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DYNAMICAL SYSTEMS APPROACH TO A BIOECONOMIC DIFFERENTIAL ALGEBRAIC PREDATOR–PREY MODEL WITH HARVESTING

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BİR BİYOEKONOMİK DİFERANSİYEL CEBİRSEL HASATLI AV-AVCI MODELİNİN DİNAMİK SİSTEMLER YAKLAŞIMI İLE İNCELENMESİ

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ABSTRACT

DYNAMICAL SYSTEMS APPROACH TO A BIOECONOMIC DIFFERENTIAL ALGEBRAIC PREDATOR–PREY MODEL WITH HARVESTING

In this work, we offer a differential algebraic population model which describe the dynamics of predator and prey species with Holling Type II functional response and a harvesting of both the prey and the predator populations. Considering the economic factor, a bioeconomic differential algebraic equation is obtained.

$$\begin{cases} \frac{dx}{dt} = rx\left(1-\frac{x}{k}\right) - \frac{a_1xy}{n+x} - \frac{qEx}{m_1E+m_2x} \\ \frac{dy}{dt} = sy\left(-1+\frac{a_2x}{n+x}\right) \\ 0 = \frac{qE}{m_1E+m_2x}(px-c) - m \end{cases}$$

We show that the above system displays an interior equilibrium point. This equilibrium is stable when the economic profit is negative. However, as the economic profit is increased this equilibrium loses stability. This phenomenon is known as bifurcation. We investigate this bifurcation both from the view point of singularity induced bifurcation as well as Hopf bifurcation. We rigorously prove that a singularity induced bifurcation occurs when the net economic profit is zero. We also study the existence of Hopf bifurcation by means of normal form analysis. Finally we investigate the theoretical findings by means of numerical simulations. We find that our theoretical results match well with the numerical simulations.

ÖZET

BİR BİYOEKONOMİK DİFERANSİYEL CEBİRSEL HASATLI AV-AVCI MODELİNİN DİNAMİK SİSTEMLER YAKLAŞIMI İLE İNCELENMESİ

Bu çalışmada, fonksiyonel tepkinin Holling 2 türü olduğu, hem av hem de avcı hasadına dayanan, biyoekonomik diferensiyel-cebirsel bir av-avcı modeli sunulmuştur. Ekonomik faktörü de göz önünde bulundurarak biyoekonomik diferansiyel-cebirsel bir denklem sistemi elde edilmiştir.

$$\begin{cases} \frac{dx}{dt} = rx\left(1 - \frac{x}{k}\right) - \frac{a_1 xy}{n+x} - \frac{qEx}{m_1 E + m_2 x} \\ \frac{dy}{dt} = sy\left(-1 + \frac{a_2 x}{n+x}\right) \\ 0 = \frac{qE}{m_1 E + m_2 x}(px - c) - m \end{cases}$$

Yukarıda verilen sistemin bir iç denge noktasına sahip olduğu gösterilmiştir. Bu denge noktası, ekonomik kar küçükken kararlı olduğu bulunmuştur. Ancak, ekonomik kar arttırıldığında denge noktasının kararlılığını kaybettiği gözlenmiştir. Bu fenomene çatallanma denilir.

Biz bu tezde denge noktasının yerel çatallanmasını hem tekillik kaynaklı çatallanma hem de Hopf çatallanması paradigmalarıyla inceledik. Matematiksel bir kesinlikle, net ekonomik karın sıfır olduğu noktada tekillik kaynaklı bir çatallanma olduğunu gösterdik. Ayrıca denge noktasının bir Hopf çatallanması gösterdiğini normal form analizi sayesinde gösterdik. Son olarak da teorik sonuçlarımızın geçerliliğini nümerik simülasyonlar kullanarak inceledik. Nümerik simülasyonlarımızın teorik sonuçlarla uyumlu olduğunu gözlemledik.

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1 INTRODUCTION

The prey-predator models are building blocks of mathematical biology. These models describe the evolution of populations of several species which effect each other. Usually, these populations are also harvested by humans for their economic benefit. The harvesting impact on the prey-predator models has been extensively studied by mathematical biology researchers. In this thesis, our goal is to understand the interaction in a nonlinear prey-predator model with harvesting and economic profit. We consider a linear harvesting on both species. Moreover, the economic balance between cost, revenue and profit is taken into account. This results in a system of differential algebraic system consisting of two ordinary differential equations describing the time evolution of the populations and a single algebraic equation describing the economic balance. To the best of our knowledge, this model has not been considered elsewhere.

In this Introduction, we will summarize a brief review of the literature on the recent progress on the dynamical systems analysis of similar models.

There are previous results on population models displaying both linear and constant harvesting [1, 21]. Sometimes the harvesting is only taken into account when one of the populations is over an economic threshold as in [21]. Nonlinear prey harvesting with bifurcation analysis of a revised Leslie – Gower prey – predator system is considered by [10] . A two-dimensional framework of ordinary prey-predator differential equation together with nonlinear prey-harvesting is studied in [9]. The model is an amended version of the famous prey-predator model of Leslie – Gower type.

In [8], a predator-prey cycle of two species is examined with stage structure and harvesting. An interesting behavior of this system is that it displays Hopf bifurcations which is then analyzed using the theory of normal form and the theorem of center manifold.

