2016

A Study of the Effect of Harvesting on a Discrete System with Two Competing Species

Rebecca G. Clark
Virginia Commonwealth University

A Study of the Effect of Harvesting on a Discrete System with Two Competing Species

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at Virginia Commonwealth University.

by

Rebecca Grace Clark
Master of Science

Director: Dr. Norma Ortiz-Robinson, Associate Professor
Department of Mathematics and Applied Mathematics

Virginia Commonwealth University
Richmond, Virginia
May 2016

Acknowledgements

I want to thank my parents, who with so much love and care were the first to interest me in learning, who taught me to be curious about the world, think analytically, and strive for excellence. I cannot thank you enough.

I would also like to thank my family, friends, and God, whose love, support, and encouragement have sustained me. I could not have made it this far without you.

Table of Contents

List of Figures

Abstract

This is a study of the effect of harvesting on a system with two competing species. The system is a Ricker-type model that extends the work done by Luis, Elaydi, and Oliveira to include the effect of harvesting on the system. We look at the uniform bound of the system as well as the isoclines and perform a stability analysis of the equilibrium points. We also look at the effects of harvesting on the stability of the system by looking at the bifurcation of the system with respect to harvesting.

Chapter 1

Introduction

Difference equations are used to describe and predict discrete events. They have widespread applications that span many fields such as economics, quantum mechanics, ecology, and meteorology [2]. Many biological situations are modeled through the use of difference equations and can be used in place of experiments that are expensive or unethical. These models have been used to predict outbreaks [18], forecast population growth [20], and propose strategies to obtain a desired state [6].

Discrete modeling was introduced and made popular more than 50 years ago through two significant papers, one authored by Ricker [15] and the other by Beverton and Holt [3]. In single species dynamics, the two models from these papers describe different forms of instraspecific competition among a single species. The Ricker model displays scramble competition, describing a situation in which fierce fighting for resources within the species decreases the size of a large population [13]. The Beverton-Holt model displays contest competition, a situation in which the species makes increasingly better use of resources [4].

One of the most popular models for describing competition between two species is the differential equation model introduced in the 1920s by Lotka and Volterra [12, 19]. The Leslie-Gower model is considered by some to be the discrete counterpart to the Lotka-Volterra model [13]. Continuous models can be more difficult to derive but less burdensome to use [11], and thus discrete models have not been studied to the same extent as their continuous counterparts [13], although recently Hone described and studied a predator-prey system with a Ricker-type model [7]. The type of population being modeled can affect whether a discrete model is used:

> Although most models are described with differential equations, the discrete-time models governed by difference equations are more appropriate than the continuous ones when the size of the population is rarely small, or the population has non-overlapping generations. It is also known that the discrete models can provide more efficient computational methods for numerical simulations. [22]

In addition to various forms of competition, the population of a species may change in size due to harvesting, which is when some of a population is removed by an external force. For instance, fisheries use harvesting to sell a portion of the raised and extracted fish [8]. In addition to modeling how a population naturally changes in size, we can incorporate harvesting in a population model by adding a term to decrease the size of a population. Understanding the effects of harvesting in a multi-species environment may facilitate the prediction and control of populations; thus, bio-economic modeling with harvesting has become increasingly important in the field of population dynamics [17].

Several different forms of harvesting that are employed in real-life situations have been studied to explore how they affect population dynamics. Wentworth et al. studied the effect of constant harvesting as well as non-autonomous harvesting on a continuous, single species model pertaining to various fishery population models [20]. They found the harvest rate leading to the maximum yield using numerical techniques and optimization. Idels and Wang also studied a single species, continuous model and the effect that a harvesting control parameter has on the equilibrium and the rate to reach equilibrium [8]. They used numerical simulations to study different harvesting strategies for fish.

Getz created a general discrete stage structured model for a single species that includes nonlinearity [6]. The model was used to study harvesting during nonequilibrium conditions as well as the role of Maximum Sustainable Yield. Yao used a single species difference equation with linear harvesting to study a variation of Nicholson's blowflies model [22]. He updated this known continuous model to take a discrete approach.

Abu-Saris et al. used constant-yield harvesting in a single species discrete model to study stability and boundedness and other dynamic properties [1]. Martin and Ruan also used constant-yield harvesting in a continuous, two species, predator-prey model [14]. They showed that in predator-prey models a higher harvesting rate can cause unstable equilibrium to become stable so long as the rate stays below a critical harvesting level. Another continuous, two species model by Sharma and Samanta used combined harvesting with imprecise parameters to study a system in which the parameter values cannot be exactly known [17]. Wu analyzed stability in a discrete, two species competitive system with harvesting [21]. Wu's system had a nonlinear, polynomial structure.

The discrete dynamical system we will be studying is an autonomous Ricker-type competition model that describes the population dynamics between two species, species x and species y, with the addition of harvesting of species x. It is similar to a system studied by Luis, Elaydi, and Oliveira [13] with the important distinction that our system includes a harvesting parameter that allows the carrying capacity of the harvested species to be controlled.

The system is as follows:

$$x_{n+1} = ux_n e^{K-x_n-ay_n} \tag{1.1}$$

$$y_{n+1} = y_n e^{L-y_n-bx_n} \tag{1.2}$$

$$a, b, K, L > 0, \quad \text{and} \quad 0 < u \leqslant 1.$$

Two main paths exist for the construction and creation of discrete mathematical models. Some discrete models are discretized versions of continuous differential equations. Other discrete models are created from the properties of the situation it is modeling [13]. This model, as well as the system this model is based off of, is of the latter type. It is created utilizing biological properties of the species interaction dynamics.

This brings us to the biological interpretation of our model. In the context of population dynamics, K and L are the carrying capacities of species x and y, respectively, if each were in isolation. Carrying capacity indicates the maximum population size that the environment can naturally sustain due to resources and other ecological constraints, and is the size toward which the population will naturally tend absent other forces. At times in the analysis of this system it will be simpler to consider the modified carrying capacity, M, of species x, where $M = K + \ln(u)$. The parameters a and b describe the effect of competition that one species has on the other. That is, the larger the value of competition parameter a, the more that the population of species x is affected by the population of species y. Likewise, a similar relationship holds for the effect of the value of competition parameter b.

The harvesting term, u, describes the proportion of the population of species x that is not harvested but instead remains in the ecosystem. We can alternatively think of harvesting some proportion, v, of the population of species x, in which case $u = 1 - v$. For example, if we harvest 20% of the population, then $v = 0.2$ and $u = 0.8$ indicating that 80% of the population is being kept. Since total harvesting of species x, i.e. $u = 0$, would lead to immediate extinction of the species, we discard this situation in the study of this system. For clarity and ease of analysis, we will use u throughout this thesis.

We note that the carrying capacity of species x is dampened by harvesting, i.e. since $\ln(u) \leqslant 0$ for the potential values of u, then $M \leqslant K$. Since the modified carrying capacity will feature prominently in the analysis of the dynamics of the system, we will see that the behavior of the system can be greatly affected by different choices of the harvesting parameter u. It is also important to note that as u increases to 1, $\ln(u)$ goes to 0, so

M approaches K. This means that as we decrease the proportion of the population that is harvested, i.e., we keep a larger proportion of the population, our modified carrying capacity for species x approaches K, the original carrying capacity without harvesting. This is the result we would expect.

As we harvest more of species x, i.e. as u decreases towards 0, then $\ln(u)$ quickly approaches negative infinity. We will see later that if we assume that K is relatively small, then $M = K + \ln(u)$ also quickly approaches negative infinity when we ignore biological constraints. In a biological context, M, the modified carrying capacity of species x, is limited to positive values. Together this implies that with enough harvesting of species x, i.e. u sufficiently small, the ecosystem quickly is unable to sustain species x.

In this thesis we study the system given in equations (1.1) and (1.2) and examine some mathematical properties and dynamics of the system, keeping in mind the biological application. In particular we consider how different levels of harvesting can affect system dynamics.

Chapter 2

Definitions and Theorems

In this chapter we will discuss the mathematical vocabulary and background that is needed to study a Ricker-type system such as in the one described by Equations (1.1) and (1.2). Throughout these definitions and theorems, we keep in mind the biological context in which we are doing our analysis. All of the following definitions are for a 2-dimensional system.

Definition 1 *A* ***discrete dynamical system*** *is a sequence of real numbers obtained from a function that is applied repeatedly.*

A discrete dynamical system describes how non-overlapping events change with time. It is frequently expressed as a difference (otherwise known as recurrence) equation with an initial condition, i.e.

$$x_{n+1} = f(x_n) \qquad \text{given } x_0. \tag{2.1}$$

Here the subscript describes the index of the element of the sequence. For example, x_4 refers to the 4^{th} element of the sequence after the initial condition.

Each term in the sequence is generated by applying the relation to the previous term. Thus, given x_0, we can find x_1 by applying the function to the initial condition, i.e., $x_1 = f(x_0)$. We then obtain x_2 from x_1 by applying the function again: $x_2 = f(x_1)$, then $x_3 = f(x_2)$, and so on.

Definition 2 *The* ***solution*** *to Equation (2.1) is the sequence*

$$\{x_n\}_{n=0}^{\infty} = \{x_0, x_1, x_2, x_3, x_4, \dots\}. \tag{2.2}$$

generated by the recurrence relation.

It is interesting to note that with discrete dynamical systems, even simple equations can have interesting dynamics. For clarity, we will show this with a one dimensional example. The system $f(x) = x^2$, given x_0, will generate very different types of solutions depending on the sign and value of the initial condition. In this situation $x_{n+1} = x_n^2$.

If $x_0 = -1$, we get the solution $\{x_n\}_{n=0}^{\infty} = \{-1, 1, 1, 1, 1, \dots\}$.

If $0 < x_0 < 1$, each term in the solution is the square of the previous term, which for positive numbers less than 1 means that the values get increasingly smaller and the solution approaches 0. If $x_0 = 0.8$ we get the solution $\{x_n\}_{n=0}^{\infty} = \{0.8, 0.64, 0.4096, 0.16777216, 0.0281474977, \dots\}$ which approaches 0.

If $x_0 = 1$, we get the solution $\{x_n\}_{n=0}^{\infty} = \{1, 1, 1, 1, 1, \dots\}$.

If $x_0 > 1$, each term in the solution is the square of the previous term, which for positive numbers greater than 1 means that the values get increasingly bigger and the solution approaches positive infinity. If $x_0 = 2$ we get the solution $\{x_n\}_{n=0}^{\infty} = \{2, 4, 16, 256, 65536, \dots\}$ which approaches infinity.

It is clear from this example that we may get very different dynamics in a discrete dynamical system from even minor changes in the initial condition.

Definition 3 *The* n^{th} ***iterate****,* x_n*, of the solution is the* n^{th} *element of the sequence after the initial condition. We say* n *is the index of the iterate.*

Definition 4 *A system of difference equations is* ***linear*** *if all iterate terms are linear for the iterate. Otherwise the system is considered nonlinear.*

Our previous example, $x_{n+1} = x_n^2$, is not linear since the n^{th} iterate is not linear. A system described by the difference equation $x_{n+2} = x_n * x_{n+1}$ is also nonlinear since it contains a product of iterates. However, the system $x_{n+1} = sin(n)x_n$ is linear since all terms involving the iterate are linear iterate terms. The $sin(n)$ is only nonlinear for n and does not affect the designation of the system as linear.

Definition 5 *A system is **homogeneous** if every term involves the iterate. Otherwise it is said to be non-homogeneous.*

The example $x_{n+1} = x_n^2$ is homogeneous, as are the examples $x_{n+2} = x_n * x_{n+1}$ and $x_{n+1} = sin(n)x_n$. However, $x_{n+1} = 3x_n + 2$ is non-homogeneous since the last term does not involve an iterate.

Definition 6 *The **order** of the system is determined by the difference between the highest index of the system and the lowest index of the system.*

The example $x_{n+2} = x_n * x_{n+1}$ is second order, while our system described by Equations (1.1) and (1.2) is a first order system.

Definition 7 *A system is **autonomous** if it does not depend explicitly on the independent variable n. Otherwise, the system is non-autonomous.*

The examples $x_{n+1} = x_n^2$, $x_{n+2} = x_n * x_{n+1}$, and $x_{n+1} = 3x_n + 2$ are all autonomous systems. However, $x_{n+1} = sin(n)x_n$ is non-autonomous since the term $sin(n)x_n$ explicitly depends on n.

We are now able to classify our autonomous system in Equations (1.1) and (1.2) as a set of first order, nonlinear, homogeneous difference equations.

A few final, very important definitions introduce a topic we will spend a great amount of time studying.

Definition 8 *A point* (x^*, y^*) *of the system given by the vector difference equation* $(x_{n+1}, y_{n+1}) = f(n, x_n, y_n)$ *with initial condition* $(x_{n_0}, y_{n_0}) = (x_0, y_0)$ *is an* ***equilibrium point*** *if* $f(n, x^*, y^*) = (x^*, y^*) \quad \forall n \geqslant n_0$.

To better understand the dynamics of the system, we will need to know the local stability of each equilibrium point, i.e. the behavior of the solution near the equilibrium point.

Suppose $f : \mathbb{R}^2 \to \mathbb{R}, g : \mathbb{R}^2 \to \mathbb{R}$ have continuous first partial derivatives.

Definition 9 *The* ***Jacobian*** *of a function* $F : \mathbb{R}^2 \to \mathbb{R}^2$ *where* $F(x, y) = (f(x, y), g(x, y))$, *is given by*

$$JF(x,y) = \begin{bmatrix} \frac{df}{dx} & \frac{df}{dy} \\ \frac{dg}{dx} & \frac{dg}{dy} \end{bmatrix} = \begin{bmatrix} f_x & f_y \\ g_x & g_y \end{bmatrix}.$$

Definition 10 *The equilibrium point* (x^*, y^*) *is* ***locally asymptotically stable*** *(LAS) if, given* λ_1 *and* λ_2 *are the eigenvalues for* (x^*, y^*),

$$max\{|\lambda_1|,\ |\lambda_2|\} < 1.$$

Otherwise, the equilibrium point is unstable.

Looking back at our one dimensional example, the value $x = 1$ is an unstable equilibrium point since an initial condition with a small perturbation away from the value results in a solution that diverges from the equilibrium point. Identifying the equilibrium points of a system and finding local stability of each equilibrium point are crucial in understanding the behavior of the system. We will discuss these ideas more thoroughly later.

Here we state a theorem by Li and Yorke [10] from 1975 along with some prerequisite definitions:

Let $F : J \to J$. For $x \in J, F^0(x)$ denotes x and $F^{n+1}(x)$ denotes $F(F^n(x))$ for $n = 0, 1, \cdots$. We will say p is a **periodic point with period** n if $p \in J$ and $p = F^n(p)$ and $p \neq F^k(p)$ for $1 \leqq k < n$. We say p is **periodic** or is a **periodic point** if p is periodic for some $n \geqq 1$....

Theorem 1 *Let* J *be an interval and let* $F : J \to J$ *be continuous. Assume there is a point* $a \in J$ *for which the points* $b = F(a)$, $c = F^2(a)$ *and* $d = F^3(a)$, *satisfy*

$$d \leqq a < b < c \text{ (or } d \geqq a > b > c\text{).}$$

Then for every $k = 1, 2, \cdots$ *there is a periodic point in* J *having period* k.

[10]

Then under the assumptions of the theorem, we would say that the given map F displays a characteristic known as chaos. This leads us to our final definition.

Definition 11 ***Chaos****, in the sense of Li and Yorke, appears in the dynamics of a map* F *any time the map has a periodic point of minimal period 3.*

Chapter 3

System Analysis

Nonlinear difference equations can be difficult to study since it can be impossible to discover a closed form solution to the system. However, we can employ certain mathematical tools to help us determine how the system behaves. In this chapter we will show much of the analysis of the system given by Equations (1.1) and (1.2), which will include finding boundedness and folding the system. We will determine the equilibrium points of our system and then identify and discuss the isoclines. We will proceed to find the stability of the equilibrium points in the following chapter.

3.1 Uniform Boundedness

A uniform bound of a function is a constant that exceeds the absolute value of any value of the function [5]. In essence, if a function has a uniform bound, it cannot outgrow this constant. The uniform bound of a system, if it exists, can tell us that the system can be contained by some value instead of growing uncontrollably. To find a uniform bound, which does not depend on x_n or y_n, we take the absolute value of the functions describing the system and find bounds for those functions. In this section we will establish the uniform bounds of our system given by Equations (1.1) and (1.2).

For reference, recall that our system is given by Equations (1.1) and (1.2):

$$x_{n+1} = ux_n e^{K-x_n-ay_n}$$

$$y_{n+1} = y_n e^{L-y_n-bx_n}$$

$$a, b, K, L > 0, \quad \text{and} \quad 0 < u \leqslant 1.$$

Before finding the uniform bound, we must first make the important note that due to the biological interpretation of the system, we will limit $x_n \geqslant 0$ and $y_n \geqslant 0$.

