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Dynamics of Mutualism in a Two Prey, One Predator System with Variable Carrying Capacity

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Dynamics of Mutualism in a Two Prey, One Predator System with Variable Carrying Capacity

by

Randy Lee

A thesis submitted to the Department of Mathematics and Statistics

in partial fulfillment of the requirements for the degree of

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UNIVERSITY OF NORTH FLORIDA

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Abstract

We considered the livelihood of two prey species in the presence of a predator species. To understand this phenomenon, we developed and analyzed two mathematical models considering indirect and direct mutualism of two prey species and the influence of one predator species. Both types of mutualism are represented by an increase in the preys' carrying capacities based on direct and indirect interactions between the prey. Because of mutualism, as the death rate parameter of the predator species goes through some critical value, the model shows transcritical bifurcation. Additionally, in the direct mutualism model, as the death rate parameter decreases to some critical value, the model shows limit cycle phenomena.

1 Introduction

When organisms of two or more different species interact, it is called symbiosis [7]. The three main types of symbiosis are mutualism, commensalism, and parasitism. Mutualism is when both interacting species benefit. An example of this is the bee and flowering plants. The bee gets nectar from the flower for food and pollen from the flower gets onto the bee and spreads to other flowers, helping the plant species reproduce. Both species benefit from each other. Commensalism is when one species benefits while the other is unaffected. An example is a vulture and a lion. The lion hunts its prey and gets its nutrition. The remainder of the prey is eaten by the vulture. The vulture benefits while the lion is unaffected. Parasitism is when one species benefits while the other is harmed. An example is the mosquito and the cow. The mosquito gets nutrients by drinking the cow's blood. The cow gets irritated skin at the bite site and possibly infected with diseases. Here, the mosquito benefits and the cow is harmed. Mathematical models for symbiosis have been developed [1, 5].

Mutualism and commensalism can be split up into further categories, such as obligate and facultative. Obligate symbiosis means that the symbiosis is necessary for the species' survival. Facultative symbiosis means that the symbiosis is helpful, but not required. Thus for mutualism, there are three subcategories: facultative-facultative, obligate-facultative, and obligate-obligate. For commensalism, there are two subcategories: facultative and obligate.

Predation is another form of interaction between different species. Consider a predator species and one of the prey species that it hunts, such as the predator wolf and the prey rabbit. When the wolf hunts the rabbit, the rabbit population decreases. When there is a small rabbit population, there is less food for the wolves, so the wolf population decreases. When there are less wolves, less rabbits are hunted, meaning the rabbit population grows. Finally, as the rabbit population increases, there

is more food for the wolves, increasing their population.

Indeed, while predator and prey species interact with each other, predation is generally not considered a form of symbiosis. This is because symbiosis is defined by the persistence of the interactions [7]. A mosquito can feed from a cow once and feed from the same organism again another time. However, once the wolf has hunted the rabbit, there is no more interaction between the two organisms.

Thus, we require a different model from symbiosis. The Lotka-Volterra system is the first to model these changing dynamics by analyzing how one predator species and one prey species affect each other. The standard two species model has been modified to simulate more specific factors regarding predator-prey interactions, such as handling rate and herding behavior [9, 10]. There have been multiple other articles that have studied a modified two prey, one predator model [2, 3, 4].

In this thesis we studied two mutualistic prey populations, by introducing the influence of a predator species. An example of this is the multi-species herd comprised of zebras and wildebeests. Both are prey to the lion and protect each other from the predator. In Chapter 2 we cover the mathematical material required to understand the rest of the paper. This includes a basic overview of dynamical systems, stability analysis, limit cycles, and bifurcations. In Chapter 3, we focus on the indirect mutualism model and study the stability and bifurcations that occur in the model. In Chapter 4, we focus on the more complex direct mutualism model. Like Chapter 3, we study the stability and bifurcations that occur in the model, which will include limit cycles. In Chapter 5, we make concluding remarks about the biological significance of our results and make suggestions for future research.

2 Background Materials

2.1 Differential Equations and Dynamical Systems

The study of dynamical systems starts with differential equations. The differential equations we are interested in involve functions of time t , say the function $x(t)$.

The order of a differential equation is the order of the highest derivative in the equation. We will only concern ourselves with first order differential equations for the rest of the paper. A differential equation is linear if every dependent variable and every derivative is to the first degree only. There must also be no products of dependent variables or derivatives. A nonlinear differential equation is a differential equation that is not linear. An autonomous differential equation is a differential equation where the independent variable, say t , does not appear explicitly. We will be focusing on nonlinear first order autonomous ordinary differential equations (ODEs) in this thesis.

Let us define a general system of first order autonomous ODEs of the form:

$$\begin{aligned}\frac{dx_1}{dt} &= f_1(x_1, x_2, \dots, x_n) \\ \frac{dx_2}{dt} &= f_2(x_1, x_2, \dots, x_n) \\ &\dots \\ \frac{dx_n}{dt} &= f_n(x_1, x_2, \dots, x_n),\end{aligned}\tag{1}$$

where f_i is a function for $1 \leq i \leq n$. The the system (1) can be written in vector form

$$\dot{\vec{x}} = f(\vec{x}),\tag{2}$$

where $\vec{x} = (x_1, x_2, \dots, x_n)^T$ and $f(\vec{x}) = (f_1(x_1, x_2, \dots, x_n), f_2(x_1, x_2, \dots, x_n), \dots, f_n(x_1, x_2, \dots, x_n))^T \in \mathbb{R}^n$.

An issue with nonlinear differential equations is that for most of them, it is impossible to find explicit solutions. Thus, we study the qualitative behavior of their solutions instead. This involves a dynamical system, which are an evolution rule that defines a trajectory as a function of a single parameter (time) on a set of states (the phase space) [29]. Dynamical systems are therefore categorized according to properties of their phase space, of their evolution rule, and of time itself. In this thesis, we consider systems with a continuous phase space, D , that is typically \mathbb{R}^n .

The evolution rule can be deterministic or stochastic. A system is deterministic if for each state in the phase space there is a unique consequent, that is, the evolution rule is a function taking a given state to a unique, subsequent state. Systems that are nondeterministic are called stochastic.

When the evolution rule is deterministic, then for each time, t , it is a mapping from the phase space to the phase space, $\phi_t : D \rightarrow D$, so that $x(t) = \phi_t(x_0)$ denotes the position of the system at time t that started at x_0 . Here we assume that t takes values in some allowed range and that the initial value of time is zero, so that $\phi_0(x_0) = x_0$.

Every dynamical system has orbits or trajectories; namely, the sequence of states that follow from or lead to a given initial state. The simplest orbit is an equilibrium, where the orbit is a single point: $\Gamma_x = \{x\}$. A periodic orbit, γ , is a closed loop. Thus, for each x on a periodic orbit, there is a time T such that the point returns to itself: $\phi_T(x) = x$.

Definition 2.1.1: Suppose the phase space of a dynamical system is D , an open subset of \mathbb{R}^n . A complete flow $\phi_t(x)$ is a one-parameter, continuously differentiable mapping $\phi : \mathbb{R} \times D \rightarrow D$, such that,

(i) $\phi_0(\vec{x}) = \vec{x}$ for all $\vec{x} \in D$,

(ii) The composition $\phi_t \circ \phi_s = \phi_{t+s}$ for each $t, s \in \mathbb{R}$ and $\vec{x} \in D$.

Since a flow is differentiable, it has an associated ODE, or more specifically, a vector field.

Definition 2.1.2: A vector field is a function $f : D \rightarrow \mathbb{R}^n$ that defines a vector $v = f(x)$ at each point x in the phase space D . The vector field associated with a flow is defined by

$$f(x) = \left. \frac{d}{dt} \phi_t(x) \right|_{t=0} \quad (3)$$

Theorem 2.1.3: If $\phi_t(x)$ is a flow, then it is a solution of the initial value problem,

$$\frac{d}{dt} \phi_t(x_0) = f(\phi_t(x_0)), \phi_0(x_0) = x_0, \quad (4)$$

for the vector field defined in (3).

Proof: Let $x(t) = \phi_t(x_0)$. From Definition 2.1.1 (ii), we get

$$\frac{dx}{dt} = \lim_{\epsilon \rightarrow 0} \frac{1}{\epsilon} [\phi_{t+\epsilon}(x_0) - \phi_t(x_0)] = \lim_{\epsilon \rightarrow 0} \frac{1}{\epsilon} [\phi_\epsilon(x(t)) - \phi_0(x(t))] = f(x(t))$$

Therefore the flow is the solution of the differential equation $\frac{dx}{dt} = f(x)$. \square

Example 2.1.4: In Figure (1), we can see an example of a flow. The first condition is shown as $\phi_0(x) = x$. The second condition is shown by $\phi_t(y) = (\phi_t \circ \phi_s)(x) = \phi_{t+s}(x)$. Thus, given

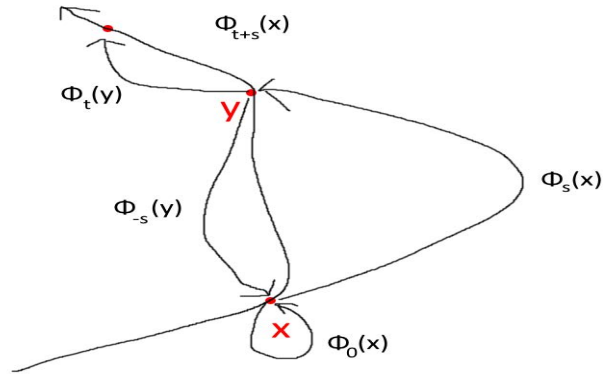


Figure 1: Illustration of a flow $\phi_t(y) = (\phi_t(\phi_s)(x)) = \phi_{t+s}(x)$

various initial conditions, we can look at a solution's behavior and analyze its properties without needing the solution itself.

2.2 Stability Analysis

As mentioned in the previous chapter, it is difficult to find solutions to systems of nonlinear differential equations, which is why we study the behavior of these systems instead. To do so, we need to look at the solutions at sufficiently large t . One of the best ways to do so is to look at the equilibrium points, or steady states, of the system.

Definition 2.2.1: A point $\bar{x} \in D$ is an equilibrium point if it satisfies $f_i(\bar{x}) = 0$ for all $i = 1, \dots, n$.

Thus the importance of the steady state is that there is no change in the solution at the equilibrium points, which make them a useful reference for solutions near those points.

The steady states can be stable, meaning the solutions go towards the equilibrium point. They

can also be unstable, where the solutions go away from the equilibrium point. Mathematically, we define stability to be the following:

Definition 2.2.2: Let \bar{x} be an equilibrium point. It is stable if for every neighborhood E of \bar{x} , there is a neighborhood E_1 of \bar{x} in E such that every solution $x(t)$ with $x(0) = x_0$ in E_1 is defined and remains in E for all $t > 0$. Additionally, if there is an E_1 such that $\lim_{t \rightarrow \infty} x(t) = \bar{x}$, then \bar{x} is asymptotically stable. \bar{x} is unstable if it is not stable.

Definition 2.2.3: Steady states can be sinks, where the solutions go directly to or away from the point. They can also be spirals, where the solutions circle to or from the steady state. Saddle nodes are unstable steady states where the solutions approach the point before going away from it.

The goal of stability analysis is to determine the conditions in which solutions go towards certain steady states. In the nonlinear system, there are multiple steady states, so we must analyse the local stability of each steady state to have a general idea of the global behavior. We find steady states of nonlinear systems through the nullclines.

Definition 2.2.4: The x_j nullcline is the set of points where $\frac{dx_j}{dt}$ vanishes. That is, the set of points determined by setting $f_j(x_1, x_2, \dots, x_n) = 0$.

After finding the steady states, we then analyze their stability by finding the linearization of the system (1). The linearization of the system (1) at a steady state $\bar{x} = (\bar{x}_1, \bar{x}_2, \dots, \bar{x}_n)$ is defined by

the linear system of differential equations:

$$\begin{aligned}
\dot{z}_1 &= \frac{\partial f_1}{\partial x_1}(\bar{x}_1, \bar{x}_2, \dots, \bar{x}_n)z_1 + \frac{\partial f_1}{\partial x_2}(\bar{x}_1, \bar{x}_2, \dots, \bar{x}_n)z_2 + \dots + \frac{\partial f_1}{\partial x_n}(\bar{x}_1, \bar{x}_2, \dots, \bar{x}_n)z_n \\
&\quad \dots \\
\dot{z}_i &= \frac{\partial f_i}{\partial x_1}(\bar{x}_1, \bar{x}_2, \dots, \bar{x}_n)z_1 + \frac{\partial f_i}{\partial x_2}(\bar{x}_1, \bar{x}_2, \dots, \bar{x}_n)z_2 + \dots + \frac{\partial f_i}{\partial x_n}(\bar{x}_1, \bar{x}_2, \dots, \bar{x}_n)z_n \\
&\quad \dots \\
\dot{z}_n &= \frac{\partial f_n}{\partial x_1}(\bar{x}_1, \bar{x}_2, \dots, \bar{x}_n)z_1 + \frac{\partial f_n}{\partial x_2}(\bar{x}_1, \bar{x}_2, \dots, \bar{x}_n)z_2 + \dots + \frac{\partial f_n}{\partial x_n}(\bar{x}_1, \bar{x}_2, \dots, \bar{x}_n)z_n
\end{aligned}$$

Thus the linearization of (1) in vector matrix form at an equilibrium is the linear system

$$\dot{z} = Jz, \tag{5}$$

where $J = \begin{bmatrix} \frac{\partial f_1}{\partial x_1}(\bar{x}_1, \bar{x}_2, \dots, \bar{x}_n) & \dots & \frac{\partial f_1}{\partial x_n}(\bar{x}_1, \bar{x}_2, \dots, \bar{x}_n) \\ \dots & & \dots \\ \frac{\partial f_i}{\partial x_1}(\bar{x}_1, \bar{x}_2, \dots, \bar{x}_n) & \dots & \frac{\partial f_i}{\partial x_n}(\bar{x}_1, \bar{x}_2, \dots, \bar{x}_n) \\ \dots & & \dots \\ \frac{\partial f_n}{\partial x_1}(\bar{x}_1, \bar{x}_2, \dots, \bar{x}_n) & \dots & \frac{\partial f_n}{\partial x_n}(\bar{x}_1, \bar{x}_2, \dots, \bar{x}_n) \end{bmatrix},$

is called the Jacobian matrix of the system (1) at an equilibrium point \bar{x} .

We can analyze the stability of the nonlinear system (1) using the Jacobian matrix due to the Hartman-Grobman Theorem.

Definition 2.2.5: A steady state \bar{x} is called hyperbolic if all eigenvalues of the Jacobian J evaluated at \bar{x} have nonzero real part.

Theorem 2.2.6: Hartman-Grobman Theorem: Assume that \bar{x} is a hyperbolic equilibrium. Then, in a small neighborhood of \bar{x} , the phase portrait of the nonlinear system (1) is equivalent to the linearized system $\dot{z} = J\bar{z}$.

After finding the Jacobian matrix, we evaluate it at each steady state and get a corresponding characteristic equation. The characteristic equation is of the form,

$$\lambda^n + a_1\lambda^{n-1} + \dots + a_{n-1}\lambda + a_n = 0. \quad (6)$$

Normally, we would solve for the eigenvalues and look at those to determine the stability.

Theorem 2.2.7: For a square matrix A, the equation $v = Av$ is:

- (i) stable if A has no eigenvalues with positive real part;
- (ii) asymptotically stable if and only if A has only eigenvalues with negative real part;
- (iii) unstable if A has at least one eigenvalue with positive real part.

However, it is sometimes too difficult to find or study the exact eigenvalues of the matrix. Thus we use the Routh-Hurwitz criteria to determine the stability of the steady state.

Theorem 2.2.8: Assuming the characteristic equation (6) has real coefficients, let H_1, \dots, H_n denote the following n matrices:

$$H_1 = (a_1)$$

...

$$H_k = \begin{bmatrix} a_1 & a_3 & a_5 & \dots & a_{2k-1} \\ 1 & a_2 & a_4 & \dots & a_{2k-2} \\ 0 & a_1 & a_3 & \dots & a_{2k-3} \\ 0 & 1 & a_2 & \dots & a_{2k-4} \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ 0 & 0 & 0 & \dots & a_k \end{bmatrix}$$

...

$$H_n = \begin{bmatrix} a_1 & a_3 & a_5 & \dots & 0 \\ 1 & a_2 & a_4 & \dots & 0 \\ 0 & a_1 & a_3 & \dots & 0 \\ 0 & 1 & a_2 & \dots & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ 0 & 0 & 0 & \dots & a_n \end{bmatrix}$$

for $1 \leq k \leq n$, where $a_k = 0$ if $j > n$. If $|H_k| > 0$ for $k = 1, \dots, n$, then all eigenvalues have negative real parts.

For $n = 2$, the steady state is stable if $a_1 > 0$ and $a_2 > 0$. For $n = 3$, the steady state is stable if $a_1 > 0$, $a_3 > 0$, and $a_1 a_2 > a_3$.

Example 2.2.9: Consider the Lotka-Volterra equations with logistic prey growth:

$$\begin{aligned}
\frac{dx}{dt} &= \frac{ax(K-x)}{K} - bxy \\
\frac{dy}{dt} &= -cy + dxy
\end{aligned} \tag{7}$$

The parameters a, b, c , and d as well as the carrying capacity K are all assumed to be positive. The biological meaning of the parameters is explained in Chapter 3.

