

Lotka Volterra Predator-Prey Model with a Predating Scavenger

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Abstract

The classic Lotka Volterra equations are used to model the population dynamics between two species: a predator and its prey. This analysis will look at the population dynamics of a three-species Lotka Volterra model: a predator, a scavenger and their common prey. We will use a set of parameters that result in stable limit cycles and the coexistence of the three species.

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1 Introduction to Population Dynamics and the Lotka-Volterra Model

We can use mathematics to predict biological situations. Population dynamics models the growth or decline of species, and enables us to predict trends over time. The classic two dimensional Lotka-Volterra predator-prey model uses a nonlinear system of equations that includes logistic growth of two species, and a predatory factor that will have an adverse effect on the prey population. The classic Lotka-Volterra predator-prey model is given by:

$$\begin{cases} x' &= x(1 - y) \\ y' &= y(-c + x), \end{cases}$$

where c is the death rate of the predator. The solution of the classic system would behave as shown in figure 1.

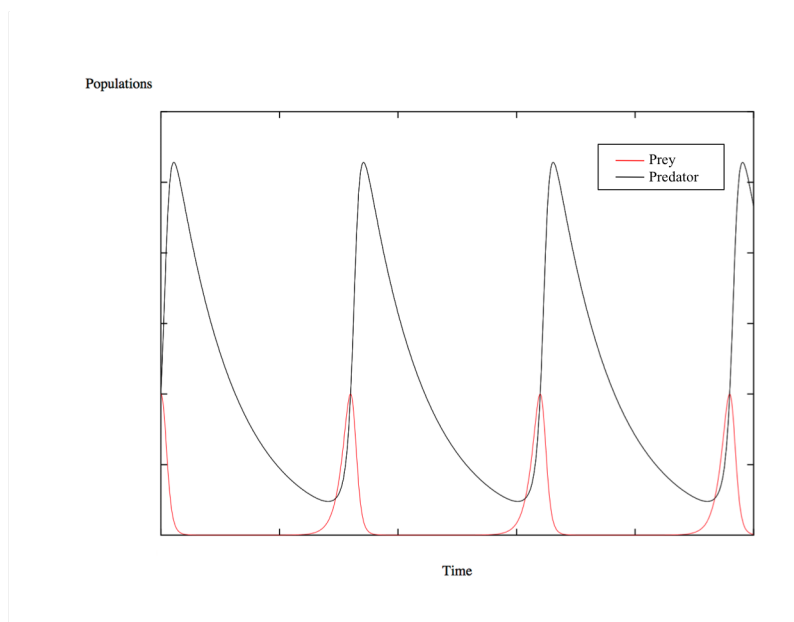


Figure 1: The behavior of the predator and prey populations over time for the classic model.

The populations are represented as a pair of lagging, oscillating curves over time. The predator population will grow according to the amount of prey. If the prey population is large, the predators will have more food to support a larger population. However, when the predator population grows too large, the prey begins to die off. This will result in a decrease in the predators. This trend continues as time goes on, implying a stable coexistence of the two populations.

The modified two dimensional Lotka-Volterra predator-prey model also uses a nonlinear system of equations that includes logistic growth of two species, a carrying capacity of the prey, and a predatory factor. The modified Lotka-Volterra predator-prey model is given by:

$$\begin{cases} x' &= x(1 - bx - y) \\ y' &= y(-c + x), \end{cases}$$

where b is the carrying capacity of the prey and c is the death rate of the predator. The solution of the modified system would behave as shown in figure 2.

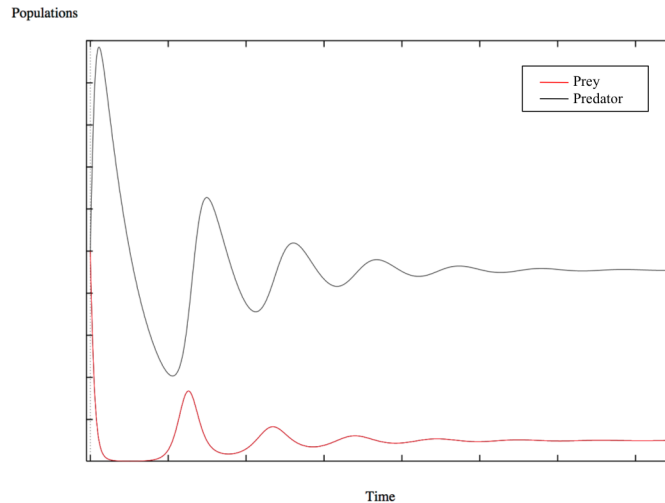


Figure 2: The behavior of the predator and prey populations over time for the modified model.

In the modified model, we find that the populations start as a pair of oscillating curves, but over time the amplitude of the oscillations decrease with each period of time until the curves flatten out. This implies that the populations experienced a stable, coexistence that saturates after sometime such that the populations will remain constant.

2 Preliminaries

2.1 Linearization of Nonlinear Systems

To analyze a nonlinear system, must linearize the system in order to classify the fixed points and predict local trajectories around the fixed points [4]. Given a system of two nonlinear differential equations

$$\begin{cases} \dot{x} &= f(x, y) \\ \dot{y} &= g(x, y), \end{cases} \quad (1)$$

we find a fixed point of the system (x_0, y_0) where $f(x_0, y_0) = 0$ and $g(x_0, y_0) = 0$. We then make a change of variables to translate the origin to the fixed point such that

$$u = x - x_0, v = y - y_0.$$

We then expand the translated system using a Taylor series expansion. First, we will expand the u -equation:

$$\begin{aligned}
\dot{u} &= \dot{x} \\
&= f(x_0 + u, y_0 + v) \\
&= f(x_0, y_0) + u \frac{\partial f}{\partial x} + v \frac{\partial f}{\partial y} + O(u^2, v^2, uv) \\
&= u \frac{\partial f}{\partial x} + v \frac{\partial f}{\partial y} + O(u^2, v^2, uv)
\end{aligned}$$

Similarly the v -equation is given by

$$\dot{v} = u \frac{\partial g}{\partial x} + v \frac{\partial g}{\partial y} + O(u^2, v^2, uv).$$

Note that $O(u^2, v^2, uv)$ represents quadratic terms in u and v . Since we want a linear system, and because we are looking only at a small area around the fixed point, we only take the first order terms of the expansion, and the small, higher order terms are truncated. Thus, it follows that the system will behave according to the linearized system:

$$\begin{pmatrix} \dot{u} \\ \dot{v} \end{pmatrix} = \begin{pmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix}$$

Now, the Jacobian is defined to be:

$$J = \begin{pmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} \end{pmatrix}.$$

We can also apply the Jacobian to a third order system of nonlinear equations.

2.2 Use of Eigenvalues in Classifying Stability

We want to solve a linear system, where $\dot{\mathbf{x}}$ is a general system of linear equations. We will find straight-line trajectories that start on one coordinate axis and follow that axis exhibiting exponential growth or decay as $t \rightarrow \pm\infty$. We will find these trajectories of the form $\mathbf{x}(t) = e^{\lambda t} \mathbf{v}$, where λ is an eigenvalues of the system.

