**STUDENT VERSION**

An Invitation to Mathematical Ecology: Visualizing Predator-Prey Cycles

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**Abstract:** In mathematical ecology models, the existence of trajectories that exhibit cyclic behavior is a very important result. These trajectories are also called limit cycles. In general, finding limit cycles, or showing that there are no limit cycles to a system are difficult problems. In this modeling scenario, we propose a gentle introduction to limit cycles using nullcline analysis and a spreadsheet graphical approach via the fourth-order Runge-Kutta method. We will be offering three predator-prey models, each more complex and realistic than the previous. We choose the nullcline method as a way to support students coming from Calculus and we choose the use of a spreadsheet, instead of commercial software, to make the activity accessible and in support of open access to educational resources. In analyzing systems of predator-prey equations, these two methods along with the equilibrium analysis present a way to detect and analyze special solutions of differential equations.

**Keywords:** predator-prey, limit cycles, fourth-order Runge-Kutta method, geometry of cycles

**Tags:** limit cycles, fourth-order Runge-Kutta, nullcline analysis

**SCENARIO DESCRIPTION**

We offer a predator prey modeling activity in which nullcline analysis and spreadsheet graphics render structured approaches to modeling.

1 Introduction

A predator eats while a prey gets eaten. As a result, the prey species decreases in number which in turn increases predator abundance due to diminishing food resources. With less predators, the prey species rebound and the the circle of life continues...
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This pleasing result in nature can be captured by differential equations using elementary methods, such as nullcline analysis and spreadsheet graphing. In this short modeling scenario, we will only highlight the use of nullclines to geometrically detect limit cycles and how to produce the corresponding graphs for these limit cycles. The analysis may then proceed, for example, to analyze stability of the limit cycles, the structural stability of the system itself, or a bifurcation analysis; these topics are not covered here.

3 Three Models of Predation

Investigations on predator-prey cycles have been a rich source of research activity in the past 100 years since Lotka published his mathematical model of autocatalytic chemical reactions in 1910 and Volterra published similar set of equations in 1926, [1], [3], [5]. Here, we consider three models of predation (see models (1), (2), (3)) where \( x(t), y(t) \) represent the population of the prey and predator species, respectively. The first model is the Lotka-Volterra model,

\[
\begin{align*}
\frac{dx}{dt} &= x(r - ax) = F_1(x, y) \\
\frac{dy}{dt} &= y(-s + ax) = G_1(x, y)
\end{align*}
\]  

(1)

The second model is a variant of the first where the growth of the prey species is assumed to be logistic with carrying capacity \( K \),

\[
\begin{align*}
\frac{dx}{dt} &= x \left( r - \frac{x}{K} - ay \right) = F_2(x, y) \\
\frac{dy}{dt} &= y(-s + ax) = G_2(x, y)
\end{align*}
\]  

(2)

The third model is a variant of the second where the interaction terms between the predator and the prey species is of the Michaelis-Menten type; with saturation:

\[
\begin{align*}
\frac{dx}{dt} &= x \left( r - \frac{x}{K} - \frac{ay}{q} \right) = F_3(x, y) \\
\frac{dy}{dt} &= y \left( -s + \frac{ax}{q} + \frac{x}{q + x} \right) = G_3(x, y)
\end{align*}
\]  

(3)

These models were intentionally chosen to demonstrate increasing complexity in models. Moreover, pedagogically speaking, these models will guide our students in understanding the theory we present here step-by-step. In particular, the nullclines for model (1) are horizontal and vertical lines, one of the nullclines for model (2) is a decreasing line, and one of the nullclines for model (3) is a parabola.

3 Nullcline Analysis

The nullcline method is a simple yet geometrically insightful way of analyzing dynamical systems. For a system of two first-order differential equations in variables \( x \) and \( y \), the nullcline method involves investigating planar curves obtained by setting the derivatives equal to zero (hence, the prefix null). Consider

\[
\begin{align*}
\frac{dx}{dt} &= F(x, y), \\
\frac{dy}{dt} &= G(x, y).
\end{align*}
\]
The $x'$ and $y'$ nullclines are the curves $F(x, y) = 0$ and $G(x, y) = 0$, respectively. The points where the $x'$ nullclines intersect the $y'$ nullclines are the equilibrium points of the system. Note that in many textbooks, the $x'$ nullclines are called $x$ nullclines; we believe that using $x'$ is a more student-friendly label for the nullclines.