To find the steady states of system (7), we must first find the nullclines of the system. The x -nullclines are $x = 0$ and $y = \frac{a(K-x)}{bK}$. The y -nullclines are $y = 0$ and $x = \frac{c}{d}$. Thus the steady states are $(0, 0)$, $(K, 0)$, and $(\frac{c}{d}, \frac{a(dK-c)}{dbK})$.

The Jacobian matrix for the system is

$$J = \begin{bmatrix} \frac{a(K-2x)}{K} - by & -bx \\ dy & -c + dx \end{bmatrix}. \quad (8)$$

The Jacobian matrix (8) evaluated at the steady state $(0, 0)$ is

$$J(0, 0) = \begin{bmatrix} a & 0 \\ 0 & -c \end{bmatrix}.$$

The eigenvalues are a and $-c$, so the steady state is always unstable.

The Jacobian matrix (8) evaluated at the steady state $(K, 0)$ is

$$J(K, 0) = \begin{bmatrix} -a & -bK \\ 0 & -c + dK \end{bmatrix}.$$

The eigenvalues are $-a$ and $-c + dK$. Thus $(K, 0)$ is stable when $dK < c$.

Figure (2) shows an example of the stable $(K, 0)$ steady state. The parameters are $a = b = d = 1$ and $c = 1.1$. The carrying capacity $K = 1$ and the initial conditions are $x = y = 0.5$.

The Jacobian matrix (8) evaluated at the steady state $(\frac{c}{d}, \frac{a(dK-c)}{dbK})$ is

$$J\left(\frac{c}{d}, \frac{a(dK-c)}{dbK}\right) = \begin{bmatrix} \frac{-ac}{dK} & \frac{-bc}{d} \\ \frac{a(dK-c)}{bK} & 0 \end{bmatrix}.$$

The characteristic equation is

$$\lambda^2 + \frac{ac\lambda}{dK} + \frac{ac((dK-c))}{dbK} = 0$$

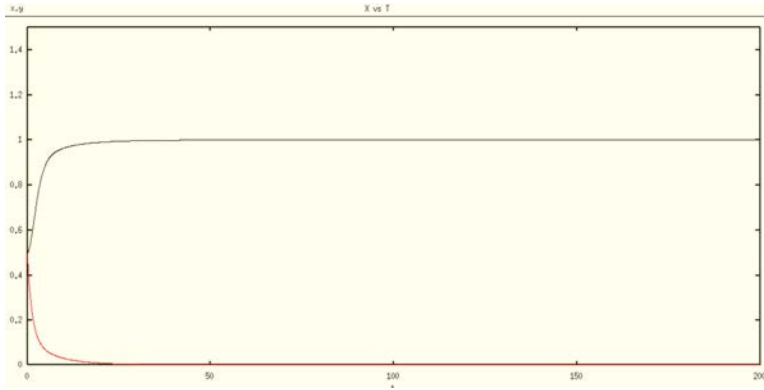


Figure 2: Stable x only steady state

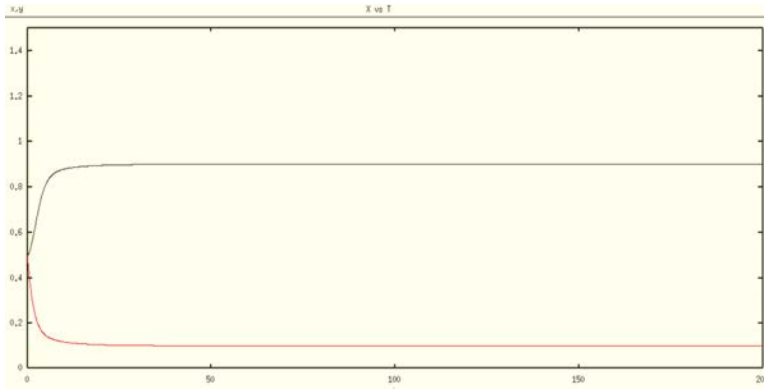


Figure 3: Stable coexistence steady state

We can use the Routh-Hurwitz criteria to analyze stability rather than finding the eigenvalues.

Thus, for $(\frac{c}{d}, \frac{a(dK-c)}{dbK})$ to be stable, $\frac{ac}{dK} > 0$ and $\frac{ac(dK-c)}{dbK} > 0$, which is only true when $dK > c$.

Figure (3) shows an example of the stable $(\frac{c}{d}, \frac{a(dK-c)}{dbK})$ steady state. The parameters are $a = b = d = 1$ and $c = 0.9$. The carrying capacity $K = 1$ and the initial conditions are $x = y = 0.5$.

2.3 Periodic Solutions and Limit Cycles

This chapter is adapted from [28]. Steady states may lead to limit cycles, where the solutions maintain a stable orbit around the steady state. Mathematically, we can define a limit cycle through the following steps.

Definition 2.3.1: Let $\phi_t(x_0)$ be a solution of the differential equation of \dot{x} , where x_0 is an initial condition and t is time and an element of the maximal interval I_{x_0} . A set $A \subset \mathbb{R}^n$ is invariant if $\phi_t(x) \in A$ for every $x \in A$ and $t \in I_x$.

Definition 2.3.2: The orbit of $x \in \mathbb{R}^n$ is defined as $\gamma(x) = \{\phi_t(x) : t \in I_x\}$.

By extension, the positive semiorbit of x is $\gamma^+(x) = \{\phi_t(x) : t \in I_x \cap \mathbb{R}^+\}$. Similarly, the negative semiorbit of x is $\gamma^-(x) = \{\phi_t(x) : t \in I_x \cap \mathbb{R}^-\}$. The invariant set A can also be seen as

$$\bigcup_{x \in A} \gamma(x).$$

The ω -limit set is

$$\omega(x) = \bigcap_{y \in \gamma(x)} \overline{\gamma^+(y)}.$$

Similarly, the α -limit set of x is

$$\alpha(x) = \bigcap_{y \in \gamma(x)} \overline{\gamma^-(y)}.$$

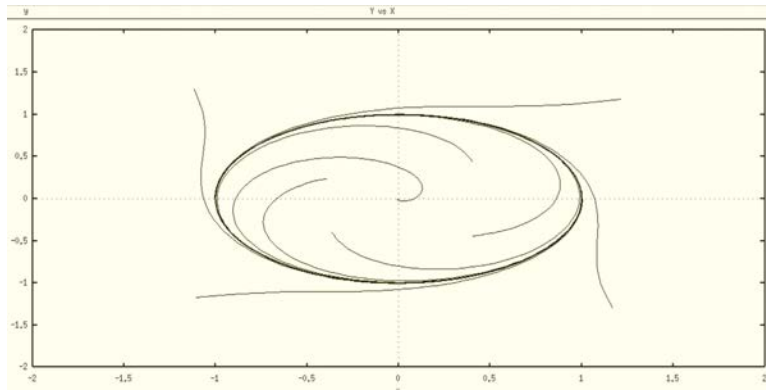


Figure 4: Stable limit cycle

Example 2.3.3: Consider the system of two equations:

$$\frac{dx}{dt} = x(1 - (x^2 + y^2)) - y$$

$$\frac{dy}{dt} = y(1 - (x^2 + y^2)) + x.$$

In polar coordinates, this system is:

$$\frac{dr}{dt} = r(1 - r^2)$$

$$\frac{d\theta}{dt} = 1.$$

As seen in Figure (4), there is a stable limit cycle at $r = 1$, which in Cartesian coordinates is the circle $x^2 + y^2 = 1$. Solutions that start inside the circle go away from the origin and towards the circle. Solutions that start outside the circle go inward to the limit cycle.

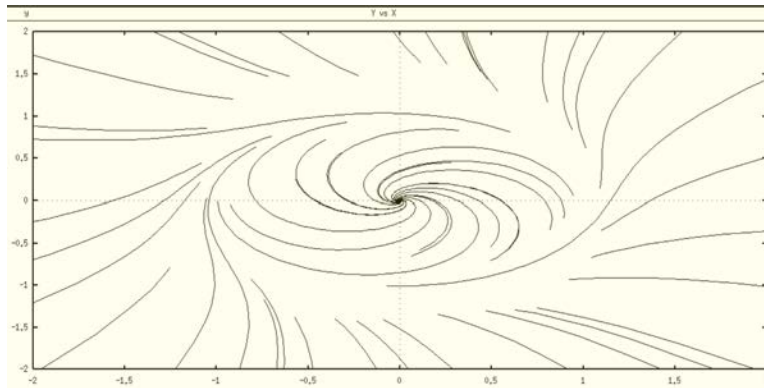


Figure 5: Unstable limit cycle

Example 2.3.4: Consider the similar system of two equations:

$$\frac{dx}{dt} = x((x^2 + y^2) - 1) - y$$

$$\frac{dy}{dt} = y((x^2 + y^2) - 1) + x.$$

In polar coordinates, this system is:

$$\frac{dr}{dt} = r(r^2 - 1)$$

$$\frac{d\theta}{dt} = 1.$$

As seen in Figure (5), there is an unstable limit cycle at $r = 1$, which in Cartesian coordinates is the circle $x^2 + y^2 = 1$. Solutions that start inside the circle go towards the origin. Solutions that start outside the circle go away from the origin.

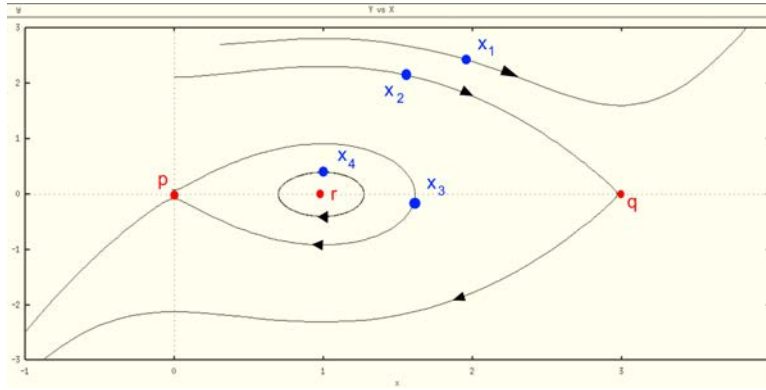


Figure 6: Limit Set Example

Example 2.3.5: Consider the system of two equations:

$$\frac{dx}{dt} = y$$

$$\frac{dy}{dt} = x(x-1)(x-3).$$

As shown in Figure (6), we can see the following limit sets:

$$\alpha(x_1) = \omega(x_1) = \emptyset;$$

$$\alpha(x_2) = \emptyset, \quad \omega(x_2) = q;$$

$$\alpha(x_3) = \omega(x_3) = p;$$

$$\alpha(x_4) = \omega(x_4) = \gamma(x_4).$$

(9)

Lemma 2.3.6: If the positive semiorbit $\gamma^+(x)$ of a point $x \in \mathbb{R}^n$ is bounded, then:

- (i) $\omega(x)$ is compact, connected, and nonempty;
- (ii) $y \in \omega(x)$ if and only if there exists a sequence $t_k \rightarrow +\infty$ such that $\phi_{t_k}(x) \rightarrow y$ when $k \rightarrow \infty$;
- (iii) $\phi_t(y) \in \omega(x)$ for every $y \in \omega(x)$ and $t > 0$;
- (iv) $\inf\{\|\phi_t(x) - y\| : y \in \omega(x)\} \rightarrow 0$ when $t \rightarrow +\infty$.

Proof: Let $W = \overline{\gamma^+(x)}$. By definition of the ω -limit set, $\omega(x)$ is closed. Since $\omega(x) \subset W$, $\omega(x)$ is also bounded. Thus $\omega(x)$ is compact.

Since $\gamma^+(x)$ is bounded, $\mathbb{R}^+ \subset I_x$, so

$$\omega(x) = \bigcap_{t>0} A_t,$$

where $A_t = \overline{\{\phi_s(x) : s > t\}}$.

If $y \in \omega(x)$, then there exists a sequence $t_k \rightarrow +\infty$ such that $y \in A_{t_k}$ for $k \in \mathbb{N}$. This means there is a sequence $s_k \rightarrow +\infty$ with $s_k \geq t_k$ for $k \in \mathbb{N}$ such that $\phi_{s_k}(x) \rightarrow y$ when $k \rightarrow \infty$. Conversely, if there exists a sequence $t_k \rightarrow +\infty$ such that $\phi_{t_k}(x) \rightarrow y$, then $y \in A_{t_k}$ and

$$y \in \bigcap_{k=1}^{\infty} A_{t_k} = \bigcap_{t>0} A_t,$$

since $A_t \subset A_{t'}$ for $t > t'$. Thus (ii) is proven.

Let $(\phi_k(x))_k$ be a sequence contained in W . By compactness, there exists a subsequence $(\phi_{t_k}(x))_k$, with $t_k \rightarrow +\infty$, converging to a point in W . Thus $\omega(x)$ is nonempty.

Assume to the contrary that $\omega(x)$ is disconnected. Then $\omega(x) = A \cup B$ for some nonempty A and

B such that $\bar{A} \cap B = A \cap \bar{B} = \emptyset$. Since $\omega(x)$ is closed,

$$\bar{A} = \bar{A} \cap \omega(x) = \bar{A} \cap (A \cup B) = (\bar{A} \cap A) \cup (\bar{A} \cap B) = A.$$

By similar reasoning, $\bar{B} = B$. Thus A and B are also closed, so they are at a positive distance, meaning

$$\delta := \inf\{\|a - b\| : a \in A, b \in B\} > 0.$$

Let the set

$$C = \{z \in \mathbb{R}^2 : \inf_{y \in \omega(x)} \|z - y\| \geq \frac{\delta}{4}\}.$$

It is trivial to show $C \cap W$ is compact and nonempty. Thus, from (ii), $C \cap W \cap \omega(x) \neq \emptyset$. This is a contradiction, since $C \cap W$ does not intersect $\omega(x)$ by the definition of C . So $\omega(x)$ is connected, proving (i).

To prove (iii), we start with the assumption that $y \in \omega(x)$. Using (ii) and the continuity of the function $z \mapsto \phi_t(z)$, for all $t > 0$ we have: $\phi_{t_k+t}(x) = \phi_t(\phi_{t_k}(x)) \rightarrow \phi_t(y)$ when $k \rightarrow \infty$. Since $t_k + t \rightarrow +\infty$ as $k \rightarrow \infty$, from (ii) we get $\phi_t(y) \in \omega(x)$.

Finally, assume to the contrary that there exists a sequence $t_k \rightarrow +\infty$ and a constant $\delta > 0$ such that $\inf\{\|\phi_{t_k}(x) - y\| : y \in \omega(x)\} \geq \delta$ for $k \in \mathbb{N}$. Since W is compact, there exists a convergent subsequence $(\phi_{t'_k}(x))_k$ of $(\phi_{t_k}(x))_k \subset W$, which by (ii) has a limit $p \in \omega(x)$. However, we established that $\|\phi_{t_k}(x) - y\| \geq \delta$ for every $y \in \omega(x)$ and $k \in \mathbb{N}$. This means $\|p - y\| \geq \delta$ for $y \in \omega(x)$, meaning $p \notin \omega(x)$. This is a contradiction, thus proving (iv). \square

Now that we have an understanding of limit cycles and limit sets, we can talk about the Poincare-Bendixson theorem. However, to do so, we must restrict our functions to \mathbb{R}^2 .

Definition 2.3.7: Let $f : \mathbb{R}^2 \rightarrow \mathbb{R}^2$ be a continuously differentiable function. A line segment L is a transversal to f if for each $x \in L$ the directions of $f(x)$ and L generate \mathbb{R}^2 .

Theorem 2.3.8: (Jordan's curve theorem) If $\gamma : [0, 1] \rightarrow \mathbb{R}^2$ is a continuous function with $\gamma(0) = \gamma(1)$ such that $\gamma|_{(0, 1)}$ is injective, then $\mathbb{R}^2 \setminus \gamma([0, 1])$ has two connected components, one bounded and one unbounded.

We will not be proving Jordan's curve theorem as it requires knowledge of topics outside of dynamical systems. However, it is necessary to prove the following lemma.

Lemma 2.3.9: Assume that L is transversal to f and let $x \in \mathbb{R}^2$. Then $\omega(x) \cap L$ contains at most one point.

Proof: Assume that $\omega(x) \cap L$ and let $q \in \omega(x) \cap L$. By Lemma 2.3.6, there exists a sequence $t_k \rightarrow +\infty$ such that $\phi_{t_k}(x) \rightarrow q$ when $k \rightarrow \infty$. Since L is a transversal to f , for each $y \in \mathbb{R}^2$ sufficiently close to L there exists a unique time s such that $\phi_s(y) \in L$ and $\phi_t(y) \notin L$ for $t \in (0, s)$ when $s > 0$, or for $t \in (s, 0)$ when $s < 0$. Mainly, for each $k \in \mathbb{N}$ there exists $s = s_k$ such that $x_k = \phi_{t_k + s_k}(x) \in L$.

There are two cases: when $(x_k)_k$ is a constant sequence, meaning the orbit of x is periodic, and when it is not. Assuming the first case, since the orbit of x is periodic, the ω -limit set $\omega(x) = \gamma(x)$

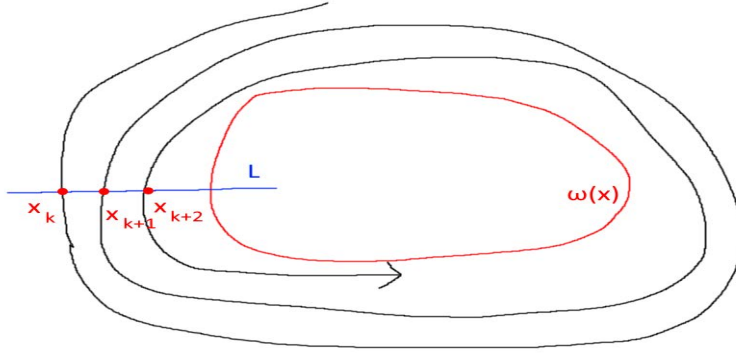


Figure 7: Intersections x_k, x_{k+1} and x_{k+2} with the transversal L

only intersect L at the constant value of the sequence $(x_k)_k$, so $\omega(x) \cap L = \{q\}$.