3.1.1 The Bound for x_{n+1}

Proposition 1 *Let* $x_0 \geqslant 0$ *and* $y_n \geqslant 0$ *for the system given in Equations (1.1) and (1.2). Then* $0 \leqslant x_{n+1} \leqslant e^{K-1}$ *for all* $n \geqslant 0$.

Proof: To find the bound for x_{n+1}, we consider Equation (1.1). Since $0 < u \leqslant 1$ and $e^{K-x_n-ay_n} > 0$ for all values of a, K, x_n, y_n, then if $x_n \geqslant 0$ we have

$$0 \leqslant \left|ux_n e^{K-x_n-ay_n}\right| \leqslant \left|x_n e^{K-x_n-ay_n}\right| = \left|x_n e^{-x_n} \cdot e^{K-ay_n}\right|. \qquad (3.1)$$

We first consider $h(x) = xe^{-x}$. Using Calculus, we can find the critical values of h:

$$h'(x) = x(-1)e^{-x} + e^{-x} = e^{-x}(1-x) = 0.$$

Thus $x = 1$ is the only critical point. We know a maximum occurs at this value since by the First Derivative Test, since $h'(0) = e^{-0}(1-0) = 1 > 0$ and $h'(2) = e^{-2}(1-2) = -e^{-2} < 0$, then $x = 1$ is where a maximum occurs for h. Thus the maximum $h(1) = 1e^{-1} = e^{-1}$, so we know $xe^{-x} \leqslant e^{-1}$ for all values of x. Now from Equation (3.1) we glean

$$0 \leqslant \left|ux_n e^{K-x_n-ay_n}\right| \leqslant \left|x_n e^{-x_n} e^{K-ay_n}\right| \leqslant \left|e^{-1} e^{K-ay_n}\right| = e^{-1} e^{K-ay_n} = e^{-ay_n} e^{K-1}.$$

When $y \geqslant 0$, the function e^{-ay} is uniformly decreasing with its maximum occurring at $y = 0$. Then its maximum is $e^{-a(0)} = e^0 = 1$.

Since $y_n \geqslant 0$, this gives us $0 \leqslant e^{-ay_n} e^{K-1} \leqslant e^{K-1}$ which is a constant. Since $x_n \geqslant 0$ as well, we can drop the absolute values, giving $0 \leqslant ux_n e^{K-x_n-ay_n} \leqslant e^{K-1} < \infty$. Therefore, $0 \leqslant x_{n+1} \leqslant e^{K-1} < \infty$ for each fixed K.

3.1.2 The Bound for y_{n+1}

Proposition 2 *Let* $x_0 \geqslant 0$ *and* $y_n \geqslant 0$ *for the system given in Equations (1.1) and (1.2). Then* $0 \leqslant y_{n+1} \leqslant e^{L-1}$ *for all* $n \geqslant 0$.

Proof: To find the bound for y_{n+1}, we consider Equation (1.2). We have

$$0 \leqslant \left|y_n e^{L-y_n-bx_n}\right| = \left|y_n e^{-y_n} e^{L-bx_n}\right|. \tag{3.2}$$

As we did in the case for x_{n+1}, let $h_2(y) = ye^{-y}$ and from the previous work we know that h_2 has a maximum value of e^{-1}. Since we assume that $x_n \geqslant 0$, the following holds:

$$\left|y_n e^{L-y_n-bx_n}\right| = \left|y_n e^{-y_n} e^{L-bx_n}\right| \leqslant \left|e^{-1} e^{L-bx_n}\right| = \left|e^{-bx_n} e^{L-1}\right| = e^{-bx_n} e^{L-1} \leqslant e^{L-1} < \infty.$$

Therefore, $0 \leqslant y_{n+1} \leqslant e^{L-1} < \infty$ for each fixed value of L.

So both x_{n+1} and y_{n+1} are uniformly bounded when x_n and y_n are nonnegative. From a biological perspective, this means that neither population will grow without bound, as we would expect to be true due to ecological constraints.

3.2 Folding the System

In this section we will apply a method known as folding wherein we write our system of two, first order difference equations as a single equation of higher order. Folding a system may allow a new type of analysis which may sometimes permit the reader to glean additional information [16], so folding our system in Equations (1.1) and (1.2) may allow us to discover dynamics of our system that are not otherwise apparent. For example, in some planar systems the method of folding allows one to discover cycles or chaos within the system that are not able to be found through more traditional methods [16]. However, sometimes the resulting second order equation is too complex for this to be true.

In order to fold the system we first solve for x_n in Equation (1.2) :

$$y_{n+1} = y_n e^{L-y_n-bx_n} \implies \frac{y_{n+1}}{y_n} = e^{L-y_n-bx_n} \implies$$

$$\ln\left(\frac{y_{n+1}}{y_n}\right) = L - y_n - bx_n \implies bx_n = L - y_n - \ln\left(\frac{y_{n+1}}{y_n}\right) \implies$$

$$x_n = \frac{1}{b}\left[L - y_n - \ln\left(\frac{y_{n+1}}{y_n}\right)\right]. \tag{3.3}$$

Now shifting the index of Equation (1.2) gives

$$y_{n+2} = y_{n+1} e^{L-y_{n+1}-bx_{n+1}}.$$

Replacing x_{n+1} with Equation (1.1) we obtain

$$y_{n+2} = y_{n+1} e^{L-y_{n+1}-b\left(ux_n e^{K-x_n-ay_n}\right)}.$$

Replacing x_n in the above equation with the right-hand side of Equation (3.3) yields

$$y_{n+2} = y_{n+1} e^{L - y_{n+1} - bu\left(\frac{1}{b}\left[L - y_n - \ln\left(\frac{y_{n+1}}{y_n}\right)\right]\right) e^{K - \left(\frac{1}{b}\left[L - y_n - \ln\left(\frac{y_{n+1}}{y_n}\right)\right]\right) - ay_n}}.$$

To simplify the right-hand side of this new equation, we use algebra to simplify the coefficients so that exponential and logarithmic expressions can be condensed as such:

$$y_{n+2} = y_{n+1} \exp\left\{L - y_{n+1} - u\left[L - y_n - \ln\left(\frac{y_{n+1}}{y_n}\right)\right] e^{K - \frac{1}{b}[L - y_n] + \ln\left(\left(\frac{y_{n+1}}{y_n}\right)^{\frac{1}{b}}\right) - ay_n}\right\}.$$

This implies

$$y_{n+2} = y_{n+1} \exp\left\{L - y_{n+1} - u\left[L - y_n - \ln\left(\frac{y_{n+1}}{y_n}\right)\right] \left(\frac{y_{n+1}}{y_n}\right)^{\frac{1}{b}} e^{K - \frac{1}{b}[L - y_n] - ay_n}\right\}.$$

We then distribute the harvesting term, u, as such:

$$\begin{aligned} y_{n+2} = \quad & y_{n+1} \exp\left\{L - y_{n+1} + u\,[y_n - L]\left(\frac{y_{n+1}}{y_n}\right)^{\frac{1}{b}} e^{K - \frac{1}{b}[L - y_n] - ay_n}\right. \\ & \left. + u \ln\left(\frac{y_{n+1}}{y_n}\right)\left(\frac{y_{n+1}}{y_n}\right)^{\frac{1}{b}} e^{K - \frac{1}{b}[L - y_n] - ay_n}\right\} \end{aligned}$$

which allows us to combine and simplify the right-hand side further into:

$$y_{n+1} \exp\left\{L - y_{n+1} + u\,[y_n - L]\left(\frac{y_{n+1}}{y_n}\right)^{\frac{1}{b}} e^{K - \frac{1}{b}[L - y_n] - ay_n}\right\} \cdot \left\{e^{\ln\left(\frac{y_{n+1}}{y_n}\right)}\right\}^{u\left(\frac{y_{n+1}}{y_n}\right)^{\frac{1}{b}} e^{K - \frac{1}{b}[L - y_n] - ay_n}}.$$

Then we find that our system in Equations (1.1) and (1.2) has been folded to become the following single equation:

$$y_{n+2} = y_{n+1} e^{\left\{L - y_{n+1} + u[y_n - L]\left(\frac{y_{n+1}}{y_n}\right)^{\frac{1}{b}} e^{K + \frac{1}{b}[y_n - L] - ay_n}\right\}} \left(\frac{y_{n+1}}{y_n}\right)^{\left\{u\left(\frac{y_{n+1}}{y_n}\right)^{\frac{1}{b}} e^{K + \frac{1}{b}[y_n - L] - ay_n}\right\}}.$$

As is sometimes the case, the folding has resulted in a very complicated second order difference equation. Because of the complexity of the folded system, we are unable to determine any additional characteristics of our system. No obvious simplifying assumptions, such as letting either $a = 0$ or $b = 0$, help us gain insight into the extinction or proliferation of either species, but further research may yield additional insights.

3.3 Equilibrium Points

An important part of the analysis of a system requires knowledge about the equilibrium points of that system. In this section we will obtain the equilibrium points (x^*, y^*) of our system. In general, the equilibrium points describe a steady state. For our system that means the points where the application of the recursive relation produces no change in either species x or in species y. Once a solution reaches an equilibrium point, it will continue to stay on the equilibrium point. In other words, once both populations simultaneously reach the equilibrium value, neither population grows or declines over time.

To find the equilibrium points, we replace all x iterates with the constant x^*, and all y iterates with the constant y^*, and then solve for x^* and y^* by solving the system of equations through elimination or substitution. This allows us to find the points where neither x nor y varies. Then Equation (1.1) becomes

$$x^*(1 - ue^{K - x^* - ay^*}) = 0.$$

Then

$$x^* = 0 \quad \text{or} \quad e^{K - x^* - ay^*} = \frac{1}{u} \implies x^* = K + \ln(u) - ay^*. \tag{3.4}$$

Equation (1.2) becomes

$$y^*(1 - e^{L - y^* - bx^*}) = 0.$$

Then

$$y^* = 0 \quad \text{or} \quad e^{L - y^* - bx^*} = 1 \implies y^* = L - bx^*.$$

We know if $x^* = 0$, then either $y^* = 0$, giving the first equilibrium point $(x^*, y^*) = (0, 0)$, or else $y^* = L - b(0) = L$, giving the second equilibrium point $(x^*, y^*) = (0, L)$. Alternately, if $x^* = K + \ln(u) - ay^*$, then $y^* = 0$ implies that $x^* = K + \ln(u) - a(0) = K + \ln(u)$, giving the third equilibrium point $(x^*, y^*) = (K + \ln(u), 0)$. Recall that $M = K + \ln(u)$. Then the third equilibrium points can be rewritten as $(x^*, y^*) = (M, 0)$.

Finally, using the substitution method the fourth scenario gives

$$y^* = L - bx^* = L - b(K + \ln(u) - ay^*) = L - bK - b\ln(u) + aby^*.$$

This then tells us that

$$y^*(1 - ab) = L - bK - b\ln(u) \implies y^* = \frac{L - b(K + \ln(u))}{1 - ab}.$$

Plugging this in to Equation (3.4) we obtain

$$x^* = \frac{K + \ln(u) - aL}{1 - ab},$$

and so the fourth equilibrium point is $(x^*, y^*) = \left(\frac{K + \ln(u) - aL}{1 - ab}, \frac{L - b(K + \ln(u))}{1 - ab}\right)$, or alternately $(x^*, y^*) = \left(\frac{M - aL}{1 - ab}, \frac{L - bM}{1 - ab}\right)$.

This can be summarized as follows:

1. $EP_1 = (0, 0)$. This is the extinction equilibrium point.
2. $EP_2 = (0, L)$. This is an exclusion equilibrium point (y survives and x is extinct).
3. $EP_3 = (M, 0)$. This is an exclusion equilibrium point (x survives and y is extinct).
4. $EP_4 = \left(\frac{M - aL}{1 - ab}, \frac{L - bM}{1 - ab}\right)$. This is the coexistence equilibrium point.

We can also use the isoclines of the system, which we will discuss in the next section, to help us find the equilibrium points.

3.4 Isoclines

Isoclines can be useful tools in aiding our understanding of system dynamics, as well as considering equilibrium points. Isoclines are curves along which one of the variables, either x or y, does not change. In this section, we will determine the isoclines with the goal of better understanding the dynamics of the system. This includes identifying necessary properties to consider only a biologically relevant coexistence equilibrium point (EP_4).

Recall again that our system is:

$$x_{n+1} = ux_n e^{K-x_n-ay_n}$$

$$y_{n+1} = y_n e^{L-y_n-bx_n}$$

$$a, b, K, L > 0, \quad \text{and} \quad 0 < u \leqslant 1.$$

We let

$$F(x,y) = (uxe^{K-x-ay}, ye^{L-y-bx}), \tag{3.5}$$

which we can rewrite as

$$F(x,y) = (f(x,y), g(x,y)) \tag{3.6}$$

where

$$f(x,y) = uxe^{K-x-ay} \tag{3.7}$$

and

$$g(x,y) = ye^{L-y-bx}. \tag{3.8}$$

To find the isoclines of the system, we consider Equations (3.7) and (3.8). We set $f(x,y) = x$ and $g(x,y) = y$. Looking at each equation separately, we hold one variable constant, and solve for that variable. For example, with Equation (3.7), the equation describing the change in population for species x, we set x equal to the constant $\overline{x}$ while still allowing y to vary, and then we solve the equation for $\overline{x}$. We repeat the process with y and $\overline{y}$ for Equation (3.8), the equation describing species y.

To find the x isoclines where the value of x does not change, we do

$\overline{x} = u\overline{x}e^{K-\overline{x}-a\overline{y}}$ then

$\overline{x}\left[ue^{K-\overline{x}-a\overline{y}} - 1\right] = 0.$

Then either $\overline{x} = 0$ or $ue^{K-\overline{x}-a\overline{y}} = 1$

$$\implies \overline{x} = K + \ln(u) - a\overline{y}. \tag{3.9}$$

The previous equation can be rearranged as $\overline{y} = \frac{1}{a}\left[K + \ln(u) - \overline{x}\right]$.

So the isoclines in x are $\overline{x} = 0$ and $\overline{y} = \frac{1}{a}\left[K + \ln(u) - \overline{x}\right]$.

Note: if we let $M = K + \ln(u)$ then the second x isocline becomes $\overline{y} = \frac{1}{a}\left[M - \overline{x}\right]$.

Similarly, to find the y isoclines where the value of y does not change, we do

$\overline{y} = \overline{y} * e^{L-\overline{y}-b\overline{x}}$ then

$\overline{y}\left[e^{L-\overline{y}-b\overline{x}} - 1\right] = 0.$

This gives us that either $\overline{y} = 0$ or $e^{L-\overline{y}-b\overline{x}} = 1$

$$\implies \overline{y} = L - b\overline{x}. \tag{3.10}$$

So the isoclines in y are $\overline{y} = 0$ and $\overline{y} = L - b\overline{x}$.

To find where the isoclines have intercepts in Quadrant 1, which is the only biologically relevant quadrant, note that

$s_1: \quad \overline{y} = \frac{1}{a}\left[M - \overline{x}\right]$ has intercepts $(M, 0)$ and $(0, \frac{M}{a})$ and

$s_2: \quad \overline{y} = L - b\overline{x}$ has intercepts $(\frac{L}{b}, 0)$ and $(0, L)$.

These isoclines can be seen in Figure 3.1. On isocline s_1 the population of species x remains constant and on isocline s_2 the population of species y remains constant.

We then have two cases. Either $ab < 1$ or $ab > 1$. We do not allow $ab = 1$ since we see from Equations (3.9) and (3.10) that the isoclines would be parallel and thus EP_4 cannot occur, a situation we do not consider.

First we will look at the x-axis. Then since $y = 0$, Equation (1.1) becomes

$$x_{n+1} = ux_n e^{K-x_n}.$$

We can write this in terms of M by rewriting the above equation as

$$x_{n+1} = e^{\ln(u)} x_n e^{K-x_n} \implies x_{n+1} = x_n e^{M-x_n}.$$

If $x_n < M$, then $e^{M-x_n} > 1$, so population x increases to M. Alternately, if $x_n > M$, then $e^{M-x_n} < 1$, so population x decreases to M. This is an expected result. In the absence of species y, species x will tend towards its modified carrying capacity M. Since on the isocline s_2 species x can change value, if s_2 intersects the x-axis while x is increasing (alternately decreasing), then x will continue to increase (alternately decrease) all along s_2.