Depending on the predator population, the dynamics of a ratio-dependent predator-prey system is studied in [16] with two different non-constant harvesting functions.

In [3], the authors consider an eco-epidemiological framework that depends on the ratio in which prey population is harvested. Mathematical results have been established such as positive invariance, limits, equilibrium stability, and system permanence.

A predator-prey system with a realistic response of Holling type II combining a constant prey refuge and prey harvesting at a constant rate are considered in [13]. Based on the constant prey refuge, which provides a prerequisite for protecting prey from predation and constant prey harvesting, some adequate conditions are obtained for the instability and global stability of the equilibrium, and the presence and uniqueness of the model's limit cycles.

The main feature in the paper [17] is to incorporate time delay into the age-structured predator – prey (natural enemy – pest) model, to show a new modeling approach that is used to investigate impulsive differential equations of delay, and to provide some reasonable suggestions for pest management.

In [15], they investigate the properties of a Michaelis-Menten predator-prey system which depends on the prey population with two non-constant harvesting functions. Equilibria and periodic orbits are measured and their properties of stability are analysed. As well as connecting orbits, many bifurcations are observed, with a focus on analyzing the equilibrium points at which the species coexist.

The goal of the paper [22] is to research the dynamic properties of the ratio-dependent predator-prey system with non-zero constant rate harvesting. A desired equilibrium population can achieve global stability by applying simple switching controls, chosen in accordance with the theory of variable structure framework. [5]

There are a lot of real life considerations where one or both of the biological stock within the predator–prey system are harvested and used for the purpose of economic profit. As the numerous studies have demonstrated, the effect of harvesting has to be taken into account in the analysis of the dynamics of the populations. In [6], the authors have applied the bioeconomic model with constant harvesting to fisheries. In [2], the authors have analyzed the global dynamics and bifurcation of a predator–prey system which exhibits a harvesting constant. The dynamical behavior of a bioeconomic predator–prey framework with relative gathering has been mentioned in [20]. In order to establish more realistic models, numerous researchers have studied the differential algebraic population systems that exhibit nonlinear harvesting terms, see for example [4, 12, 7, 11, 14, 19].

2 MATERIALS AND METHODS

Consider the equation

$$\dot{x} = f(x) \tag{2.1}$$

where $x : I \subset \mathbb{R} \rightarrow \mathbb{R}^n$ is the unknown function and $f : \mathbb{R}^n \rightarrow \mathbb{R}^n$ is the vector field.

We call $x = x^*$, a **fixed point** of (2.1) if $f(x^*) = 0$.

2.1 Stability Definitions

Let $x(t)$ be the solution of (2.1). We call a fixed point $x = x^*$ **Lyapunov stable** if for any $\epsilon > 0$ there exists $\delta > 0$ such that if

$$|x(0) - x^*| < \delta \implies |x(t) - x^*| < \epsilon \quad \forall t \geq 0.$$

We call a fixed point $x = x^*$ **locally asymptotically stable** if it is Lyapunov stable and there exists $\delta > 0$ such that

$$|x(0) - x^*| < \delta \implies \lim_{t \to \infty} |x(t) - x^*| = 0$$

A fixed point $x = x_0$ is called **globally asymptotically stable** if it is locally asymptotically stable and the definition holds for every $\delta > 0$.

2.2 Linear Stability Analysis

The stability of the fixed point $x = x_0$ can be determined by a linear analysis. Let

$$A = Df(x^*)$$

where $Df(x^*)$ is the **Jacobian matrix** of f evaluated at x^*. When $n = 2$, the case which interests us the most, the Jacobian matrix is defined as

$$A = Df(x^*) = \begin{bmatrix} \frac{\partial f_1}{\partial x_1}(x^*) & \frac{\partial f_1}{\partial x_2}(x^*) \\ \frac{\partial f_2}{\partial x_1}(x^*) & \frac{\partial f_2}{\partial x_2}(x^*) \end{bmatrix}$$

where $f = (f_1, f_2)$ and $x = (x_1, x_2)$.

$$\dot{x} = Ax \tag{2.2}$$

The linear system (2.2) has always the fixed point $(0,0)$. The eigenvalue problem of A is defined as

$$Ax = \lambda x$$

The eigenvalues which are roots of the characteristic equation.

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

The relation between the eigenvalues of A and the stability of the fixed point x^* of (2.1) is summarized by the following theorem.

Main Theorem of Linear Stability Analysis. Consider the equation (2.1). Let x^* be a fixed point and let $A = Df(x^*)$.

1. If all the eigenvalues of A have a real part which is negative , then the equilibrium point x^* of is **locally asymptotically stable**.

2. If one of the eigenvalues of A have a real part which is positive, then the equilibrium point x^* is **unstable**.

3. If all of the eigenvalues of A have real part which is less than or equal to zero, then the stability of the fixed point x^* can not be concluded by the linear stability analysis.

Let us consider the case where A is a 2×2 matrix.

