MATH 221 Biocalculus II
Enrichment

Goals

- BIO: To examine the effects of nutritional enrichment in two species predator-prey interactions.
- MATH: To perform stability analysis on a system of nonlinear differential equations.

Computational Tool: Maple

Introduction

We will study the following predator-prey (or exploiter-victim) model analyzed by Rozenzweig [1]:

$$\frac{dN}{dt} = rN\left(1-\frac{N}{K}\right) - aP(1-e^{-cN}) \tag{1}$$

$$\frac{dP}{dt} = baP(1-e^{-cN}) - dP \tag{2}$$

Here, N represents the density of the prey, and P represents the density of the predator. For this particular investigation, we will think of N as a plant species and P as an herbivore species that eats the plant. The model assumes that the plant species grows logistically in the absense of the herbivore species, with growth parameter r and carrying capacity K. We can think of e^{-cN} as the probability of an individual plant not being consumed by the herbivore. Hence $a(1-e^{-cN})$ is the number of plants consumed by an individual herbivore in a unit of time. The parameter b is the conversion rate from consumption to births of new individuals in the herbivore species. We assume a death rate of d for the herbiovore species.

The phenomenon that will investigate here is the effect of nutritional *enrichment* of the plant species on the entire two-species population. Enrichment is the process of increasing the nutrient flow to the plant species, which in turn increases the carrying capacity K for the plant species in the ecosystem. We will interpret enrichment in our model as an increase in K.

For this investigation, we set the parameter values to be $r = 1.5$, $a = 1$, $b = 1$, $c = 0.1$, and $d = 0.95$. As the analysis depends on using different values of K, we will assign specific values to K as needed.

1. In terms of the parameters, find the nullclines of this system. The nontrivial dP/dt nullcline should be a vertical line, and the dN/dt should be express P as a function of N. We are specificially interested in the nontrivial equilbrium of this system. Find the coordinates of the nontrivial equilibrium $(\hat{N}, \hat{P})$ in terms of the parameters. Notice that $\hat{N}$ does not depend on K.
2. Prepare a blank Maple worksheet by loading in the *DETools*, *plots*, *LinearAlgebra*, and *VectorCalculus* packages.
3. Enter the values of your parameters (except for K) in Maple. (You will come back to this input line momemtarily with your value of K.)
4. Enter the system of differential equations into Maple.
5. We will now analyze this system for a "small" value for K. Now set $K = 34$ and perform the following steps in Maple.
   (a) Set $K = 34$ in Maple in the line with your other parameter values.
   (b) Let $N0 = \hat{N}$. Enter $N0$ into Maple in terms of the parameters. Let $P0 = \hat{P}$. Enter $P0$ into Maple in terms of $N0$ and the remaining parameters.

(c) Enter the system of differential equations into Maple.

(d) Create a plot in the (N, P)-plane containing the plots of the nontrivial nullclines found above, the nontrivial equilibrium point, and the solution with initial conditions $N_0 = 50$, $P_0 = 50$. Print out this plot.

(e) Notice that dN/dt nullcline is concave down and has a single local maximum. Let $N^\star$ denote the N-coordinate of this local maximum point. Also note whether the dP/dt nullcline lies to the left or right of this local maximum point.

(f) Observe (by checking sample values) that dN/dt is positive below its nullcline and negative above its nullcine. Observe that dP/dt is negative to the left of its nullcline ($N = \hat{N}$) and positive to the right of its null cline.

(g) Using your printed plot, perform graphical analysis to determine the stability of the nontrivial equilibrium.

(h) Confirm the graphical analysis symbolically by computing the Jacobian of the system, evaluating it at $(\hat{N}.\hat{P})$, and by computing the determinant and trace of the resulting matrix.

(i) Create a plot of N and P versus t using $N_0 = 50$ and $P_0 = 50$. This graph should also confirm the graphical and numerical analysis.

(j) What does the analysis indicate about whether the system will persist or be in danger of extinction? What does the system indicate about the proficiency of the herbivore in relation to the availability of the plant?

6. Now consider the larger value $K = 200$ and repeat the same steps as in the $K = 34$ case. (To save time, either cut and paste your Maple code, or simply change the value of K and re-evaluate the worksheet). What does the analysis indicate about whether the system will persist or be in danger of extinction? What does the system indicate about the proficiency of the herbivore in relation to the availability of the plant?

7. Experiment with several other values of K by repeating the steps above. What conclusions can you make about whether the system will persist or die out based on the positions of $\hat{N}$ and $N^\star$?

8. We will observe that $N^\star$ increases with K while the dP/dt nullcline $N = \hat{N}$ remains fixed as K increases. We will then be able to draw a conclusion about the effect of enrichment (increasing K!) on the ecosystem. The following steps should be completed in terms of the parameters.

   (a) We previously expressed the nontrivial dN/dt nullcline as P as function of N. Using this equation, compute dP/dN.

   (b) The value $N^\star$ is the value of N that makes dP/dN equal to zero. Solving for $N^\star$ explicitly is not possible. Instead, set dP/dN equal to zero and solve for K. Replace N by $N^\star$ in this new equation so that we have K as a function of $N^\star$.

   (c) We want to show that $dN^\star/dK$ is positive to obtain our desired result. Consider a point (n, k) on the graph of the function K of $N^\star$ in the previous step. The Inverse Function Theorem, guarantees that $dN^\star/dK(k)$ is positive if and only if $dK/dN^\star(n)$ is positive. Compute $dK/dN^\star$.

   (d) Using the fact that the Taylor series for e^x at $x = 0$ is given by $e^x = \sum_{i=0}^{\infty} \frac{x^i}{i!}$ conclude that $dK/dN^\star$ is positive for $N^\star > 0$ and $c > 0$.

9. Finally, draw a conclusion about the whether the two species ecosystem will persist or become extinct when significant enrichment is provided for the plant species.

References

[1] M.L. Rosenzweig, "Paradox of Enrichment: Destabilization of Exploitation Ecosystems in Ecological Time," *Science* **171**, 385-387, 1971.