Now we will look at the y-axis. Since $x = 0$, Equation (1.2) becomes

$$y_{n+1} = y_n e^{L-y_n}.$$

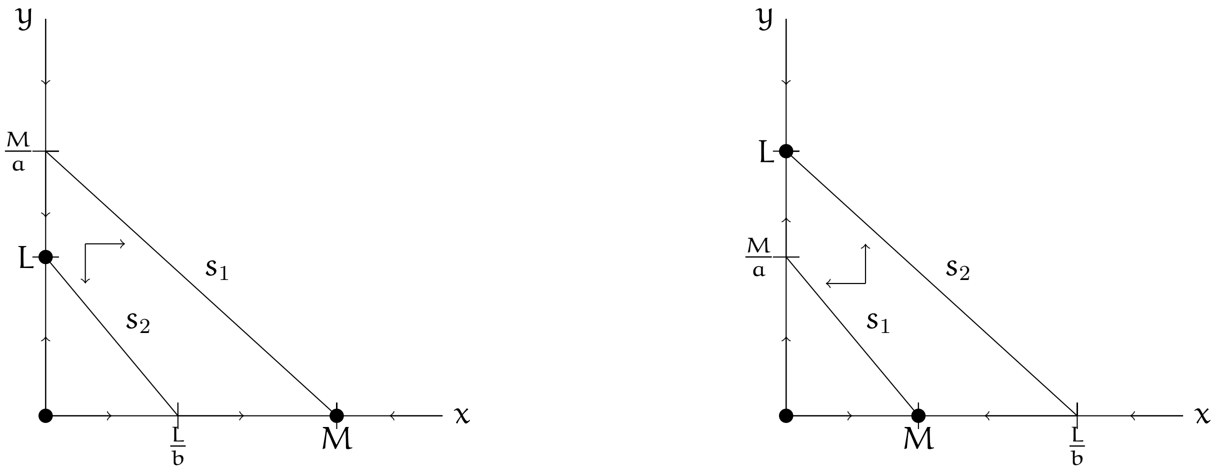
If $y_n < L$, then $e^{L-y_n} > 1$, so population y increases to L. Alternately, if $y_n > L$, then $e^{L-y_n} < 1$, so population y decreases to L. This is also an expected result. In the absence of species x, species y will tend towards its carrying capacity L. Since on the isocline s_1 species y can change value, if s_1 intersects the y-axis while y is increasing (alternately decreasing), then y will continue to increase (alternately decrease) all along s_1.

We will describe two scenarios for the exclusion equilibrium points, as seen in Figure 3.1. Recall that x tends towards M on the x-axis and y tends towards L on the y-axis.

Then equilibrium point $(0, 0)$ is clearly unstable in both cases.

In Case 1, s_2 intersects the x-axis while x is increasing; thus x is increasing on s_2. Meanwhile s_1 intersects the y-axis when y is decreasing; thus y is decreasing on s_1. From this we conclude that if M is bounded so that chaos cannot occur, and if $L < bM$, then the exclusion equilibrium point $(M, 0)$ is locally asymptotically stable and species y goes extinct.

In Case 2, s_2 intersects the x-axis while x is decreasing; thus x is decreasing on s_2. Meanwhile s_1 intersects the y-axis when y is increasing; thus y is increasing on s_1. From this we conclude that if L is bounded so that chaos cannot occur, and if $L > \frac{M}{a}$, then the exclusion equilibrium point $(0, L)$ is locally asymptotically stable and species x goes extinct.



Case 1 Case 2

Figure 3.1: Two cases for the exclusion equilibrium points.

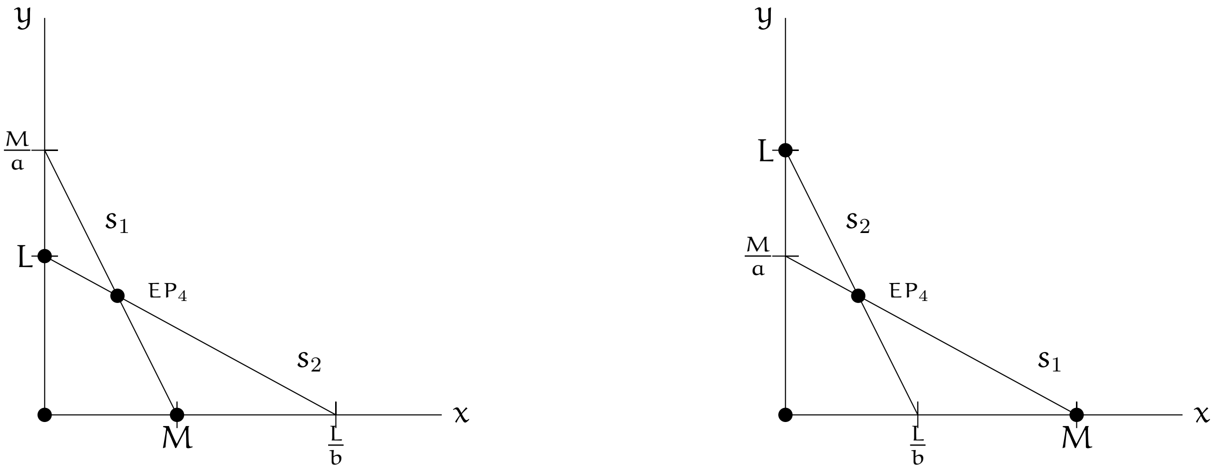
It is interesting to note that as the term ab grows from a value less than 1 to a value greater than 1, s_1 and s_2 briefly intersect to yield EP_4 (see Figure 3.2) and then the lines along with their intercepts switch places.

When s_1 and s_2 intersect in Quadrant 1, then we obtain the fourth equilibrium point EP_4. This coexistence equilibrium point occurs in two cases.

The coexistence equilibrium point exists if $bM < L < \frac{M}{a}$ and $ab < 1$. In this case, s_1 intersects s_2 at EP_4 because when $M < \frac{L}{b}$ it implies $bM < L$. Also, in this case $L < \frac{M}{a}$ implies $aL < M$. Multiplying by b on both sides implies $abL < bM$. Together we get that $abL < bM < L$ which by the Transitive Property means that $abL < L$. The only way for this to be true is for $ab < 1$.

The coexistence equilibrium point also exists if $\frac{M}{a} < L < bM$ and $ab > 1$. In this case, s_1 intersects s_2 at EP_4 because when $\frac{L}{b} < M$ it implies $L < bM$. Multiplying by a on both sides yields $aL < abM$. In addition, $\frac{M}{a} < L$ which implies that $M < aL$. Together we get that $M < aL < abM$ which by the Transitive Property means that $M < abM$. The only way for this to be true is for $ab > 1$.

These two cases can be seen in Figure 3.2.



$ab < 1$

$ab > 1$

Figure 3.2: Two cases for the coexistence equilibrium point.

In cases 1 and 2, no coexistence equilibrium point exists and thus no possibility exists for the population of species x to change between increasing and decreasing along s_1. Similarly, no possibility exists for the population of species y to change between increasing and decreasing along s_2. However, the cases illustrated by Figure 3.2 do allow a change to happen, and thus we will perform further analysis to determine the stability of EP_4.

It is also important to note that when looking at the biologically relevant Quadrant 1, $M \geqslant 0$ which implies that $u \geqslant e^{-K}$. The previous four cases assume that $M > 0$. This is especially obvious when $ab < 1$, since in those cases $0 < \frac{L}{b} < M \implies 0 < M$. In the previous scenarios when $ab > 1$, note that either $L < bM$ (as with the exclusion scenario) or $L < \frac{M}{a}$ (as with the coexistence scenario). Since $a, b, L > 0$, in the former case $0 < L < bM \implies 0 < bM \implies M > 0$ and in the latter case $0 < L < \frac{M}{a} \implies 0 < \frac{M}{a} \implies M > 0$.

When looking at scenarios in which $M < 0$, we see that EP_4 can only occur in either Quadrant 2 or Quadrant 4, neither of which are biologically relevant. This can be seen in Figure 3.3. For the rest of this thesis, we will only consider $M \geqslant 0$.

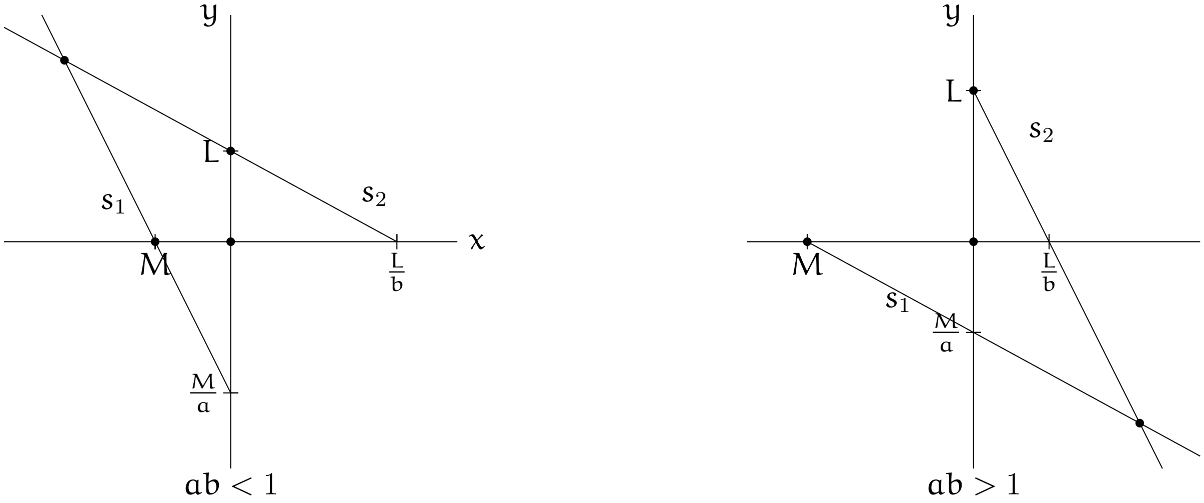


Figure 3.3: Two cases for the coexistence equilibrium point when $M < 0$.

Chapter 4

Local Stability Analysis

In this chapter, we analyze the local stability of the equilibrium points of our system. In order to analyze the local stability of an equilibrium point, we find the eigenvalues of the Jacobian evaluated at the equilibrium point and look at the modulus of each eigenvalue. If the modulus for both eigenvalues is less than one, the equilibrium point is stable. If the modulus of either eigenvalue is greater than one, the equilibrium point is unstable. For many systems, since the eigenvalues may depend on parameters, this involves looking at multiple cases of the parameters involved in the system.

4.1 Eigenvalues

To find the eigenvalues λ_1 and λ_2 of equilibrium point (x^*, y^*), we first evaluate the Jacobian of a map $F = (f, g)$ at (x^*, y^*). Next, we find the matrix formed by taking the difference of the Jacobian evaluated at the equilibrium point and the matrix λI, where I is the identity matrix. We then take the determinant of this newly found matrix and set it equal to zero as seen here:

$$\det\left(JF(x^*, y^*) - \lambda I\right) = \begin{bmatrix} f_x(x^*, y^*) - \lambda & f_y(x^*, y^*) \\ g_x(x^*, y^*) & g_y(x^*, y^*) - \lambda \end{bmatrix} \overset{\text{set}}{=} 0. \tag{4.1}$$

The characteristic equation then becomes:

$$\lambda^2 - (f_x + g_y)\lambda + f_x g_y - g_x f_y = 0 \tag{4.2}$$

which is a quadratic in λ. The eigenvalues λ_1, λ_2 of equalibrium point (x^*, y^*) are the roots of the characteristic equation.

Once we know the local stability of every equilibrium point in a system, we have a better understanding of how the system behaves and what the solution of the system will look like. Although not in general true, the terms stable and locally asymptotically stable are used here interchangeably. Every reference in this thesis to asymptotic stability indicates local asymptotic stability as the stability analysis of this paper has been limited to local analysis. Finding the global stability of a system is outside the scope of this thesis.

To find the eigenvalues for our system, we again consider the function $F(x, y) = (uxe^{K-x-ay}, ye^{L-y-bx})$, where f and g represent Equations (1.1) and (1.2), respectively. The Jacobian of F is then

$$JF(x, y) = \begin{bmatrix} ue^{K-x-ay}(1-x) & -auxe^{K-x-ay} \\ -bye^{L-y-bx} & e^{L-y-bx}(1-y) \end{bmatrix}$$

which yields the characteristic equation

$$\lambda^2 - \left[e^{L-y-bx}(1-y) + ue^{K-x-ay}(1-x)\right]\lambda + e^{K-x-ay}e^{L-y-bx}(u(1-x)(1-y) - abuxy) = 0.$$

In what follows, we determine the eigenvalues λ in this equation by substituting the values of each equilibrium point.

4.2 Local Stability of the Extinction and Exclusion Equilibrium Points

We will now find the Jacobian evaluated at each point and obtain its eigenvalues. We then determine where the equilibrium point is asymptotically stable, which as previously stated holds where $\max\{|\lambda_1|,\ |\lambda_2|\} < 1$.

1. For the extinction equilibrium point $(0, 0)$, the Jacobian is

$$JF(0,0) = \begin{bmatrix} ue^{K} & 0 \\ 0 & e^{L} \end{bmatrix}.$$

   The eigenvalues of the extinction equilibrium point are found through the characteristic equation: $(ue^K - \lambda)(e^L - \lambda) - 0^2 = 0$. Alternatively, note that this is a diagonal matrix. This implies $(0, 0)$ has eigenvalues $\lambda_1 = ue^K, \lambda_2 = e^L$.

   Then $(0, 0)$ is locally asymptotically stable if $|\lambda_1| < 1$ and $|\lambda_2| < 1$. That is, if $|ue^K| < 1$ and $|e^L| < 1$. Since we have limited $L > 0$, then $e^L > 1$, so $(0, 0)$ is unstable. This generalizes the result we found using isoclines.

   An example of the instability of $(0, 0)$ can be seen in Figure 4.1. Here even a small perturbation from $(0, 0)$ results in the system being drawn to $(0, L)$. We see that while we began with small population values for both species, as time progresses species x goes extinct but species y increases and eventually remains at the population value given by its carrying capacity.

2. The exclusion equilibrium point $(0, L)$ has the Jacobian

$$JF(0,L) = \begin{bmatrix} ue^{K-aL} & 0 \\ -bL & 1-L \end{bmatrix}.$$

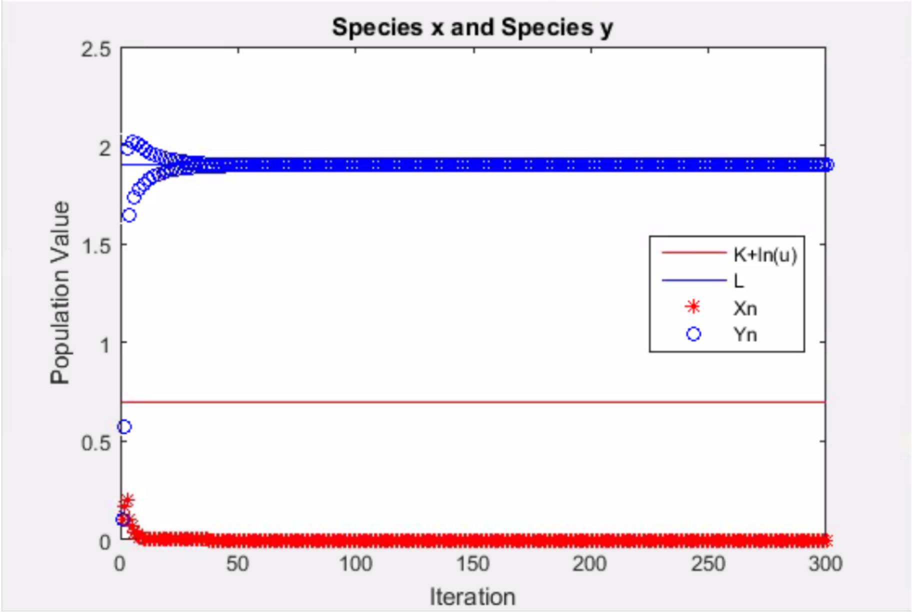


Figure 4.1: An example of the instability of the equilibrium point $(0,0)$, with parameter values $a = 0.6, b = 0.5, K = 3, L = 1.9$, and $u = 0.1$

The characteristic equation $(ue^{K-aL} - \lambda)(1 - L - \lambda) = 0$ yields $\lambda_1 = ue^{K-aL}, \lambda_2 = 1 - L$.

Then $(0, L)$ is locally asymptotically stable if

(a) $|ue^{K-aL}| < 1$ and

(b) $|1 - L| < 1$.

From (a), and noting that $u > 0$, we obtain $0 < ue^{K-aL} < 1$. Thus $0 < u < e^{-(K-aL)}$ is required for stability. However, while it can be informative to discuss stability in terms of the harvesting parameter u, at this equilibrium point species x is nonexistent. Thus we will look at the stability of this equilibrium point with respect to the parameter L.

$$0 < ue^{K-aL} < 1 \iff 0 < e^{-aL} < \frac{e^{-K}}{u}$$

$$\iff -aL < \ln\left(\frac{e^{-K}}{u}\right)$$

$$\iff -aL < -K - \ln(u)$$

$$\iff L > \frac{K + \ln(u)}{a}$$

$$\iff L > \frac{M}{a}.$$

Condition (b) implies

$$-1 < 1 - L < 1 \implies -2 < -L < 0$$

$$\implies 0 < L < 2.$$

From (a) and (b) we conclude that $(0, L)$ is locally asymptotically stable if $L > \dfrac{M}{a}$ and $0 < L < 2$. Since we only consider $M \geqslant 0$, then together these become $\dfrac{M}{a} < L < 2$. When this condition is met, species y remains but species x becomes extinct. This matches the result we found in Case 2 when studying the isoclines of the system. This analysis then provides the upper bound needed for L.