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

In this situation, the characteristic equation is

$$\det(A - \lambda I) = \lambda^2 - \tau\lambda + \Delta = 0$$

Here $\tau = a + d$ is the trace of A, and $\Delta = ad - bc$ is the determinant of A. Since

$$(\lambda - \lambda_1)(\lambda - \lambda_2) = \det(A - \lambda I)$$

it follows that

$$\tau = \lambda_1 + \lambda_2, \qquad \Delta = \lambda_1\lambda_2.$$

The exact expressions of the eigenvalues are

$$\lambda_{1,2} = \frac{1}{2}(\tau \pm \sqrt{\tau^2 - 4\Delta})$$

The classification of fixed points:

1. If $\lambda_1, \lambda_2 \in \mathbb{R}$ and $\lambda_2 > 0 > \lambda_1$, then the fixed point is called a **saddle point**. This happens when $\Delta < 0$.

2. If $\lambda_1, \lambda_2 \in \mathbb{R}$ and $\lambda_2 > \lambda_1 > 0$, then the fixed point is called a **unstable node**.

3. If $\lambda_2, \lambda_1 \in \mathbb{R}$ and $\lambda_2 < \lambda_1 < 0$, then the fixed point is named a **stable node**.

4. If $\lambda_1 = \overline{\lambda_2} = i\mu$ with $\mu \in \mathbb{R}$ then the fixed point is named a **center**.

5. If $\lambda_1 = \overline{\lambda_2} = \beta + i\mu$ with $\beta, \mu \in \mathbb{R}$ and $\Re\beta < 0$ then the fixed point is named a **stable focus**.

6. If $\lambda_1 = \overline{\lambda_2} = \beta + i\mu$ with $\beta, \mu \in \mathbb{R}$ and $\Re\beta > 0$ then the fixed point is named a **unstable focus**.

Some of the results mentioned above can be displayed in Figure 1.

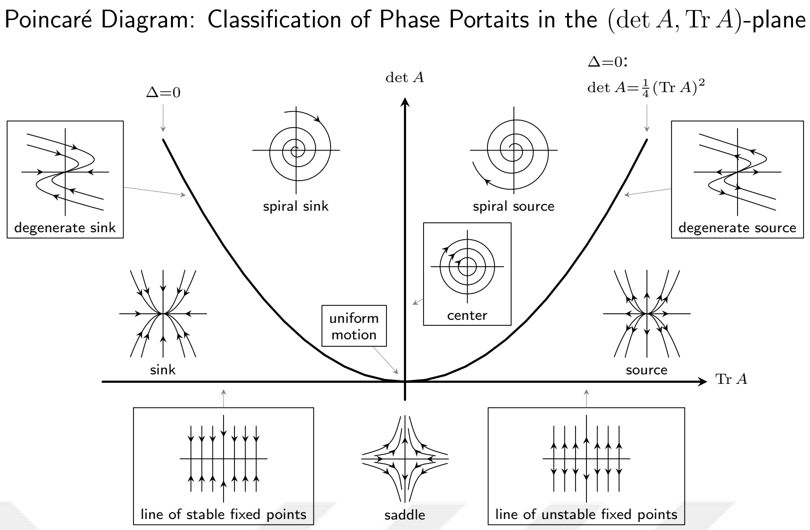

Figure 1: The trace-determinant plane describing the stability of 2×2 linear systems.

Note that a center fixed point is Lyapunov stable but it is not asymptotically stable fixed points of the linear system (2.2). Stable node and stable focus are globally asymptotically stable fixed points of (2.2). Unstable node and unstable focus are unstable.

2.3 Hopf Bifurcation

Normal form of the Supercritical Hopf Bifurcation

Let us observe the differential equation system with a single parameter a

$$\begin{aligned} \dot{x_1} &= x_1 a - x_2 - (x_2^2 + x_1^2)x_1 \\ \dot{x_2} &= x_1 + x_2 a - (x_2^2 + x_1^2)x_2 \end{aligned} \tag{2.3}$$

We can easily notice that this system has an fixed point at

$$x_1 = x_2 = 0.$$

The Jacobian matrix of the system (2.3) is obtained as

$$J = \begin{bmatrix} a & -1 \\ 1 & a \end{bmatrix}$$

The matrix J has eigenvalues

$$\lambda_1 = a + i, \qquad \lambda_2 = a - i$$

By the linear stability analysis, the equilibrium $(x_1, x_2) = (0, 0)$ is a stable focus if $a < 0$, a center if $a = 0$ and an unstable focus if $a > 0$. By the main theorem of linear stability analysis, the origin is still stable for $a < 0$ and unstable for $a > 0$. For $a = 0$, the main theorem of linear stability analysis does not give any conclusion since in this situation the stability of the fixed point may change in the presence of nonlinear terms.