We consider $\dot{\mathbf{x}}$, a general system of differential equations:

$$\begin{aligned}
\dot{x} &= ax + by \\
\dot{y} &= cx + dy.
\end{aligned}$$

We want to solve the linear system $\dot{\mathbf{x}} = A\mathbf{x}$, where $\dot{\mathbf{x}}$ the general system of linear equations, \mathbf{x} is the eigenvector, corresponding to an eigenvalues λ , and

$$A = \begin{pmatrix} a & b \\ c & d \end{pmatrix}.$$

We will find eigensolutions \mathbf{x} . This is done by solving the characteristic equation

$$\det(A - \lambda I) = 0,$$

which will yield

$$\lambda^2 - \tau\lambda + \Delta = 0,$$

where

$$\tau = \text{trace}(A) = a + d \text{ and } \Delta = \det(A) = ad - bd.$$

By solve the characteristic equation, we find eigenvalues

$$\lambda_1 = \frac{\tau + \sqrt{\tau^2 - 4\Delta}}{2} \text{ and } \lambda_2 = \frac{\tau - \sqrt{\tau^2 - 4\Delta}}{2}.$$

When λ_1 and λ_2 are distinct the corresponding eigenvectors \mathbf{x}_1 and \mathbf{x}_2 are linearly independent. An initial condition \mathbf{x}_0 can be writing as a linear combination, $\mathbf{x}_0 = c_1\mathbf{x}_1 + c_2\mathbf{x}_2$. The general solution for $\mathbf{x}(t)$ is

$$\mathbf{x}(t) = c_1e^{\lambda_1 t}\mathbf{v}_1 + c_2e^{\lambda_2 t}\mathbf{v}_2.$$

This is a solution since it is a linear combination of the general system $\dot{\mathbf{x}} = A\mathbf{x}$, and it satisfies the initial condition $\mathbf{x}(0) = \mathbf{x}_0$.

Rewriting Δ and τ in terms of λ_1, λ_2 such that $\Delta = \lambda_1\lambda_2$ and $\tau = \lambda_1 + \lambda_2$, we can see that the sign of the eigenvalues determines the stability. We can classify the stability of the fixed points based on the sign of the eigenvalues as shown in the figure below [4]:

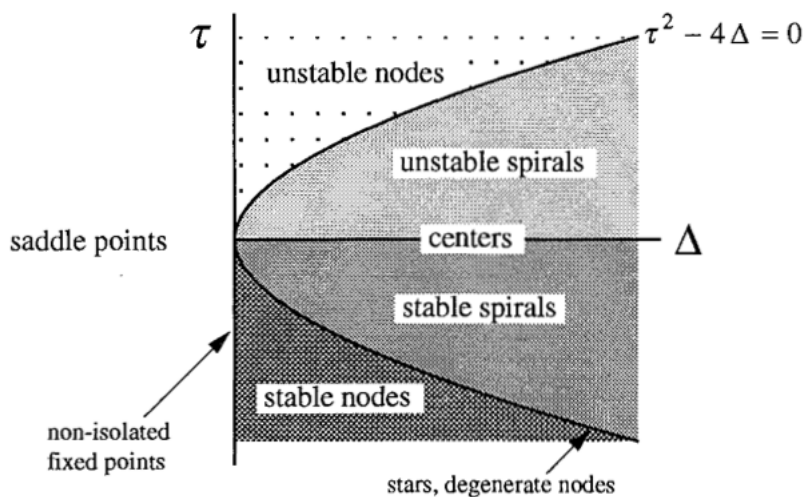


Figure 3: Fixed Point Stability Classification

By finding eigensolutions of our nonlinear systems, we can predict the trajectories and classify the stability of our model.

2.3 Bifurcations

The model we are using depends on parameters. This means that the flow of the system changes as parameters are varied. These changes in dynamics are called bifurcations. Bifurcations can create new fixed points, destroy existing fixed points, or change the stability of fixed points. In our model, we will look at a specific type of bifurcation called a Hopf bifurcation. These occur when two complex conjugate eigenvalues cross the imaginary axis. We will see two specific types of Hopf bifurcations: supercritical and subcritical. A supercritical Hopf bifurcation results in a stable limit cycle and a subcritical Hopf bifurcation results in an unstable limit cycle. We will look at an example of both of these. Consider the system of equations:

$$\begin{cases} \dot{x} = y \\ \dot{y} = -x + ay - x^2y. \end{cases} \quad (2)$$

By looking at the phase planes of system (2), we can see when the Hopf bifurcation occurs:

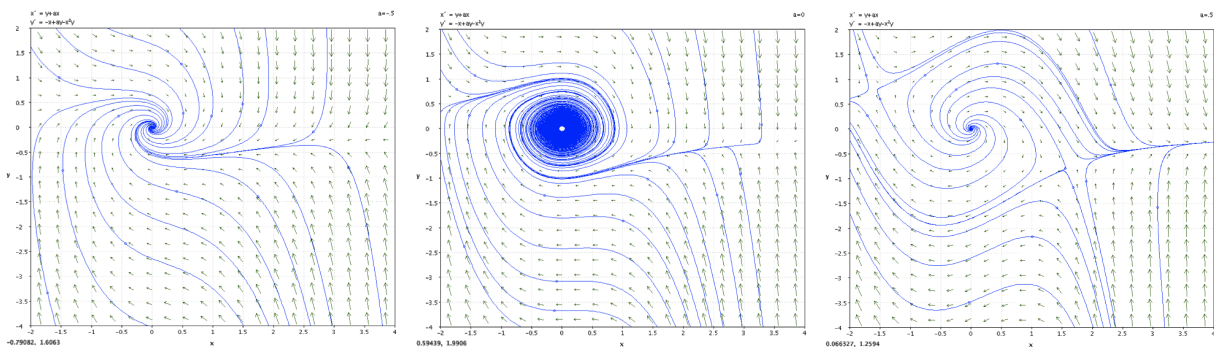


Figure 3: Phase planes of system (2) where $a = -0.5$ (left), $a = 0$ (center), $a = 0.5$ (right).

A supercritical Hopf bifurcation occurs when $a = 0$ which results in a stable limit cycle centered at the origin. Note that the trajectories spiral into the limit cycle.

Now, consider the system of equations:

$$\begin{cases} \dot{x} = -y + ax + xy^2 \\ \dot{y} = x + ay - x^2. \end{cases} \quad (3)$$

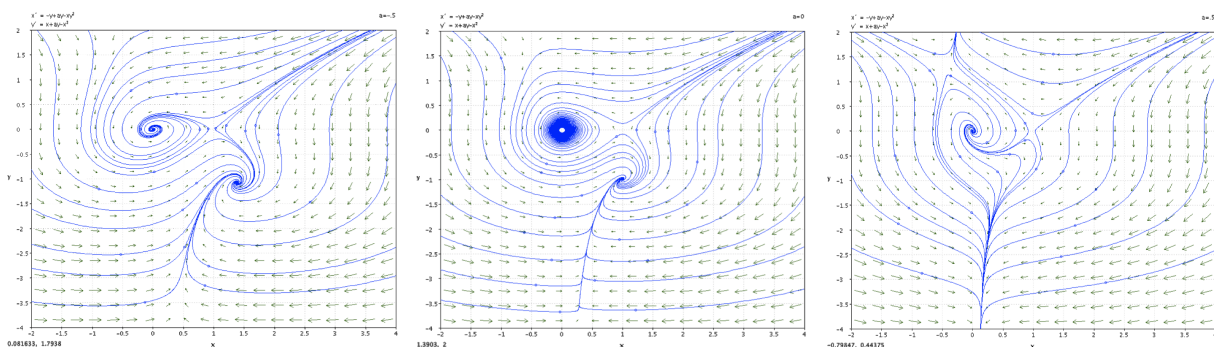


Figure 4: Phase planes of system (3) where $a = -0.5$ (left), $a = 0$ (center), $a = 0.5$ (right).