As harvesting is increased (u decreases to zero), M also decreases to zero; that is, the modified carrying capacity for species x decreases to 0 and the system will not as easily sustain species x. Thus the lower bound decreases such that for any given L, the condition $L > \frac{M}{a}$ will be more easily met and $(0, L)$ will more easily be LAS. That is, with sufficient harvesting, species x will become extinct and species y will persist at population value L.

This can be seen in Figure 4.2. For these parameter values in this example, species x does not become extinct nor does the population value of species y tend towards its carrying capacity, L, when harvesting is at 20% of the species x population. However, when harvesting is increased to 90%, species x goes extinct while species y persists at population value L.

3. The exclusion equilibrium point $(K + \ln(u), 0) = (M, 0)$ has the Jacobian

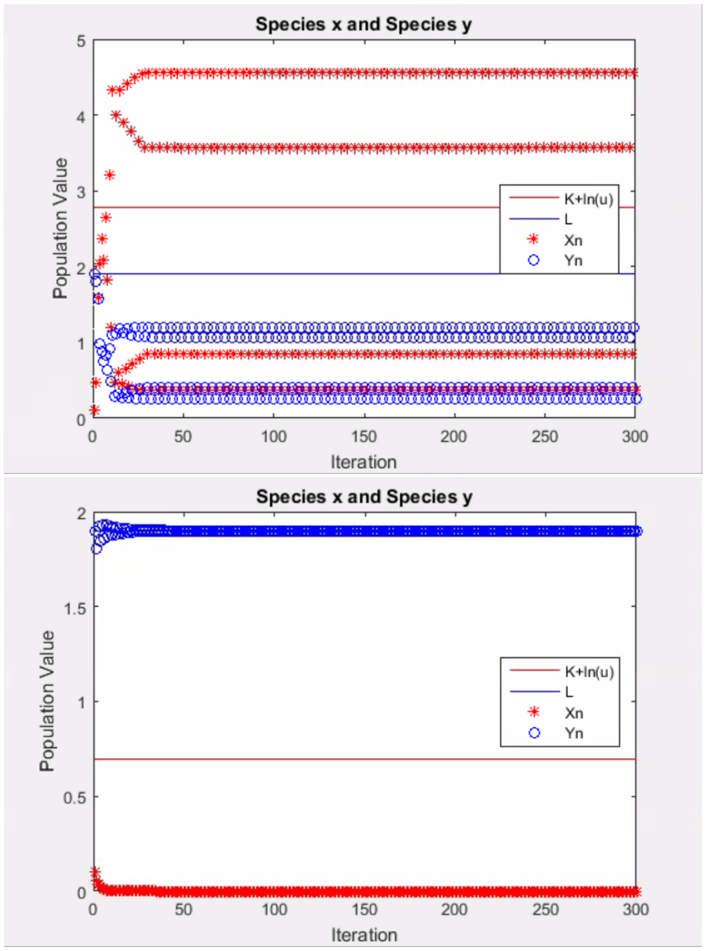


Figure 4.2: For $a = 0.6, b = 0.5, K = 3, L = 1.9$, and $u = 0.8$ (top) or $u = 0.1$ (bottom). We observe that the stability of $(0, L)$ changes with harvesting.

$$JF(K + \ln(u), 0) = \begin{bmatrix} 1 - (K + \ln(u)) & -a(K + \ln(u)) \\ 0 & e^{L-b(K+\ln(u))} \end{bmatrix} = \begin{bmatrix} 1 - M & -aM \\ 0 & e^{L-bM} \end{bmatrix}.$$

The characteristic equation $(1 - (K + \ln(u)) - \lambda)(e^{L-b(K+\ln(u))} - \lambda) - 0 = 0$

yields the eigenvalues $\lambda_1 = 1 - (K + \ln(u)), \qquad \lambda_2 = e^{L-b(K+\ln(u))}$.

$(K + \ln(u), 0)$ is locally asymptotically stable if

(a) $|1 - (K + \ln(u))| < 1$ and

(b) $|e^{L-b(K+\ln(u))}| < 1$.

From (a), we obtain

$$-1 < 1 - (K + \ln(u)) < 1$$

$$\implies 0 < K + \ln(u) < 2 \text{ or } 0 < M < 2.$$

For $K < 2$ this implies that

$$e^{-K} < u < e^{2-K}.$$

From condition (b) we note that the exponential allows us to drop the absolute value and obtain

$$e^{L-b(K+\ln(u))} < 1 \implies L - b(K + \ln(u)) < 0.$$

From this we obtain

$$K + \ln(u) > \frac{L}{b} \text{ or } M > \frac{L}{b}.$$

This can also be written as $u > e^{\frac{L}{b}-K}$.

Making the substitution for M, from (a) and (b) we conclude that $(M, 0)$ is locally asymptotically stable if $0 < M < 2$ and $M > \frac{L}{b}$. That is, if $\frac{L}{b} < M < 2$, then species x persists at its modified carrying capacity, while species y goes extinct. This matches the result we found in Case 1 when studying the isoclines of the system. This analysis then provides the upper bound needed for M.

As harvesting is increased, i.e., as M decreases, the condition $L < bM$ for any given L is more difficult to satisfy while the condition $M < 2$ is easier to satisfy. That is, harvesting can move $(M, 0)$ into or out of a region of stability.

In Figure 4.3 we show that a change in harvesting affects the stability of $(M, 0)$.

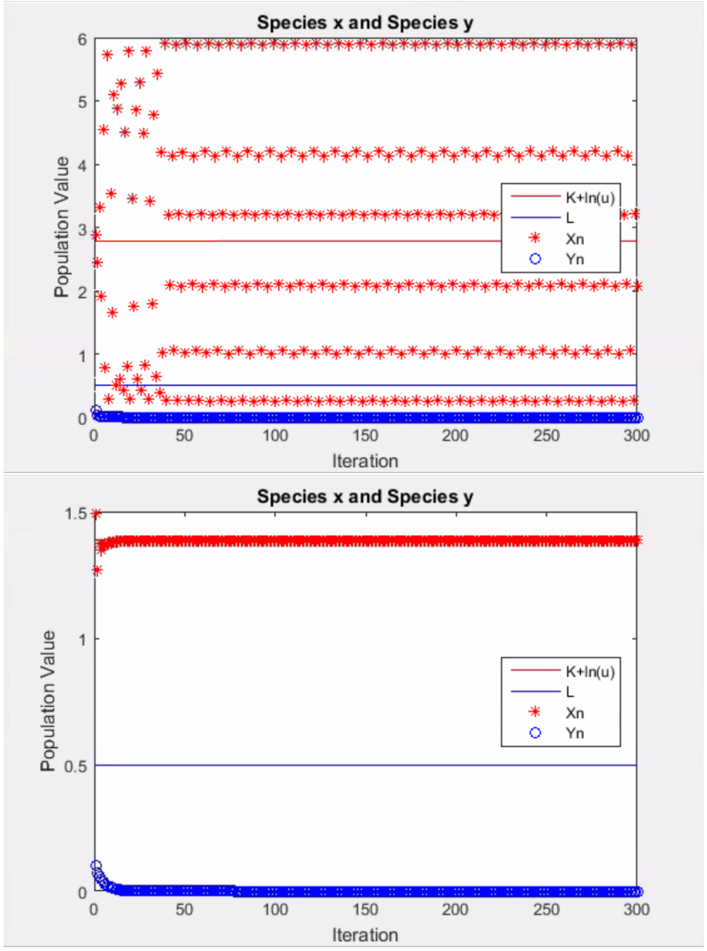


Figure 4.3: For $a = 0.6, b = 0.5, K = 3, L = 0.5$, and $u = 0.8$ (top) or $u = 0.2$ (bottom). We observe that the stability of $(M, 0)$ changes with harvesting.

4.3 Local Stability of the Coexistence Equilibrium Point

The rest of our analysis will focus on the stability of the coexistence equilibrium point $\left(\frac{K+\ln(u)-aL}{1-ab}, \frac{L-b(K+\ln(u))}{1-ab}\right)$. For the purpose of clarity, throughout the analysis of EP_4 we will use the notation λ^+ and λ^- in place of λ_1 and λ_2.

The Jacobian of the coexistence equilibrium point is

$$\begin{aligned} JF&\left(\frac{K+\ln(u)-aL}{1-ab}, \frac{L-b(K+\ln(u))}{1-ab}\right) \\ &= \frac{1}{1-ab}\begin{bmatrix} 1+aL-ab-(K+\ln(u)) & a^2L-a(K+\ln(u)) \\ b^2(K+\ln(u))-bL & b(K+\ln(u))-ab-L+1 \end{bmatrix}. \end{aligned}$$

Making the substitution $M = K + \ln(u)$ allows us to simplify our calculations but hides the system's reliance on the harvesting factor u, and for this reason we will switch between the two notational styles to emphasize different qualities. Recall from our discussion on isoclines that we only consider positive values for M to ensure a biologically relevant coexistence equilibrium point. Hence, the above Jacobian can also be written as the following:

$$\begin{aligned} & JF\left(\frac{M-aL}{1-ab}, \frac{L-bM}{1-ab}\right) \\ & \quad = \frac{1}{1-ab}\begin{bmatrix} 1+aL-ab-M & a^2L-aM \\ b^2M-bL & bM-ab-L+1 \end{bmatrix}. \end{aligned}$$

Using the before-mentioned process of finding the eigenvalues, we find that the eigenvalues of EP_4 are:

$$\begin{aligned} \lambda^{\pm} = & \frac{1}{2}\frac{1}{(1-ab)}\left[2+aL-2ab-L+b\left(K+\ln(u)\right)-\left(K+\ln(u)\right)\right. \\ & \pm(K^2+2K\ln(u)+(\ln(u))^2+b^2\left(K^2+2K\ln(u)+(\ln(u))^2\right)-4ab^2\left(K^2+2K\ln(u)+(\ln(u))^2\right) \\ & +2b\left(K^2+2K\ln(u)+(\ln(u))^2\right)+2abL\left(K+\ln(u)\right)-2bL\left(K+\ln(u)\right) \\ & \left.-2aL\left(K+\ln(u)\right)+4a^2b^2L\left(K+\ln(u)\right)-2L\left(K+\ln(u)\right)+a^2L^2-4a^2bL^2+2aL^2+L^2)^{\frac{1}{2}}\right]. \end{aligned}$$

Again using the substitution $M = K + \ln(u)$ our eigenvalues become:

$$\begin{aligned} \lambda^{\pm} = & \frac{1}{2}\frac{1}{(1-ab)}[2+aL-2ab-L+bM-M \\ & \pm\{M^2+b^2M^2-4ab^2M^2+2bM^2+2abLM-2bLM \\ & -2aLM+4a^2b^2LM-2LM+L^2(a^2-4a^2b+2a+1)\}^{\frac{1}{2}}]. \end{aligned} \tag{4.3}$$

We simplify Equation (4.3) to obtain:

$$\begin{aligned} & \lambda^{\pm} = 1+\tfrac{1}{2}\tfrac{1}{(1-ab)}[L(a-1)+M(b-1) \\ & \pm\sqrt{M^2(b^2-4ab^2+2b+1)+2LM(2a^2b^2+ab-a-b-1)+L^2(a^2-4a^2b+2a+1}]. \end{aligned}$$

To determine the stability of EP_4, we must consider multiple cases. For simplicity, we allow $D = M^2(b^2 - 4ab^2 + 2b + 1) + 2LM(2a^2b^2 + ab - a - b - 1) + L^2(a^2 - 4a^2b + 2a + 1$, so our eigenvalues become

$$\lambda^{\pm} = 1 + \frac{1}{2}\frac{1}{(1-ab)}\left[L(a-1) + M(b-1) \pm \sqrt{D}\right].$$

Case I: Complex Eigenvalues ($D < 0$)

First we will assume that $D < 0$. In this case, $\lambda^{\pm}$ are complex.

Letting $A = 1 + \frac{1}{2}\frac{1}{(1-ab)}[L(a-1) + M(b-1)]$ and $B = \frac{1}{2}\frac{1}{(1-ab)}\sqrt{-1(D)}$, we rewrite $\lambda^{\pm}$ as

$$\lambda^{\pm} = A + Bi.$$

Then $|\lambda^{\pm}| < 1$ if $\sqrt{A^2 + B^2} < 1$:

$$\sqrt{\left(1 + \frac{1}{2}\frac{1}{(1-ab)}[L(a-1) + M(b-1)]\right)^2 + \left(\frac{1}{2}\frac{1}{(1-ab)}\sqrt{-1(D)}\right)^2} < 1$$

$$\implies \sqrt{\left(1 + \frac{1}{2}\frac{1}{(1-ab)}[L(a-1) + M(b-1)]\right)^2 - \frac{1}{4}\frac{1}{(1-ab)^2}D} < 1$$

This implies:

$$\left(1 + \frac{1}{(1-ab)}[L(a-1) + M(b-1)] \right.$$
$$\left. + \frac{1}{4}\frac{1}{(1-ab)^2}[L^2(a-1)^2 + 2LM(a-1)(b-1) + M^2(b-1)^2] - \frac{1}{4}\frac{1}{(1-ab)^2}D\right)^{\frac{1}{2}} < 1,$$

which simplifies to:

$$\left(1 + \frac{1}{(1-ab)}[L(a-1) + M(b-1)] \right.$$
$$\left. + \frac{1}{4}\frac{1}{(1-ab)^2}[L^2(a-1)^2 + 2LM(a-1)(b-1) + M^2(b-1)^2 - D]\right)^{\frac{1}{2}} < 1.$$

Substituting in for D and simplifying we obtain

$$\left(1 + \frac{1}{(1-ab)}[L(a-1) + M(b-1)] \right.$$
$$\left. - \frac{1}{(1-ab)^2}[aL^2(1+ab) - LM(1-a^2b^2) + bM^2(1+ab)]\right)^{\frac{1}{2}} < 1$$

and squaring both sides and subtracting 1, we observe:

$$\frac{1}{(1-ab)}\left[L(a-1)+M(b-1)\right]-\frac{1}{(1-ab)^2}\left[aL^2(1+ab)-LM(1-a^2b^2)+bM^2(1+ab)\right]<0.$$

Multiplying by $(1-ab)^2$ we obtain:

$$(1-ab)\left[L(a-1)+M(b-1)\right]-aL^2(1+ab)+LM(1-a^2b^2)-bM^2(1+ab)<0,$$

which rearranges to

$$M^2\left(-b(1+ab)\right)+M\left[L(1-ab)(1+ab)+(b-1)(1-ab)\right]+(1-ab)(a-1)L-a(1+ab)L^2<0. \tag{4.4}$$

Let

$$\psi(M)=M^2\left(-b(1+ab)\right)+M\left[L(1-ab)(1+ab)+(b-1)(1-ab)\right]+(1-ab)(a-1)L-a(1+ab)L^2.$$

We note $\psi(M)$ is a downward-facing parabola since the coefficient of M^2 is clearly negative. Consider the following cases:

1. If $a>1$ and $b>1$, then $1-ab<0$ and clearly (4.4) is satisfied.

2. If the conditions of Case 1 are not met, consider the roots of $\psi(M)$:

$$\begin{aligned}M^{\pm}=&\frac{1}{2b(1+ab)}\Big[L(1-a^2b^2)+(b-1)(1-ab)\\&\pm\sqrt{(L(1-a^2b^2)+(b-1)(1-ab))^2+4b(1+ab)\left[(1-ab)(a-1)L-a(1+ab)L^2\right]}\Big].\end{aligned}$$

   Clearly $M^+\geqslant M^-$. Recall for biological relevance we only consider $M>0$. If $M^-<0$, then we discard this root as well as the values to the left of it and (4.4) holds true if $M>M^+$. If both roots are greater than zero, then (4.4) holds true if either $M<M^-$ or $M>M^+$. We illustrate this in Figure 4.4.

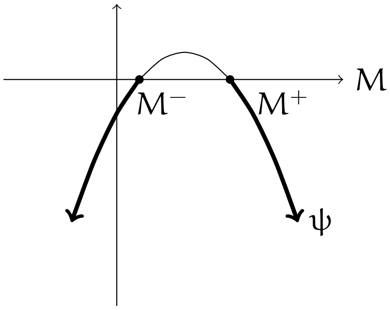


Figure 4.4: The regions for M where $\psi(M)$ is negative.

Case II: Real Eigenvalues ($D \geqslant 0$)

Now we consider the case when $D \geqslant 0$. In this case, $\lambda^{\pm}$ are real. The majority of the analysis for the stability of EP_4 will be in this case.