We want to analyze the system (2.3) in complex variable

$$z = ix_2 + x_1,$$

Using the facts that

$$\overline{z} = -ix_2 + x_1 \quad \text{and} \quad |z|^2 = z\overline{z} = x_1^2 + x_2^2$$

we obtain the below ODE for z,

$$\begin{aligned} \dot{z} &= i\dot{x_2} + \dot{x_1} \\ &= (x_1 + ix_2)a - (x_1 + ix_2)(x_1^2 + x_2^2) + (x_1 + ix_2)i \end{aligned}$$

That is, the system (2.3) in the complex variable z becomes

$$\dot{z} = z(a + i) - z|z|^2 \tag{2.4}$$

To analyze the above differential equation, we make use of the polar coordinates

$$z(t) = r(t)e^{i\theta(t)}$$

Taking derivative with respect to t, we obtain

$$\dot{z} = \dot{r}e^{i\theta} + rie^{i\theta}\dot{\theta}$$

Now the equation (2.4) becomes,

$$\dot{r}e^{i\theta} + rie^{i\theta}\dot{\theta} = re^{i\theta}(a + i - r^2)$$

By considering the imaginary and real parts of the above equation, we obtain the system (2.3) in polar form

$$\begin{aligned} \dot{r} &= r(a - r^2) \\ \dot{\theta} &= 1 \end{aligned} \tag{2.5}$$

The bifurcations of the system's phase portrait as a traverses zero can be easily analyzed using the above polar system.

The second equation in (2.5) defines a constant-speed counter clockwise rotation.

The first equation has the equilibrium point $r = 0$ for all $a \in \mathbb{R}$ which is a focus. This equilibrium point is globally asymptotically stable if $a \leq 0$ since $\dot{r} < 0$ in this case hence r is decreasing. That is, the distance to the origin is decreasing in time. Since there are no other solutions of $\dot{r} = 0$ in this case, the solution must approach to the origin as $t \to \infty$.

On the other hand, if $a > 0$, the equilibrium $r = 0$ would be unstable.

For $a > 0$, the system has a so called **stable limit cycle** $r = \sqrt{a}$. Noticing that, for $a > 0$,

$$\begin{cases} 0 < \dot{r} & \text{if } \sqrt{a} > r \\ 0 > \dot{r} & \text{if } \sqrt{a} < r \end{cases}$$

we find that the limit cycle $r = \sqrt{a}$ is stable for $a > 0$. We recall the definition of a limit cycle, which is an isolated, closed orbit. All of the orbits which are starting outside or within the limit cycle except at the origin tend to approach to this limit cycle as t goes to infinity. This case has the special name **supercritical Andronov-Hopf Bifurcation**.

We plot the phase portrait near the origin using the below Mathematica code.

```
a = -.4;
p1 = StreamPlot[{a*x - (y^2 + x^2 )x -y,
    x + a*y - (x^2 + y^2) y}, {x, -1, 1}, {y, -1, 1}];
a = 0.0;
p2 = StreamPlot[{a*x - (y^2 + x^2) x -y,
    x + a*y - (x^2 + y^2) y}, {x, -1, 1}, {y, -1, 1}];
a = .4;
p3 = StreamPlot[{a*x - (y^2 + x^2) x -y,
    x - (y^2 + x^2) y + a*y}, {x, -1, 1}, {y, -1, 1}];
GraphicsRow[{p1, p2, p3},
 PlotLabel -> "Super Critical Andronov-Hopf Bifurcation"]
```

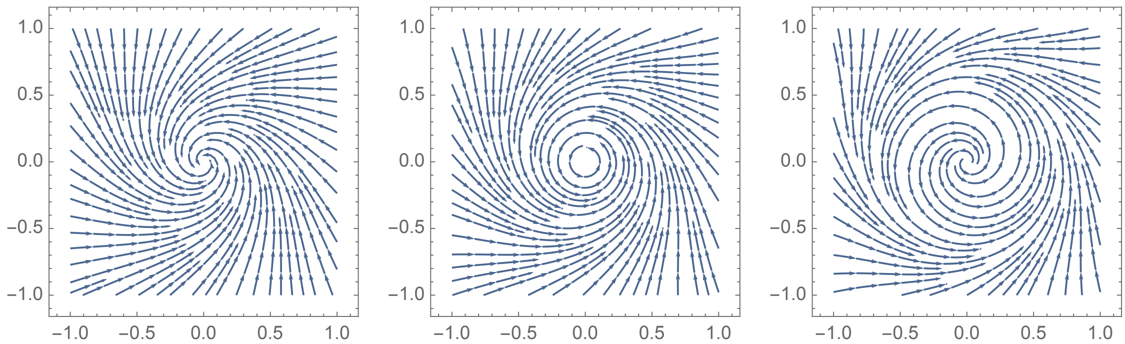

Figure 2: The phase portrait of the super critical Andronov-Hopf bifurcation (2.3) with (a) $a < 0$, (b) $a = 0$, (c) $a > 0$.

To see the animated phase portrait of the stable limit cycle, one can use the below GLSL (Open GL Shading languange) code in the `https://anvaka.github.io/fieldplay/`.

```
// p.x and p.y are current coordinates
```

```
// v.x and v.y is a velocity at point p
vec2 get_velocity(vec2 p) {
vec2 v = vec2(0., 0.);
float a = 0.4;
// change this to get a new vector field
v.x = a* p.x - p.y - p.x * (p.x*p.x +p.y*p.y);
v.y = p.x + a* p.y - p.y * (p.x*p.x +p.y*p.y);

return v;
}
```

Normal form of the Subcritical Hopf Bifurcation

Now, instead of (2.3), we consider

$$\begin{aligned} \dot{x_1} &= x_1 a - x_2 + (x_1^2 + x_2^2)x_1 \\ \dot{x_2} &= x_1 + x_2 a + (x_1^2 + x_2^2)x_2 \end{aligned} \tag{2.6}$$

In this case, if we repeat the same analysis of converting the system in a complex variable z, we get

$$\dot{z} = z(a+i) + z|z|^2 \tag{2.7}$$

which in polar form reads

$$\begin{aligned} \dot{r} &= r(a+r^2) \\ \dot{\theta} &= 1 \end{aligned} \tag{2.8}$$

Since the linear part of (2.6) is identical to (2.3), the linear stability analysis does not change. Hence in this case the fixed point is an unstable focus $a > 0$ and a stable focus for $a < 0$.