A subcritical Hopf bifurcation occurs when $a = 0$. This results in a unstable limit cycle centered at the origin in which local trajectories spiral out from the limit cycle.

2.4 Routh-Hurwitz Theorem

Consider an n degree polynomial:

$$P(\lambda) = a_n \lambda^n + a_{n-1} \lambda^{n-1} + \dots + a_1 \lambda + a_0,$$

where $a_i \in \mathbb{R}$ for $i = 0, 1, \dots, n$, and $a_n > 0$, and $a_0 \neq 0$. The construction of the Routh Array is as follows,

$$\begin{bmatrix} a_n & a_{n-2} & a_{n-4} & \cdots \\ a_{n-1} & a_{n-3} & a_{n-5} & \cdots \\ b_{n-1} & b_{n-3} & b_{n-5} & \cdots \\ c_{n-1} & c_{n-3} & c_{n-5} & \cdots \\ \vdots & \vdots & \ddots & \end{bmatrix},$$

where the b_i, c_i, \dots coefficients

$$\begin{aligned} b_{n-1} &= \frac{a_{n-1}a_{n-1} - a_n a_{n-3}}{a_{n-1}} \\ b_{n-3} &= \frac{a_{n-1}a_{n-4} - a_n a_{n-5}}{a_{n-1}} \\ &\vdots \\ c_{n-1} &= \frac{b_{n-1}a_{n-3} - a_{n-1}b_{n-2}}{b_{n-1}} \\ c_{n-3} &= \frac{b_{n-1}a_{n-5} - a_{n-1}b_{n-3}}{b_{n-1}} \\ &\vdots \end{aligned}$$

are generated until coefficients in subsequent columns are equal to zero and the n th row of the array is reached. Then, we analyze the first column of coefficients in the array for changes in sign. For each change in sign going down the column, there exists a root. If all coefficients are positive, such that there does not exist a sign change in the first column, then the roots of the n degree polynomial are stable, meaning they have negative real parts. If there exists a sign change, this implies that the roots are unstable, meaning they have positive real parts [2].

3 Three Dimensional Lotka Volterra Model

We consider the modified three dimensional Lotka-Volterra model, a system of differential equations modeling the population dynamics of a predator Y , a scavenger Z , and the prey X ,

$$\begin{cases} \frac{dX}{d\tau} = X(A - BX - CY - DZ) \\ \frac{dY}{d\tau} = Y(-E + FX) \\ \frac{dZ}{d\tau} = Z(-G - HZ + IX + JY), \end{cases} \quad (4)$$

where,

- A is the growth rate of X
- B is related to the carrying capacity of X
- C is the rate of change of the X due to the presence of Y
- D is the rate of change of X due the the presence of Z
- E is the natural death rate of Y
- F is the rate of change of Y due to the presence of X
- G is the natural death rate of Z
- H is related to the carrying capacity of Z
- I is the rate of change of Z due the the presence of X
- J is the rate of change of Z due to the presence of Y .

We assume all parameters are positive and all variables are non-negative. Now, we will find a change of coordinates to transform system (4).

$$\begin{aligned} \frac{dX}{d\tau} &= X(A - BX - CY - DZ) \\ \frac{dY}{d\tau} &= Y(-E + FX) \\ \frac{dZ}{d\tau} &= Z(-G + HZ + IX + JY) \end{aligned}$$

Using $t = A\tau$ we achieve the following system:

$$\begin{aligned}\frac{dX}{dt} &= X\left(1 - \frac{B}{A}X - \frac{C}{A}Y - \frac{D}{A}Z\right) \\ \frac{dY}{dt} &= Y\left(-\frac{E}{A} + \frac{F}{A}X\right) \\ \frac{dZ}{dt} &= Z\left(-\frac{G}{A} - \frac{H}{A}Z + \frac{I}{A}X + \frac{J}{A}Y\right)\end{aligned}$$

Considering the change of variables $x = \frac{F}{A}X$, $y = \frac{C}{A}Y$, and $z = \frac{D}{A}Z$, the system becomes the following:

$$\begin{aligned}\frac{dx}{dt} &= x\left(1 - \frac{B}{F}x - y - z\right) \\ \frac{dy}{dt} &= y\left(-\frac{E}{A} + x\right) \\ \frac{dz}{dt} &= z\left(-\frac{G}{A} - \frac{H}{D}z + \frac{I}{F}x + \frac{J}{C}y\right)\end{aligned}$$

Renaming the constants $b = \frac{B}{F}$, $c = \frac{E}{A}$, $e = \frac{G}{A}$, $f = \frac{I}{F}$, $g = \frac{J}{C}$, and $h = \frac{H}{D}$, we obtain the final system for the scavenger model where $x' = \frac{dx}{dt}$, $y' = \frac{dy}{dt}$, and $z' = \frac{dz}{dt}$:

$$\begin{cases} x' &= x(1 - bx - y - z) \\ y' &= y(-c + x) \\ z' &= z(-e - hz + fx + gy). \end{cases} \quad (5)$$

The new system will behave similarly to the original system where each new variable and coefficient is related to the variables and coefficients of system (4). We can now begin our analysis of this new simplified system.

4 Analysis of the Coordinate Planes

Since our three dimensional system is invariant, we can look at each planar system individually. We will look at the behavior of the predator-prey population in the absence of the scavenger, the predator-scavenger population in the absence of the prey, and the scavenger-prey population in the absence of the predator.