For EP_4 to be stable, we must determine when $|\lambda^-| < 1$ and $|\lambda^+| < 1$. This is equivalent to saying $-1 < \lambda^{\pm} < 1$, which results in

$$-2 < \frac{1}{2}\frac{1}{(1-ab)}\left[L(a-1) + M(b-1) \pm \sqrt{D}\right] < 0$$

$$\iff \quad -4 < \frac{1}{(1-ab)}\left[L(a-1) + M(b-1) \pm \sqrt{D}\right] < 0. \tag{4.5}$$

Below we consider some special cases.

4.3.1 Real Eigenvalues Case (i) $1 - ab > 0$

Throughout this section we assume that $1 - ab > 0$, which implies $ab < 1$. Multiplying (4.5) by $(1 - ab)$ on all sides does not change the direction of the inequality signs. Thus (4.5) becomes

$$-4(1-ab) < L(a-1) + M(b-1) \pm \sqrt{D} < 0. \tag{4.6}$$

We will look at λ^+ and λ^- separately.

Left-hand Side ($-1 < \lambda^-$)

In this case we investigate under what conditions the following inequality is true.

$$-4(1-ab) < L(a-1) + M(b-1) - \sqrt{D}$$

$$\implies \sqrt{D} < L(a-1) + M(b-1) + 4(1-ab). \tag{4.7}$$

If $L(a-1) + M(b-1) + 4(1-ab) \leqslant 0$, then Equation (4.7) is never satisfied and the equilibrium point is unstable. If instead $L(a-1) + M(b-1) + 4(1-ab) > 0$, that is if

1. for $b > 1$, $M > \dfrac{-L(a-1) - 4(1-ab)}{b-1}$, or
2. for $b < 1$, $M < \dfrac{-L(a-1) - 4(1-ab)}{b-1}$

then we can safely square both sides to obtain

$$D < [L(a-1) + M(b-1) + 4(1-ab)]^2 . \tag{4.8}$$

Substituting in the value of D and expanding (4.8) gives

$$bM^2(1-ab) + aL^2(1-ab) + LM(a^2b^2-1) - 2L(1-ab)(a-1) - 2M(1-ab)(b-1) - 4(1-ab)^2 < 0.$$

Since $1 - ab > 0$, we can divide both sides of the inequality by $(1 - ab)$; hence

$$bM^2 + aL^2 - LM(ab+1) - 2L(a-1) - 2M(b-1) - 4(1-ab) < 0 \tag{4.9}$$

which is a quadratic in M.

Let $\gamma(M) = bM^2 + aL^2 - LM(ab+1) - 2L(a-1) - 2M(b-1) - 4(1-ab)$. Then $-1 < \lambda^-$ when $\gamma(M) < 0$. We know that γ is an upward-facing parabola since b, which is the coefficient of M^2, is positive. The roots of γ are as follows:

$$
\begin{aligned}
M_1 = &\ \frac{1}{2b}\left[2(b-1)+(1+ab)L\right.\\
&\left.-\sqrt{(1-2ab+a^2b^2)L^2+(4ab^2+4ab-4b-4)L+(4b^2+8b-16ab^2+4)}\right]\\
M_2 = &\ \frac{1}{2b}\left[2(b-1)+(1+ab)L\right.\\
&\left.+\sqrt{(1-2ab+a^2b^2)L^2+(4ab^2+4ab-4b-4)L+(4b^2+8b-16ab^2+4)}\right].
\end{aligned}
$$

As long as the discriminant of M_1 and M_2 is nonnegative (and thus M_1 and M_2 are real), it is possible for $\gamma(M) < 0$ for some M between M_1 and M_2. Since the quadratic is upward-facing, the critical point must be a minimum. If the minimum value of γ is negative, we are guaranteed that γ is negative between M_1 and M_2.

To find the minimum value of γ, we first take the derivative of γ and set it equal to zero in order to find the critical point, $\overline{M}$, as follows:

$$\frac{d\gamma}{dM} = 2bM - (1+ab)L - 2(b-1) \overset{\text{set}}{=} 0$$

$$\Longleftrightarrow \quad \overline{M} = \frac{1}{2b}\left[(1+ab)L + 2(b-1)\right].$$

Finally, to find the minimum of γ we evaluate γ at $\overline{M}$:

$$\gamma(\overline{M}) = \frac{-1}{4b}\left[(1-ab)^2L^2 + 4(b+1)(ab-1)L + 4\left(b^2(1-4a)+2b+1\right)\right].$$

Letting

$$\tau(L) = (1-ab)^2L^2 + 4(b+1)(ab-1)L + 4\left(b^2(1-4a)+2b+1\right)$$

we see that the above equation becomes $\gamma(\overline{M}) = \dfrac{-1}{4b}\tau(L)$. Note that τ is a quadratic in L.

Recall that within this case if $\gamma(\overline{M})$ is negative, which occurs when $\tau(L)$ is positive, there will be a region of M for which γ is negative. If $\gamma(M)$ is negative, $-1 < \lambda^-$, and there is a possibility for the stability of EP_4, as seen in Figure 4.5.

In order to show where $\gamma(\overline{M})$ is negative, we first notice that since $b > 0$, the first factor of $\gamma(\overline{M})$ is negative. It is then sufficient to show that where τ is positive, $\gamma(\overline{M})$ is

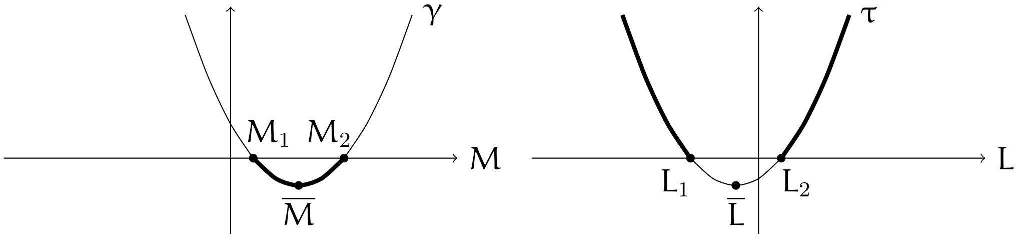


Figure 4.5: The regions where γ is negative for M and τ is positive for L

negative so that stability is possible.

The function τ is an upward-facing parabola since $(1-ab)^2$, the coefficient of L^2, is clearly positive. This is illustrated in Figure A.1. Since τ is upward-facing, we are guaranteed that $\tau > 0$ for some region or regions of L.

In order to find where these regions of L may occur, we use the quadratic formula and get that the roots of L are as follows:

$$L_1 = \frac{1}{(1-ab)}\left[2(b-1) - 4b\sqrt{a}\right], \qquad L_2 = \frac{1}{(1-ab)}\left[2(b-1) + 4b\sqrt{a}\right].$$

Clearly L_1 is less than L_2. We make a note about the behavior of τ by determining where its minimum occurs. In order to find the critical point, $\overline{L}$, we take the derivative and set it equal to zero:

$$\frac{d\tau}{dL} = 2(1-ab)^2 L + 4(b+1)(ab-1) \overset{\text{set}}{=} 0$$

$$\implies \overline{L} = \frac{2(b+1)}{1-ab} \quad .$$

Since we have $1-ab > 0$ (Case i), then $\overline{L} > 0$ always, so $\tau(L)$ is positive for all values of L, and thus $\gamma(\overline{M}) < 0$. This guarantees there will be a region for which stability is possible.

In summary of $-1 < \lambda^-$:

1. if $b > 1$ and $M > \dfrac{-L(a-1) - 4(1-ab)}{b-1}$ and $M_1 < M < M_2$, or

2. if $b < 1$ and $M < \dfrac{-L(a-1) - 4(1-ab)}{b-1}$ and $M_1 < M < M_2$,

then the conditions for $-1 < \lambda^-$ are met.

Right-hand Side ($\lambda^- < 1$)

In this case we investigate the following inequality.

$$L(a-1) + M(b-1) - \sqrt{D} < 0$$

$$\implies L(a-1) + M(b-1) < \sqrt{D}. \tag{4.10}$$

It is not guaranteed that both sides of inequality (4.10) are nonnegative, so we must consider two cases.

1. If $L(a-1) + M(b-1) < 0$, then (4.10) is clearly true. That is,
   (a) if $b > 1$, then $M < \dfrac{-L(a-1)}{b-1}$; otherwise
   (b) if $b < 1$, then $M > \dfrac{-L(a-1)}{b-1}$.
2. If instead $L(a-1) + M(b-1) \geqslant 0$, we note the following conditions must hold
   (a) if $b > 1$, then $M \geqslant \dfrac{-L(a-1)}{b-1}$, or
   (b) if $b < 1$, then $M \leqslant \dfrac{-L(a-1)}{b-1}$.

   Now we can safely square both sides of (4.10) and substitute in the value for D.

   $$bM^2(ab-1) + LM(1-ab)(1+ab) + aL^2(ab-1) < 0.$$

   Dividing both sides of this inequality by $(ab-1)$ will change the sign of the inequality since $1 - ab > 0$.

   $$bM^2 - (1+ab)LM + aL^2 > 0,$$

which implies

$$(bM - L)(M - aL) > 0. \tag{4.11}$$

Note that since $1 - ab > 0$ (Case i), then $a < \frac{1}{b}$, and hence $aL < \frac{L}{b}$. Using this, we can see that (4.11) is true in two cases: either both factors are greater than 0 or both factors are less than 0. That is

(a) $M > \frac{L}{b}$ and $M > aL$, which implies that $M > \frac{L}{b}$, or

(b) $M < \frac{L}{b}$ and $M < aL$, which implies that $M < aL$.

In summary of $\lambda^{-} < 1$:

1. if $b > 1$ and if $M < \dfrac{-L(a-1)}{b-1}$, or
2. if $b < 1$ and if $M > \dfrac{-L(a-1)}{b-1}$, or
3. if $b > 1$, $M \geqslant \dfrac{-L(a-1)}{b-1}$, and either $M < aL$ or $M > \frac{L}{b}$, or
4. if $b < 1$, $M \leqslant \dfrac{-L(a-1)}{b-1}$, and either $M < aL$ or $M > \frac{L}{b}$,

then the conditions for $\lambda^{-} < 1$ are met.

Left-hand Side ($-1 < \lambda^{+}$)

In this case we investigate the following inequality.

$$-4(1 - ab) < L(a-1) + M(b-1) + \sqrt{D}$$

$$\implies -4(1 - ab) - L(a-1) - M(b-1) < \sqrt{D}. \tag{4.12}$$

It is not guaranteed that both sides of inequality (4.12) are nonnegative, so we must consider two cases.

1. If $-4(1-ab) - L(a-1) - M(b-1) < 0$, then (4.12) is clearly true. That is,
   (a) if $b > 1$, then $M > \dfrac{-L(a-1) - 4(1-ab)}{b-1}$; otherwise

   (b) if $b < 1$, then $M < \dfrac{-L(a-1)-4(1-ab)}{b-1}$.

2. If instead $-4(1-ab)-L(a-1)-M(b-1) \geqslant 0$, we note the following conditions must hold

   (a) $b > 1$, then $M \leqslant \dfrac{-L(a-1)-4(1-ab)}{b-1}$, or

   (b) $b < 1$, then $M \geqslant \dfrac{-L(a-1)-4(1-ab)}{b-1}$.

Now we can safely square both sides of (4.12) and substitute in the value for D.

$$\begin{aligned} &bM^2(ab-1)+aL^2(ab-1)+(1-ab)(1+ab)LM \\ &+2L(a-1)(1-ab)+2M(b-1)(1-ab)+4(1-ab)^2 < 0. \end{aligned}$$

Dividing both sides of this inequality by $(ab-1)$ will change the sign of the inequality since $1-ab > 0$.

$$bM^2+aL^2-(1+ab)LM-2(a-1)L-2(b-1)M-4(1-ab) > 0. \tag{4.13}$$

Using our previous definition of $\gamma(M)$, we see that (4.13) is equivalent to the condition that $\gamma(M) > 0$. Recall that γ defines an upward-facing parabola, so we are guaranteed that $\gamma(M) > 0$ for some values of M. Let $\overline{M}$ denote the point at which γ takes a minimum as seen before. Then we know the following is true regarding γ.

(a) if $\gamma(\overline{M}) > 0$, then $\gamma(M) > 0$ for all M.

(b) If $\gamma(\overline{M}) = 0$, then $\gamma(M) > 0$ for all $M \neq \overline{M}$.

(c) If $\gamma(\overline{M}) < 0$, then γ has roots M_1 and M_2, where $M_1 < M_2$. In this case, $\gamma(M) > 0$ for values of M satisfying $M < M_1$ or $M > M_2$, where the first of these conditions can be discarded if $M_1 < 0$.

This is illustrated in Figure 4.6.

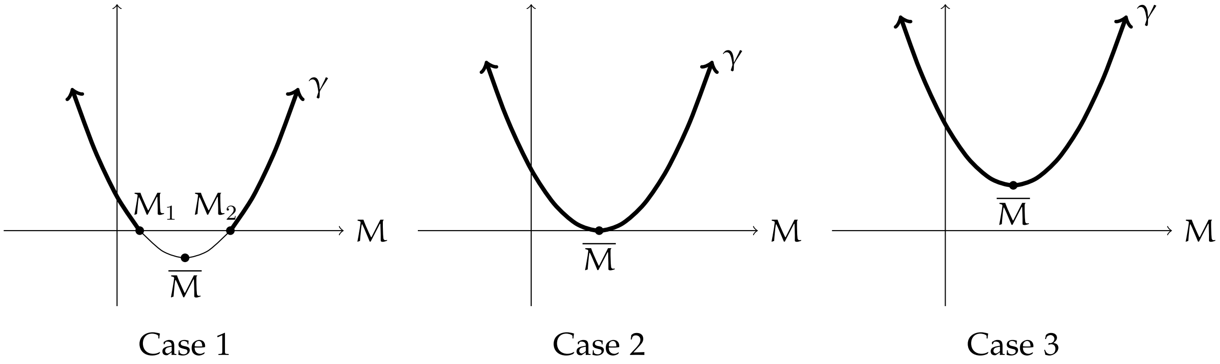


Figure 4.6: Cases for $\gamma(M) > 0$

In summary of $-1 < \lambda^+$:

1. if $b > 1$ and if $M > \dfrac{-L(a-1) - 4(1-ab)}{b-1}$, or
2. if $b < 1$ and if $M < \dfrac{-L(a-1) - 4(1-ab)}{b-1}$, or
3. if one of conditions (a) or (b) hold, and if one of conditions (i), (ii), or (iii) hold
   (a) $b > 1$ and if $M \leqslant \dfrac{-L(a-1) - 4(1-ab)}{b-1}$
   (b) $b < 1$ and if $M \geqslant \dfrac{-L(a-1) - 4(1-ab)}{b-1}$
   (i) if $\gamma(\overline{M}) > 0$, then $\gamma(M) > 0$ for all M
   (ii) if $\gamma(\overline{M}) = 0$, then $\gamma(M) > 0$ for all $M \neq \overline{M}$
   (iii) if $\gamma(\overline{M}) < 0$, then $M < M_1$ or $M > M_2$, where the first of these conditions can be discarded if $M_1 < 0$.

then the conditions for $-1 < \lambda^+$ are met.

Right-hand Side ($\lambda^+ < 1$)

In this case we investigate the following inequality.

$$L(a-1) + M(b-1) + \sqrt{D} < 0$$

$$\Longrightarrow \sqrt{D} < -L(a-1) - M(b-1).$$

If $-L(a-1) - M(b-1) \leqslant 0$, then the above inequality is never satisfied. If instead $-L(a-1) - M(b-1) > 0$, that is, when

1. if $b > 1$ and $M < \dfrac{-L(a-1)}{b-1}$, or
2. if $b < 1$ and $M > \dfrac{-L(a-1)}{b-1}$

then both sides are nonnegative and we can safely square both sides to obtain

$$D < (-1)^2[L(a-1) - M(b-1)]^2. \tag{4.14}$$

Substituting in the value of D and expanding (4.14) we obtain

$$0 < bM^2(ab-1) + LM(1-a^2b^2) + aL^2(ab-1).$$

Dividing both sides of this inequality by $ab-1$ will change the sign of the inequality since $1 - ab > 0$.

$$bM^2 + aL^2 - (1+ab)LM < 0$$

$$\Longrightarrow (bM - L)(M - aL) < 0. \tag{4.15}$$

Note that since $1 - ab > 0$ (Case i), then $a < \dfrac{1}{b}$, and hence $aL < \dfrac{L}{b}$. We have two cases to consider for when (4.15) is true.

1. $M < \dfrac{L}{b}$ and $M > aL$, which implies that $aL < M < \dfrac{L}{b}$.
2. $M > \dfrac{L}{b}$ and $M < aL$. However, this can never occur since $aL < \dfrac{L}{b}$, so we discard this case.

In summary, we conclude that $\lambda^+ < 1$ if $aL < M < \dfrac{L}{b}$.

Summary of Conditions for Stability when $1 - ab > 0$ (Case i

A condition from each of the following four cases must be true for the stability of EP_4 to occur.