This time, there is an unstable limit cycle for $a < 0$ given by $r = \sqrt{-a}$. We show the phase portrait in Figure 3.

We remark here the effect of nonlinear terms on the linear stability. For (2.6), we

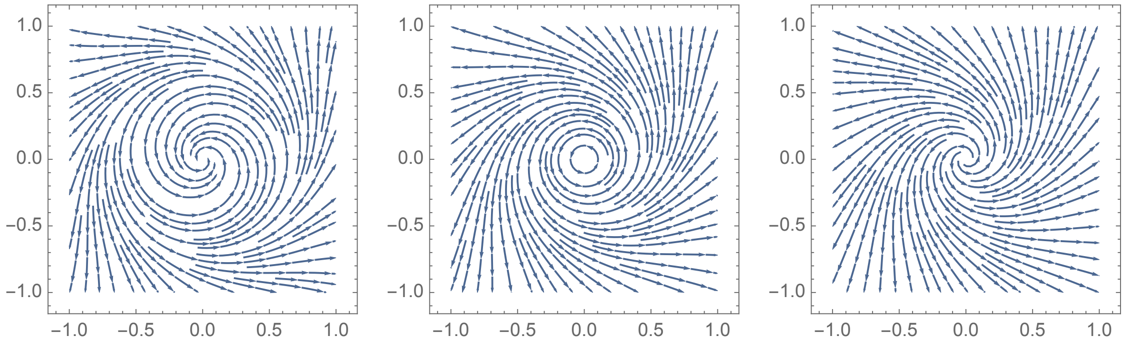

Figure 3: The phase portrait of the sub critical Andronov-Hopf bifurcation (2.6) with (a) $a < 0$, (b) $a = 0$, (c) $a > 0$.

note that the origin is a center of the linearized system which is stable in the sense of Lyapunov. However, for the nonlinear system, the origin is unstable.

2.4 Singularity Induced Bifurcation

In this part we analyze a system of differential algebraic equations which can be put in the form

$$\begin{aligned} \dot{x} &= f(x,y,m), \qquad f : \mathbb{R}^{n+k+d} \mapsto \mathbb{R}^n \\ 0 &= g(x,y,m), \qquad g : \mathbb{R}^{n+k+d} \mapsto \mathbb{R}^k, \end{aligned} \tag{2.9}$$

This system consists of n-ODE's and k-algebraic equations which determine $n+k$ unknowns given by the n-vector x and k-vector y. We note that the time-evolution of the x variables are given explicitly while the time evolution of the y-variables are not given. Finally m denotes a d-vector of parameters.

We suppose that the system has an interior equilibrium point $(x,y) = (x_0(m), y_0(m))$ for all parameters m. We say that the system has a **singularity induced bifurcation** at $(x,y,m) = (x_0(m_0), y_0(m_0), m_0)$ if the stability of the equilibrium point $(x_0(m), y_0(m))$ switches from stable to unstable as m crosses $m = m_0$.

Lemma1

Let us define

$$T = \det D_y g$$

The differential algebraic framework (2.9) owns a singularity induced bifurcation at

$(x,y) = (x_0(m), y_0(m))$ and $m = 0$ if the following conditions are satisfied at the point $(x,y,m) = (x_0(m_0), y_0(m_0), m_0)$:

- **Condition 1**. $T = D_y g$ has a simple zero eigenvalue,
- **Condition 2**. $trace(D_x f\, adj(D_y g) D_x g)$ is non-zero,
- **Condition 3**. The matrix
$$\begin{bmatrix} D_x f & D_y f \\ D_x g & D_y g \end{bmatrix}$$
is nonsingular.
- **Condition 4**. The matrix
$$\begin{bmatrix} D_x f & D_y f & D_m f \\ D_x g & D_y g & D_m g \\ D_x T & D_y T & D_m T \end{bmatrix}$$
is also nonsingular.

As we shall see, this Lemma is very useful in analyzing prey-predator populations with harvesting. In those models the dynamic variable vector x consists of the population sizes of the prey and predators, the y-vector denotes the vector of harvesting effort and m is the profit due to harvesting. That system will have a interior equilibrium point depending on m which is stable for $m < 0$ and which becomes unstable for $m > 0$. Thus increasing the harvesting over a critical threshold $m = 0$ may cause a dramatic change in the populations of predators and preys which could even cause economic disparity. That is the biological meaning of the bifurcation phenomenon caused by singularity.