4.1 The Predator-Prey System

By analyzing the xy plane alone, we can predict the behavior of a predator-prey model:

$$\begin{cases} x' = x(1 - bx - y) \\ y' = y(-c + x) \end{cases} \quad (6)$$

We find the equilibrium points $(0, 0)$, $(c, 1 - bc)$, $(\frac{1}{b}, 0)$. We can find the eigenvalues of the Jacobian. For our system (6),

$$J = \begin{pmatrix} 1 - 2bx - y & -x \\ y & -c + x \end{pmatrix}.$$

Now, we calculate the Jacobian for each equilibrium point.

$$J|_{(0,0)} = \begin{pmatrix} 1 & 0 \\ 0 & -c \end{pmatrix}.$$

Since $J(0, 0)$ is diagonal, it follows that the eigenvalues are 1 and $-c$. Since c must be greater than zero, the eigenvalues differ in sign. This implies that the point $(0, 0)$ is a saddle node, with the y -axis at the stable manifold and the x -axis as the unstable manifold. Next, we look at $J(\frac{1}{b}, 0)$:

$$J|_{(\frac{1}{b}, 0)} = \begin{pmatrix} -1 & \frac{1}{b} \\ 0 & -c + \frac{1}{b} \end{pmatrix}.$$

Since $J(\frac{1}{b}, 0)$ is an upper triangular matrix, we can conclude that the eigenvalues are 1 and $-c + \frac{1}{b}$. Thus, if $c < \frac{1}{b}$, then the eigenvalues differ in sign, and $(\frac{1}{b}, 0)$ is a saddle node with a stable manifold in the positive x -axis. If $c > \frac{1}{b}$, then the eigenvalues are both negative, then $(\frac{1}{b}, 0)$ is a stable node. If $c = \frac{1}{b}$, then the critical point is a singular stable node. Now, we look at the last critical point in the analysis of the xy plane. Note that

$$J|_{(c, 1-bc)} = \begin{pmatrix} -bc & -c \\ 1 - bc & 0 \end{pmatrix}.$$

Here we can calculate the characteristic polynomial,

$$\lambda^2 + bc\lambda + c - bc^2,$$

and find the eigenvalues to be

$$\frac{-bc + \sqrt{b^2c^2 - 4(c - bc^2)}}{2}, \frac{-bc - \sqrt{b^2c^2 - 4(c - bc^2)}}{2}.$$

Here, we can see that if $bc = 1$, then the point behaves as the previous critical point $(\frac{1}{b}, 0)$. If $1 - bc > 0$, then the eigenvalues are negative, and we have stable equilibrium. Now, we analyze the value under the square root to determine when the eigenvalues are real:

$$\begin{aligned}
 b^2c^2 - 4(c - bc^2) &> 0 \\
 b^2c^2 - 4c + 4bc^2 &> 0 \\
 b^2c - 4 + 4bc &> 0 \\
 b^2c + 4bc &> 4 \\
 bc(b + 4) &> 4 \\
 bc &> \frac{4}{b + 4}.
 \end{aligned}$$

So, when $bc > \frac{4}{b+4}$, the eigenvalues are real, and the critical point is a stable node. Thus, if $bc < \frac{4}{b+4}$, then the eigenvalues are imaginary, and it is a stable spiral. When $1 - bc < 0$, the equilibrium point is not applicable biologically.

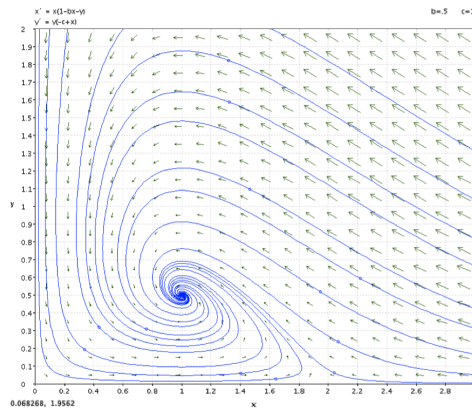


Figure 5(a): The phase plane of the predator-prey system when $c < \frac{1}{b}$ and $bc < \frac{4}{b+4}$.

The phase plane in figure 5(a) shows that the trajectories near the equilibrium will spiral into the fixed point, showing coexistence of the predator and prey.

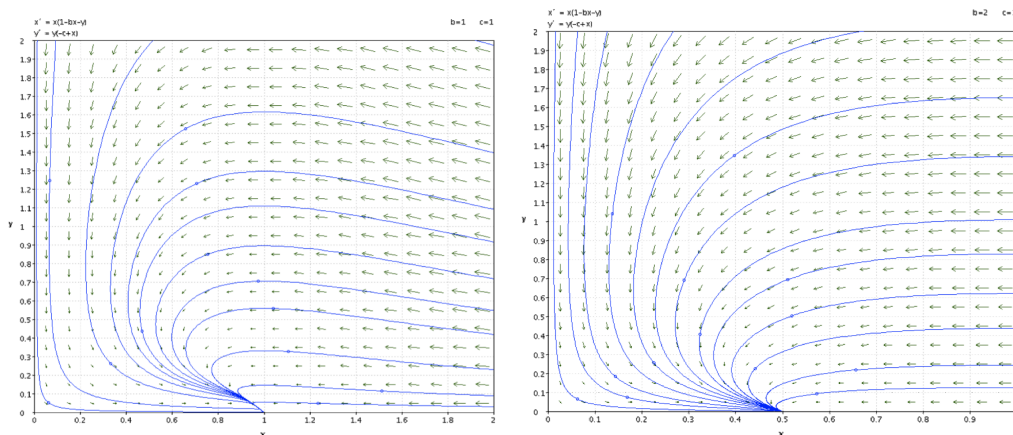


Figure 5(b): The phase planes of the predator-prey system when $c = \frac{1}{b}$ (left) and $c > \frac{1}{b}$ (right).

In both cases in figure 5(b), all trajectories flow to the x -axis. This means in either of these cases the predator population will die off, and only the prey will survive.

4.2 The Predator-Scavenger System

An analysis of the yz plane represents a predator-scavenger system, and is given by the system,

$$\begin{cases} y' = -cy \\ z' = z(-e - hz + gy). \end{cases} \quad (7)$$

Similarly to our analysis of the xy plane. By setting the equations of (7) equal to each other, we find the critical points $(0, 0)$ and $(0, -\frac{e}{h})$. Since $(0, -\frac{e}{h})$ does not occur in the first quadrant, we can ignore this point, as it is of no biological relevance. Now, we find the Jacobian of system (7):

$$J = \begin{pmatrix} -c & 0 \\ gz & -e + 2hz \end{pmatrix}.$$

Computing the Jacobian at our equilibrium point, we find

$$J|_{(0,0)} = \begin{pmatrix} -c & 0 \\ 0 & -e \end{pmatrix}.$$

Our eigenvalues are $-c$ and $-e$. Since both eigenvalues are negative, the origin is a stable fixed point.

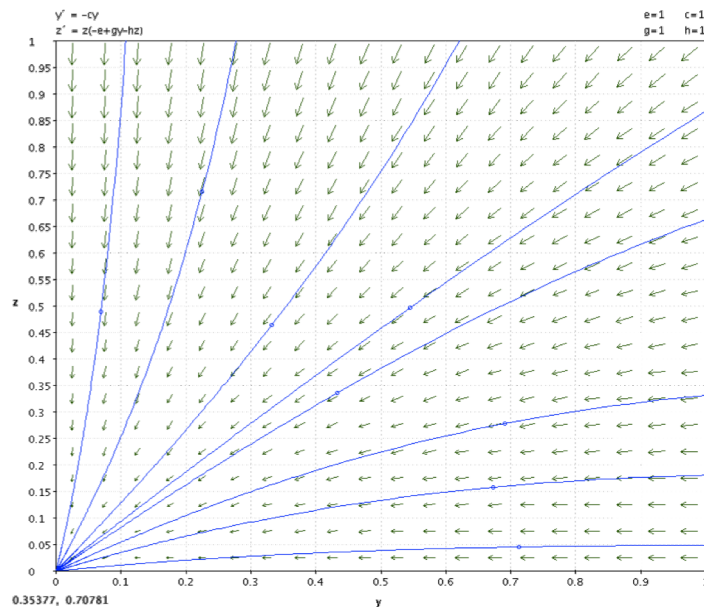


Figure 6: The behavior of the predator-scavenger populations in absence of the prey.