1. $-1 < \lambda^-$ if:
   (a) $b > 1$ and $M > \dfrac{-L(a-1) - 4(1-ab)}{b-1}$ and $M_1 < M < M_2$, or
   (b) $b < 1$ and $M < \dfrac{-L(a-1) - 4(1-ab)}{b-1}$ and $M_1 < M < M_2$.
2. $\lambda^- < 1$ if:
   (a) $b > 1$ and if $M < \dfrac{-L(a-1)}{b-1}$, or
   (b) $b < 1$ and if $M > \dfrac{-L(a-1)}{b-1}$, or
   (c) $b > 1$, $M \geqslant \dfrac{-L(a-1)}{b-1}$, and either $M < aL$ or $M > \frac{L}{b}$, or
   (d) $b < 1$, $M \leqslant \dfrac{-L(a-1)}{b-1}$, and either $M < aL$ or $M > \frac{L}{b}$.
3. $-1 < \lambda^+$ if:
   (a) $b > 1$ and if $M > \dfrac{-L(a-1) - 4(1-ab)}{b-1}$, or
   (b) $b < 1$ and if $M < \dfrac{-L(a-1) - 4(1-ab)}{b-1}$, or
   (c) one of conditions (a) or (b) hold, and if one of conditions (i), (ii), or (iii) hold
      (a) $b > 1$ and if $M \leqslant \dfrac{-L(a-1) - 4(1-ab)}{b-1}$
      (b) $b < 1$ and if $M \geqslant \dfrac{-L(a-1) - 4(1-ab)}{b-1}$
      (i) if $\gamma(\overline{M}) > 0$, then $\gamma(M) > 0$ for all M
      (ii) if $\gamma(\overline{M}) = 0$, then $\gamma(M) > 0$ for all $M \neq \overline{M}$
      (iii) if $\gamma(\overline{M}) < 0$, then $M < M_1$ or $M > M_2$, where the first of these conditions can be discarded if $M_1 < 0$.
4. $\lambda^+ < 1$ if:

(a) $b > 1$ and $M < \dfrac{-L(a-1)}{b-1}$ and $aL < M < \dfrac{L}{b}$, or

(b) $b < 1$ and $M > \dfrac{-L(a-1)}{b-1}$ and $aL < M < \dfrac{L}{b}$.

Stability Interpretation when $1 - ab > 0$ (Case i)

For the coexistence equilibrium point, $\left(\dfrac{M-aL}{1-ab}, \dfrac{L-bM}{1-ab}\right)$, to have biological relevance and be distinct from the other three equilibrium points, then $x > 0$ and $y > 0$ must be true. Since $1 - ab > 0$ (Case i), then to ensure that this condition is met, it must be that

1. $\dfrac{M-aL}{1-ab} > 0 \implies M - aL > 0 \implies M > aL$, and
2. $\dfrac{L-bM}{1-ab} > 0 \implies L - bM > 0 \implies M < \dfrac{L}{b}$.

The previous conditions together require that $aL < M < \frac{L}{b}$ since $1 - ab > 0$, which implies that $aL < \frac{L}{b}$.

This condition for biological relevance indicates that condition 2 parts (c) and (d) can be discarded. The remaining conditions indicate that stability for EP_4 is possible. We will discuss the effect harvesting has on the stability of EP_4 in the next chapter.

4.3.2 Real Eigenvalues Case (ii) $1 - ab < 0$

Throughout this section, we assume $1 - ab < 0$, which implies $ab > 1$. Multiplying (4.5) by $(1 - ab)$ on all sides changes the direction of the inequality signs. Thus (4.5) becomes

$$0 < L(a-1) + M(b-1) \pm \sqrt{D} < -4(1-ab). \tag{4.16}$$

Again, for the coexistence equilibrium point, $\left(\dfrac{M-aL}{1-ab}, \dfrac{L-bM}{1-ab}\right)$, to have biological relevance and be distinct from the other three equilibrium points, then $x > 0$ and $y > 0$. Since $1 - ab < 0$ (Case ii), then to ensure that this condition is met, it must be that

1. $\dfrac{M - aL}{1 - ab} > 0 \implies M - aL < 0 \implies M < aL$, and
2. $\dfrac{L - bM}{1 - ab} > 0 \implies L - bM < 0 \implies M > \dfrac{L}{b}$.

Since $1 - ab < 0$, then $\frac{L}{b} < aL$, and conditions 1 and 2 together require that $\frac{L}{b} < M < aL$. We keep this in mind as we look at λ^+ and λ^- separately.

Stability Conditions from λ^-

For the stability of EP_4 in this case, recall the necessary (but not sufficient) condition $|\lambda^-| < 1$, which implies

$$0 < L(a-1) + M(b-1) - \sqrt{D} < -4(1 - ab). \tag{4.17}$$

To find the stability conditions given by λ^-, we will separately look at the left-hand side of (A.2) which corresponds to $\lambda^- < 1$, and the right-hand side of (A.2) which corresponds to $-1 < \lambda^-$.

Left-hand Side ($\lambda^- < 1$):

Consider the left-hand side of (A.2). Because multiplying by $(1 - ab)$ changes the direction of the inequality,

$$\lambda^- < 1 \implies 0 < L(a-1) + M(b-1) - \sqrt{D}$$

$$\sqrt{D} < L(a-1) + M(b-1). \tag{4.18}$$

Note that since $D \geqslant 0$ (Case II), then $\sqrt{D} \geqslant 0$. Thus we are guaranteed that the right-hand side of the inequality is also nonnegative.

We can then square both sides of (A.3) to get:

$$\left(\sqrt{D}\right)^2 < (L(a-1) + M(b-1))^2$$

$$\implies D < M^2(b-1)^2 + 2LM(a-1)(b-1) + L^2(a-1)^2. \tag{4.19}$$

Plugging in the value of D gives

$$M^2(b^2 - 4ab^2 + 2b + 1) + 2LM(2a^2b^2 + ab - a - b - 1) + L^2(a^2 - 4a^2b + 2a + 1)$$

$$< M^2(b^2 - 2b + 1) + 2LM(ab - a - b + 1) + L^2(a^2 - 2a + 1).$$

Upon simplification and collecting like terms, we obtain

$$0 < bM^2(ab - 1) + LM(1 - a^2b^2) + aL^2(ab - 1) \tag{4.20}$$

and since $1 - ab < 0$, then $ab - 1 > 0$. Dividing (A.5) by $(ab - 1)$ we get

$$0 < bM^2 - (1 + ab)LM + aL^2 \tag{4.21}$$

which is a quadratic in M.

Let $\phi = bM^2 - (1 + ab)LM + aL^2$. We set $\phi = 0$ and use the quadratic formula to find the factored form of the equation $(bM - L)(M - aL) = 0$.

Then (A.6) becomes $(bM - L)(M - aL) > 0$. Thus (A.6) is true in two cases: either both factors are greater than 0 or both factors are less than 0. That is

1. $M > \frac{L}{b}$ and $M > aL$, or
2. $M < \frac{L}{b}$ and $M < aL$.

Since $ab > 1$, we know $a > \frac{1}{b}$. Then multiplying by L on both sides gives us $aL > \frac{L}{b}$. Then case 1 implies that $M > aL$, and case 2 implies $M < \frac{L}{b}$.

In summary, $\lambda^- < 1$ if $M < \frac{L}{b}$ or if $M > aL$. However, this violates the condition for the biological relevance of the coexistence equilibrium point. To see additional work, consult Appendix A.

Thus the condition for biological relevance can never be simultaneously true with the conditions for stability when $1 - ab < 0$. We conclude that in Case (ii), regardless of how much species x is being harvested, EP_4 must be unstable.

4.3.3 Implications of an Unstable Coexistence Equilibrium Point

To conclude this chapter, we will briefly consider what can happen to the stability of the exclusion equilibrium points in the case that the coexistence equilibrium point is unstable. Conducting a full analysis of this question is beyond the scope of this thesis, but by examining some examples we can gain some insight about possible outcomes.

When the coexistence equilibrium point, EP_4, is unstable, we observe multiple possible behaviors of the system. Without harvesting, it is possible to have no stable equilibrium points. For example, taking our system with parameter values $a = 2, b = 2, L = 1.4, K = 3$, and $u = 1$, then $1 - ab < 0$, so we know EP_4 is unstable. Using the conditions for stability for the exclusion equilibrium points, we observe that neither $\frac{M}{a} < L < 2$ nor $\frac{L}{b} < M < 2$ is satisfied. Then neither of these equilibrium points is stable, and in every case the extinction equilibrium point is unstable.

If we add harvesting in this example, it is possible for both exclusion equilibrium points to be stable. Taking the parameter values from above while changing the value of the harvesting parameter, u, to be 0.333, we observe that the conditions for stability for both EP_2 and EP_3 are satisfied. The long-term population values for species x and y will depend on the initial population values, i.e. the initial conditions of the system.

It is also possible for one of the exclusion equilibrium points to be stable while the other is not. Continuing our example, consider when $u = 0.08$. In this case, we see that the conditions for stability are satisfied for EP_2 but not for EP_3. That is, if we harvest 92% of species x, the population values will tend towards the extinction of species x and the persistence of species y regardless of the initial values of each population.

Chapter 5

Bifurcation Analysis

Bifurcation diagrams show the relationship between a bifurcation parameter and the long term behavior of a system. When the dynamics of a system drastically change based on the value of some parameter, a bifurcation diagram allows us to visualize where and how this happens. A bifurcation diagram illustrates the asymptotic behavior of a system by graphing a portion of the iterates of a solution at each value of the bifurcation parameter. Any vertical slice of a bifurcation diagram indicates the period number at that bifurcation value, and dense black strips indicate chaos.

To create our bifurcation diagrams, we first specify the parameter values for each diagram. We then use the program MATLAB to calculate the first 500 iterates of a solution, using an initial condition slightly perturbed from EP_4, and then plot the last 200 iterates from these calculations. This gives us the endpoint behavior. Thus, where a single value appears in a vertical strip of the diagram, the species has the same population value for 300 iterates, and this indicates an equilibrium point. Where two points appear in a vertical strip, the species oscillates between two population values. This indicates a two period solution. We can alter the number of iterates calculated and plotted with no change in the diagram.

Below we explore a specific case using the bifurcation parameter ν which is equivalent to $1-u$. We have already noted that different levels of harvesting can impact the stability of the other equilibrium points in the system, and a bifurcation diagram can give us additional insight into this effect on the stability of EP_4. We plot v, a term indicating the proportion of population x that is harvested, instead of u, the proportion of the population that is retained after harvesting, for ease of interpretation. Note that $0 \leqslant v < 1$. The value $v = 0$ implies $u = 1$, which indicates no harvesting of species x, while v close to 1 indicates that almost the entire population of species x has been harvested. Recall that for biological relevance, $M \geqslant 0$, i.e. $u \geqslant e^{-K}$ which implies $v \leqslant 1 - e^{-K}$. Thus we see the values of v in the diagram do not extend all the way to 1. The values of $v > 1$ have no biological meaning.

We will look at an example of a bifurcation diagram for species x and y when $a < 1$ and $b < 1$. This is an example of when $1 - ab > 0$ (Case i) and can be seen in Figure 5.1. It is clear by inspection that chaos, in the sense of Li and Yorke, exists. The non-pattern, or chaotic, behavior occurs when approximately $0 < v < 0.12$. Note that chaos disappears as v increases towards 1; that is, as harvesting of species x increases, period halving occurs and the system stabilizes. With the parameter values in this example, an eight period exists from approximately $0.13 < v < 0.16$, a four period exists from approximately $0.16 < v < 0.27$, a two period exists from approximately $0.27 < v < 0.6$, and an equilibrium exists starting at $v = 0.6$ for both species. Starting at approximately $v = 0.84$, species x goes extinct while species y reaches its carrying capacity.

In the example given in Figure 5.1, chaos exists if harvesting is below 12% of species x, while harvesting 70% of species x results in the persistence of both species. However, with 85% harvesting, species x goes extinct while species y persists and eventually reaches and maintains a population size determined by its carrying capacity.

These same system dynamics can be seen in Figure 5.2, which is created using the same parameter values for a, b, K, and L as is used in the example given in Figure 5.1. Using Matlab we observe the behavior of the first 300 iterations of both species populations given a value of u, the proportion of species x that remains after harvesting. In the top left diagram when $u = 0.9$, that is, only 10% of the species x population is harvested, chaos occurs. In the top right diagram when $u = 0.8$, i.e. 20% harvesting occurs, both species x and species y display a four period. The middle left diagram shows that both species display a two period when $u = 0.6$, that is, 40% of the species x population is harvested. In the middle right diagram when $u = 0.3$, i.e. 70% harvesting, both species persist at steady population values. This indicates that species x and species y are at an equilibrium and will coexist in the environment. Finally, in the bottom diagram we observe the effect of heavy harvesting when $u = 0.15$, that is, 85% harvesting of the species x population. In this scenario, species x goes extinct, while species y persists at its carrying capacity.

Clearly, harvesting can change the dynamics of the system. Both species are affected by changing the proportion of species x harvested, since the population of species y depends on the population of species x. With small amounts of harvesting, we observe chaos. As harvesting increases, we observe four periods, two periods, stability, and extinction.

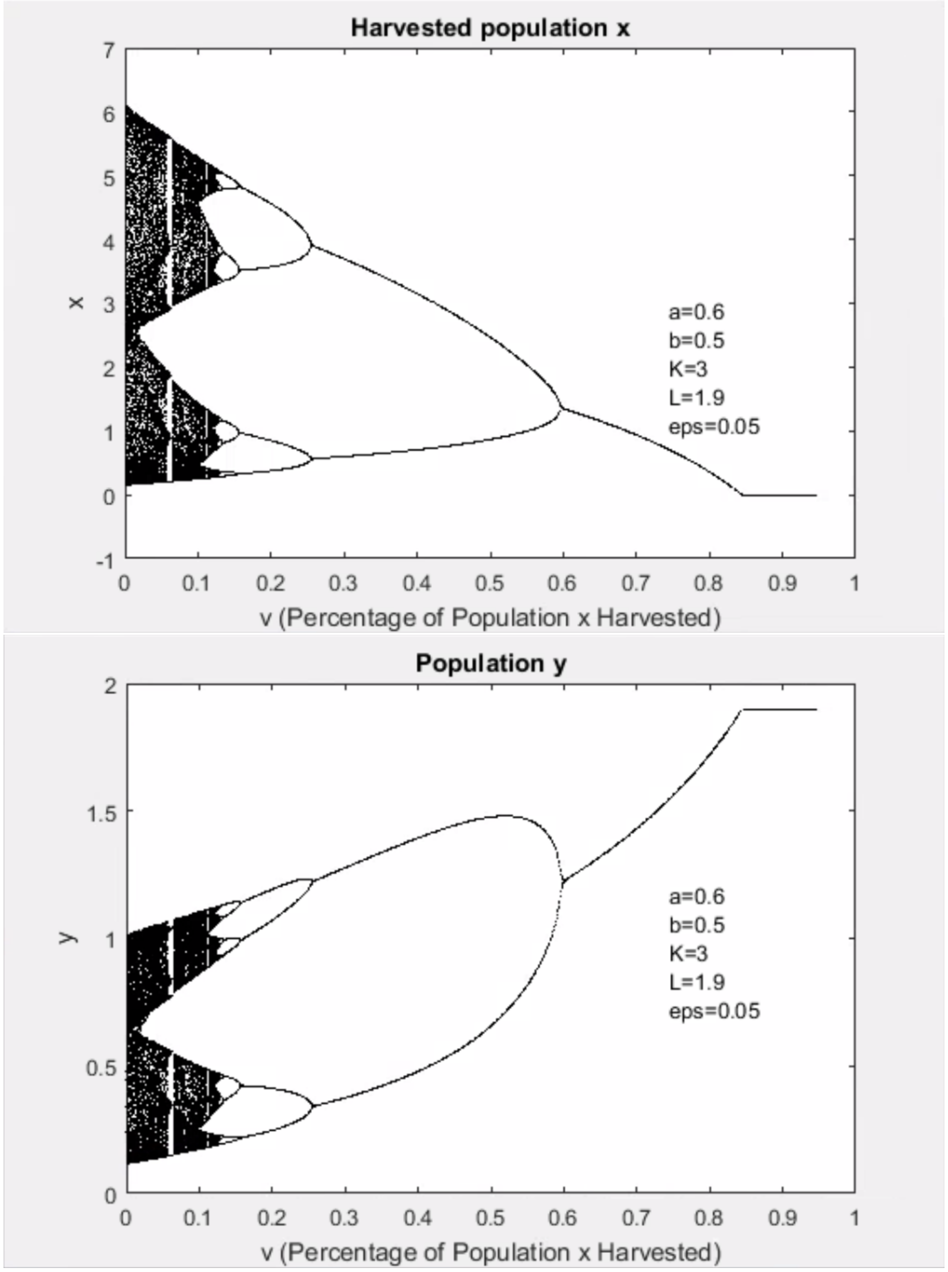


Figure 5.1: An example of bifurcation of harvesting with species x and y when $ab < 1$