2.5 Lotka Volterra Model

Predator prey models are given by the following form.

$$\begin{aligned} \dot{x} &= F(x,y)x \\ \dot{y} &= G(x,y)y \end{aligned} \tag{2.10}$$

In the most basic scenario, one considers the Lotka-Volterra system which was proposed by Lotka (1920)

$$\begin{aligned} \dot{x} &= (a - by)x \\ \dot{y} &= (cx - d)y \end{aligned} \tag{2.11}$$

which corresponds to (2.10) with

$$F(x,y) = a - by, \quad G(x,y) = cx - d.$$

In the Lotka-Volterra model (2.11), without predator, that is $y = 0$, prey grows exponentially, $x(t) = e^{at}x(0)$. On the other hand, in the absence of prey, that is $x = 0$, the predator will go extinct exponentially, $y(t) = e^{-dt}y(0)$. These solutions are purely unrealistic. When both species are present, prey contributes to the growth of predator by cxy while predator reduces per capita growth rate of the prey by bxy.

The Lotka-Volterra model has two fixed points: $(0,0)$ and $(d/c, a/b)$. The fixed point $(0,0)$ represents the disappearance of both species, while the fixed point $(d/c, a/b)$ represents coexistence of both species. These fixed points' stability can be analyzed using the Jacobian matrix

$$Df(x,y) = \begin{bmatrix} (a - by) & (-bx) \\ (yc) & (cx - d) \end{bmatrix}$$

where $f(x,y) = (x(a - by), y(cx - d))$. At the first equilibrium, the Jacobian matrix becomes

$$Df(0,0) = \begin{bmatrix} a & 0 \\ 0 & -d \end{bmatrix}$$

which has eigenvalues $\lambda_1 = a$ and $\lambda_2 = -d$. Since a and b are positive, one of the eigenvalue is positive and other is negative, $(0,0)$ is **a saddle point**. We know that saddle points are unstable.

The Jacobian matrix at the second equilibrium is

$$Df(d/c, a/b) = \begin{bmatrix} 0 & -(bd)/c \\ (ac)/b & 0 \end{bmatrix}$$

The characteristic equation of the system is

$$\lambda^2 + dc = 0$$

The eigenvalues are given by

$$\lambda_1 = \sqrt{dc}i, \qquad \lambda_2 = -\sqrt{dc}i$$

Since all of the eigenvalues are imaginary , the fixed point (d/c, a/b) is a center which is linearly stable. As discussed in the Introduction, the stability of the fixed point $(d/c, a/b)$ can not be concluded by the linear stability analysis, since both eigenvalues have zero real part.

To determine the stability of $(d/c, a/b)$, we write

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

and note that the above equation is a separable ODE

$$\frac{(a-by)}{y}dy - \frac{cx-d}{x}dx = 0.$$

We can integrate the above ODE manually or alternatively use the following Mathematica code

```
In[1]:= Integrate[(a - b y)/y, y] - Integrate[(c x - d)/x, x]
Out[1]= -c x - b y + d Log[x] + a Log[y]
```

We find that the solution curves are given by

$$V(x, y) = C$$

where

$$V = -cx - by + d \ln x + a \ln y.$$

and C is a constant depending on the initial condition. This means that the trajectories in the phase portrait correspond to level curves of V. To sketch the phase portrait, we use

```
ContourPlot[-3 x - 2 y + Log[x] + Log[y], {x, 0, 5}, {y, 0, 5},
    ContourShading -> None]
```

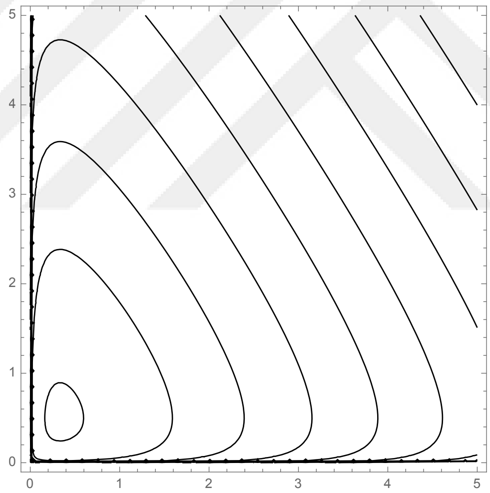

Figure 4: The phase portrait of the Lotka-Volterra model (2.11) with $a = 1$, $b = 2$, $c = 3$, $d = 1$.

In (4), we see that the system has infinitely many periodic solutions centered around the fixed point $(d/c, a/b)$.

It is well known that this model has serious drawbacks and one should consider more realistic models.

2.6 More Realistic Predator Prey Models

A more realistic prey population model is

$$\dot{x} = xr\left(1 - \frac{x}{K}\right) - xyR(x)$$

which corresponds to

$$F(x,y) = r\left(1 - \frac{x}{K}\right) - yR(x)$$

Here the growth of the prey is not unbounded in the absence of the predator. In particular, in the absence of predator, easily can be seen that the prey stabilizes at $x = K$ since $\dot{x} > 0$ if K> x >0 and $\dot{x} < 0$ if $x > K$. For this reason, K is named the **capacity of carrying**. This type of growth is known as **logistic growth**.