All trajectories of the phase plane of the scavenger-prey system flow to the origin. This means that both populations will die off. Biologically, this makes sense, because without the prey, the predator will have no food. As the predator population dies off, the scavenger also loses its source food, and the scavenger will die off too. Thus, the predator and scavenger populations cannot exist in the absence of the prey.

4.3 The Scavenger-Prey System

Finally, we look at the xz plane that represents a scavenger-prey model by the system

$$\begin{cases} x' &= x(1 - bx - z) \\ z' &= z(-e - hz + fx). \end{cases} \quad (8)$$

We find equilibrium points at $(0, 0)$, $(\frac{1}{b}, 0)$, $(0, -\frac{e}{h})$, and $(\frac{e+h}{f+hb}, \frac{f-be}{f+hb})$. Once again, $(0, -\frac{e}{h})$ is of no importance. So we begin our analysis of the other three equilibria. The Jacobian of (8) is as follows:

$$J = \begin{pmatrix} 1 - z - 2bx & -x \\ fz & -e + fx - 2hz \end{pmatrix}.$$

Now we find the Jacobian of (8) at $(0, 0)$:

$$J|_{(0,0)} = \begin{pmatrix} 1 & 0 \\ 0 & -e \end{pmatrix}.$$

Our eigenvalues 1 and $-e$ differ in sign, so $(0, 0)$ is a saddle node. Now, note that

$$J|_{(\frac{1}{b}, 0)} = \begin{pmatrix} -1 & -\frac{1}{b} \\ 0 & -e + \frac{f}{b} \end{pmatrix}.$$

The eigenvalues are -1 and $-e + \frac{f}{b}$. If $eb < f$, then both values are negative, and the critical point is stable. If $eb > f$, then the eigenvalues differ in sign, and the critical point is a saddle node. For our final equilibrium point,

$$J|_{(\frac{e+h}{f+hb}, \frac{f-be}{f+hb})} = \begin{pmatrix} -\frac{b(h+e)}{bh+f} & -\frac{e+h}{f+hb} \\ \frac{f(f-be)}{f+hb} & -\frac{h(f-be)}{f+hb} \end{pmatrix}.$$

We calculate the characteristic polynomial to be

$$(\lambda^2 + \lambda(h\beta + b\alpha) + \beta\alpha h + \alpha f\beta),$$

where $\alpha = \frac{h+e}{bh+f}$ and $\beta = \frac{f-be}{bh+f}$, and find the eigenvalues,

$$\frac{-(h\beta + b\alpha) \pm \sqrt{(h\beta + b\alpha)^2 - 4\alpha\beta(hb + f)}}{2}.$$

Only when $f - be > 0$, is the equilibria of biological relevance. If $(h\beta + b\alpha)^2 - 4\alpha\beta(hb + f) < 0$, then the eigenvalues will be complex conjugates, resulting in a spiral. In either case, the eigenvalues are negative so the fixed point is stable.

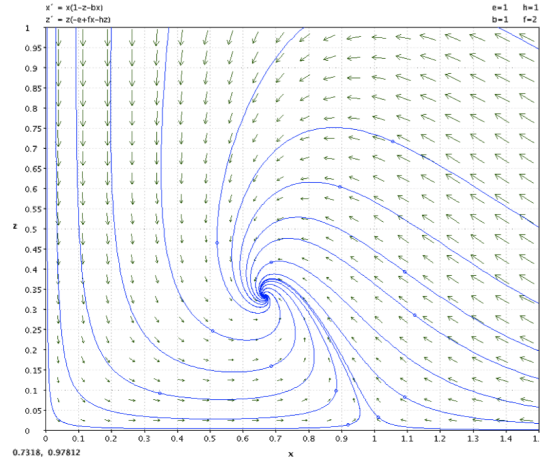


Figure 7(a): The phase plane of the scavenger-prey system when $f > be$ and $(h\beta + b\alpha)^2 - 4\alpha\beta(hb + f) < 0$.

The phase plane in figure 7(a) shows that trajectories will spiral into the fixed point, achieving equilibrium. Thus, the populations will coexist under the given conditions.

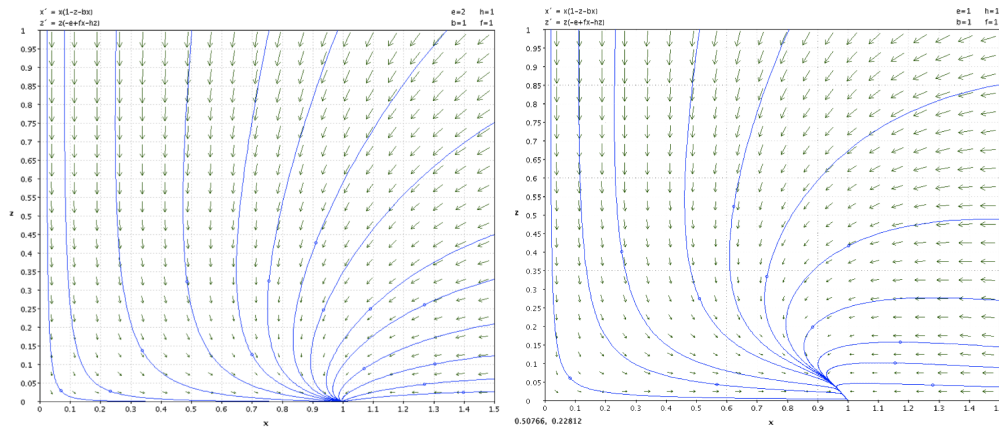


Figure 7(b): The phase planes of the scavenger-prey system when $f < be$ (left) and $f = be$ (right).

In either case shown in figure 7(b), the scavenger population will die off, and only the prey population will survive.