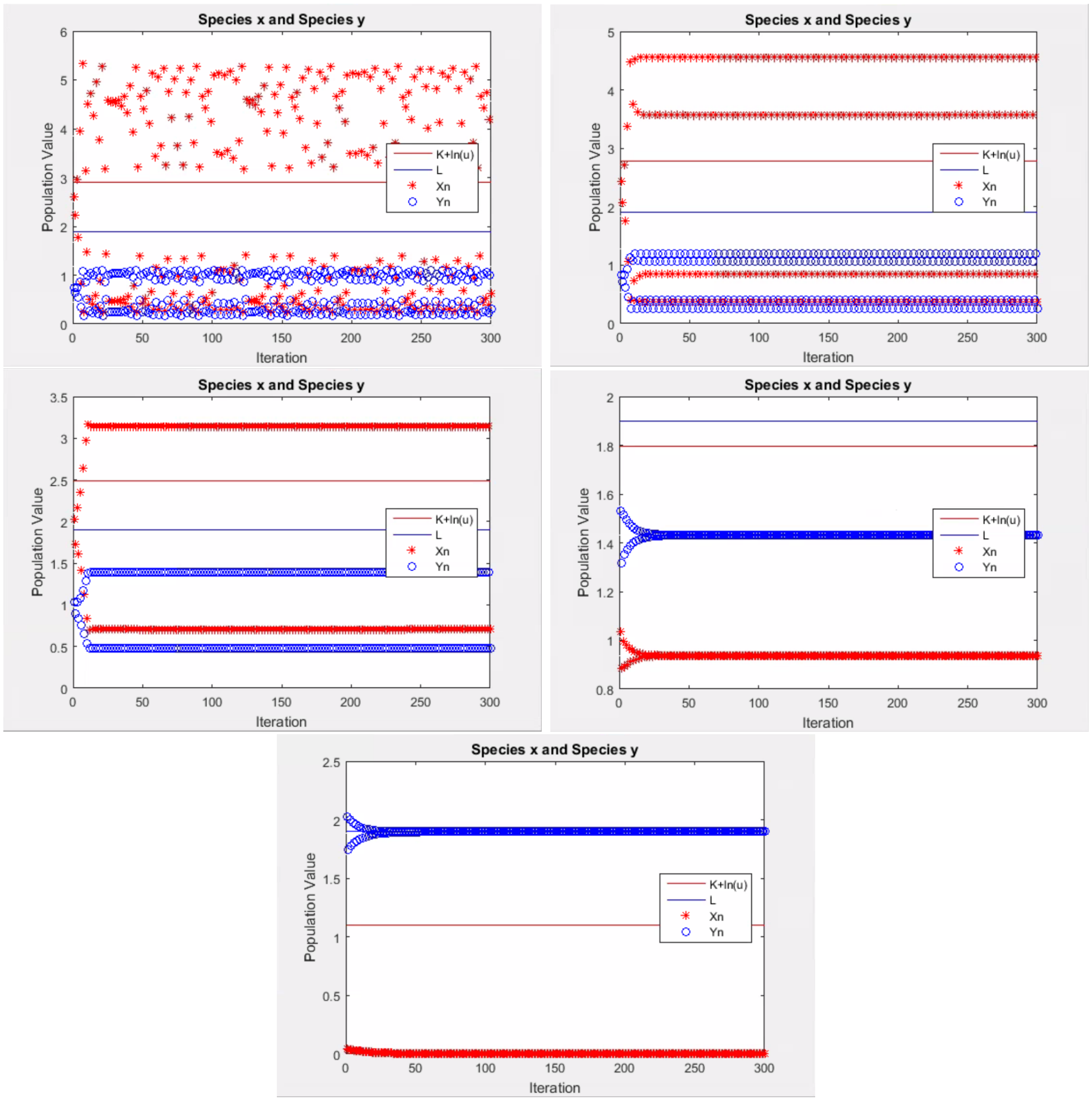


Figure 5.2: For $a = 0.6, b = 0.5, K = 3, L = 1.9$ and $u = 0.9$ (top left), $u = 0.8$ (top right), $u = 0.6$ (middle left), $u = 0.3$ (middle right), or $u = 0.15$ (bottom).

Chapter 6

Biological Interpretation and Summary

Our analysis of the system from Equations (1.1) and (1.2) has included multiple techniques. We have found the existence and value of the uniform bound of our system. The existence of the bound indicates neither species x nor species y can grow without restraint due to the limitations of resources in the system. We have also derived the isoclines and the equilibrium points of our system. We then have proceeded to analyze the stability of the equilibrium points and have performed a bifurcation analysis of the coexistence equilibrium point in our system in order to glean additional insights into the effects of harvesting of the population of species x.

It is clear from our work that the extinction equilibrium point $(0, 0)$ is unstable. This indicates that for even small values of the populations of species x and species y, at least one of the species will increase in population size instead of becoming extinct.

The exclusion equilibrium point $(0, L)$ is locally asymptotically stable under the condition $\frac{K + \ln(u)}{a} < L < 2$ (i.e. $\frac{M}{a} < L < 2$). This condition is more easily met as harvesting is increased. That is, species x will become extinct with sufficient harvesting.

Likewise, we have determined that if M is bounded such that $\frac{L}{b} < M < 2$, then the exclusion equilibrium point $(M, 0)$ is locally asymptotically stable. Recall that as harvesting is increased the condition $L < bM$, for any given L, is harder to satisfy, while

$M < 2$ is more easy to satisfy. That is, when $M < 2$, additional harvesting makes it more difficult for species x to persist and species y to become extinct.

If harvesting increases, i.e. as M decreases, then if the intercepts of the isoclines switch positions; that is, if $M > \frac{L}{b}$ becomes $M < \frac{L}{b}$ and if $L < \frac{M}{a}$ becomes $L < \frac{M}{a}$, then the isoclines s_1 and s_2 also switch positions. Then the system can change from a scenario where $(M, 0)$ is LAS and y goes extinct to a system where $(0, L)$ is LAS and species x goes extinct. We conclude that with sufficient harvesting, an otherwise stable x population will go extinct.

When s_1 and s_2 intersect in Quadrant 1, then we obtain the fourth equilibrium point EP_4. This coexistence equilibrium point occurs in two cases. In the case that $1 - ab > 0$, EP_4 may be stable if the necessary conditions are met. Then it is possible for species x and species y to coexist in a stable manner. In the case that $1 - ab < 0$, EP_4 is unstable regardless of harvesting. In the event that EP_4 is unstable, any, none, or all of the exclusion equilibrium points may become stable. More analysis of this situation is discussed in further detail by Luis et al. [13].

When we analyze the bifurcation diagram, we see the asymptotic, or eventual, behavior of a solution. We see from the bifurcation diagram example that with sufficient harvesting, period doubling and chaotic behavior can occur.

We observe changes in stability as we vary the proportion of species x that is harvested. We can conclude that the coexistence of species x and species y can occur for specific harvesting conditions. As harvesting is decreased, we also see that period doubling can replace a single equilibrium point in the system for species x. That is, instead of the population remaining at a particular size, with sufficient harvesting species x may oscillate between two population sizes.

Thus, we have found that harvesting has the possibility to significantly alter the dynamics of the system. Sufficient harvesting can result in the extinction of the harvested species. In addition, harvesting has the ability to change stability, eliminate chaos, produce period halving, and cause extinction.

Bibliography

[1] R. Abu-Saris, Z. AlSharawi, M. Rhouma, *The dynamics of some discrete models with delay under the effect of constant yield harvesting*, Chaos, Solitons & Fractals 54 (2013), pp. 26–38.

[2] L. C. Becker, *Ordinary Differential Equations: Concepts, Methods, and Models*. 2012-2013 ed. Memphis: n.p., n.d. Print.

[3]] R. Beverton and S. Holt, On the dynamics of exploited fish populations, Fishery Investigations Series II, Volume XIX (1957). Ministry of Agriculture, Fisheries and Food.

[4] A. Brannstrom and D. Sumpter, The role of competition and clustering in population dynamics, Proc. R. Soc. B 272 (2005), pp. 2065–2072.

[5] S. Elaydi, *An Introduction to Difference Equations*. 3rd ed. New York: Springer, 2005. Print.

[6] W. M. Getz, *Harvesting discrete nonlinear age and stage structured populations*, J. Optim. Theory Appl. 57 (1988), no. 1, pp. 69–83.

[7] A. Hone, M. Irle, and G. Thurura, *On the Neimark–Sacker bifurcation in a discrete predator-prey system*, J. Biol. Dyn. 4(6) (2010), pp. 594–606.

[8] L. Idels and M. Wang. *Harvesting fisheries management strategies with modified effort function*, International Journal of Modelling, Identification and Control 3.1 (2008), pp. 83-87.

[9] P. Leslie and J. Gower, *The properties of a stochastic model for two competing species*, Biometrica 45 (1958), pp. 316–330.

[10] T. Li and J. Yorke, *Period three implies chaos*, Amer. Math. Monthly 82 (1975), no. 10, 985–992.

[11] P. Lindstrom, *Discrete Models and Fisher's Maximum Principle in Ecology*, Proceedings of the Fourth International Conference on Dynamical Systems and Difference Equations, 2002, pp. 571–579.

[12] A. Lotka, *Elements of Physical Biology*, Williams & Wiliams, Baltimore, MD, 1925.

[13] Rafael Luis, Saber Elaydi, and Henrique Oliveira, *Stability of a Ricker-type competition model and the competitive exclusion principle*, *Journal of Biological Dynamics*, **5** (2011) 636–660.

[14] A. Martin, S. Ruan, *Predator-prey models with delay and prey harvesting*, J. Math. Biol. 43 (2001), no. 3, pp. 247–267.

[15] E. Ricker, *Handbook of Computation for Biological Statistics of Fish Populations*, Bulletin 119 of the Fisheries Resource Board Canada, Ottawa, 1958.

[16] H. Sedaghat, *Folding, Cycles and Chaos in Discrete Planar Systems*, preprint, available at: https://arxiv.org/abs/1406.6721

[17] S. Sharma and G. P. Samanta, *Optimal harvesting of a two species competition model with imprecise biological parameters*, Nonlinear Dynam. 77 (2014), no. 4, pp. 1101–1119.

[18] X. Shen, L. Ou, X. Chen, X. Zhang, and X. Tan, *The application of the grey disaster model to forecast epidemic peaks of typhoid and paratyphoid fever in China*, PloS one 8.4 (2013): e60601.

[19] V. Volterra, *Variations and fluctuations of the number of individuals in animal species living together in animal ecology*, in Animal Ecology, R.N. Chapman, ed., McGraw-Hill, New York, 1931, pp. 409–448.

[20] C. Wentworth, M. Fujiwara, and J. Walton, *Optimum Harvesting Models for Fishery Populations*, 2011.

[21] T. Wu, *Harvesting analysis of a discrete competitive system*, Advances in Difference Equations 2014.1 (2014), pp. 1.

[22] Z. Yao, *Existence and exponential convergence of almost periodic positive solution for Nicholson's blowflies discrete model with linear harvesting term*, Mathematical Methods in the Applied Sciences 37.16 (2014), pp. 2354-2362.

Appendix A

Recall that this work refers to Case (ii) of Case II.

Throughout this section, we assume $1 - ab < 0$, which implies $ab > 1$. Multiplying (4.5) by $(1 - ab)$ on all sides changes the direction of the inequality signs. Thus (4.5) becomes

$$0 < L(a - 1) + M(b - 1) \pm \sqrt{D} < -4(1 - ab). \tag{A.1}$$

We will look at λ^+ and λ^- separately.

Stability Conditions from λ^-

For the stability of EP_4 in this case, recall the necessary (but not sufficient) condition $|\lambda^-| < 1$, which implies

$$0 < L(a - 1) + M(b - 1) - \sqrt{D} < -4(1 - ab). \tag{A.2}$$

To find the stability conditions given by λ^-, we will separately look at the left-hand side of (A.2) which corresponds to $\lambda^- < 1$, and the right-hand side of (A.2) which corresponds to $-1 < \lambda^-$.

Left-hand Side ($\lambda^- < 1$):

Consider the left-hand side of (A.2). Because multiplying by $(1 - ab)$ changes the direction of the inequality,

$$\lambda^{-} < 1 \implies 0 < L(a-1) + M(b-1) - \sqrt{D}$$

$$\sqrt{D} < L(a-1) + M(b-1). \tag{A.3}$$

(A.3) is only true if $L(a-1) + M(b-1) > 0$. We then get two cases.

1. If $b > 1$, then we obtain the condition $M > \dfrac{-L(a-1)}{b-1}$.
2. If $b < 1$, then we obtain the condition $M < \dfrac{-L(a-1)}{b-1}$.

Suppose the conditions from one of these cases hold. We can then square both sides of (A.3) to get:

$$\left(\sqrt{D}\right)^2 < (L(a-1) + M(b-1))^2$$

$$\implies D < M^2(b-1)^2 + 2LM(a-1)(b-1) + L^2(a-1)^2. \tag{A.4}$$

Substituting in the value of D gives

$$M^2(b^2 - 4ab^2 + 2b + 1) + 2LM(2a^2b^2 + ab - a - b - 1) + L^2(a^2 - 4a^2b + 2a + 1)$$

$$< M^2(b^2 - 2b + 1) + 2LM(ab - a - b + 1) + L^2(a^2 - 2a + 1).$$

Upon simplification and collecting like terms, we obtain

$$0 < bM^2(ab-1) + LM(1 - a^2b^2) + aL^2(ab-1) \tag{A.5}$$

and since $1 - ab < 0$, then $ab - 1 > 0$. Dividing (A.5) by $(ab-1)$ we obtain

$$0 < bM^2 - (1+ab)LM + aL^2 \tag{A.6}$$

which is a quadratic in M.

Let $\phi = bM^2 - (1 + ab)LM + aL^2$. We set $\phi = 0$ and use the quadratic formula to find the factored form of the equation $(bM - L)(M - aL) = 0$.

Then (A.6) becomes $(bM - L)(M - aL) > 0$. Thus (A.6) is true in two cases: either both factors are greater than 0 or both factors are less than 0. That is

1. $M > \frac{L}{b}$ and $M > aL$, or
2. $M < \frac{L}{b}$ and $M < aL$.

Since $ab > 1$, we know $a > \frac{1}{b}$. Then multiplying by L on both sides gives us $aL > \frac{L}{b}$. Then case 1 implies that $M > aL$, and case 2 implies $M < \frac{L}{b}$.

In summary, $\lambda^- < 1$ if

1. $b > 1$, $M > \dfrac{-L(a-1)}{b-1}$ and either $M < \frac{L}{b}$ or $M > aL$, or
2. $b < 1$, $M < \dfrac{-L(a-1)}{b-1}$ and either $M < \frac{L}{b}$ or $M > aL$.

Right-hand Side ($-1 < \lambda^-$):

Since multiplying by $(1 - ab)$ changes the direction of the inequality,

$$-1 < \lambda^- \implies L(a-1) + M(b-1) - \sqrt{D} < -4(1 - ab).$$

This implies

$$L(a-1) + M(b-1) + 4(1-ab) < \sqrt{D}. \tag{A.7}$$

We have two possibilities.

1. If $L(a-1) + M(b-1) + 4(1-ab) < 0$, that is,
   (a) for $b > 1$ if $M < \frac{-L(a-1)-4(1-ab)}{b-1}$, or
   (b) for $b < 1$ if $M > \frac{-L(a-1)-4(1-ab)}{b-1}$.

   Then (A.7) is clearly true and the condition for $-1 < \lambda^-$ is met.

2. If instead $L(a-1)+M(b-1)+4(1-ab) \geqslant 0$, we note the following conditions must hold
   (a) for $b > 1$, $M \geqslant \frac{-L(a-1)-4(1-ab)}{b-1}$, or
   (b) for $b < 1$ if $M \leqslant \frac{-L(a-1)-4(1-ab)}{b-1}$.

   These conditions ensure that the left-hand side of (A.7) is nonnegative so that we may square both sides.

   Squaring both sides of (A.7) we get

$$(L(a-1)+M(b-1)+4(1-ab))^2 < \left(\sqrt{D}\right)^2, \tag{A.8}$$

and plugging in the value of D and collecting like terms gives

$$bM^2(ab-1)+aL^2(ab-1)+(1-a^2b^2)LM+2L(a-1)(1-ab)+2M(b-1)(1-ab)+4(1-ab)^2 < 0. \tag{A.9}$$

Since $1-ab<0$ (Case ii) dividing (A.9) by $(ab-1)$ gives

$$bM^2+aL^2-(1+ab)LM-2L(a-1)-2M(b-1)-4(1-ab) < 0, \tag{A.10}$$

which is a quadratic in M.