In the second case, consider two points of the intersection x_k and x_{k+1} . The projection of f on the perpendicular to L always has the same direction. The segment of orbit between x_k and x_{k+1} together with the line segment between these two points form a continuous curve C whose complement $\mathbb{R}^2 \setminus C$ has two connected components, due to Jordan's curve theorem. Due to the direction of f on the segment between x_k and x_{k+1} , the positive semiorbit $\gamma^+(x)$ is contained in the unbounded connected component. This implies the next intersection x_{k+2} does not belong to the line segment between x_k and x_{k+1} . Therefore the points x_k, x_{k+1} , and x_{k+2} are ordered along the transversal L , as seen in Figure (7). Since the sequence $(x_k)_k$ is monotonic along L , it has at most one accumulation point in L and $\omega(x) \cap L = \{q\}$. \square

These two lemmas help prove the Poincaré-Bendixson theorem, which states the following:

Theorem 2.3.10: Let $f : \mathbb{R}^2 \rightarrow \mathbb{R}^2$ be a continuously differentiable function. Then for the differential equations $x' = f(x)$, if the positive semiorbit of x , $\gamma^+(x)$, is bounded and $\omega(x)$ has no critical points, then $\omega(x)$ is a limit cycle.

Proof: Since the semiorbit $\gamma^+(x)$ is bounded, by Lemma 2.3.6 (i), $\omega(x)$ is nonempty. Let $p \in \omega(x)$. From Lemma 2.3.6 (i) and (iii), and the definition of the ω -limit set, $\omega(p)$ is nonempty and $\omega(p) \subset \omega(x)$. Let $q \in \omega(p)$. Since we are assuming $\omega(x)$ has no critical points, q is not a critical point and so there exists a line segment L containing q that is transverse to f . By Lemma 2.3.6 (ii), since $q \in \omega(p)$, there exists a sequence $t_k \rightarrow +\infty$ such that $\phi_{t_k}(p) \rightarrow q$ when $k \rightarrow \infty$. Following the proof of Lemma 2.3.9, we can assume $\phi_{t_k}(p) \in L$ for $k \in \mathbb{N}$. Since $p \in \omega(x)$, by Lemma 2.3.6 (iii), $\phi_{t_k}(p) \in \omega(x)$ for $k \in \mathbb{N}$. Thus $\phi_{t_k}(p) \in L \cap \omega(x)$ and by Lemma 2.3.9, $\phi_{t_k}(p) = q$ for every $k \in \mathbb{N}$. This implies $\gamma(p) \subset \omega(x)$.

Now, assume to the contrary that $\omega(x) \setminus \gamma(p)$ is nonempty. Since $\omega(x)$ is connected, in each neighborhood of $\gamma(p)$ there exist points of $\omega(x)$ that are not in $\gamma(p)$. Thus there exists a transversal L' to f containing one of these points, which is in $\omega(x)$, and a point of $\gamma(p)$. This would mean $\omega(x) \cap L'$ contains at least two points. However, this contradicts Lemma 2.3.9, so $\omega(x) = \gamma(p)$ and $\omega(x)$ is a limit cycle. \square

From the Poincaré-Bendixson theorem, we can obtain additional results.

Corollary 2.3.11: Let γ be an ω -limit cycle. If $\gamma = \omega(x)$ where $x \notin \gamma$, then x has a neighborhood O such that $\gamma = \omega(y)$ for all $y \in O$. That is, the set $\{y \mid \omega(y) = \gamma\} - \gamma$ is open.

Corollary 2.3.12: A compact set K that is positively or negatively invariant contains either a limit cycle or an equilibrium point.

Corollary 2.3.13: Let γ be a closed orbit and let U be the open region in the interior of γ . Then U contains either an equilibrium point or a limit cycle.

Proof: Let D be the compact set $U \cup \gamma$. Then D is invariant since no solution in U can cross γ . If U contains no limit cycle and no equilibrium, then, for any $x \in U$, $\omega(x) = \alpha(x) = \gamma$ by Poincare-Bendixson. If S is a local section at a point $z \in \gamma$, there are sequences $t_n \rightarrow \infty, s_n \rightarrow -\infty$ such that $\phi_{t_n}(x), \phi_{s_n}(x) \in S$ and both $\phi_{t_n}(x)$ and $\phi_{s_n}(x)$ tend to z as $n \rightarrow \infty$. However this is a contradiction about the properties of monotone sequences. \square

Corollary 2.3.14: Let γ be a closed orbit that forms the boundary of an open set U . Then U contains an equilibrium point.

Proof: Suppose U has no equilibrium points. Consider first the case that there are only finitely many closed orbits in U . We may choose the closed orbit that bounds the region with the smallest area. There are then no closed orbits or equilibrium points inside this region, which contradicts Corollary 2.3.13.

Now suppose that there are infinitely many closed orbits in U . If $x_n \rightarrow x$ in U and each x_n lies on a closed orbit, then x must lie on a closed orbit. Otherwise the solution through x would spiral toward a limit cycle since there are no equilibria in U . By Corollary 2.3.11, so would the solution through some nearby x_n , which is impossible.

Let $v \geq 0$ be the greatest lower bound of the areas of regions enclosed by the closed orbits in U . Let $\{\gamma_n\}$ be a sequence of closed orbits enclosing regions of areas v_n such that $\lim_{n \rightarrow \infty} v_n = v$. Let $x_n \in \gamma_n$. Since $\gamma \cup U$ is compact, we may assume that $x_n \rightarrow x \in U$. Then if U contains no equilibrium, x lies in a closed orbit β bounding a region of area v . The usual section argument shows that as $n \rightarrow \infty$, γ_n gets arbitrarily close to β and hence the area $v_n - v$ of the region between γ_n and β goes to 0. Then the argument above shows that there can be no closed orbits or equilibrium points inside γ , which contradicts Corollary 2.3.13. \square

2.4 Bifurcations

Mathematical models often involve multiple parameters in their differential equations. When the parameter values are changed, we may expect a change in the behavior of the solution of the differential equations. If variation of a parameter changes the qualitative behavior of the solution, it is called a bifurcation.

Definition 2.4.1: Consider the scalar differential equation $x' = f(x, \beta)$, where $x, \beta \in \mathbb{R}$, β is the parameter, and $f : \mathbb{R}^2 \rightarrow \mathbb{R}$ is continuously differentiable.

We call \bar{x} a bifurcation point and $\bar{\beta}$ a bifurcation value if $f(\bar{x}, \bar{\beta}) = 0$ and $\frac{\partial}{\partial x} f(\bar{x}, \bar{\beta}) = 0$, where $\frac{\partial}{\partial x} f$ denotes the partial derivative with respect to x .

We can extend this definition to apply to a system with multiple variables. We can analyze bifurcations qualitatively with a bifurcation diagram, which plots a variable's steady state value with a parameter. In this diagram we indicate what parameter values will cause a steady state to be stable or unstable.

There are multiple types of bifurcations.

Definition 2.4.2: A saddle node bifurcation occurs when two steady states are created or destroyed.

Example 2.4.3: In the system of equations

$$\frac{dx}{dt} = a - x^2$$

$$\frac{dy}{dt} = -y,$$

the system has a saddle node bifurcation at the parameter value $a = 0$. There is no steady state when $a < 0$ and two when $a > 0$. The phase diagrams of Figure (8) demonstrates the change in the system's behavior when the parameter a goes from -1 to 0 to 1 . The bifurcation diagram in Figure (9) also demonstrates this change.

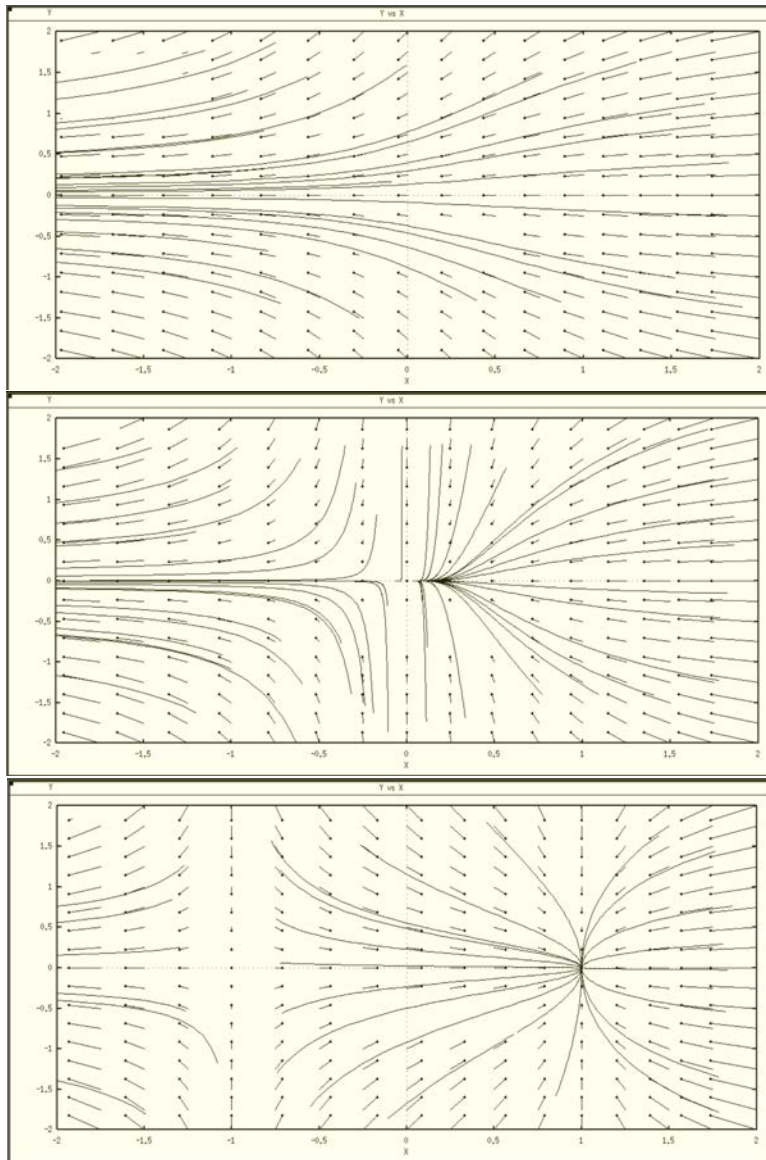


Figure 8: Saddle Node Bifurcation Phase Diagrams

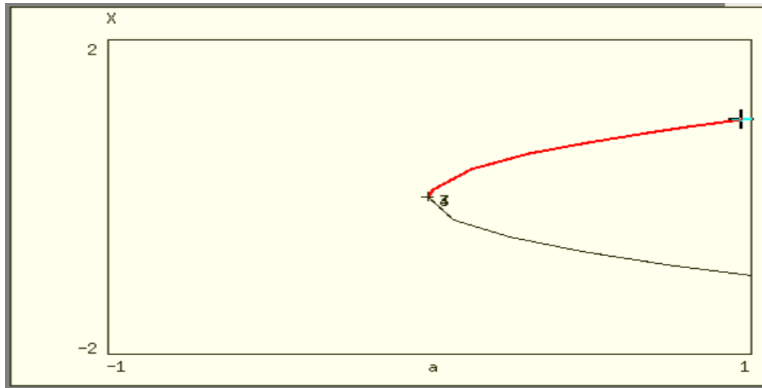


Figure 9: Saddle Node Bifurcation Diagram

Definition 2.4.4: Transcritical bifurcations occur when two steady state change their stability from stable to unstable and vice versa.

Example 2.4.5: In the system of equations

$$\frac{dx}{dt} = ax - x^2$$

$$\frac{dy}{dt} = -y,$$

the system has a transcritical bifurcation at the parameter value $a = 0$. As a goes from negative to positive, the steady state at the origin goes from stable to unstable. Meanwhile, the steady state $(a, 0)$ goes from unstable to stable. The phase diagrams of Figure (10) demonstrates the change in the system's behavior when the parameter a goes from -1 to 0 to 1 . The bifurcation diagram in Figure (11) also demonstrates this change.

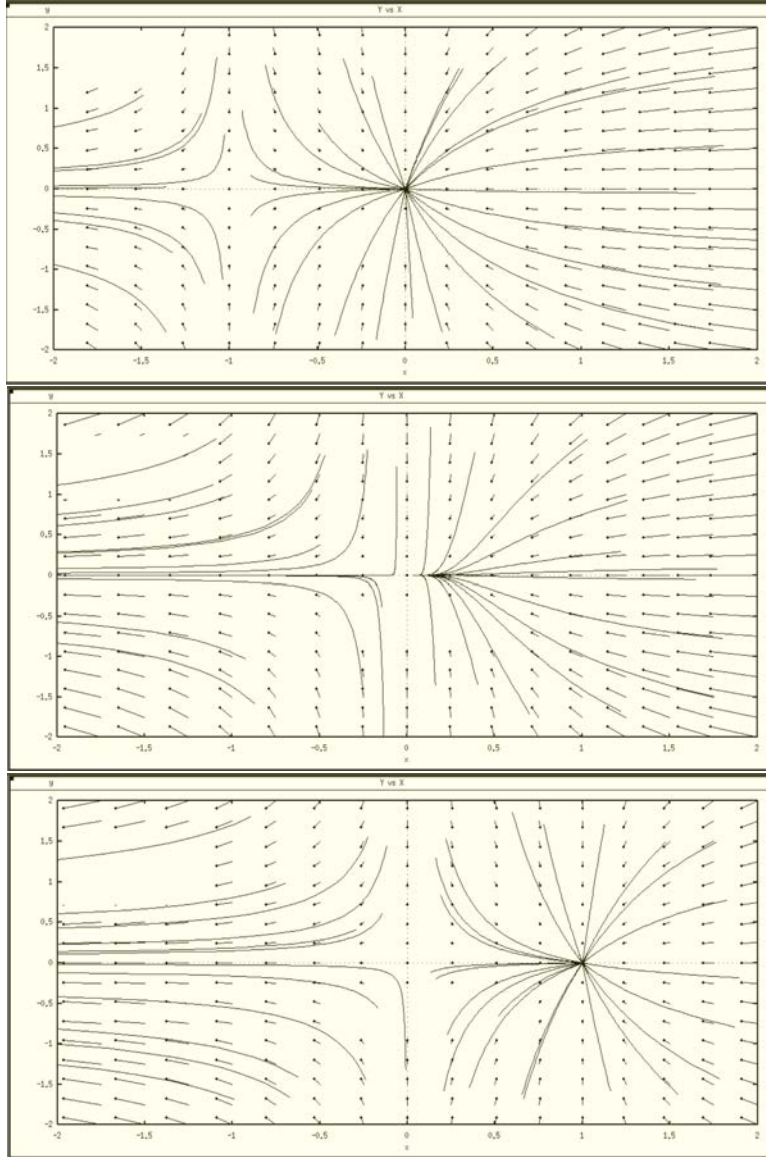


Figure 10: Transcritical Bifurcation Phase Diagrams

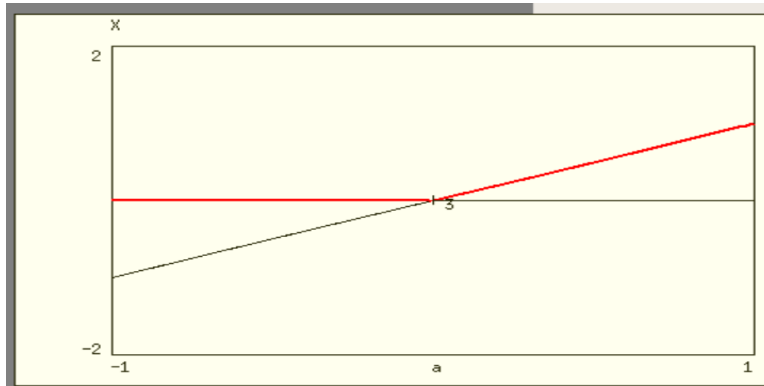


Figure 11: Transcritical Bifurcation Diagram

Definition 2.4.6: Pitchfork bifurcations are a combination of saddle node and transcritical bifurcations. They are called that because the bifurcation diagrams look like pitchforks. There are two types, supercritical and subcritical. Supercritical pitchfork bifurcations have stable branches. Subcritical pitchfork bifurcations have unstable branches.

Since this type of bifurcation does not occur in the models we studied in this thesis, we will not elaborate further with examples. However, we acknowledge its existence here since pitchfork bifurcations are one of the three basic types of bifurcations.

Here we discuss a new type of bifurcation that is not found in the one-dimensional continuous system; namely the bifurcation that gives to limit cycle. Figures (12) and (13) show a typical way that limit cycles are represented in a bifurcation plot. Plotted for each parameter value are both the maximum and minimum values of some function of the state variables as they traverse the limit cycle. Such a bifurcation is known as the Hopf bifurcation.

The next two theorems come from [15]. The next theorem is stated for $n = 2$. A key requirement that the given steady state be associated with complex eigenvalues where the real part changes sign

(e.g. from negative to positive). In popular phrasing, such eigenvalues are said to “cross the real axis”.