5 Analysis of Equilibria in the Three-Species Model

There exists four equilibrium points from the coordinate plane analysis $(0, 0, 0)$, $(1/b, 0, 0)$, $(c, 1 - bc, 0)$, $\left(\frac{h+e}{bh+f}, 0, \frac{-be+f}{bh+f}\right)$. We also find one interior equilibrium point,

$$\left(c, \frac{h+e-fc-bch}{g+h}, \frac{-e+fc+g-gbc}{g+h}\right).$$

We continue the analysis of the equilibria by computing the Jacobian J of the three-dimensional system given by

$$J = \begin{pmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} & \frac{\partial f}{\partial z} \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} & \frac{\partial g}{\partial z} \\ \frac{\partial h}{\partial x} & \frac{\partial h}{\partial y} & \frac{\partial h}{\partial z} \end{pmatrix},$$

where $f(x, y, z) = x'$, $g(x, y, z) = y'$, and $h(x, y, z) = z'$. The Jacobian of system (5) is as follows:

$$J = \begin{pmatrix} 1 - y - z - 2bx & -x & -x \\ y & -c + x & 0 \\ fz & gz & -e + fx + gy - 2hz \end{pmatrix}.$$

By finding the Jacobian of system (5) at each of the equilibria, we can predict the stability.

$$J|_{(0,0,0)} = \begin{pmatrix} 1 & 0 & 0 \\ 0 & -c & 0 \\ 0 & 0 & -e \end{pmatrix}.$$

Since $J(0, 0, 0)$ is a diagonal matrix, the eigenvalues are $1, -c, -e$. Because the eigenvalues are real and differ in sign, we have a saddle node at $(0, 0, 0)$, with a stable manifold in the yz plane and an unstable manifold in the x axis.

$$J|_{(\frac{1}{b}, 0, 0)} = \begin{pmatrix} -1 & \frac{1}{b} & \frac{1}{b} \\ 0 & -c + \frac{1}{b} & 0 \\ 0 & 0 & -e + \frac{f}{b} \end{pmatrix}.$$

It follows that the eigenvalues of $J(\frac{1}{b}, 0, 0)$ are $1, -c + \frac{1}{b}, -e + \frac{f}{b}$, since $J(\frac{1}{b}, 0, 0)$ is an upper triangular matrix. When $be > f$ and $1 - bc < 0$, all of the eigenvalues are negative and, we have a stable node at $(\frac{1}{b}, 0, 0)$. If either of these conditions or both of these conditions do not hold, then the eigenvalues are real and differ in sign and the equilibrium point is a saddle.

$$J|_{(c, 1-bc, 0)} = \begin{pmatrix} -bc & -c & -c \\ 1 - bc & 0 & 0 \\ 0 & 0 & -e + fc + g - gbc \end{pmatrix}.$$

Now, we can calculate the characteristic polynomial:

$$((-e + fc + g - bcg) - \lambda)(\lambda^2 + bc\lambda + c - bc^2).$$

Thus, we find that the eigenvalues of $J(c, 1 - bc, 0)$ are

$$-e + fc + g - gbc, \frac{-bc + \sqrt{bc^2 - 4(c - bc)^2}}{2}, \frac{-bc - \sqrt{bc^2 - 4(c - bc)^2}}{2}.$$

Note that if $-e + fc + g - gbc < 0$, all of the eigenvalues are negative, and the critical point is stable. The eigenvalues, $\frac{-bc + \sqrt{bc^2 - 4(c-bc)^2}}{2}$ and $\frac{-bc - \sqrt{bc^2 - 4(c-bc)^2}}{2}$ will have an imaginary part given that $bc^2 - 4(c-bc)^2 < 0$, which implies $\frac{4}{b+4} < bc$. This will result in a stable spiral in the xy plane. Otherwise, the two eigenvalues will be real, resulting in a stable node in the xy plane.

$$J|_{\left(\frac{h+e}{bh+f}, 0, \frac{f-be}{bh+f}\right)} = \begin{pmatrix} -b\left(\frac{h+e}{bh+f}\right) & -\frac{h+e}{bh+f} & -\frac{h+e}{bh+f} \\ 0 & -c + \frac{h+e}{bh+f} & 0 \\ f\left(\frac{f-be}{bh+f}\right) & g\left(\frac{f-be}{bh+f}\right) & -h\left(\frac{f-be}{bh+f}\right) \end{pmatrix}.$$

To simplify our calculations we let $\alpha = \frac{h+e}{bh+f}$ and $\beta = \frac{f-be}{bh+f}$. We calculate the characteristic polynomial:

$$(-c + \alpha - \lambda)(-\lambda^2 - (h\beta + b\alpha)\lambda - bh\alpha\beta - f\alpha\beta),$$

thus, finding the eigenvalues of $J\left(\frac{h+e}{bh+f}, 0, \frac{f-be}{bh+f}\right)$ are $-c + \alpha$,

$$\frac{-(h\beta + \alpha b) + \sqrt{(h\beta + b\alpha)^2 - 4\alpha\beta(bh + f)}}{2}, \text{ and } \frac{-(h\beta + \alpha b) - \sqrt{(h\beta + b\alpha)^2 - 4\alpha\beta(bh + f)}}{2}.$$

For the equilibrium to be stable, it must be true that $\alpha < c$. If $\alpha > c$ and $\beta > 0$, then the equilibria will be a saddle node.

Analyzing the interior equilibrium point,

$$\left(c, \frac{h + e - fc - bch}{g + h}, \frac{-e + fc + g - gbc}{g + h}\right),$$

requires more work. Letting $(x^*, y^*, z^*) = \left(c, \frac{h+e-fc-bch}{g+h}, \frac{-e+fc+g-gbc}{g+h}\right)$, we can find the Jacobian:

$$J|_{(x^*, y^*, z^*)} = \begin{pmatrix} -bx^* & -x^* & -x^* \\ y^* & 0 & 0 \\ fz^* & gz^* & -hz^* \end{pmatrix}.$$

The characteristic polynomial becomes

$$\lambda^3 + (hz^* + bx^*)\lambda^2 + x^*(bh z^* + y^* + fz^*)\lambda + x^*y^*z^*(g + h).$$

The eigenvalues are more complex, so we will use the Routh-Hurwitz method [2].

The Routh-Hurwitz method used for a third-degree polynomial

$$a_3\lambda^3 + a_2\lambda^2 + a_1\lambda + a_0$$

can be applied to our system, where $a_3 = 1$, $a_2 = (hz^* + bx^*)$, $a_1 = x^*(bh z^* + y^* + fz^*)$, and $a_0 = x^*y^*z^*(g + h)$. The Routh array for the third order polynomial is

$$\begin{bmatrix} a_3 & a_1 \\ a_2 & a_0 \\ H & 0 \\ a_0 & 0 \end{bmatrix},$$

where $H = \frac{a_2 a_1 - a_3 a_0}{a_1}$. Since we know $a_3 = 1$ and $a_2, a_1, a_0 > 0$, we are only concerned with the sign of H . If $a_2 a_1 > a_0$, then H is positive, and there does not exist a sign change in the first column of the Routh array. Thus, the roots of the third order polynomial are negative, meaning the eigenvalues of our characteristic polynomial are negative. This implies that the equilibrium point $J(x^*, y^*, z^*)$ is stable. If $a_2 a_1 < a_0$, then H is negative, and there exists two sign changes in the first column of the Routh array, one from a_2 to H and one from H to a_0 . This means that the third order characteristic polynomial has two roots or eigenvalues, both being positive, and the equilibrium is unstable. If $a_2 a_1 = a_0$, then the characteristic polynomial has two purely imaginary roots.

We will use the parameters $b = 0.9, c = 0.1, f = 0.1$, and $g = 13$. By plotting $H = x^*(hz^* + bx^*)(bhz^* + y^* + fz^*) - x^*y^*z^*(g + h) = 0$ as a implicit function of e and h , we can determine which values of e and h will result in stable equilibria, unstable equilibria, or a hopf bifurcation. When $H = 0$, the eigenvalues or roots of the polynomial are crossing the imaginary axis, and we see changes in equilibrium stability [4].

