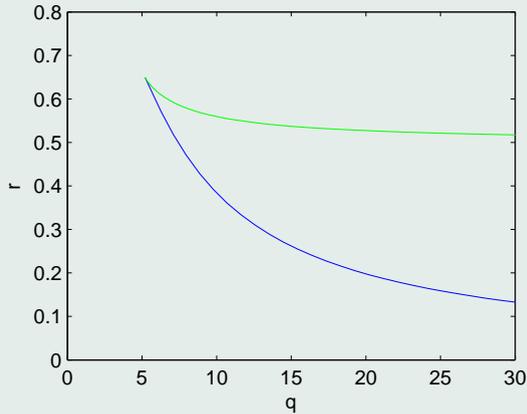


Figure 7: The figure on the left shows the graph of the cusp in the qr -plane. The figure on the right shows a detailed depiction of the varying r -values and a fixed q -value that correlates to Figures 2-6. In the case where $r = .25$, there exist exactly one equilibrium solution. The case where $r = .3840$ and $r = .56$, there exists one stable and one unstable equilibrium, which occurs along the boundaries. The case where $r = .5$ occurs three equilibria, two stable, and one unstable.



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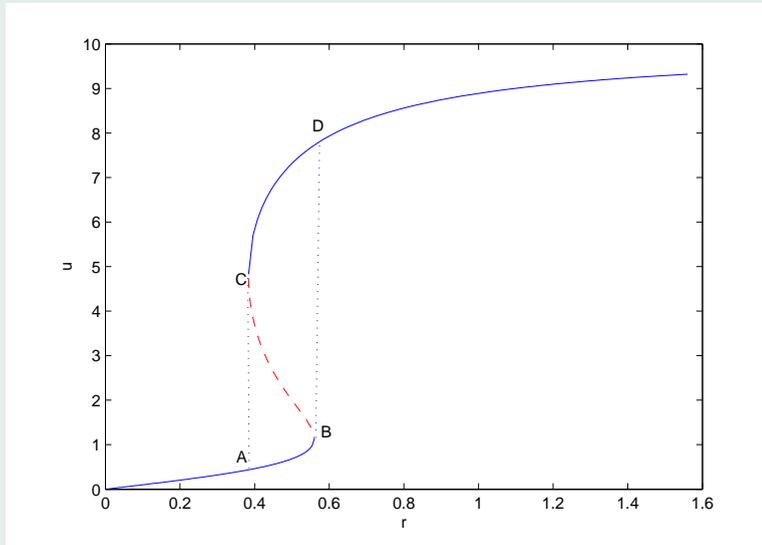


Figure 8: The *hysteresis effect* of the curves on the ru plane.

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undergoes a significant increase in their population. The point at which this occurs is known as the *cusps* of the graph in the rq plane. The term *cusps catastrophe* refers to “explosion” of the population of this pest when their reproductive rate reaches a certain level.

The same cannot be said when the r -values are *decreasing*. As the r -values decrease, the u -values remain high until point C is reached (see Figure 8), then the u -value suddenly decreases back to point A. Notice that in doing so, it took a different and much longer path to suddenly decrease in u -values than it did to increase.

Figure 9 shows a three-dimensional contour graph of the complete model in qru -space. The graph on the left displays the contours as r increases. This graph gives a 3D depiction of what happens when r reaches a value of roughly .56 (as compared with Figure 8), the contour *folds* and the stable equilibrium dramatically increases in the u -direction to the upper surface of the model. The graph on the right in Figure 9 shows the contours as q increases. Notice the similarities of the this graph when $q = 10$ in comparison with that of the hysteresis effect.

Conclusion

Upon examination of the models and graphs we have created, it is now clear to see the behavior of the spruce budworm population. We observe a dramatic increase in the population when it reaches a certain level. However, the same cannot be said as the population recedes, as it takes much longer for their populations to decrease than to increase. Thus, the coniferous forests are constantly threatened as the budworm population explodes into an almost uncontrollable outbreak.

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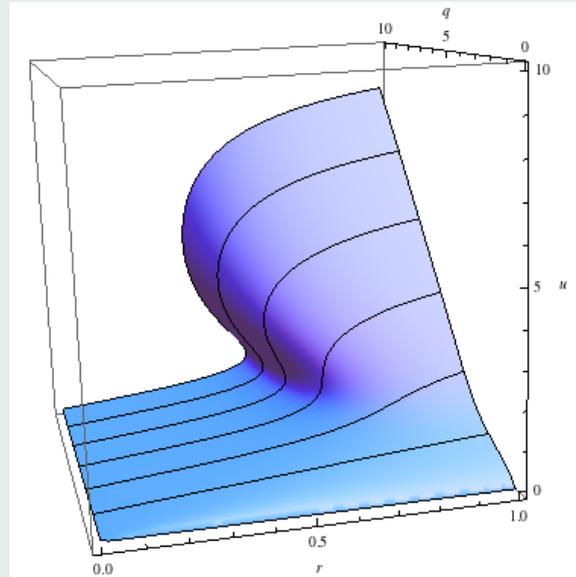
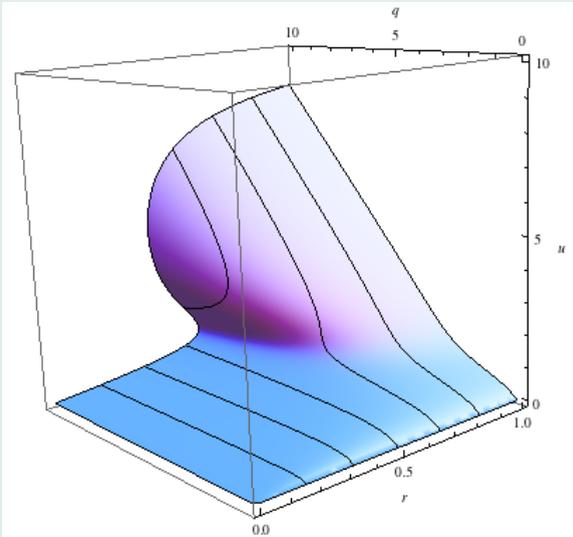


Figure 9: The figure on the left displays an emphasis of the contours as r increases. The figure on the right shows the contours as q increases.

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