Theorem 2.4.7: (The Hopf-Bifurcation Theorem for the case $n = 2$.)

Consider the system of two differential equations which contains a parameter β ,

$$\begin{aligned}\frac{dx_1}{dt} &= f_1(x_1, x_2, \beta) \\ \frac{dx_2}{dt} &= f_2(x_1, x_2, \beta)\end{aligned}$$

where f_1 and f_2 are continuous and have partial derivatives. Suppose that for each value of β the equations admit a steady state whose value may depend on β , that is $(\bar{x}(\beta), \bar{y}(\beta))$, and consider the Jacobian matrix evaluated at the parameter-dependent steady state,

$$J(\beta) = \begin{pmatrix} \frac{\partial f_1}{\partial x_1} & \frac{\partial f_1}{\partial x_2} \\ \frac{\partial f_2}{\partial x_1} & \frac{\partial f_2}{\partial x_2} \end{pmatrix}_{(\bar{x}, \bar{y})}$$

Suppose eigenvalues of this matrix are $\lambda(\beta) = a(\beta) \pm b(\beta)i$. Also suppose that there is a value β^* , called the bifurcation value, such that $a(\beta^*) = 0$, $b(\beta^*) \neq 0$, and as β is varied through β^* , the real parts of the eigenvalues change signs ($\frac{da}{d\beta} \neq 0$ at $\beta = \beta^*$). Then the following three are possible,

(i) At the value $\beta = \beta^*$ a center is created at the steady state, and thus infinitely many neutrally stable concentric closed orbits surround the point (\bar{x}, \bar{y}) .

(ii) There is a range of β values such that $\beta^* < \beta < c$ for which a single closed orbit (a limit cycle) surrounds (\bar{x}, \bar{y}) . As β is varied, the diameter of the limit cycle changes in proportion to $|\beta - \beta^*|^{1/2}$. There are no other closed orbits near (\bar{x}, \bar{y}) . Since the limit cycle exists for β values

above β^* , this phenomenon is known as a supercritical bifurcation.

(iii) There is a range of values such that $d < \beta < \beta^*$ for which a conclusion similar to case (ii) holds, and it is called a subcritical bifurcation.

One of the attractive features of the Hopf bifurcation theorem is that it applies to larger systems of equations. This makes it somewhat more applicable than the Poincare-Bendixson theorem, which holds only for the case $n=2$.

Theorem 2.4.8: (The Hopf-Bifurcation Theorem for the case $n > 2$.)

Consider a system of n variables as in (1), with the appropriate smoothness assumptions on f_i that are functions of the variables and a parameter β . If \bar{x} is an equilibrium point of this system and linearization about this fixed point yields n eigenvalues,

$$\lambda_1, \lambda_2, \dots, \lambda_{n-2}, a + bi, a - bi$$

where eigenvalues λ_1 through λ_{n-2} have negative real parts and exactly λ_{n-1}, λ_n are complex conjugates that cross the imaginary axis when β varies through some critical value, then there exist limit-cycle solutions.

Example 2.4.9: Consider the system:

$$\frac{dx}{dt} = y$$

$$\frac{dy}{dt} = -y^3 + \beta y - x.$$

As β goes from negative to positive, the system goes from a spiral sink to a stable limit cycle, as seen in figures (12) and (13).

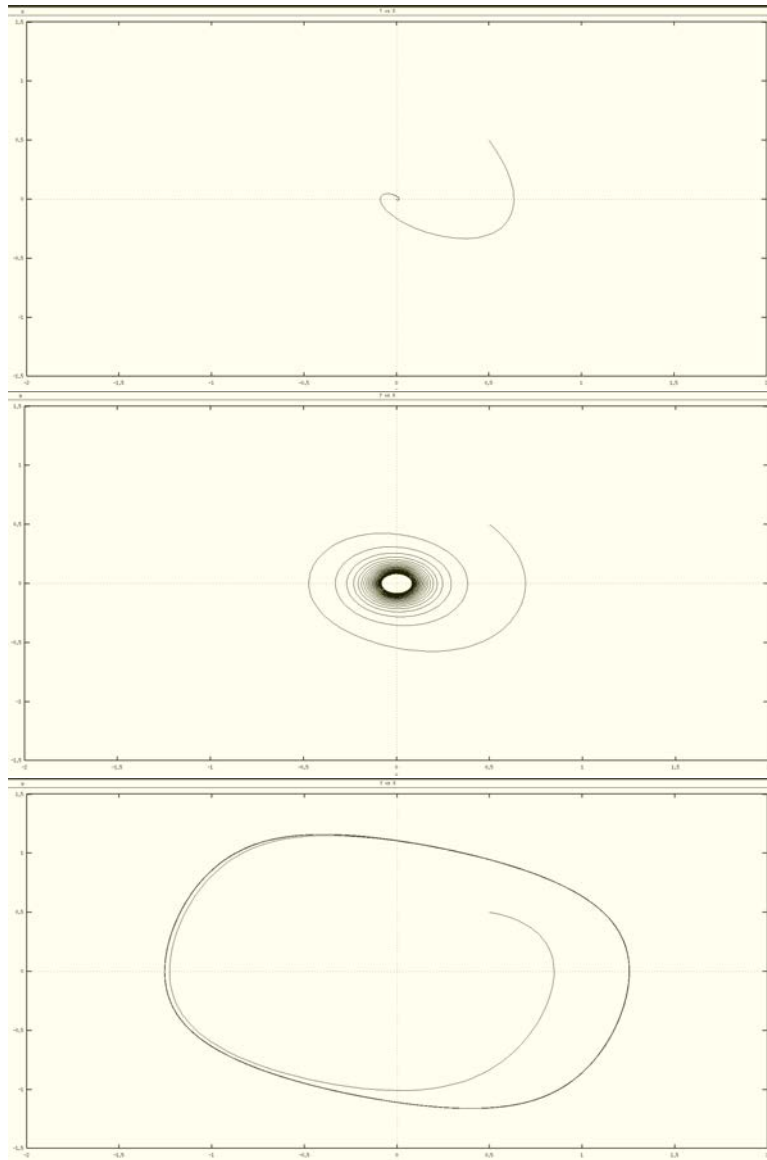


Figure 12: Hopf Bifurcation Example Phase Diagrams where $\beta = -1$ to $\beta = 0$ to $\beta = 1$

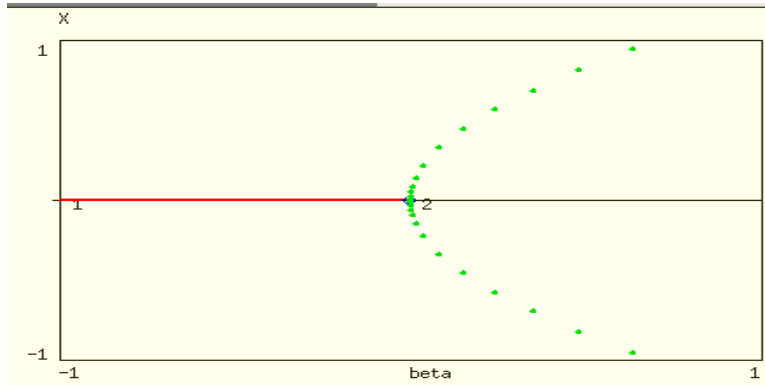


Figure 13: Hopf Bifurcation Diagram

2.5 Nondimensionalization

Some systems have parameters, which affect the behavior of the system in various ways. Since these parameters are unknown, we would like to limit the number of parameters in our model. Thus we nondimensionalize the model. First we scale our current variables in relation to our current parameters. Then we adjust our time variable. Finally, we choose new parameters to replace the ones currently in the model. The qualitative behavior of the system remains the same after nondimensionalization and it reduces the complexity of studying the model.

Example 2.5.1: Consider this system from [15]:

$$\frac{dN}{dt} = \left(\frac{K_{max}C}{K_n + C}\right)N - \frac{FN}{V}$$

$$\frac{dC}{dt} = -\alpha\left(\frac{K_{max}C}{K_n + C}\right)N - \frac{FC}{V} + \frac{FC_0}{V}.$$

Here, N and C are variables and K_{max} , F , V , K_n , α , and C_0 are parameters. We will want to reduce the number of parameters to more easily analyze the behavior of the system.

To nondimensionalize, we use the fact that our variables and time are the product of a scalar multiple and a unit carrying dimensions. As such:

$$N = N^* \times \hat{N}$$

$$C = C^* \times \hat{C}$$

$$t = t^* \times \tau.$$

We want the scalar multiple of time and our variables. First we substitute our original variables and time with the product.

$$\frac{d(N^* \hat{N})}{d(t^* \tau)} = \left(\frac{K_{max} C^* \hat{C}}{K_n + C^* \hat{C}} \right) N^* \hat{N} - \frac{F N^* \hat{N}}{V}$$

$$\frac{d(C^* \hat{C})}{d(t^* \tau)} = -\alpha \left(\frac{K_{max} C^* \hat{C}}{K_n + C^* \hat{C}} \right) N - \frac{F C^* \hat{C}}{V} + \frac{F C_0}{V}.$$

Next we multiply both sides by τ , divide by \hat{N} and \hat{C} , and group constants together. Thus we get

$$\frac{dN^*}{dt^*} = \tau K_{max} \left(\frac{C^*}{K_n / \hat{C} + C^*} \right) N^* - \frac{\tau F N^*}{V}$$

$$\frac{dC^*}{dt^*} = \left(\frac{-\alpha \tau K_{max} \hat{N}}{\hat{C}} \right) \left(\frac{C^*}{K_n / \hat{C} + C^*} \right) N^* - \frac{\tau F C^*}{V} + \frac{\tau F C_0}{V \hat{C}}.$$

At this stage, we determine which values for τ , \hat{N} , and \hat{C} would best simplify the model. In this example we choose

$$\tau = \frac{V}{F}, \hat{C} = K_n, \hat{N} = \frac{K_n}{\alpha \tau K_{max}},$$

and we get

$$\begin{aligned}\frac{dN^*}{dt^*} &= \alpha_1 \left(\frac{C^*}{1+C^*} \right) N^* - N^* \\ \frac{dC^*}{dt^*} &= - \left(\frac{C^*}{1+C^*} \right) N^* - C^* + \alpha_2.\end{aligned}$$

where

$$\begin{aligned}\alpha_1 &= \tau K_{max} = \frac{VK_{max}}{F} \\ \alpha_2 &= \frac{\tau FC_0}{V\hat{C}} = \frac{C_0}{K_n}.\end{aligned}$$

Now we have a system of equations with two parameters instead of six, which is much easier to analyze. After this, we usually drop the * to simplify writing the equations. We use these results to aid in our analysis of the models presented in the following two chapters.

3 Mathematical Model of Indirect Mutualism

Mutualism means the relations in which two or more species benefit from their relationship. To develop our model of mutualism, we will be using the basic Lotka-Volterra model [10] and modifying it to include two prey species that affect each other in mutualism. The standard Lotka-Volterra system of equations is

$$\frac{dx}{dt} = (a - by)x$$
$$\frac{dy}{dt} = (cx - d)y.$$

The parameters a , b , c , and d are assumed to be non-negative. The first equation represents the change in population of the prey species. It is increased by the population available to reproduce, as well as its ability, represented by parameter a . It is decreased by the amount of prey hunted by the predator species, which is limited by the amount of prey that can be hunted. This is also adjusted by the ability of the predator to hunt the prey, represented by parameter b . The second equation represents the change in population of the predator species. It is increased by the amount by the amount of prey that can be hunted and the amount of predators that can hunt and reproduce. The hunting and reproductive ability of the predator is represented by the parameter c . It is decreased by the natural death rate of the predator, which is parameter d . This system does not represent the death rate of prey by natural causes.

Next we will account for the prey's carrying capacity with another term as

$$\frac{dx}{dt} = ax\left(1 - \frac{x}{N}\right) - bxy$$
$$\frac{dy}{dt} = (cx - d)y,$$

where N is the carrying capacity. When the prey population is lower than the carrying capacity, the $(1 - \frac{x}{N})$ term is positive, so the prey population will always grow if there is no predator. When the prey population is higher than the carrying capacity, the $(1 - \frac{x}{N})$ term is negative, so the prey population will shrink, even without the predator.

We can further extend this model to account for two prey species and one predator species:

$$\begin{aligned}\frac{dx}{dt} &= ax\left(1 - \frac{x}{N}\right) - bxz \\ \frac{dy}{dt} &= cy\left(1 - \frac{y}{M}\right) - dyz \\ \frac{dz}{dt} &= -ex + fxz + gyz.\end{aligned}\tag{10}$$

Here, x and y are the prey species and z is the predator species. The parameters a and c are the growth rates of x and y , respectively. Meanwhile, the parameters b and d are their respective death rates. The parameter e is the predator's death rate while f and g are the growth rates of the predator due to the respective prey species. Finally, N is the carrying capacity of the x species while M is the carrying capacity of the y species.

Now we wish to consider mutualism among two prey species. It is now generally accepted that symbiotic organisms influence the carrying capacities of each other, hence the carrying capacities of symbiotes are not fixed quantities, but should be considered as functions of population size. To model mutualism among prey species, we will be incorporating two expressions studied in [1], corresponding to indirect and direct interactions. The system of equations for symbiotic species with indirect interactions (defined as “without direct interaction” in [1]) is

$$\frac{dx}{dt} = x\left(1 - \frac{x}{1 + ay}\right)$$

$$\frac{dy}{dt} = y\left(1 - \frac{y}{1 + bx}\right),$$

where x and y are the interacting species and a and b are parameters showing the type and strength of their symbiosis. In the following chapter, we suggest a mathematical foundation of this idea to an extended three species model and investigate its dynamics.

3.1 Model Development

In this chapter, we introduce a mathematical model of symbiosis between three different species by taking into account that the carrying capacity of the X species is a function of the Y species and vice versa. Our model with indirect interaction is

$$\frac{dX}{dt} = AX\left(1 - \frac{X}{1 + \mu Y}\right) - BXZ$$

$$\frac{dY}{dt} = CY\left(1 - \frac{Y}{1 + \nu X}\right) - DYZ \tag{11}$$

$$\frac{dZ}{dt} = -EZ + FXZ + GYZ,$$

where X and Y are the symbiotic prey species while Z is the predator species. The parameters A and C are the natural birth rates of their respective prey species. The parameters B and D are the death rates due to predation. The parameter E is the natural death rate of the predator. The parameters F and G are the respective growth rates of the predator due to the respective prey species. All of these parameters are positive. The parameters μ and ν show how much symbiosis

affect the respective species' carrying capacity. Since we are only considering mutualism in this model, μ and ν are nonnegative.

Before proceeding with analysis, some scaling needs to take place so as to be better able to understand how the parameters affect the dynamics. To this end, the variables are scaled as,

$$x = X, y = Y, z = \frac{B}{A}Z, t_{new} = \frac{t_{old}}{A}.$$

Thus we get

$$\begin{aligned} \frac{dx}{d(\frac{t}{A})} &= Ax(1 - \frac{x}{1 + \mu y}) - Bx \frac{Az}{B} \\ \frac{dy}{d(\frac{t}{A})} &= Cy(1 - \frac{y}{1 + \nu x}) - Dy \frac{Az}{B} \\ \frac{d(\frac{Az}{B})}{d(\frac{t}{A})} &= -E \frac{Az}{B} + Fx \frac{Az}{B} + Gy \frac{Az}{B}, \end{aligned} \tag{12}$$

which becomes

$$\begin{aligned} \frac{dx}{dt} &= x(1 - \frac{x}{1 + \mu y}) - xz \\ \frac{dy}{dt} &= \frac{C}{A}y(1 - \frac{y}{1 + \nu x}) - Dy \frac{z}{B} \\ \frac{dz}{dt} &= -E \frac{z}{A} + Fx \frac{z}{A} + Gy \frac{z}{A}, \end{aligned} \tag{13}$$

We also use the following parameters:

$$a = \frac{C}{A}, b = \frac{D}{B}, c = \frac{E}{A}, d = \frac{F}{A}, e = \frac{G}{A}, \mu = \alpha, \nu = \beta.$$

Thus we get our nondimensionalized model:

$$\begin{aligned}\frac{dx}{dt} &= x\left(1 - \frac{x}{1 + \alpha y}\right) - xz \\ \frac{dy}{dt} &= ay\left(1 - \frac{y}{1 + \beta x}\right) - byz \\ \frac{dz}{dt} &= -cz + dxz + eyz.\end{aligned}\tag{14}$$

We still have seven parameters, which is difficult to analyze quantitatively, so we will make a few assumptions to simplify our model even further. First, we will assume the x and y species have the same death rate, causing our b parameter to be 1. Second, we will assume the two prey have the same beneficial effect on the predator population, causing $d = e$. Finally, we assume the prey have the same symbiotic effect on each other, meaning $\alpha = \beta$. Thus we have four parameters in our final model:

$$\begin{aligned}\frac{dx}{dt} &= x\left(1 - \frac{x}{1 + \alpha y}\right) - xz \\ \frac{dy}{dt} &= ay\left(1 - \frac{y}{1 + \alpha x}\right) - yz \\ \frac{dz}{dt} &= -cz + dz(x + y).\end{aligned}\tag{15}$$

Note that our parameters a , c , d , and α retain the property that they are always positive. Additionally, for biological study, the region of interest in \mathbb{R}^3 remains the positive octant $H = \{(x, y, z) \in \mathbb{R}^3 | x > 0, y > 0, z > 0\}$.