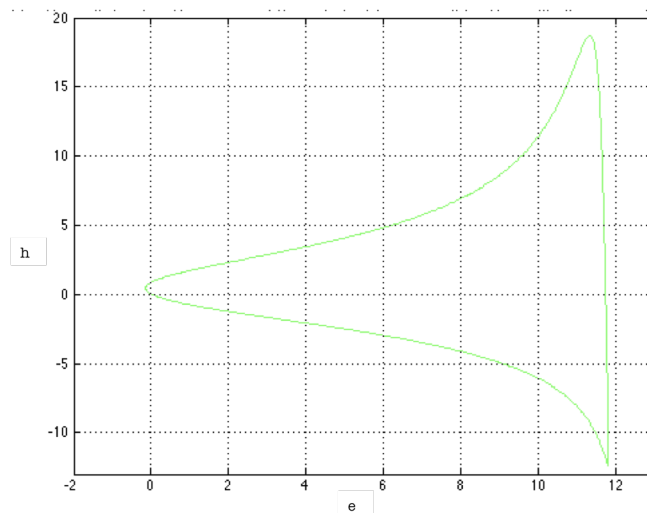


Figure 8: The Hopf Curve

The inside of the curve in figure 8 represents all points such that $H < 0$. This implies that at the values of e and h that occur inside the curve will result in unstable equilibria. Alternatively, the outside of the curve represents points such that $H > 0$, implying stable equilibria will occur. The curve itself clearly denotes when $H = 0$. Since we are only concerned with parameters with positive values, we can see that for all positive values of h , there are two values of e for which a Hopf bifurcation occurs, which implies existence of a limit cycle for the given parameters. This curve will motivate our choice of the parameters e and h when plotting the trajectories of the system.

We start by choosing the values $e = 11$ and $h = 18$ to plot the trajectories of the system. We obtain the following bifurcation diagram.

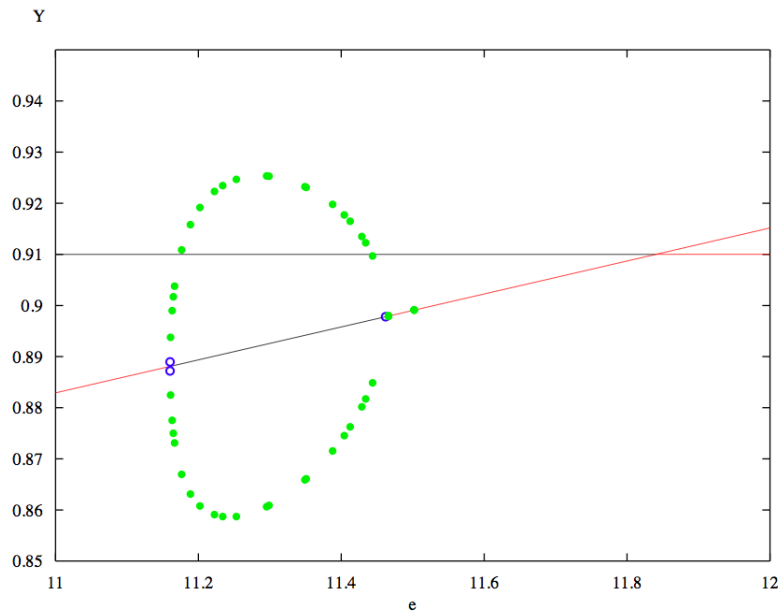


Figure 9: Hopf Bifurcation Diagram, $h=18$

Using the parameters $b = 0.9, c = 0.1, e = 11, f = 0.1, g = 13, h = 18$, we achieve the bifurcation diagram in figure 9. The black line shows values for which the equilibrium is unstable. When the line is red, the equilibrium point is stable. The open blue circles indicate the points of the supercritical Hopf bifurcations from which the periodic orbit will emanate. The first point at which the Hopf bifurcation occurs is $e \approx 11.16$ and the second point is $e \approx 11.46$. The green dotted curve of filled circles then shows the maximum and minimum values of y that result in a stable periodic orbit.

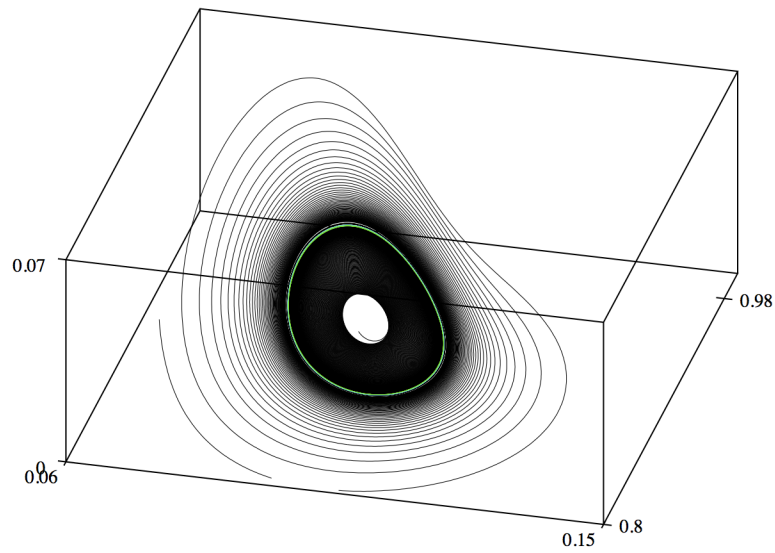
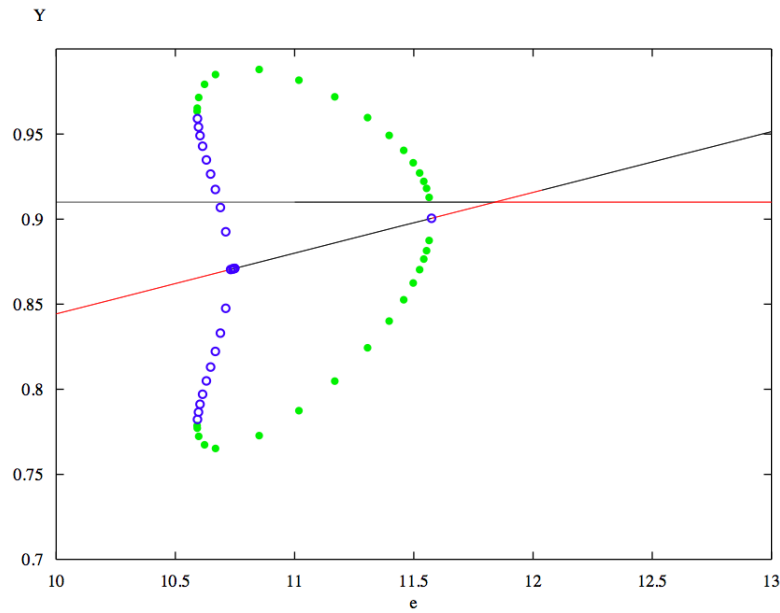


Figure 10: The trajectory plot using $e=11.23$ and $h=18$ resulting in a stable limit cycle.