The term $R(x)$ corresponds to the **predation term**. The predation term is a functional response of the predator to change in the prey density. In the classical Lotka-Volterra model (2.11), $R(x) = c$ is constant. In more realistic models, usually this term shows some **saturation effect**, and can be chosen depending on the model as

$$R(x) = \frac{A}{x+B}, \quad R(x) = \frac{Ax}{x^2+B^2}, \quad R(x) = \frac{A(1-e^{-ax})}{x} \tag{2.12}$$

In all cases we note that

$$\lim_{x \to \infty} xR(x) = A$$

That is, for all three above predation $xR(x)$ saturates at the level A. The difference is in the rate of convergence to this saturation level.

```
p1 = Plot[x/(x + 2), {x, 0, 20}];
p2 = Plot[x^2/(x^2 + 2), {x, 0, 20}];
p3 = Plot[x (1 - Exp[-x])/x, {x, 0, 20}];
GraphicsRow[{p1, p2, p3},
PlotLabel -> "Various Predation Response to Prey Density"]
```

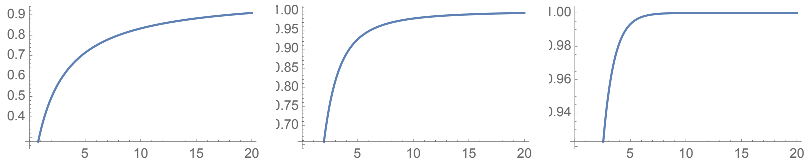

Figure 5: The predator response functions $xR(x)$ given in (2.12) to prey density for various choices showing different rates of convergence to saturation level A. (a) $xR(x) = R(x) = \frac{Ax}{x+B}$, (b) $xR(x) = \frac{Ax^2}{x^2+B^2}$, (c) $xR(x) = A(1-e^{-ax})$.

The predator population equation can also be made more realistic by choosing

$$f_2(x,y) = yG(x,y)$$

with possible forms of G as given as

$$G(x,y) = s\left(1 - h\frac{y}{x}\right), \qquad G(x,y) = -d + eR(x)$$

where $R(x)$ is given as (2.12). We remark here that in the classical Lotka-Volterra model, $G(x,y) = -d + cx$.

There are many more realistic models that can be chosen. For further reference please see [18].

Analysis of a Predator-Prey model. Let us analyze this more realistic predator-prey system

$$\begin{aligned} \dot{x} &= xr\left(1 - \frac{x}{K}\right) - xy\left(\frac{A}{x+B}\right) \\ \dot{y} &= sy\left(1 - h\frac{y}{x}\right) \end{aligned}$$

which corresponds to (2.10)

$$\dot{x} = F(x,y)x \qquad \dot{y} = G(x,y)y$$

with

$$F(x,y) = r\left(1 - \frac{x}{K}\right) - R(x)y$$

the predation term

$$R(x) = \frac{A}{x+B},$$

and

$$G(x,y) = s\left(1 - h\frac{y}{x}\right)$$

To nondimensionalize this system, let us define the following:

$$u(\tau) = x(t)/K, \qquad v(\tau) = hy(t)/K, \qquad \tau = rt$$

$$a = A/(hr) \qquad b = s/r \qquad d = B/K$$

Then comparing,

$$\frac{dx}{dt} = \frac{du}{d\tau}\frac{d\tau}{dt}K = Kr\frac{du}{d\tau}$$

and

$$\begin{aligned} xr\left(1 - \frac{x}{K}\right) - xy\left(\frac{A}{x+B}\right) &= uKr(1-u) - uKv\frac{K}{h}\left(\frac{A}{uK+B}\right) \\ &= uKr(1-u) - uKv\frac{K}{h}A\frac{1}{K}\left(\frac{1}{u+B/K}\right) \end{aligned}$$

we find

$$\frac{du}{d\tau} = u(1-u) - \frac{auv}{u+d}$$

Similarly comparing,

$$\frac{dy}{dt} = \frac{dv}{d\tau}\frac{d\tau}{dt}\frac{K}{h} = \frac{Kr}{h}\frac{dv}{d\tau}$$

and

$$\begin{aligned} sy\left(1 - h\frac{y}{x}\right) &= s\frac{K}{h}v\left(1 - h\frac{vK/h}{uK}\right) \\ &= s\frac{K}{h}v\left(1 - \frac{v}{u}\right) \end{aligned}$$

We find

$$\begin{aligned} \frac{Kr}{h}\frac{dv}{d\tau} &= s\frac{K}{h}v\left(1 - \frac{v}{u}\right) \\ \frac{dv}{d\tau} &= bv\left(1 - \frac{v}{u}\right) \end{aligned}$$

Thus the non-dimensional model becomes

$$\frac{du}{d\tau} = u(1-u) - \frac{auv}{u+d} := f(u,v)$$
$$\frac{dv}{d\tau} = bv\left(1 - \frac{v}{u}\right) := g(u,v)$$

We should find fixed points (u^*, v^*) of the system such that

$$f(u^*, v^*) = 0, \qquad g(u^*, v^*) = 0$$

The trivial fixed point of the system is $u^* = v^* = 0$, but this point is irrelevant for us because it means that there are no prey and predator in the population.