3.2 Steady States, Stability Analysis, and Bifurcations

There are seven steady states of equation (15):

- (1) Complete extinction, $(0, 0, 0)$
- (2) Prey x only, $(1, 0, 0)$
- (3) Prey y only, $(0, 1, 0)$
- (4) Prey x and predator, $(\frac{c}{d}, 0, \frac{d-c}{d})$
- (5) Prey y and predator, $(0, \frac{c}{d}, \frac{a(d-c)}{d})$
- (6) Prey only, $(\frac{1}{1-\alpha}, \frac{1}{1-\alpha}, 0)$
- (7) Coexistence, $(\bar{x}, \bar{y}, \bar{z})$ is the solution to the system of equations:

$$\begin{aligned}
 1 - \frac{\bar{x}}{1 + \alpha\bar{y}} &= \bar{z} \\
 a(1 - \frac{\bar{y}}{1 + \alpha\bar{x}}) &= \bar{z} \\
 \bar{y} &= \frac{c - d\bar{x}}{d}.
 \end{aligned} \tag{16}$$

More specifically, when $a \neq 1$ the solutions are:

$$\begin{aligned}
 \bar{x} &= \frac{d(a+1) + c\alpha(2a + \alpha(a-1)) \mp q}{2d\alpha(\alpha+1)(a-1)} \\
 \bar{y} &= \frac{d(a+1) + c\alpha(2 + \alpha(1-a)) \mp q}{2d\alpha(\alpha+1)(1-a)} \\
 \bar{z} &= \frac{(a+1)(d + 2d\alpha + c\alpha^2) \mp q}{2\alpha(2d + c\alpha)},
 \end{aligned}$$

where

$$q = \sqrt{4\alpha(1-a)(a(c-d)+d)(\alpha+1)(d+c\alpha) + (d(a+1) + c\alpha(2a + \alpha(a-1)))^2}. \quad (17)$$

We denote these steady states as $(\bar{x}_-, \bar{y}_-, \bar{z}_-)$ and $(\bar{x}_+, \bar{y}_+, \bar{z}_+)$, corresponding to the respective signs of q . When $a = 1$, the coexistence steady state is $(\frac{c}{2d}, \frac{c}{2d}, \frac{2d+c\alpha-c}{2d+c\alpha})$, which is biologically significant when $\frac{2d}{c} + \alpha > 1$.

Lemma 3.2.1: For system (16) with positive parameters α, a, c, d and $a \neq 1$, of the two steady states $(\bar{x}_-, \bar{y}_-, \bar{z}_-)$ and $(\bar{x}_+, \bar{y}_+, \bar{z}_+)$, there is only one possible positive coexistence steady state, $(\bar{x}_-, \bar{y}_-, \bar{z}_-)$ if and only if one of the following set of conditions is met.

- i. $a \neq 1$ and $d < c < 2d$;
- ii. $a \neq 1, c > 2d$, and $\frac{2d}{c} + \alpha > 1$;
- iii. $a < 1, a + \frac{c}{d} > 1$ and $c < d$;
- iv. $1 < a < \frac{d}{d-c}$ and $c < d$.

Proof: To show this is true, we must first show the steady states are real. To do this, we must show q (equation 17) is real. We can rewrite the expression under the radical of q as $d^2(a+1)^2 + 8acd\alpha + 4ac^2\alpha^2 + \alpha(4d^2(\alpha+1) + 2\alpha cd + 4cd\alpha^2 + c^2\alpha^3)(a-1)^2$, which is greater than zero due to squared terms and our parameters being positive, meaning q is real.

We will start with the \bar{z} terms. The term \bar{z}_+ is obviously positive. For the term \bar{z}_- , we know the denominator is always positive. We can multiply both numerator and denominator by the conjugate of the numerator. We know the conjugate is positive, so the sign of the numerator is preserved. Doing so, we get the numerator to be $4a\alpha(\alpha+1)(2d+c\alpha)(2d+c\alpha-c)$.

Thus, the numerator is positive when $2d + c\alpha > c$, which can be rewritten as $\frac{2d}{c} + \alpha > 1$.

Now we will look at the \bar{x}_+ and \bar{y}_+ terms. The numerator of \bar{x}_+ is obviously positive when $a > 1$.

When $a < 1$, we do not know the sign of $d(a + 1) + c\alpha(2a + \alpha(a - 1)) = r$. If $r \geq 0$, then the numerator is obviously positive.

If $r < 0$, then $q - r > 0$, since q is positive. To show $q + r > 0$, we can show $(q + r)(q - r) = q^2 - r^2 > 0$. $q^2 - r^2 = 4\alpha(1 - a)(ac + d(1 - a))(\alpha + 1)(d + c\alpha) > 0$, since $a < 1$. Thus the numerator of \bar{x}_+ is always positive.

Similarly, the numerator of \bar{y}_+ is positive when $a < 1$. When $a > 1$, if $d(a + 1) + c\alpha(2 + \alpha(1 - a)) \geq 0$, the numerator is still positive. If $d(a + 1) + c\alpha(2 + \alpha(1 - a)) < 0$, then by similar reasoning as above, we can write $q^2 - (d(a + 1) + c\alpha(2 + \alpha(1 - a)))^2 = 4\alpha(a - 1)(c + d(a - 1))(\alpha + 1)(d + c\alpha) > 0$. This is the case since $a > 1$, so the numerator of \bar{y}_+ is always positive.

Therefore, when $a < 1$, $\bar{x}_+ < 0$ and $\bar{y}_+ > 0$. However, when $a > 1$, $\bar{x}_+ > 0$ and $\bar{y}_+ < 0$. Thus $(\bar{x}_+, \bar{y}_+, \bar{z}_+)$ is not biologically significant.

Since we know the conjugates of the numerators of \bar{x}_- and \bar{y}_- are always positive, we can use that to find conditions for when \bar{x}_- and \bar{y}_- are positive. The numerator of \bar{x}_- multiplied by its conjugate is $4\alpha(\alpha + 1)(d + c\alpha)(a - 1)(a(c - d) + d)$. The relevant part is $(a - 1)(a(c - d) + d)$.

The numerator of \bar{y}_- multiplied by its conjugate is $-4\alpha(\alpha + 1)(d + c\alpha)(a - 1)(c + d(a - 1))$. The relevant part is $-(a - 1)(c + d(a - 1))$.

For $\bar{x}_- > 0$, we must have $ac + d > ad$. For $\bar{y}_- > 0$, we must have $c + ad > d$. For $\bar{z}_- > 0$, we need to have $2d + c\alpha > c$. Thus for the steady state to exist, we need ranges of parameter values that satisfy all three conditions.

If $a < 1$, \bar{x}_- is always positive. Then, if $d < c < 2d$, \bar{y}_- and \bar{z}_- will also be positive. However, if $c > 2d$, \bar{y}_- is still positive, but we also need $2d + c\alpha > c$ for \bar{z}_- to be positive. If $c < d$, then \bar{z}_-

will be positive, but we also need $c + ad > d$ for \bar{y}_- to be positive.

If $a > 1$, \bar{y}_- is always positive. Like above, if $d < c < 2d$, \bar{x}_- and \bar{z}_- will also be positive. However, if $c > 2d$, \bar{x}_- is still positive, but we also need $2d + c\alpha > c$ for \bar{z}_- to be positive. If $c < d$, then \bar{z}_- will be positive, but we also need $a < \frac{-d}{c-d} = \frac{d}{d-c}$ for \bar{x}_- to be positive.

Thus we have shown the conditions for which $(\bar{x}_-, \bar{y}_-, \bar{z}_-)$ is positive. \square

The linear stability of these steady states is determined by considering the eigenvalues of the Jacobian matrix,

$$J_1(x, y, z) = \begin{bmatrix} 1 - \frac{2x}{1+\alpha y} - z & \frac{\alpha x^2}{(1+\alpha y)^2} & -x \\ \frac{\alpha \alpha y^2}{(1+\alpha x)^2} & a - \frac{2\alpha y}{1+\alpha x} - z & -y \\ dz & dz & -c + d(x + y) \end{bmatrix}, \quad (18)$$

evaluated at each of these steady states.

3.2.1 Complete Extinction: $x = 0, y = 0, z = 0$

When the Jacobian matrix (18) is evaluated at $x = 0, y = 0$, and $z = 0$:

$$J_1(0, 0, 0) = \begin{bmatrix} 1 & 0 & 0 \\ 0 & a & 0 \\ 0 & 0 & -c \end{bmatrix}.$$

Since this is a diagonal matrix, the eigenvalues are 1, a , and $-c$. This means the origin is always unstable. Biologically, this means that assuming there all three species at the start, there will never be a time when all three species go extinct.

3.2.2 The prey x only: $x = 1, y = 0, z = 0$

When the Jacobian matrix (18) is evaluated at $x = 1, y = 0$, and $z = 0$:

$$J_1(1, 0, 0) = \begin{bmatrix} -1 & \alpha & -1 \\ 0 & a & 0 \\ 0 & 0 & -c + d \end{bmatrix}.$$

Since this is an upper triangular matrix, the eigenvalues are $-1, a$, and $d - c$. This steady state is always unstable.

3.2.3 The prey y only: $x = 0, y = 1, z = 0$

When the Jacobian matrix (18) is evaluated at the steady state $x = 0, y = 1$, and $z = 0$

$$J_1(0, 1, 0) = \begin{bmatrix} 1 & 0 & 0 \\ a\alpha & -a & -1 \\ 0 & 0 & -c + d \end{bmatrix}.$$

The characteristic equation for the Jacobian matrix is

$$-((-1 + \lambda)(a + \lambda)(c - d + \lambda)) = 0 \tag{19}$$

Thus the eigenvalues are $1, -a$, and $d - c$. This point is always unstable.

3.2.4 Prey x and Predator: $x = \frac{c}{d}, y = 0, z = \frac{d-c}{d}$

When the Jacobian matrix (18) is evaluated at the steady state $x = \frac{c}{d}, y = 0$, and $z = \frac{d-c}{d}$:

$$J_1\left(\frac{c}{d}, 0, \frac{d-c}{d}\right) = \begin{bmatrix} -\frac{c}{d} & \alpha \frac{c^2}{d^2} & -\frac{c}{d} \\ 0 & a - \frac{d-c}{d} & 0 \\ d-c & d-c & 0 \end{bmatrix}.$$

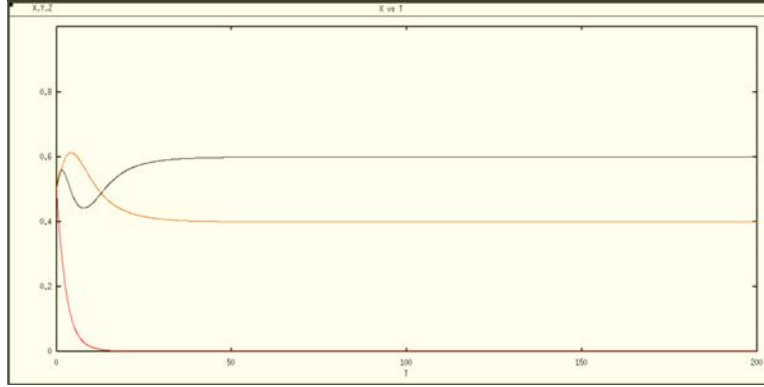


Figure 14: Prey x and predator only steady state

The characteristic equation for the Jacobian is

$$\left(a - \frac{d-c}{d} - \lambda\right)\left(c - \frac{c^2}{d} + \frac{c\lambda}{d} + \lambda^2\right) = 0. \quad (20)$$

The eigenvalues are $\frac{c-d+ad}{d}$ and $\frac{-c \mp \sqrt{c(c+4cd-4d^2)}}{2d}$. For this steady state to be biologically significant, $d > c$. Thus $4cd - 4d^2$ is negative and the real part of $\frac{-c \mp \sqrt{c(c+4cd-4d^2)}}{2d}$ is always negative.

This steady state is stable when $a + \frac{c}{d} < 1$.

The plot of the trajectory in Figure (14) for x , y , and z shows that each species travels directly towards its steady state with initial conditions $x(0) = y(0) = z(0) = 0.5$ and the parameters are $a = d = 0.25$, $\alpha = 1$, and $c = 0.15$.

Biologically, this makes sense. If the prey y cannot reproduce faster than the predator, then it will go extinct.

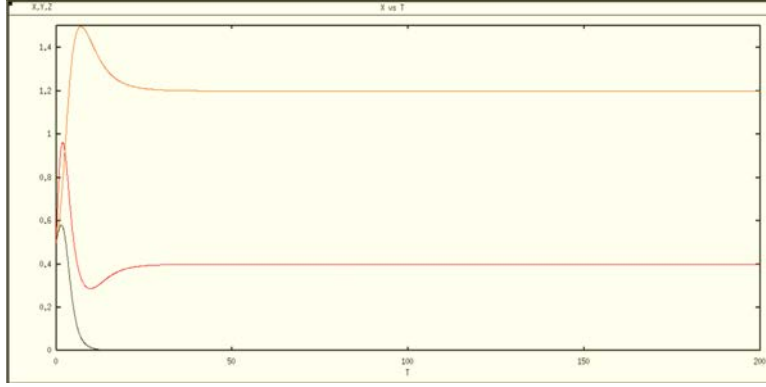


Figure 15: Prey y and predator only steady state

3.2.5 Prey y and Predator: $x = 0$, $y = \frac{c}{d}$, $z = \frac{a(d-c)}{d}$

When the Jacobian matrix (18) is evaluated at the steady state $x = 0$, $y = \frac{c}{d}$, and $z = \frac{a(d-c)}{d}$:

$$J_1\left(0, \frac{c}{d}, \frac{a(d-c)}{d}\right) = \begin{bmatrix} 1 - \frac{a(d-c)}{d} & 0 & 0 \\ a\alpha \frac{c^2}{d^2} & -a\frac{c}{d} & -\frac{c}{d} \\ a(d-c) & a(d-c) & 0 \end{bmatrix}.$$

The characteristic equation for the Jacobian is

$$\left(1 - \frac{a(d-c)}{d} - \lambda\right)\left(ac - \frac{ac^2}{d} + \frac{ac\lambda}{d} + \lambda^2\right) = 0. \quad (21)$$

The eigenvalues are $\frac{ac+d-ad}{d}$ and $\frac{-ac \mp \sqrt{ac(ac+4cd-4d^2)}}{2d}$. For this steady state to be biologically significant, $d > c$. Thus $4cd - 4d^2$ is negative and the real part of $\frac{-ac \mp \sqrt{ac(ac+4cd-4d^2)}}{2d}$ is always negative. This steady state is stable when $a > \frac{d}{d-c}$.

The plot of the trajectory in Figure (15) for x , y , and z shows that each species travels directly towards its steady state with initial conditions $x(0) = y(0) = z(0) = 0.5$ and the parameters are $a = 2$, $d = 0.25$, $\alpha = 1$ and $c = 0.1$.

Biologically, this means the prey x will go extinct if it cannot reproduce faster than the predator.

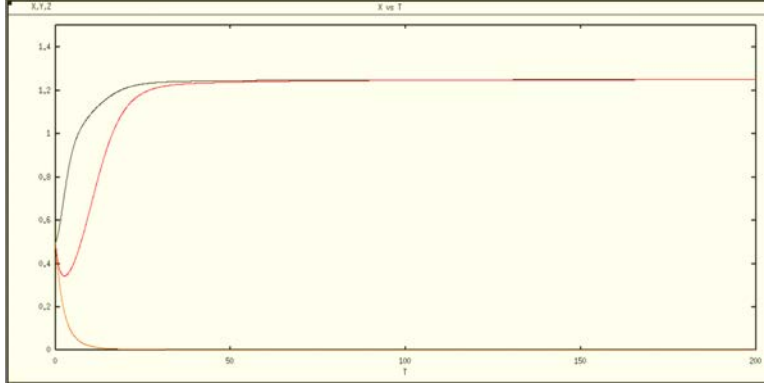


Figure 16: Prey-only steady state

Note that both mathematically and logically, the “prey x and predator only” steady state and “prey y and predator only” steady state cannot both be stable at the same time. That is because $a < 1$ for the former to be stable while $a > 1$ for latter.

3.2.6 The prey x and y only: $x = \frac{1}{1-\alpha}$, $y = \frac{1}{1-\alpha}$, $z = 0$

When the Jacobian matrix (18) is evaluated at the steady state $x = \frac{1}{1-\alpha}$, $y = \frac{1}{1-\alpha}$, and $z = 0$:

$$J_1\left(\frac{1}{1-\alpha}, \frac{1}{1-\alpha}, 0\right) = \begin{bmatrix} -1 & \alpha & -\frac{1}{1-\alpha} \\ a\alpha & -a & -\frac{1}{1-\alpha} \\ 0 & 0 & -c + \frac{2d}{1-\alpha} \end{bmatrix}.$$

The characteristic equation for the Jacobian is

$$(2d + c(\alpha - 1) + (\alpha - 1)\lambda)(a(-1 + \alpha^2 - \lambda) - \lambda(1 - \lambda)) = 0 \quad (22)$$

The eigenvalues of the matrix are $\frac{2d+c\alpha-c}{1-\alpha}$ and $\frac{-(a+1) \mp \sqrt{(a-1)^2 + 4a\alpha^2}}{2}$. To be biologically significant, $\alpha < 1$. The conjugate eigenvalues are always negative and real. The steady state will be stable when $2d < c(1 - \alpha)$ and unstable otherwise.