The green curve in figure 10 is the stable limit cycle. Choosing initial points near the curve, inside or outside of the curve, will result in periodic trajectories, spiraling into the stable limit cycle. This implies that the populations will coexist oscillating between stable population sizes over time.

Now, we choose $e = 11$ and $h = 15$ to obtain the following bifurcation seen in figure 11.

Figure 11: Hopf Bifurcation Diagram, $h=15$

Using the parameters $b = 0.9, c = 0.1, e = 11, f = 0.1, g = 13, h = 15$, we achieve the bifurcation diagram in figure 11. The red lines indicate stable when equilibrium occur, and the black lines indicate when unstable equilibrium occur. The open blue circles that lie on the the upward sloping line indicate the points of one subcritical Hopf bifurcation and one supercritical Hopf bifurcation. The subcritical Hopf bifurcation occurs when $e \approx 11.57$. The supercritical Hopf bifurcations occurs when $e \approx 10.73$. The curve of filled green circle again represents the maximum and minimum values of a stable period orbit. The curve of open blue circles indicates the maximum and minimum values of an unstable periodic orbit.

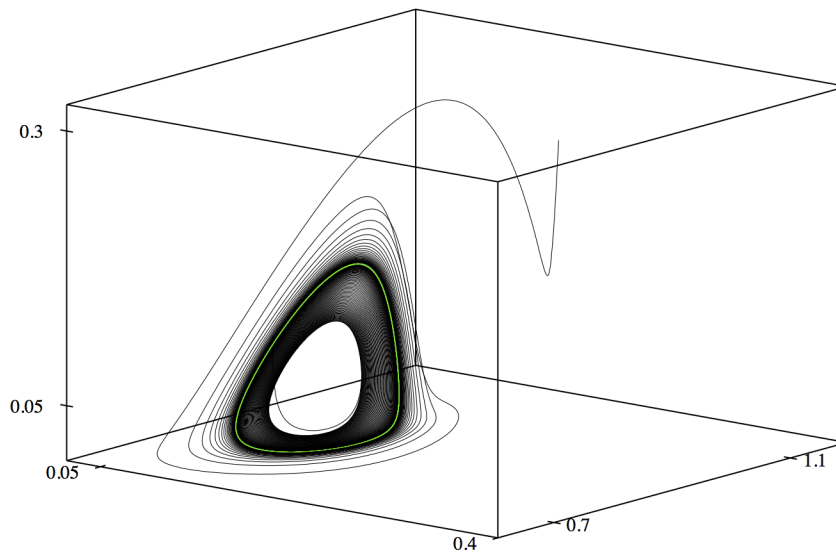


Figure 12: The trajectory using $e=10.67$ and $h=15$ resulting in a stable limit cycle.

Similarly to the trajectory in figure 12, the green curve in figure 11 is a stable limit cycle. Choosing initial points near the curve, inside or outside of the curve, will result in periodic trajectories, spiraling into the stable limit cycle. Once again, this implies that the populations will coexist oscillating between stable population sizes over time.

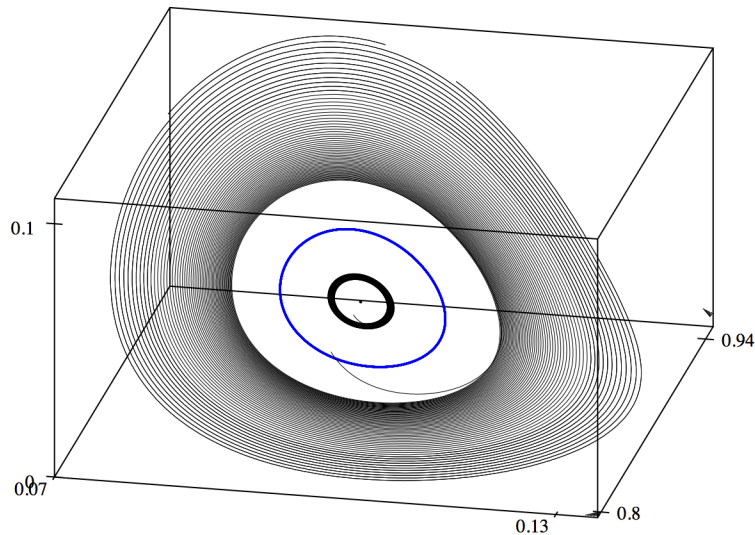


Figure 13: The trajectory using $e=10.71$ and $h=15$ resulting in an unstable limit cycle.

The blue curve in figure 13 is an unstable limit cycle. Choosing initial points on the limit cycle will result in a trajectory that will oscillate over time, following the path of the limit cycle. By choosing initial points outside of the limit cycle, the trajectories from the initial point will spiral outward away from the limit cycle. We can assume the trajectories are flowing to another fixed point such than one of the population die out. By choosing an initial point inside the limit cycle, the trajectories spiral inward away from the limit cycle to the stable equilibrium in the center of the limit cycle. This implies that the populations will oscillate for some time until they saturate at the stable equilibrium and remain constant over time. In this case, the populations coexist.

6 Summary

Our Lotka Volterra predator prey model with a scavenger demonstrates the possible population trends when a predator, a prey and a scavenger population interact. We have found that the predator and the prey can coexist in the absence of the scavenger, and the scavenger and the prey can coexist in the absence of the predator. However, the scavenger and the predator cannot coexist without the prey. Biologically this is reasonable, because without the prey, the predator will have no food and will die off. The scavenger will then lose all sources of food and will too die off. We have also found that the three populations can coexist in two ways: they will oscillate between stable populations over time, or the populations will oscillate until they saturate and remain constant over time.

7 Appendix

Provided below is the code needed to produce the three-dimensional Lotka-Volterra model solutions and diagrams using the program XPPAUT.

```
#Three-Dimensional Lotka Volterra Equations
x'=x*(1-b*x-y-z)
y'=y*(-c+x)
z'=z*(-e-h*z+f*x+g*y)
par b=0.9,c=0.1,e=11,f=0.1,g=13,h=15
init x=1,y=1,z=0
@ xplot=x,yplot=y,zplot=z,axes=3d
@ xmin=0,xmax=1,ymin=0,zmin=0,zmax=.08
@ dt=.05,total=200
done
```

References

- [1] Hoffman, Kathleen A., and Joseph P. Previte. "Period Doubling Cascades in a Predator-Prey Model with a Scavenger." *SIAM* 55.3 (2012): 523-46.
- [2] Koskie, Sarah. "Rouths Stability Criterion." IUPIU. Purdue School of Engineering and Technology, 13 Jan. 2007. Web. 1 Nov. 2013. <http://www.engr.iupui.edu/skoskie/ECE680/Routh.pdf>.
- [3] Hackborn, W. "Classification of Fixed Points of Two-Dimensional Continuous Systems." *augustana.com*. University of Alberta. 2010. Web. 22 Nov. 2013. <http://www.augustana.ualberta.ca/>.
- [4] Strogatz, S. "Nonlinear Dynamics and Chaos with Applications to Physics, Biology, Chemistry and Engineering." Addison Wesley (1996): 15-264.