Nullcline analysis consists of first sketching the nullclines for the system and realizing the sub-regions that will come from the relative positions of the two nullclines. The next step is to analyze the direction of the vector fields in each of these sub-regions; in predator-prey models, we consider only the first quadrant. The directions of the vector field will then help in visualizing the existence of predator-prey limit cycles.

For example, consider the first model (1). The $x'$ nullclines and $y'$ nullclines are, respectively,

$$
\begin{align*}
\{ x(r - ay) = 0 & \Rightarrow x = 0 \text{ or } y = \frac{r}{a} \} \\
\{ y(-s + ax) = 0 & \Rightarrow y = 0 \text{ or } x = \frac{s}{aa} \}
\end{align*}
$$

These nullclines divide the first quadrant into four sub-regions I, II, III, and IV, as illustrated, see Figure 1.

![Figure 1](image.png)

**Figure 1.** The $x'$ and $y'$ nullclines are the thick and thin lines, respectively. These nullclines intersect at the origin and at the coexistence equilibrium $P$. They divide the first quadrant into four sub-regions I, II, III, and IV. We choose a test point for each region to determine the direction of the vector field. The number $\epsilon > 0$ is chosen such that the test point stays in the region.

The next step is to evaluate the sign of $F_1$ and $G_1$ at each of the test points for each of the sub-regions I,
II, III, IV. For example, considering model (1), we have

\[
\begin{aligned}
\text{Region I:} & \quad F_1(P_I) < 0 \quad \text{and} \quad G_1(P_I) > 0 \uparrow, \\
\text{Region II:} & \quad F_1(P_{II}) < 0 \quad \text{and} \quad G_1(P_{II}) < 0 \downarrow, \\
\text{Region III:} & \quad F_1(P_{III}) > 0 \quad \text{and} \quad G_1(P_{III}) < 0 \downarrow, \\
\text{Region IV:} & \quad F_1(P_{IV}) > 0 \quad \text{and} \quad G_1(P_{IV}) > 0 \uparrow.
\end{aligned}
\]

The resulting vector direction can be obtained by adding up the vector directions; for example, in Region I, since $F_1(P_I)$ gives a vector pointing to the west and $G_1(P_I)$ gives a direction pointing north, the resultant direction is a vector pointing northwest. See Figure 2.

![Diagram](image)

**Figure 2.** The purple arrows result from taking the sum of the vectors $F_1(P_I)$ and $G_1(P_I)$ for region I, where $P_I$ is the test point for region I. Apply a similar reasoning to the other regions.

We observe that there is a counter-clockwise circulation of vectors forming a set of closed orbits concentric to the coexistence equilibrium $P$. Mathematically, what causes this circulation of vectors around $P$? The answer comes from the purely imaginary eigenvalues of the Jacobian. The Jacobian is the gradient of the first order derivative and the eigenvalues represent the condition of stability. The Jacobian at $P$:

\[
J(P) = J \left( \frac{s}{\alpha}, \frac{r}{\alpha} \right) = \begin{pmatrix} 0 & \frac{\tau}{\alpha} \\
\frac{-\tau}{\alpha} & 0 \end{pmatrix}.
\]

where the trace (the sum of the elements in the diagonal matrix) $\tau = 0$, the determinant which is the scalar value associated with the square matrices $\Delta = rs > 0$, and the discriminant (which tells us if there is one,
two, or no solutions to the system) \( \tau^2 - 4\Delta = -4rs \) of the characteristic equation is negative. Since \( \tau = 0 \), notice that the coexistence equilibrium can become a spiral sink or a spiral source with a slight change in the system. Moreover, the Jacobian at the origin tells us that the origin is a saddle with the \( x \)-axis as its stable manifold and the \( y \)-axis as its unstable manifold:

\[
J(0, 0) = \begin{pmatrix}
r & 0 \\
0 & -s
\end{pmatrix},
\]

Finally, it is an important pedagogical step to guide the students in thinking about interpreting the mathematics result: what is the ecological meaning of this cyclic behavior of trajectories around the coexistence equilibrium? Ecologically speaking, what does it mean when the origin is a saddle? In order to visualize the evolution or time-series of the solutions, we proceed to solve the system using an approximation solution method called Runge-Kutta.