The plot of the trajectory in Figure (16) for x , y , and z shows that each species travels directly towards its steady state with initial conditions $x(0) = y(0) = z(0) = 0.5$ and the parameters are $a = d = 0.25$, $\alpha = 0.2$ and $c = 0.65$.

Biologically, this means that if the predator dies faster than it can grow from food supply, it will go extinct.

3.2.7 The Coexistence Steady State Behavior

Theorem 3.2.2: The coexistence steady state $(\bar{x}, \bar{y}, \bar{z})$ of the system (15) is always stable when it is biologically significant.

Proof: The Jacobian matrix (18) evaluated at $(\bar{x}, \bar{y}, \bar{z})$ is given as follows:

$$J_1(\bar{x}, \bar{y}, \bar{z}) = \begin{bmatrix} 1 - \frac{2\bar{x}}{1+\alpha\bar{y}} - \bar{z} & \frac{\alpha\bar{x}^2}{(1+\alpha\bar{y})^2} & -\bar{x} \\ \frac{a\alpha\bar{y}^2}{(1+\alpha\bar{x})^2} & a - \frac{2a\bar{y}}{1+\alpha\bar{x}} - \bar{z} & -\bar{y} \\ d\bar{z} & d\bar{z} & -c + d(\bar{x} + \bar{y}) \end{bmatrix}.$$

which, in turn, yields a cubic characteristic polynomial equation in λ , given by

$$P(\lambda) = \lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0, \quad (23)$$

where the coefficients a_1 , a_2 , and a_3 are expressed in terms of parameters of (15) as

$$a_1 = 2\bar{z} + \frac{2a\bar{y}}{1+\alpha\bar{x}} + \frac{2\bar{x}}{1+\alpha\bar{y}} + c - d(\bar{x} + \bar{y}) - a - 1$$

$$\begin{aligned}
a_2 = & a - c - ac + d(\bar{x} + \bar{y}) + ad(\bar{x} + \bar{y}) - \bar{z} - a\bar{z} + 2c\bar{z} + 2d(\bar{x} + \bar{y})\bar{z} + \bar{z}^2 \\
& + \frac{2ac\bar{y} + 2a\bar{y}\bar{z} - 2a\bar{y} - 2ad\bar{y}(\bar{x} + \bar{y})}{1 + \alpha\bar{x}} + \frac{2c\bar{x} + 2\bar{x}\bar{z} - 2a\bar{x} - 2d\bar{x}(\bar{x} + \bar{y})}{1 + \alpha\bar{y}} \\
& + \frac{4a\bar{x}\bar{y}}{(1 + \alpha\bar{x})(1 + \alpha\bar{y})} - \frac{a\bar{x}^2\bar{y}^2\alpha^2}{(1 + \alpha\bar{x})^2(1 + \alpha\bar{y})^2}
\end{aligned}$$

$$\begin{aligned}
a_3 = & ac - ad(\bar{x} + \bar{y}) - c\bar{z} - ac\bar{z} - ad\bar{x}\bar{z} - d\bar{y}\bar{z} + d(\bar{x} + \bar{y})\bar{z} + ad(\bar{x} + \bar{y})\bar{z} + c\bar{z}^2 + d\bar{x}^2\bar{z}^2 + d\bar{y}\bar{z}^2 - d(\bar{x} + \bar{y})\bar{z} \\
& + \frac{2a\bar{y}d(\bar{x} + \bar{y}) + 2ac\bar{y}\bar{z} + 2ad\bar{x}\bar{y}^2 - 2ac\bar{y} - 2ad(\bar{x} + \bar{y})\bar{y}\bar{z}}{1 + \alpha\bar{x}} \\
& + \frac{2ad(\bar{x} + \bar{y})\bar{x} + 2c\bar{x}\bar{z} + 2d\bar{x}\bar{y}\bar{z} - 2ac\bar{x} - 2d(\bar{x} + \bar{y})\bar{x}\bar{z}}{1 + \alpha\bar{y}} \\
& + \frac{ad\alpha\bar{x}\bar{y}^2\bar{z}}{(1 + \alpha\bar{x})^2} + \frac{d\alpha\bar{x}^2\bar{y}\bar{z}}{(1 + \alpha\bar{y})^2} + \frac{4ac\bar{x}\bar{y} - 4ad\bar{x}\bar{y}(\bar{x} + \bar{y})}{(1 + \alpha\bar{x})(1 + \alpha\bar{y})}.
\end{aligned}$$

Using (16), we can simplify the terms into

$$\begin{aligned}
a_1 &= \frac{\bar{x}(1 + \alpha\bar{x}) + a\bar{y}(1 + \alpha\bar{y})}{(1 + \alpha\bar{x})(1 + \alpha\bar{y})} \\
a_2 &= \frac{d\bar{x}\bar{z} + d\bar{y}\bar{z}(1 + \alpha\bar{x})^2(1 + \alpha\bar{y})^2 + a\bar{x}\bar{y} + a\alpha\bar{x}^2\bar{y} + a\alpha\bar{x}\bar{y}^2}{(1 + \alpha\bar{x})^2(1 + \alpha\bar{y})^2} \\
a_3 &= \frac{d\bar{x}\bar{y}\bar{z}(a\alpha\bar{y}(1 + \alpha\bar{y})^2 + a(1 + \alpha\bar{x})(1 + \alpha\bar{y})^2 + \alpha\bar{x}(1 + \alpha\bar{x})^2 + (1 + \alpha\bar{y})(1 + \alpha\bar{x})^2)}{(1 + \alpha\bar{x})^2(1 + \alpha\bar{y})^2}
\end{aligned}$$

By the Routh-Hurwitz criteria, $(\bar{x}, \bar{y}, \bar{z})$ will be stable if $a_1 > 0$, $a_3 > 0$, and $a_1a_2 > a_3$. Since $\bar{x}, \bar{y}, \bar{z}$, and all parameters are positive, it is clear that $a_1 > 0$ and $a_3 > 0$. The last criterion

$$a_1a_2 - a_3 = d\bar{x}^2\bar{z}(1 + \alpha\bar{x})^3(1 + \alpha\bar{y}) + a^2\bar{x}\bar{y}^2(1 + \alpha\bar{y})(1 + \alpha\bar{x} + \alpha\bar{y}) + a\bar{y}(1 + \alpha\bar{x})(\alpha\bar{x}^3 + \bar{x}^2(1 + \alpha\bar{y} + d\bar{y}\bar{z}(1 + \alpha\bar{y})^3)),$$

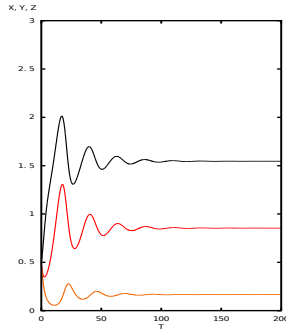


Figure 17: Time plot of the coexistence steady state

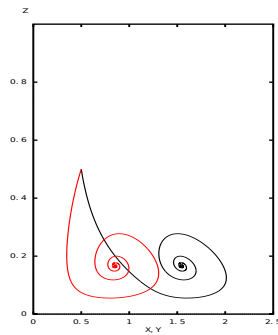


Figure 18: Phase Diagram of the coexistence steady state

is greater than zero, so $a_1 a_2 > a_3$. Thus $(\bar{x}, \bar{y}, \bar{z})$ is always stable if it is biologically significant. \square

A plot of the trajectory in Figure (17) for x , y , and z shows that each species travels directly towards its steady state with initial conditions $x(0) = y(0) = z(0) = 0.5$ and the parameters are $a = d = 0.25$, $\alpha = 1$ and $c = 0.6$.

In Figure (18) is a phase diagram of z vs. x and y , where the black curve is the x population and the red curve is the y population.

Figure (19) is a 3D phase diagram of z vs. x vs. y .

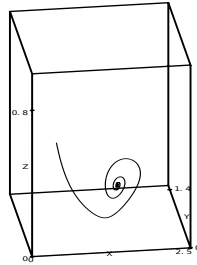


Figure 19: 3D Phase Diagram of the coexistence steady state

Biologically, this means that if the predator death rate is too low, there will be too many predators, causing one of the prey species to go extinct. As the predator death increases, there are less prey that will be killed, so all three species will stay around. However, the prey populations will not explode in growth due to the continual presence of the predator.

3.2.8 Bifurcation Analysis

We now look at the steady states of (15) as a collective whole with bifurcation analysis. The first diagram in Figure (20) is the bifurcation diagram of the x population vs the c parameter. The other parameters are set to $a = d = 0.25$ and $\alpha = 1$. As with all of these bifurcations diagrams, the red line is stable while the black line is unstable. From bottom to top according to starting position along the left axis, the corresponding steady states are the prey x and predator only steady state, the coexistence steady state, and the x only steady state. The transcritical bifurcation occurs at $c = 0.1875$.

The second diagram in Figure (21) is the bifurcation diagram of the y population vs the c parameter. Similar to the first diagram, the other parameters are set to $a = d = 0.25$ and $\alpha = 1$.

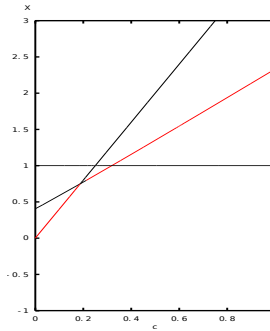


Figure 20: Bifurcation diagram of the x population vs the c parameter

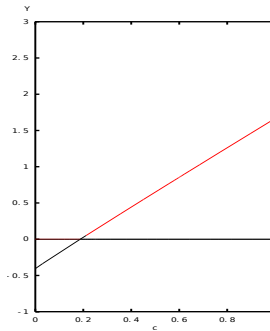


Figure 21: Bifurcation diagram of the y population vs the c parameter.

From bottom to top according to starting position along the left axis, the first corresponding steady states is the coexistence steady state. Next is the prey x and predator only steady state and the x only steady state along $y = 0$. Since these are the same set parameters, the transcritical bifurcation occurs at $c = 0.1875$.

The third diagram in Figure (22) is the bifurcation diagram of the z population vs the α parameter. The other parameters are set to $a = d = 0.25$ and $c = 0.65$. The two steady states displayed are the prey-only steady state and the coexistence steady state. There is a transcritical bifurcation

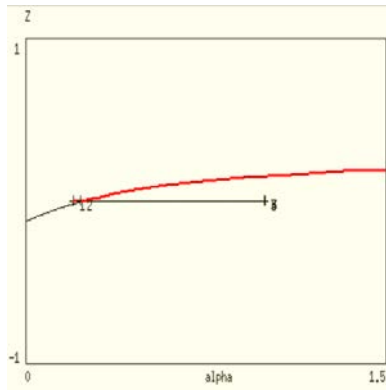


Figure 22: Bifurcation diagram of the z population vs the α parameter.

at $\alpha = 0.2308$. When $\alpha < 0.2308$, coexistence steady state is unstable while the prey-only steady state is stable. When $\alpha > 0.2308$, the coexistence steady state is stable while the prey-only steady state is unstable. The prey-only steady state disappears once $\alpha = 1$.

We notice many similarities between this model and the next model, as some major differences.

4 Mathematical Model of Direct Symbiosis

Considering direct interaction among symbiotic prey species, we derive our model in the same way as our indirect interaction model, except that we will use the direct interaction term (defined as “mutual interactions” in [1]. While “asymmetrical interactions” is a third term in [1] and would fall under our phrasing of “direct interactions”, unequal symbiosis is outside the scope of our research, so the term and its specific biological implications will be ignored for this paper.) The system of equations for symbiotic species with direct interactions is

$$\begin{aligned}\frac{dx}{dt} &= x\left(1 - \frac{x}{1 + axy}\right) \\ \frac{dy}{dt} &= y\left(1 - \frac{y}{1 + bxy}\right),\end{aligned}$$

where x and y are the interacting species and a and b are parameters showing the type and strength of their symbiosis [1].

4.1 Model Development

We will now use the direct interaction term. Our model with direct interaction is

$$\begin{aligned}\frac{dX}{dt} &= AX\left(1 - \frac{X}{1 + \mu XY}\right) - BXZ \\ \frac{dY}{dt} &= CY\left(1 - \frac{Y}{1 + \nu XY}\right) - DYZ \\ \frac{dZ}{dt} &= -EZ + FXZ + GYZ.\end{aligned}\tag{24}$$

X and Y are the symbiotic prey species while Z is the predator species. The parameters A and C are the natural growth rates of their respective prey species. The parameters B and D are the death rates due to predation. The parameter E is the natural death rate of the predator. The parameters F and G are the respective growth rates of the predator due to the respective prey species. All of these parameters are positive. The parameters μ and ν show how much symbiosis affect the respective species' carrying capacity. Since we are only considering mutualism and commensalism in this model, μ and ν are nonnegative.

Before proceeding with analysis, some scaling needs to take place so as to be better able to understand how the parameters affect the dynamics. To this end, the variables are scaled as,

$$x = X, y = Y, z = \frac{B}{A}Z, t_{new} = at_{old}.$$

We also use the following parameters:

$$a = \frac{C}{A}, b = \frac{D}{B}, c = \frac{E}{A}, d = \frac{F}{A}, e = \frac{G}{A}.$$

With these changes, Equations (24) become

$$\begin{aligned}\frac{dx}{dt} &= x\left(1 - \frac{x}{1 + \alpha xy}\right) - xz \\ \frac{dy}{dt} &= ay\left(1 - \frac{y}{1 + \beta xy}\right) - byz \\ \frac{dz}{dt} &= -cz + dxz + eyz.\end{aligned}\tag{25}$$

We still have seven parameters, so we will make the same three assumptions as our previous model

(15). Thus we have four parameters in our final model:

$$\begin{aligned}\frac{dx}{dt} &= x\left(1 - \frac{x}{1 + \alpha xy}\right) - xz \\ \frac{dy}{dt} &= ay\left(1 - \frac{y}{1 + \alpha xy}\right) - yz \\ \frac{dz}{dt} &= -cz + dz(x + y).\end{aligned}\tag{26}$$

Note that our parameters a , c , d , and α retain the property that they are always positive. Additionally, for biological study, the region of interest in \mathbb{R}^3 remains the positive octant $H = \{(x, y, z) \in \mathbb{R}^3 | x > 0, y > 0, z > 0\}$.

4.2 Steady States, Stability Analysis, and Bifurcations

There are eight steady states of equation (26):

- (1) Complete extinction, $(0, 0, 0)$
- (2) Prey x only, $(1, 0, 0)$
- (3) Prey y only, $(0, 1, 0)$
- (4) Prey x and predator, $(\frac{c}{d}, 0, \frac{d-c}{d})$
- (5) Prey y and predator, $(0, \frac{c}{d}, \frac{a(d-c)}{d})$
- (6) Prey only: the two steady states are $(\frac{1 \pm \sqrt{1-4\alpha}}{2\alpha}, \frac{1 \mp \sqrt{1-4\alpha}}{2\alpha}, 0)$
- (7) Coexistence, $(\bar{x}, \bar{y}, \bar{z})$ is the solution to the system of equations:

$$1 - \frac{\bar{x}}{1 + \alpha \bar{x} \bar{y}} = \bar{z}$$

$$a\left(1 - \frac{\bar{y}}{1 + \alpha\bar{x}\bar{y}}\right) = \bar{z} \quad (27)$$

$$\bar{y} = \frac{c - d\bar{x}}{d}.$$

More specifically, when $a \neq 1$, the coexistence steady state is:

$$\begin{aligned} \bar{x} &= \frac{d(a+1) + c\alpha(a-1) \mp q}{2d\alpha(a-1)} \\ \bar{y} &= \frac{d(a+1) + c\alpha(1-a) \mp q}{2d\alpha(1-a)} \\ \bar{z} &= \frac{a((4d^2 + \alpha c^2 - cd)(a+1) \mp cq)}{2(d^2(a+1)^2 + a\alpha c^2)} \end{aligned}$$

where

$$q = \sqrt{4\alpha d(a-1)(c + d(a-1)) + (d(a+1) + c\alpha(1-a))^2}. \quad (28)$$

We denote these steady states as $(\bar{x}_-, \bar{y}_-, \bar{z}_-)$ and $(\bar{x}_+, \bar{y}_+, \bar{z}_+)$, corresponding to the respective signs of q .

When $a = 1$, the coexistence steady state is $(\frac{c}{2d}, \frac{c}{2d}, \frac{4d^2 + c^2\alpha - 2cd}{4d^2 + c^2\alpha})$, which is biologically significant when $\alpha > \frac{2d(c-2d)}{c^2}$.

Lemma 4.2.1: For system (26) with positive parameters and $a \neq 1$, of the two steady states $(\bar{x}_-, \bar{y}_-, \bar{z}_-)$ and $(\bar{x}_+, \bar{y}_+, \bar{z}_+)$, there is only one possible positive coexistence steady state, $(\bar{x}_-, \bar{y}_-, \bar{z}_-)$, which exists if and only if one of the following set of conditions is met:

- i. $a \neq 1$ and $d < c < 2d$;
- ii. $a \neq 1$, $c > 2d$, and $\alpha > \frac{2d(c-2d)}{c^2}$;
- iii. $a < 1$, $c < d$, and $a + \frac{c}{d} > 1$;
- iv. $1 < a < \frac{d}{d-c}$ and $c < d$.

Proof: To show this is true, we must first show the steady states are real. To do this, we must show q is real (28). We can rewrite the expression under the radical of q as

$$(4d^2\alpha + (d - c\alpha)^2)(a - 1)^2 + 4ad^2,$$

which is greater than zero due to squared terms and our parameters being positive, meaning q is real.