Recall $\gamma(M) = bM^2+aL^2-(1+ab)LM-2L(a-1)-2M(b-1)-4(1-ab)$. Then $-1 < \lambda^-$ when $\gamma(M) < 0$. We know that γ is an upward-facing parabola since b, which is the coefficient of M^2, is positive. Recall that the roots of γ are as follows:

$$\begin{aligned} M_1 = {} & \frac{1}{2b}\Big[2(b-1)+(1+ab)L \\ & -\sqrt{(1-2ab+a^2b^2)L^2+(4ab^2+4ab-4b-4)L+(4b^2+8b-16ab^2+4)}\Big] \\ M_2 = {} & \frac{1}{2b}\Big[2(b-1)+(1+ab)L \\ & +\sqrt{(1-2ab+a^2b^2)L^2+(4ab^2+4ab-4b-4)L+(4b^2+8b-16ab^2+4)}\Big]. \end{aligned}$$

As long as the discriminant of M_1 and M_2 is nonnegative (and thus M_1 and M_2 are real), it is possible for $\gamma(M) < 0$ for some M between M_1 and M_2. Since the quadratic is upward-facing, the critical point must be a minimum. If the minimum value of γ is negative, we are guaranteed that γ is negative between M_1 and M_2.

To find the minimum value of γ, we first take the derivative of γ and set it equal to zero in order to find the critical point, $\overline{M}$, as follows:

$$\frac{d\gamma}{dM} = 2bM - (1+ab)L - 2(b-1) \overset{\text{set}}{=} 0$$

$$\iff \overline{M} = \frac{1}{2b}\left[(1+ab)L + 2(b-1)\right].$$

Finally, to find the minimum of γ we evaluate γ at $\overline{M}$:

$$\gamma(\overline{M}) = \frac{-1}{4b}\left[(1-ab)^2L^2 + 4(b+1)(ab-1)L + 4\left(b^2(1-4a) + 2b + 1\right)\right].$$

Letting

$$\tau(L) = (1-ab)^2L^2 + 4(b+1)(ab-1)L + 4\left(b^2(1-4a) + 2b + 1\right)$$

the above equation becomes $\gamma(\overline{M}) = \frac{-1}{4b}\tau(L)$. Note that τ is a quadratic in L.

Recall that within this case if $\gamma(\overline{M})$ is negative, there will be a region of M for which γ is negative. If $\gamma(M)$ is negative, $-1 < \lambda^-$, and there is a possibility for the stability of EP_4, as seen in Figure A.1.

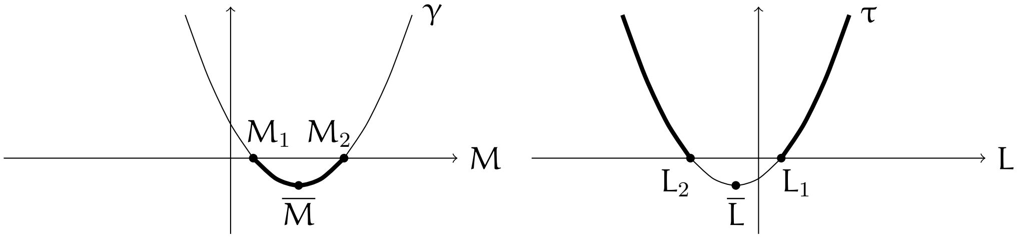


Figure A.1: The regions where γ is negative for M and τ is positive for L

In order to show where $\gamma(\overline{M})$ is negative, we first notice that since $b > 0$, the first factor of $\gamma(\overline{M})$ is negative. It is then sufficient to show that where τ is positive, $\gamma(\overline{M})$ is negative so that stability is possible.

Note that the coefficients of L^2 and L are positive. This is since we are assuming $1 - ab < 0$, i.e., $ab - 1 > 0$. Thus clearly $\tau > 0$ if $a < \frac{1}{4}$. We can also see the possibility that $\tau > 0$ for additional values of a, which we will now explore.

The function τ is an upward-facing parabola since $(1-ab)^2$, the coefficient of L^2, is clearly positive. This is illustrated in Figure A.1. Since τ is upward-facing, we are guaranteed that $\tau > 0$ for some region or regions of L.

In order to find where these regions of L may occur, we use the quadratic formula and get that the roots of L are as follows:

$$L_1 = \frac{1}{(1-ab)}\left[2(b-1) - 4b\sqrt{a}\right], \qquad L_2 = \frac{1}{(1-ab)}\left[2(b-1) + 4b\sqrt{a}\right].$$

In order to explore the roots of τ more fully, we let

$$L_{11} = 2(b-1) - 4b\sqrt{a} \quad \text{and} \quad L_{22} = 2(b-1) + 4b\sqrt{a}, \tag{A.11}$$

so L_1 and L_2 become :

$$L_1 = \frac{1}{(1-ab)}(L_{11}) \quad \text{and} \quad L_2 = \frac{1}{(1-ab)}(L_{22}). \tag{A.12}$$

Note that L_{11} is clearly less than L_{22}. Since the first factor of L_1 and L_2 is negative because $1 - ab < 0$ (Case ii), then L_2 is clearly less than L_1.

We make a note about the behavior of τ by determining where its minimum occurs.

In order to find the critical point, $\overline{L}$, we take the derivative and set it equal to zero:

$$\frac{d\tau}{dL} = 2(1-ab)^2L + 4(b+1)(ab-1) \overset{\text{set}}{=} 0$$

$$\implies \overline{L} = \frac{2(b+1)}{1-ab} \quad .$$

Clearly $\overline{L} < 0$ since the numerator is positive and $1 - ab < 0$ (Case ii). Mathematically, the minimum of τ occurs when $L < 0$, which indicates that at least one of the roots of τ must be negative and thus discarded when looking at the biological application of this system introduced by Equations (1.1) and (1.2).

The root L_2 must be less than $\overline{L}$ and thus is guaranteed to be negative. We then discard root L_2 since it does not have a biological application.

(a) If $L_1 > 0$, then $\tau(L) > 0$ for $L > L_1$.

(b) If $L_1 < 0$, then $\tau(L) > 0$ for all $L > 0$.

    Note that $L_1 < 0 \implies L_{11} > 0 \implies 2(b+1) - 4b\sqrt{a} > 0$. We can rewrite our new result as $a \leqslant \frac{1}{4} + b + \frac{1}{b^2}$. This is a more generalized statement of the earlier observation that $\tau > 0$ if $a < \frac{1}{4}$. Recall that L denotes the carrying capacity for our y population, so that $L > 0$ by assumption. Since $L_2 < 0$ and $L_1 < 0$, we are guaranteed that $L > L_1$ regardless of the parameter values for $a, b,$ and u.

When $\tau > 0$, then $\gamma(\overline{M}) < 0$, which means that there exists a range of values for M in which for $M_1 < M < M_2$, then $-1 < \lambda^-$.

In summary of $-1 < \lambda^-$:

1. If $b > 1$ and if $M < \frac{-L(a-1)-4(1-ab)}{b-1}$, or
2. If $b < 1$ and if $M > \frac{-L(a-1)-4(1-ab)}{b-1}$, or

3. If $b > 1$, $M \geqslant \frac{-L(a-1)-4(1-ab)}{b-1}$, $\gamma(\overline{M}) < 0$, and $M_1 < M < M_2$, or
4. If $b < 1$, $M \leqslant \frac{-L(a-1)-4(1-ab)}{b-1}$, $\gamma(\overline{M}) < 0$, and $M_1 < M < M_2$,

then the conditions for $-1 < \lambda^-$ are met.

Stability Conditions from λ^+

To find where EP_4 might be stable, we now look at the conditions given by λ^+. As before, we will look at the left-hand side and right-hand side of the inequality separately. For stability it is necessary

$$|\lambda^+| < 1 \implies -1 < \lambda^+ < 1 \implies 0 < L(a-1) + M(b-1) + \sqrt{D} < -4(1-ab).$$

Left-hand Side ($\lambda^+ < 1$):

Recall since $1 - ab < 0$, then $\lambda^+ < 1$ becomes

$$0 < L(a-1) + M(b-1) + \sqrt{D}. \tag{A.13}$$

This implies

$$-M(b-1) - L(a-1) < \sqrt{D}. \tag{A.14}$$

We then have the following cases.

1. If $-M(b-1) - L(a-1) < 0$, that is,
   (a) for $b > 1$ if $M > \frac{-L(a-1)}{b-1}$, or
   (b) for $b < 1$ if $M < \frac{-L(a-1)}{b-1}$.

   Then (A.14) is clearly true and the condition for $\lambda^+ < 1$ is met.

2. If instead $-M(b-1) - L(a-1) \geqslant 0$, we note the following conditions must hold

(a) for $b > 1$, $M \leqslant \frac{-L(a-1)}{b-1}$, or

(b) for $b < 1$, $M \geqslant \frac{-L(a-1)}{b-1}$.

These conditions guarantee that both sides of (A.14) are nonnegative, and we can safely square both sides:

$$M^2(b-1)^2 + 2LM(a-1)(b-1) + L^2(a-1)^2 < D.$$

Note that this is the reverse inequality of (A.4), so upon simplification we get

$$bM^2(ab-1) + LM(1-a^2b^2) + aL^2(ab-1) < 0. \tag{A.15}$$

Dividing by $(ab-1)$ which is positive since we are in Case (ii), this simplifies to

$$bM^2 - (1+ab)LM + aL^2 < 0 \tag{A.16}$$

which is a quadratic in M, and is the same inequality as in (A.6) but with the reverse direction.

Using our knowledge from the case of $\lambda^- < 1$, the left-hand side of (A.16) factors into $(bM - L)(M - aL)$. Thus (A.16) holds when one factor is negative and one factor is positive, that is

(a) $M > \frac{L}{b}$ and $M < aL$ or

(b) $M < \frac{L}{b}$ and $M > aL$.

Since we are in Case (ii) where $ab > 1$, we know $a > \frac{1}{b}$. Then multiplying by L on both sides gives us $aL > \frac{L}{b}$. Then case (a) implies that $\frac{L}{b} < M < aL$, and case (b) contains two conditions that can never be simultaneously true. Then (A.16) implies $\frac{L}{b} < M < aL$.

In summary of $\lambda^+ < 1$:

1. If $b > 1$ and if $M > \frac{-L(a-1)}{b-1}$, or
2. If $b < 1$ and if $M < \frac{-L(a-1)}{b-1}$, or
3. If $b > 1$, $M \leqslant \frac{-L(a-1)}{b-1}$, and $\frac{L}{b} < M < aL$, or
4. If $b < 1$, $M \geqslant \frac{-L(a-1)}{b-1}$, and $\frac{L}{b} < M < aL$,

then the conditions for $\lambda^+ < 1$ are met.

Right-hand Side ($-1 < \lambda^+$):

Recall since $1 - ab < 0$, then $-1 < \lambda^+$ becomes

$$L(a-1) + M(b-1) + \sqrt{D} < -4(1-ab). \tag{A.17}$$

To simplify this inequality, we would like to isolate the $\sqrt{D}$ term as such:

$$\sqrt{D} < -L(a-1) - M(b-1) - 4(1-ab) \tag{A.18}$$

and then square both sides. The above inequality is only true if $L(a-1) + M(b-1) + 4(1-ab) < 0$. We then get two cases.

1. If $b > 1$ then we obtain the condition $M < \frac{-L(a-1)-4(1-ab)}{b-1}$.
2. If $b < 1$ then we obtain the condition $M > \frac{-L(a-1)-4(1-ab)}{b-1}$.

If either of the above cases hold, then both sides of (A.18) will be nonnegative, and we can square both sides of (A.18) to reach:

$$\left(\sqrt{D}\right)^2 < (-1)^2 \left[L(a-1) + M(b-1) + 4(1-ab)\right]^2$$

which is the reverse inequality of (A.8) that we see in the $-1 < \lambda^-$ case.

As in the $-1 < \lambda^-$ case, simplifying and collecting like terms we obtain:

$$bM^2(ab-1)+aL^2(ab-1)+(1-a^2b^2)LM+2L(a-1)(1-ab)+2M(b-1)(1-ab)+4(1-ab)^2 > 0 \tag{A.19}$$

Since $1 - ab < 0$ (Case ii), then $ab - 1 > 0$. Dividing (A.19) by $(ab - 1)$ gives us

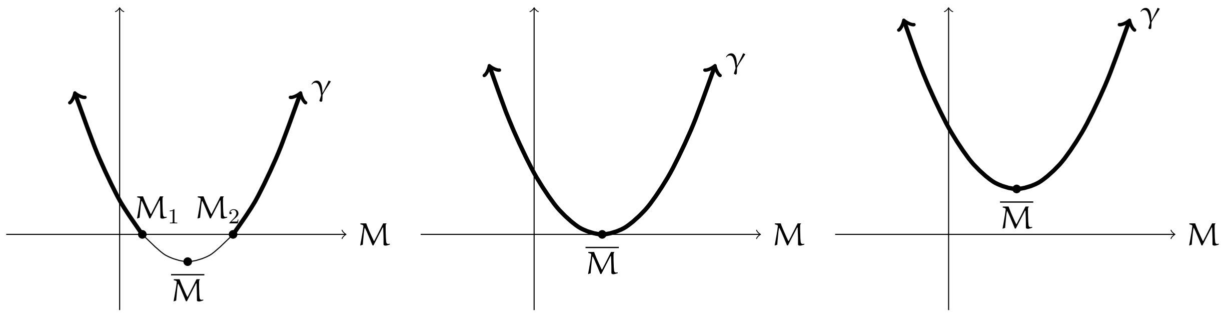
$$bM^2 + aL^2 - (1 + ab)LM - 2L(a - 1) - 2M(b - 1) - 4(1 - ab) > 0 \tag{A.20}$$

which is still a quadratic in M. This can also be written as $\gamma(M) > 0$, where γ is an upward-facing parabola.

Using our work from the $-1 < \lambda^-$ case, we know that the minimum of γ is found at $\overline{M}$, the roots of γ (when real) are M_1 and M_2, and the minimum of γ is $\gamma(\overline{M})$. From here we see that we have three possible cases illustrated in Figure A.2:

1. If $\gamma(\overline{M}) < 0$ then $\gamma(M) > 0$ if $M < M_1$ (for $M_1 > 0$ else discard) or $M > M_2$. We note that if both M_1 and M_2 are negative, $\gamma(M) > 0$ for all $M > 0$.
2. If $\gamma(\overline{M}) = 0$ then $\gamma(M) > 0$ for all $M \neq \overline{M}$.
3. If $\gamma(\overline{M}) > 0$ then $\gamma(M) > 0$ for all M.

Then $-1 < \lambda^+$ if one of the previous conditions holds.



Case 1 Case 2 Case 3

Figure A.2: Cases for $\gamma(M) > 0$

Summary of Conditions for Stability when $1 - ab < 0$ (Case ii)

A condition from each of the following four cases must be true for the stability of EP_4 to occur.

1. $\lambda^{-} < 1$ if :
   (a) $b > 1$, $M > \dfrac{-L(a-1)}{b-1}$ and either $M < \frac{L}{b}$ or $M > aL$, or
   (b) $b < 1$, $M < \dfrac{-L(a-1)}{b-1}$ and either $M < \frac{L}{b}$ or $M > aL$.
2. $-1 < \lambda^{-}$ if:
   (a) $b > 1$ and if $M < \frac{-L(a-1)-4(1-ab)}{b-1}$, or
   (b) $b < 1$ and if $M > \frac{-L(a-1)-4(1-ab)}{b-1}$, or
   (c) $b > 1$, $M \geqslant \frac{-L(a-1)-4(1-ab)}{b-1}$, $\gamma(\overline{M}) < 0$, and $M_1 < M < M_2$, or
   (d) $b < 1$, $M \leqslant \frac{-L(a-1)-4(1-ab)}{b-1}$, $\gamma(\overline{M}) < 0$, and $M_1 < M < M_2$.
3. $\lambda^{+} < 1$ if:
   (a) $b > 1$ and if $M > \frac{-L(a-1)}{b-1}$, or
   (b) $b < 1$ and if $M < \frac{-L(a-1)}{b-1}$, or
   (c) $b > 1$, $M \leqslant \frac{-L(a-1)}{b-1}$, and $\frac{L}{b} < M < aL$, or
   (d) $b < 1$, $M \geqslant \frac{-L(a-1)}{b-1}$, and $\frac{L}{b} < M < aL$.
4. $-1 < \lambda^{+}$ if:
   (a) either $b > 1$ and $M < \frac{-L(a-1)-4(1-ab)}{b-1}$, or $b < 1$ and $M > \frac{-L(a-1)-4(1-ab)}{b-1}$, and
   (b) one of the following holds:
      i. $\gamma(\overline{M}) < 0$ and if $M < M_1$ (for $M_1 > 0$ else discard) or $M > M_2$, or
      ii. $\gamma(\overline{M}) = 0$ and if $M \neq \overline{M}$, or
      iii. $\gamma(\overline{M}) > 0$.

Vita

Rebecca Clark was born in the beautiful state of Virginia, where she grew up learning how to describe the world with math. After graduating as valedictorian of her high school class, she became a proud Monarch at Old Dominion University where she earned the Top Math Graduate Award and her bachelor's degree in applied mathematics in 2007. She then started her own tutoring business, which she greatly enjoyed, in an attempt to spread a love of mathematics to anyone who would listen.