4 Runge-Kutta Method

Mathematics software currently used by professionals include commercial products such as Matlab, Mathematica, and Maple. To support the teaching and learning of differential equations in an open access setting, we recommend using a spreadsheet, which is often under-rated, to perform elementary experiments of differential equations. We utilize the fourth-order Runge-Kutta method (RK4) to sketch the time-evolutions or time-series of our limit cycle.

The fourth-order Runge-Kutta method to solve a system of two differential equations is given by

\[
\begin{aligned}
x_{n+1} &= x_n + \frac{h}{6}(k_1 + 2k_2 + 2k_3 + k_4) \\
y_{n+1} &= y_n + \frac{h}{6}(l_1 + 2l_2 + 2l_3 + l_4),
\end{aligned}
\]

where \( k_i, l_i \) are steps given by

\[
\begin{aligned}
k_1 &= hf(t_n, x_n, y_n) \\
l_1 &= hg(t_n, x_n, y_n) \\
k_2 &= hf(t_n + \frac{h}{2}, x_n + \frac{k_1}{2}, y_n + \frac{l_1}{2}) \\
l_2 &= hg(t_n + \frac{h}{2}, x_n + \frac{k_1}{2}, y_n + \frac{l_1}{2}) \\
k_3 &= hf(t_n + \frac{h}{2}, x_n + \frac{k_2}{2}, y_n + \frac{l_2}{2}) \\
l_3 &= hg(t_n + \frac{h}{2}, x_n + \frac{k_2}{2}, y_n + \frac{l_2}{2}) \\
k_4 &= hf(t_n + h, x_n + k_3, y_n + l_3) \\
l_4 &= hg(t_n + h, x_n + k_3, y_n + l_3)
\end{aligned}
\]

with \( h \) the step-size. By implementing the fourth-order Runge-Kutta method to model (1) and using the graphing capabilities of Excel, we produce graphs as in Figure 3. Observe that the variable \( t \) is considered the parameter. There are four limit cycles on the right (because the graphs for prey and predators have 4 peaks), corresponding to each time-periodic picture on the left.

See the supplementary Excel file for the implementation of the RK4 method to the model (1).
Figure 3. The sketch on the left is the time-series or evolution graphs for the prey $x(t)$ and the predator $y(t)$. The graph on the right is the corresponding limit cycle. These pictures are produced in Excel using the Runge Kutta 4th order method. The time series may be used to visually estimate the period of the (approximately periodic) behavior of the prey and predator.

The parameter values that were used to create this model were $r = 1$, $\alpha = 0.2$, $s = 0.9$, $a\alpha = 0.2$, and the time increment was 0.5.

Teaching and Learning Activities for Students

1. For each of models (2) and (3), do the following:
   (a) Compute the $x'$ and $y'$ nullclines.
   (b) Sketch the nullclines. Produce a graph similar to Figure 1.
   (c) Choose test points for each of the sub-regions.
   (d) Determine the signs of $\frac{dx}{dt}$ and $\frac{dy}{dt}$ of the respective $F$ and $G$ functions at your chosen test points.
   (e) Determine the direction of the vector fields in each of the sub-regions. Do you geometrically confirm the existence of a limit cycle? Explain.
   (f) Use the attached Excel file to generate the time-series and limit cycles for the model. Visual approximate a period for the prey and predator interactions.

2. Consider model (1). Add a harvesting term to each differential equation, as follows:
   \[
   \begin{align*}
   \frac{dx}{dt} &= x(r - \alpha y) - h_1x, \\
   \frac{dy}{dt} &= y(-s + a\alpha x) - h_2y.
   \end{align*}
   \]

   Repeat the steps above to this new model. Where is the coexistence equilibrium of the new model in relation to the old model? What conditions on the parameter guarantee non-extinction?

3. Consider models (2) and (3). As in the previous problem, add harvesting terms to each equation and analyze the resulting model using the steps shown above.
References