Next we will show the numerators of $(\bar{x}_+, \bar{y}_+, \bar{z}_+)$ are always positive. When $a > 1$, the numerator of \bar{x}_+ is obviously positive. If $a < 1$, there are two cases. If $d(a+1) + c\alpha(a-1) \geq 0$ then the numerator of \bar{x}_+ is still positive. If $d(a+1) + c\alpha(a-1) < 0$, we need to show $q^2 - (d(a+1) + c\alpha(a-1))^2 > 0$, as explained in Lemma 3.2.1.

$$q^2 - (d(a+1) + c\alpha(a-1))^2 = 4d\alpha(a-1)(c + d(a-1)),$$

which is positive since we assume $a > 1$.

Similarly, when $a < 1$, the numerator of \bar{y}_+ is positive. If $a > 1$, there are two cases. If $d(a+1) + c\alpha(1-a) \geq 0$ then the numerator of \bar{y}_+ is still positive. If not, then

$$q^2 - (d(a+1) + c\alpha(1-a))^2 = 4d\alpha(a-1)(c + d(1-a)) > 0,$$

since $a < 1$. Thus the numerator of \bar{y}_+ is always positive.

For the numerator of \bar{z}_+ , when $4d^2 + \alpha c^2 > cd$, the numerator of \bar{z}_+ is positive. If $4d^2 + \alpha c^2 < cd$, $c^2q^2 - ((4d^2 + \alpha c^2 - cd)(a+1))^2 = 4(2cd - 4d^2 - c^2\alpha)(d^2(a+1)^2 + \alpha c^2) > 0$, due to our assumption. Thus the numerator of \bar{z}_+ is always positive.

Note that when $a < 1$, $\bar{x}_+ < 0$ and $\bar{y}_+ > 0$. However, when $a > 1$, $\bar{x}_+ > 0$ and $\bar{y}_+ < 0$. Thus $(\bar{x}_+, \bar{y}_+, \bar{z}_+)$ is not biologically significant.

Since we know the conjugates of the numerators of $\bar{x}_-, \bar{y}_-,$ and \bar{z}_- are always positive, we can use them to find the conditions for when $(\bar{x}_-, \bar{y}_-, \bar{z}_-)$ is positive by multiplying both numerator and denominator by the respective conjugate. The numerator of \bar{x}_- multiplied by its conjugate is $4d\alpha(a-1)(a(c-d) + d)$. The relevant part is $(a-1)(a(c-d) + d)$.

The numerator of \bar{y}_- multiplied by its conjugate is $4d\alpha(1-a)(c+d(a-1))$. The relevant part is $(1-a)(c+d(a-1))$.

The numerator of \bar{z}_- multiplied by its conjugate is $4a^2(-2cd+4d^2+c^2\alpha)((a+1)^2d^2+ac^2\alpha)$. The relevant part is $(-2cd+4d^2+c^2\alpha)$.

\bar{z}_- is positive when $4d^2+c^2\alpha > 2cd$, which is the same as $\alpha > \frac{2d(c-2d)}{c^2}$. This condition is unnecessary if $c < 2d$.

If $a < 1$, the numerator of \bar{x}_- needs to be negative and the numerator of \bar{y}_- needs to be positive. Thus we need $ac+d(1-a) > 0$ and $c+ad-d > 0$, the second inequality requiring additional conditions. If $c < d$, then $c+ad > d$, which is the same as $a + \frac{c}{d} > 1$. If $d < c < 2d$, no other conditions are necessary. If $c > 2d$, then $\alpha > \frac{2d(c-2d)}{c^2}$ is needed to make \bar{z}_- positive.

If $a > 1$, the numerator of \bar{x}_- needs to be positive and the numerator of \bar{y}_- needs to be negative. Thus we need $ac+d-ad > 0$ and $c+d(a-1) > 0$, the first inequality requiring additional conditions. If $c < d$, then $a(c-d)+d > 0$, which is the same as $a < \frac{d}{d-c}$. If $d < c < 2d$, no other conditions are necessary. If $c > 2d$, then $\alpha > \frac{2d(c-2d)}{c^2}$ is needed to make \bar{z}_- positive.

Thus we have shown the conditions for which $(\bar{x}_-, \bar{y}_-, \bar{z}_-)$ is positive. \square

Like our first model, if the initial conditions have a species with zero population, that species will never change and we can effectively remove that equation from the model under such conditions. Thus we can analyze different cases where a species is included or not by adjusting the Jacobian matrix.

The linear stability of these steady states is determined by considering the eigenvalues of the Jacobian matrix,

$$J_2(x, y, z) = \begin{bmatrix} 1 - \frac{x(2+\alpha xy)}{(1+\alpha xy)^2} - z & \frac{\alpha x^3}{(1+\alpha xy)^2} & -x \\ \frac{a\alpha y^3}{(1+\alpha xy)^2} & a - \frac{ay(2+\alpha xy)}{(1+\alpha xy)^2} - z & -y \\ dz & dz & -c + d(x+y) \end{bmatrix}, \quad (29)$$

evaluated at each of these steady states.

4.2.1 Complete Extinction: $x = 0, y = 0, z = 0$

When the Jacobian matrix (29) is evaluated at $x = 0, y = 0$, and $z = 0$:

$$J_2(0, 0, 0) = \begin{bmatrix} 1 & 0 & 0 \\ 0 & a & 0 \\ 0 & 0 & -c \end{bmatrix}.$$

Since this is a diagonal matrix, the eigenvalues are 1, a , and $-c$. For the entire system, this means the origin is unstable.

4.2.2 The prey x only: $x = 1, y = 0, z = 0$

When the Jacobian matrix (29) is evaluated at $x = 1, y = 0$, and $z = 0$:

$$J_2(1, 0, 0) = \begin{bmatrix} -1 & \alpha & -1 \\ 0 & a & 0 \\ 0 & 0 & -c + d \end{bmatrix}.$$

Since this is an upper triangular matrix, the eigenvalues are $-1, a$, and $d - c$. This point is unstable.

4.2.3 The prey y only: $x = 0, y = 1, z = 0$

When the Jacobian matrix (29) is evaluated at the steady state $x = 0, y = 1$, and $z = 0$:

$$J_2(0, 1, 0) = \begin{bmatrix} 1 & 0 & 0 \\ a\alpha & -a & -1 \\ 0 & 0 & -c + d \end{bmatrix}.$$

The characteristic equation for the Jacobian matrix is

$$-((-1 + \lambda)(a + \lambda)(c - d + \lambda)) = 0. \quad (30)$$

Thus the eigenvalues are $1, -a$, and $d - c$. This point is unstable.

4.2.4 Prey x and Predator: $x = \frac{c}{d}, y = 0, z = \frac{d-c}{d}$

When the Jacobian matrix (29) is evaluated at the steady state $x = \frac{c}{d}, y = 0$, and $z = \frac{d-c}{d}$:

$$J_2\left(\frac{c}{d}, 0, \frac{d-c}{d}\right) = \begin{bmatrix} -\frac{c}{d} & \alpha \frac{c^3}{d^3} & -\frac{c}{d} \\ 0 & a - \frac{d-c}{d} & 0 \\ d-c & d-c & 0 \end{bmatrix}.$$

The characteristic equation for the Jacobian matrix is

$$\left(a - \frac{d-c}{d} - \lambda\right)\left(c - \frac{c^2}{d} + \frac{c\lambda}{d} + \lambda^2\right) = 0. \quad (31)$$

The eigenvalues are $\frac{c-d+ad}{d}$ and $\frac{-c \mp \sqrt{c(c+4cd-4d^2)}}{2d}$. For this steady state to be biologically significant, $d > c$. Thus $4cd - 4d^2$ is negative and the real part of $\frac{-c \mp \sqrt{c(c+4d(c-d))}}{2d}$ is always negative.

This steady state is stable when $a < 1$ and $a + \frac{c}{d} < 1$.

The plot of the trajectory in Figure (23) for x, y , and z shows that each species travels directly towards its steady state with initial conditions $x(0) = y(0) = z(0) = 0.5$ and the parameters are

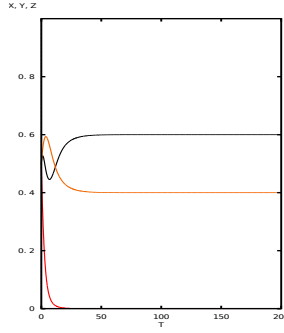


Figure 23: Prey x and Predator only steady state time plot

$a = d = 0.25$, $\alpha = 1$, and $c = 0.15$. The bifurcation occurs at the parameter $c = 0.1875$. Note that the behavior of the species' populations matches those found in the corresponding steady state of the indirect symbiosis model.

Biologically, this makes sense. If the prey y cannot reproduce faster than the predator, then it will go extinct.

4.2.5 Prey y and Predator: $x = 0$, $y = \frac{c}{d}$, $z = \frac{a(d-c)}{d}$

When the Jacobian matrix (29) is evaluated at the steady state $x = 0$, $y = \frac{c}{d}$, and $z = \frac{a(d-c)}{d}$:

$$J_2\left(0, \frac{c}{d}, \frac{a(d-c)}{d}\right) = \begin{bmatrix} 1 - \frac{a(d-c)}{d} & 0 & 0 \\ a\alpha \frac{c^3}{d^3} & -a\frac{c}{d} & -\frac{c}{d} \\ a(d-c) & a(d-c) & 0 \end{bmatrix}.$$

The characteristic equation for the Jacobian matrix is

$$\left(1 - \frac{a(d-c)}{d} - \lambda\right)\left(ac - \frac{ac^2}{d} + \frac{ac\lambda}{d} + \lambda^2\right) = 0. \quad (32)$$

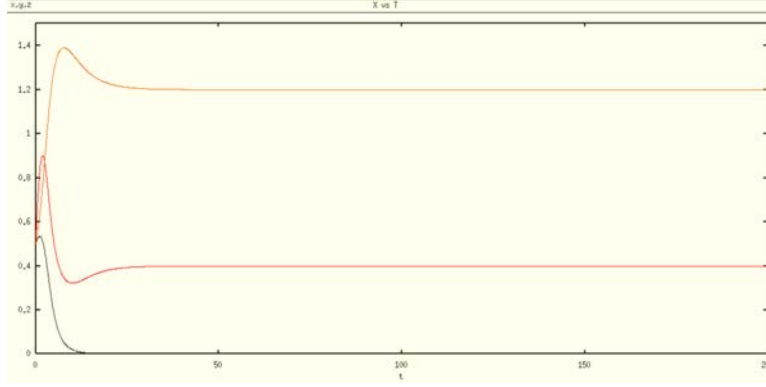


Figure 24: Prey y and Predator only steady state time plot

The eigenvalues are $\frac{ac+d-ad}{d}$ and $\frac{-ac \mp \sqrt{ac(ac+4cd-4d^2)}}{2d}$. For this steady state to be biologically significant, $d > c$. Thus $4cd - 4d^2$ is negative and the real part of $\frac{-ac \mp \sqrt{ac(ac+4cd-4d^2)}}{2d}$ is always negative. This steady state is stable when $1 < a$ and $a > \frac{d}{d-c}$.

The plot of the trajectory in Figure (24) for x , y , and z shows that each species travels directly towards its steady state with initial conditions $x(0) = y(0) = z(0) = 0.5$ and the parameters are $a = 2$, $d = 0.25$, $\alpha = 1$ and $c = 0.1$. Note that the behavior of the species' populations matches those found in the corresponding steady state of the indirect symbiosis model.

Biologically, this means the prey x will go extinct if it cannot reproduce faster than the predator. Note that this and the previous steady state cannot both be stable. That is because $a < 1$ to be stable in the previous steady state while $a > 1$ for this steady state to be stable.

4.2.6 The prey x and y only: $x = \frac{1 \mp \sqrt{1-4\alpha}}{2\alpha}$, $y = \frac{1 \mp \sqrt{1-4\alpha}}{2\alpha}$, $z = 0$

We will denote the two prey species only steady states as follows: $(\bar{x}_1, \bar{y}_1, 0) = (\frac{1-\sqrt{1-4\alpha}}{2\alpha}, \frac{1-\sqrt{1-4\alpha}}{2\alpha}, 0)$ and $(\bar{x}_2, \bar{y}_2, 0) = (\frac{1+\sqrt{1-4\alpha}}{2\alpha}, \frac{1+\sqrt{1-4\alpha}}{2\alpha}, 0)$. Note that for either steady state to be biologically significant, $0 < \alpha \leq 0.25$. Also, for $(\bar{x}_1, \bar{y}_1, 0)$ to be biologically significant, $1 > \sqrt{1-4\alpha}$.

When the Jacobian matrix (29) is evaluated at the steady state $x = \bar{x}_1$, $y = \bar{y}_1$, and $z = 0$:

$$J_2(\bar{x}_1, \bar{y}_1, 0) = \begin{bmatrix} -\frac{1}{x_1} & \alpha x_1 & -x_1 \\ a\alpha x_1 & -\frac{a}{x_1} & -x_1 \\ 0 & 0 & \frac{d(1-\sqrt{1-4\alpha})-c\alpha}{\alpha} \end{bmatrix}.$$

The characteristic equation for the Jacobian matrix is

$$(-a\alpha x_1 + a\alpha + \frac{a}{(1 + \alpha x_1^2)^2} + \frac{\lambda(a+1)}{1 + \alpha x_1^2} + \lambda^2)(-c + \frac{d(1 - \sqrt{1-4\alpha}}{\alpha} - \lambda) = 0. \quad (33)$$

The eigenvalues are $\frac{d(1-s)-c\alpha}{\alpha}$ and $\frac{\alpha(a+1)+r}{-(1-s)}$,

where $r = \sqrt{2a(1-s) - 8a\alpha + 4a\alpha s + (a+1)^2\alpha^2}$ and $s = \sqrt{1-4\alpha}$.

The second eigenvalue $\frac{\alpha(a+1)+r}{-(1-s)}$ is obviously always negative with our assumptions that the parameters a and α are positive and $1 > \sqrt{1-4\alpha}$. The third eigenvalue will be negative when $\alpha(a+1) > r$, which is when $2a(1-s-4\alpha+2\alpha s) < 0$. Following this, we need to have $1-4\alpha < s(1-2\alpha)$. We know $1-4\alpha > 0$ and $s(1-2\alpha) > 0$, so this is equivalent to the condition $(1-4\alpha)^2 < (s(1-2\alpha))^2$, which is the same as $1-4\alpha < 1-4\alpha+4\alpha^2$. This is the same as requiring $0 < 4\alpha^2$, which is always true due to our assumptions. Thus, the third eigenvalue is always negative.

This means, $(\bar{x}_1, \bar{y}_1, 0)$ is stable when the first eigenvalue is negative, which is when $\alpha < \frac{2d(c-2d)}{c^2}$.

Similarly, when the Jacobian matrix (29) is evaluated at the steady state $x = \bar{x}_2$, $y = \bar{y}_2$, and $z = 0$:

$$J_2(\bar{x}_2, \bar{y}_2, 0) = \begin{bmatrix} -\frac{1}{x_2} & \alpha x_2 & -x_2 \\ a\alpha x_2 & -\frac{a}{x_2} & -x_2 \\ 0 & 0 & \frac{d(1+\sqrt{1-4\alpha})-c\alpha}{\alpha} \end{bmatrix}.$$

The characteristic equation for the Jacobian matrix is

$$(-a\alpha x_2 + a\alpha + \frac{a}{(1 + \alpha x_2^2)^2} + \frac{\lambda(a+1)}{1 + \alpha x_2^2} + \lambda^2)(-c + \frac{d(1 + \sqrt{1-4\alpha}}{\alpha} - \lambda) = 0. \quad (34)$$

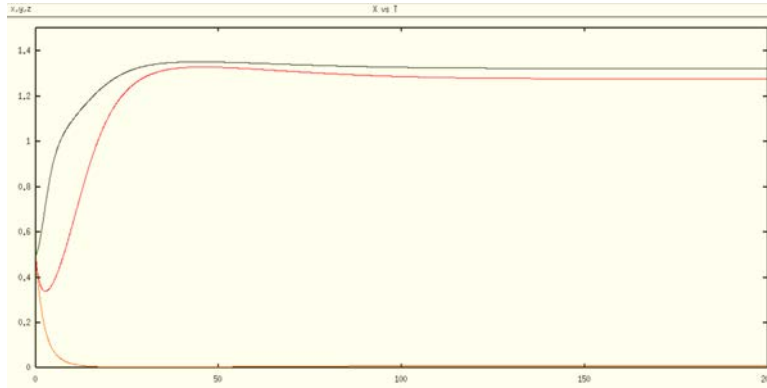


Figure 25: Prey only steady state time plot

The eigenvalues are $\frac{d(1+s)-c\alpha}{\alpha}$ and $\frac{-\alpha(a+1)\mp u}{1+s}$,

where $u = \sqrt{2a(1+s) - 8a\alpha - 4a\alpha s + (a+1)^2\alpha^2}$ and $s = \sqrt{1-4\alpha}$, as above. We can show the third eigenvalue, $\frac{-\alpha(a+1)+u}{1+s}$, is always positive. To do this, we show $u > \alpha(a+1)$, which is true if $2a(1+s) - 8a\alpha - 4a\alpha s = 2a(1+s - 4\alpha - 2\alpha s) = 2a((1-4\alpha) + (1-2\alpha)s) > 0$, which it is due to our assumptions. Thus, $(\bar{x}_2, \bar{y}_2, 0)$ is always unstable.

The plot of the trajectory in Figure (25) for x , y , and z shows that each species travels directly towards its steady state with initial conditions $x(0) = y(0) = z(0) = 0.5$ and the parameters are $a = d = 0.25$, $\alpha = 0.2$ and $c = 0.65$.

Biologically, this makes sense as a high predator death rate and low growth rate will lead to the predator's extinction. The prey species help each other grow, but not enough for there to be an abundance of prey for the predator to eat.

4.2.7 The Coexistence Steady State Behavior

As we proved in Lemma 4.2.1, the coexistence steady state exists with certain conditions of parameter values.

Theorem 4.2.2: For the parameter values $a, c, d,$ and α satisfying the conditions in Lemma 4.2.1, the steady state $(\bar{x}, \bar{y}, \bar{z})$ is stable if

$$\frac{(1 + \alpha\bar{x}\bar{y} - 2a\alpha\bar{y}^2)}{d(\bar{x}^2 + a\bar{y}^2)(1 + \alpha\bar{x}\bar{y})^2} > \frac{(-1 + \bar{x} + \alpha\bar{x}^2\bar{y}(\alpha\bar{y} - 1))}{\bar{x}^2(\bar{x} + a\bar{y})}.$$

Proof: First we evaluate the Jacobian matrix (29) at $x = \bar{x}, y = \bar{y},$ and $z = \bar{z}$ to get:

$$J_2(\bar{x}, \bar{y}, \bar{z}) = \begin{bmatrix} 1 - \frac{2\bar{x}}{1 + \alpha\bar{x}\bar{y}} - \bar{z} & \frac{\alpha\bar{x}^2}{(1 + \alpha\bar{x}\bar{y})^2} & -\bar{x} \\ \frac{a\alpha\bar{y}^2}{(1 + \alpha\bar{x}\bar{y})^2} & a - \frac{2a\bar{y}}{1 + \alpha\bar{x}\bar{y}} - \bar{z} & -\bar{y} \\ d\bar{z} & d\bar{z} & -c + d(\bar{x} + \bar{y}) \end{bmatrix}.$$

The characteristic equation for the evaluated Jacobian matrix is

$$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0, \quad (35)$$

where

$$a_1 = 2\bar{z} + \frac{(\bar{x} + a\bar{y})(2 + \alpha\bar{x}\bar{y})}{(1 + \alpha\bar{x}\bar{y})^2} + c - d(\bar{x} + \bar{y}) - a - 1 \quad (36)$$

$$\begin{aligned} a_2 = & a - c - ac + d(\bar{x} + \bar{y}) + ad(\bar{x} + \bar{y}) - \bar{z} - a\bar{z} + 2c\bar{z} + d\bar{x}\bar{z} + d\bar{y}\bar{z} - 2d(\bar{x} + \bar{y})\bar{z} + \bar{z}^2 \\ & + \frac{(2 + \alpha\bar{x}\bar{y})(-a\bar{x} + c\bar{x} - a\bar{y} + ac\bar{y} - d\bar{x}(\bar{x} + \bar{y}) - ad\bar{y}(\bar{x} + \bar{y}) + \bar{x}\bar{z} + a\bar{y}\bar{z})}{(1 + \alpha\bar{x}\bar{y})^2} \\ & + \frac{a\bar{x}\bar{y}(2 + \alpha\bar{x}\bar{y})^2 - a\alpha^2\bar{x}^3\bar{y}^3}{(1 + \alpha\bar{x}\bar{y})^4} \end{aligned} \quad (37)$$

$$\begin{aligned}
a_3 = & ac - ad(\bar{x} + \bar{y}) - c\bar{z} - ac\bar{z} - ad\bar{x}\bar{z} - d\bar{y}\bar{z} + d(\bar{x} + \bar{y})\bar{z} + ad(\bar{x} + \bar{y})\bar{z} + c\bar{z}^2 + d\bar{x}^2\bar{z}^2 + d\bar{y}\bar{z}^2 - d(\bar{x} + \bar{y})\bar{z} \\
& + \frac{2d\bar{x}\bar{y}\bar{z} + 2ad\bar{x}\bar{y}\bar{z} + d\alpha\bar{x}^3\bar{y}\bar{z} + d\alpha\bar{x}^2\bar{y}^2\bar{z} + ad\alpha\bar{x}^2\bar{y}^2\bar{z} + ad\alpha\bar{x}\bar{y}^3\bar{z}}{(1 + \alpha\bar{x}\bar{y})^2} \\
& + \frac{(2 + \alpha\bar{x}\bar{y})(-ac\bar{x} - ac\bar{y} + ad\bar{x}(\bar{x} + \bar{y}) + ad\bar{y}(\bar{x} + \bar{y})) + c\bar{x} + c\bar{y} - d\bar{x}(\bar{x} + \bar{y}) - d\bar{y}(\bar{x} + \bar{y})}{(1 + \alpha\bar{x}\bar{y})^2} \\
& + \frac{ad\alpha^2\bar{x}^3\bar{y}^3(\bar{x} + \bar{y}) + ac\bar{x}\bar{y}(2 + \alpha\bar{x}\bar{y})^2 - ac\alpha^2\bar{x}^3\bar{y}^3 - ad\bar{x}\bar{y}(\bar{x} + \bar{y})(2 + \alpha\bar{x}\bar{y})^2}{(1 + \alpha\bar{x}\bar{y})^4}.
\end{aligned}$$

Using (27), we can simplify the terms to

$$\begin{aligned}
a_1 &= \frac{\bar{x} + a\bar{y}}{(1 + \alpha\bar{x}\bar{y})^2} \\
a_2 &= \frac{(d\bar{x}\bar{z} + d\bar{y}\bar{z})(1 + \alpha\bar{x}\bar{y})^3 + \bar{x}^2(1 + \alpha\bar{x}\bar{y} - 2a\alpha\bar{y})}{(1 + \alpha\bar{x}\bar{y})^3} \\
a_3 &= \frac{d\bar{x}\bar{y}\bar{z}(1 + a + \alpha\bar{x}^2 + a\alpha\bar{y}^2)}{(1 + \alpha\bar{x}\bar{y})^2}.
\end{aligned}$$

By the Routh-Hurwitz criterion, $(\bar{x}, \bar{y}, \bar{z})$ will be stable if $a_1 > 0$, $a_3 > 0$, and $a_1a_2 > a_3$. Since $\bar{x}, \bar{y}, \bar{z}$, and all parameters are positive, it is clear that $a_1 > 0$ and $a_3 > 0$.

$$a_1a_2 - a_3 = \bar{x}^2(\bar{x} + a\bar{y})(1 + \alpha\bar{x}\bar{y} - 2a\alpha\bar{y}^2) - d(\bar{x}^2 + a\bar{y}^2)(1 + \alpha\bar{x}\bar{y})^2(-1 + \bar{x} + \alpha\bar{x}^2\bar{y}(\alpha\bar{y} - 1)) \quad (38)$$

By inputting certain test values, it is easy to see there will be conditions for which $a_1a_2 - a_3 > 0$.

Through algebraic manipulation, we get our condition from the theorem. \square

Since this is a complicated expression analytically, to better understand the periodic solution branch of system (26), we numerically show the time plots and phase portraits of the unstable periodic solution for different values of c . Figures (26) and (27) show the time plot of the unstable

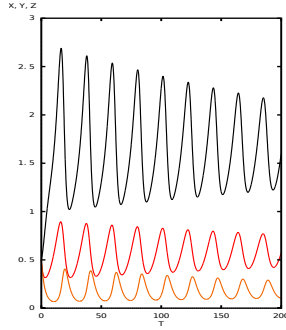


Figure 26: x , y , and z vs. t . Initial conditions are $x = 0.5$, $y = 0.5$, $z = 0.5$, $a = d = 0.25$, $\alpha = 1$, and $c = 0.55$.

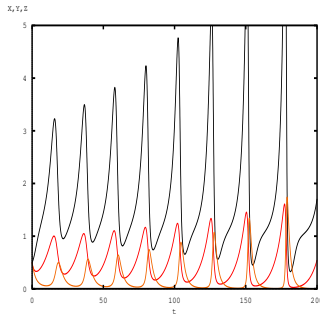


Figure 27: x , y , and z vs. t . The populations have become unstable. Initial conditions are $x = 0.5$, $y = 0.5$, $z = 0.5$, $a = d = 0.25$, $\alpha = 1$, and $c = 0.6$.

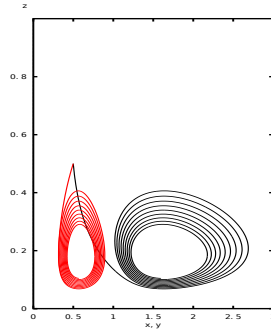


Figure 28: Phase diagram of z vs. x and y . Initial conditions are $x = 0.5$, $y = 0.5$, $z = 0.5$, $a = d = 0.25$, $\alpha = 1$, and $c = 0.55$.

periodic solutions for different values of c . Black curve represents the x population, the red curve represents the y population, and the orange curve represents the z population.

Additionally, figures (28) and (29) show the phase portrait of the unstable periodic solutions for different values of c . The black curve represents the x - z diagram while the red curve represents the y - z diagram. The populations are in an unstable limit cycle. As is evident from the figure, it is clear that as c decreases to c^* , the unstable periodic solution amplitude increases rapidly.

Finally, figures (30) and (31) show the 3D phase portraits of the unstable periodic solutions for different values of c .

Biologically, this means that as the predator death rate or symbiosis parameter increases, there are less prey that will be killed, so all three species will stay around. However, after a certain point, the prey population has uncontrollable growth and causes the system to become unstable. This is likely due to the stronger impact mutualism has on carrying capacity when there are direct interactions between the symbiotic species.

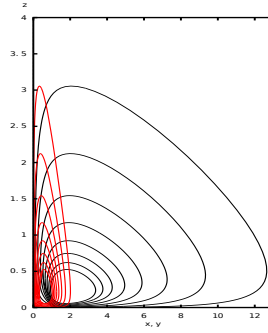


Figure 29: Phase diagram of z vs. x and y . The populations have become unstable. Initial conditions are $x = 0.5$, $y = 0.5$, $z = 0.5$, $a = d = 0.25$, $\alpha = 1$, and $c = 0.6$.

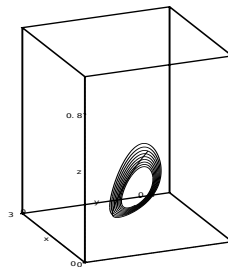


Figure 30: 3D phase diagram of z vs. x vs. y . Initial conditions are $x = 0.5$, $y = 0.5$, $z = 0.5$, $a = d = 0.25$, $\alpha = 1$, and $c = 0.55$.

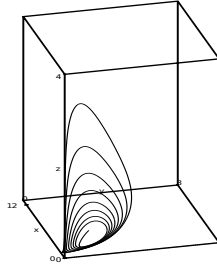


Figure 31: 3D phase diagram of z vs. x vs. y . Initial conditions are $x = 0.5$, $y = 0.5$, $z = 0.5$, $a = d = 0.25$, $\alpha = 1$, and $c = 0.6$.

4.2.8 Bifurcation Analysis

In Figure (32), a bifurcation diagram is shown with c as the bifurcation parameter. The other parameters are set to $a = d = 0.25$ and $\alpha = 1$. The red line corresponds to a stable steady state while the black line is unstable. For the periodic solutions (which are unstable), both the maximum and minimum values of $x(t)$ are depicted as circles. It is noteworthy that the amplitude of the periodic solutions increases as c decreases from the Hopf bifurcation value, $c = 0.5462$, and the periodic solution branch forms at some critical value $c^* > 0$.

Note, too, the periodic solution branch only occurs over a small range of parameter c . As the c parameter decreases, the system has another bifurcation at $c = 0.1875$, which is a transcritical bifurcation.

In Figure (33), a bifurcation diagram is shown with α as the bifurcation parameter. The other parameters are set to $a = d = 0.25$ and $c = 0.9$. For the periodic solutions, both the maximum and minimum values of $x(t)$ are depicted as circles. The green circles are stable limit cycles while the open circles are unstable limit cycles. It is noteworthy that the amplitude of the periodic solutions increases as α decreases from the Hopf bifurcation value, $\alpha = 0.31$, and the periodic solution branch

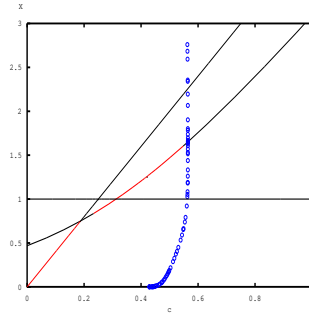


Figure 32: Bifurcation diagram of the x population vs the c parameter.

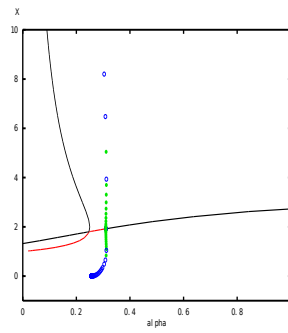


Figure 33: Bifurcation diagram of the x population vs the α parameter.

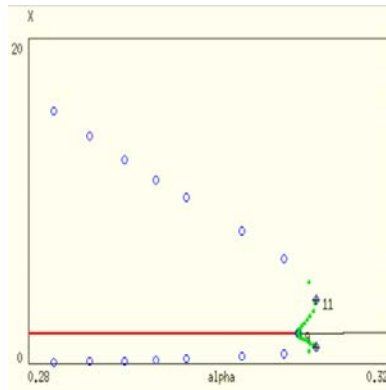


Figure 34: Bifurcation diagram of the x population vs the α parameter focused on the limit cycles.

forms at some critical value $\alpha^* > 0$.

Note too the saddle node bifurcation that occurs at $\alpha = 0.25$. This corresponds to the prey only steady state, which no longer exists when $\alpha > 0.25$.

Figure (34) shows a bifurcation diagram with the same initial conditions as Figure (33), with a close-up on the stable and unstable limit cycles. We can see the turning point of the branch that occurs at $\alpha = 0.3119$. Before the Hopf bifurcation point we see large, unstable limit cycles. For a small range of α between the Hopf bifurcation and the turning point, there is a stable limit cycle.

5 Conclusion

In this thesis, we have examined two models that simulate the effect of indirect and symmetrically direct symbiosis in a two prey, one predator system. These models can have the alternate interpretation of two mutualistic species withstanding the effect of a predator. This is different from previously studied models about mutualism and predation, which only have one prey species while the other mutualistic species is not directly affected by the predator.

For both models, only one species will go extinct at most. They also share a transcritical bifurcation that occurs as c decreases and the disappearance of the prey only steady state when α increases.

However, as expected, the models made of two different functional responses will have some different behavior. Symbiosis with indirect interactions keeps the system stable, like in the normal Lotka-Volterra model with carrying capacity. However, symbiosis with direct interaction can lead to unstable limit cycles once the c or α parameters are sufficiently large. This unbounded growth shares similarities with other mutualism models.

To start with the study of our model, we have made some assumptions to reduce the amount of parameters. Additionally, we did not study the asymmetric case of mutualism. Finally, we did not look at the possibility of commensalism and parasitism between the two prey species, which the functional response in carrying capacity can account for. Further research can be done with this model and some simple changes alone. With greater adjustments, future models may also account for the specific mutualistic cases, such as the multispecies herd using a square root functional response [9-10].

6 Appendix

6.1 XPPAUT Code of Indirect Mutualism Model

```
init x=0.5 y=0.5 z=0.5  
para a=0.25 c=1 d=0.25 alpha=1  
x'=x*(1-(x/(1+alpha*y)))-x*z  
y'=a*y*(1-(y/(1+alpha*x)))-y*z  
z'=-c*z+d*x*z+d*y*z  
done
```

6.2 XPPAUT Code of Direct Mutualism Model

```
init x=0.5 y=0.5 z=0.5  
para a=0.25 c=1 d=0.25 alpha=1  
x'=x*(1-(x/(1+alpha*x*y)))-x*z  
y'=a*y*(1-(y/(1+alpha*x*y)))-y*z  
z'=-c*z+d*x*z+d*y*z  
done
```

6.3 Mathematica Code

```
Solve[{1-x/(1+[Alpha]*y)==z, (a)(1-(y/(1+[Alpha]*x)))==z,c==d(x+y)},{x,y,z}, PositiveReals]
```

Solve[{1-x/(1+\[Alpha]*x*y)==z, (a)(1-(y/(1+\[Alpha]*x*y)))==z,c==d(x+y)},{x,y,z},PositiveReals]

j={{1-2x/(1+\[Alpha]*y)-z, \[Alpha]*x^2/(1+\[Alpha]*y)^2,-x},
{a*\[Alpha]*y^2/(1+\[Alpha]*x)^2,a-2*a*y/(1+\[Alpha]*x)-z,-y},{d*z,d*z,-c+d*(x+y)}}

MatrixForm[j]

Eigenvalues[j]

CharacteristicPolynomial[j,\[Lambda]]

k={{1-x (2+\[Alpha]*x*y)/(1+\[Alpha]*x*y)^2-z, \[Alpha]*x^3/(1+\[Alpha]*x*y)^2,-x},
{a*\[Alpha]*y^3/(1+\[Alpha]*x*y)^2,a-a*y (2+\[Alpha]*x*y)/(1+\[Alpha]*x*y)^2-z,-y},
{d*z,d*z,-c+d(x+y)}}

MatrixForm[k]

Eigenvalues[k]

CharacteristicPolynomial[k,\[Lambda]]

We set x, y , and z to the appropriate steady state values to get eigenvalues and characteristic polynomials.

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