Let us find the other fixed point. By using $g(u^*, v^*) = 0$ we can observe that

$$u^* = v^*$$

and we can find u^* by solving this equation

$$f(u^*, v^*) = u^*(1-u^*) - \frac{av^*u^*}{(u^*+d)} = 0 \tag{2.13}$$

Let us put u^* to v^*, also simplify the equation and find the roots of

$$(1-u^*)(u^*+d) - au^* = 0$$

Simplfiy the equation to

$$(u^*)^2 + u^*(d+a-1) - d = 0$$

We are concerned with positive root

$$u^* = \frac{(1-d-a)+\sqrt{(-1+d+a)^2+4d}}{2}$$

We can use the Mathematica code

```
Solve[u^2 + (a + d - 1) u - d == 0, u]
```

to solve the roots of the above equation.

The Jacobian matrix at u^* is

$$Df(u^*,u^*) = \begin{bmatrix} 1+\frac{a(u^*)^2}{(u^*+d)^2}+u^*(-2-\frac{a}{u^*+d}) & \frac{-au^*}{d+u^*} \\ b & -b \end{bmatrix}$$

The Jacobian matrix can be computed with the following Mathematica code

```
f1 = u (1 - u) - a u v /(u + d);
f2 = b v (1 - v/u);
m = D[{f1, f2}, {{u, v}}];
mm = m /. v->u;
mm // Simplify // MatrixForm
```

If we use the equation (2.13), we get

$$\frac{au^*}{(u^*+d)} = 1-u^*$$

Using this in the Jacobian matrix gives,

$$Df(u^*,u^*) = \begin{bmatrix} u^*\left(\frac{au^*}{(u^*+d)^2}-1\right) & \frac{-au^*}{d+u^*} \\ b & -b \end{bmatrix}$$

We use the Mathematica code to find the determinant and the trace;

```
mmm = {{u ((a*u)/(u + d)^2 - 1), (-a u)/(u + d)}, {b, -b}};
Det[mmm] // Simplify
```

```
Tr[mmm] // Simplify
```

$$\det Df(u^*,u^*) = bu\left(1+\frac{ad}{(d+u^*)^2}\right)$$

which is always positive. Hence both eigenvalues have the same sign. The trace is

$$\mathrm{trace}(Df(u^*,u^*)) = -b+u^*\left(-1+\frac{au^*}{(d+u^*)^2}\right)$$

However, the trace can be positive or negative depending on the parameters.

Thus the determinant is always positive and trace may change sign depending on the parameters. If the trace is negative but small then the equilibrium is a stable spiral, while if the trace is positive but small then the equilibrium is an unstable spiral according to Figure 1. Moreover, the parameter values at which the trace is zero corresponds to Hopf bifurcation. We will make this analysis for the main model we investigate in the next section.

2.7 Predator Prey Model with Harvesting

Harvesting can be considered as a function of the the prey stock x and/or the predator stock y, the catch-ability q of the prey, and the harvesting effort E. Usually, three types of harvesting are generally considered in the literature:

1. Constant harvesting where H is a constant, i.e. $H = C$.
2. Proportionate harvesting $H = qEx$ where harvesting is proportional to the stock and effort.
3. Nonlinear harvesting

   $$H = \frac{qEx}{m_1E+m_2x}$$

   where m_1 and m_2 are suitable constants.

These harvesting models can be put in the framework of functional response theory of Holling. Here by a functional response we mean the intake rate of a consumer as a function of food density. In this theory, proportionate harvesting is known as Holling Type-I functional response, while the above nonlinear harvesting corresponds to Holling Type-II. In this theory there is also a Type-III functional response with similar saturation properties as of Type-II. A model of Type-III functional response can be given as

$$H = \frac{qEx^2}{m_1 E + m_2 x^2}$$

Of course, compared to the other two types of harvesting, the nonlinear harvesting enjoys the more realistic saturation effects by taking into account both stock abundance x and the harvesting effort E. That is for large E, the harvesting saturates as $\frac{qx}{m_1}$ while for large x the harvesting saturates as $\frac{qE}{m_2}$.

An algebraic equation is also included at the same time due to consideration of the economic benefit of harvesting. The economic equilibrium is obtained when the proceeds from the sale of harvested biomass

$$TR = Hp$$

equals to the costs

$$TC = Hc$$

used in the harvesting activities. In the economic equilibrium, the net profit defined as

$$P = TR - TC$$

is identically zero that is

$$P = 0$$

When the biological equilibrium

$$\frac{dx}{dt} = \frac{dy}{dt} = 0$$

is considered together with the economic equilibrium, it is called a **bionomic equilibrium**.

3 RESULTS and DISCUSSION

3.1 Equation of the Model

In this thesis, we study the following model which describes a prey-predator interaction with harvesting.

$$\begin{cases} \frac{dx}{dt} = rx\left(1-\frac{x}{k}\right) - \frac{a_1xy}{n+x} - q_1E_1x \\ \frac{dy}{dt} = sy\left(-1+\frac{a_2x}{n+x}\right) - q_2E_2y \\ 0 = q_1E_1(p_1x-c_1) + q_2E_2(p_2y-c_2) - m \end{cases} \tag{3.1}$$

where m is the net economic profit. The meaning of the symbols are given in Table 1.

In this chapter, we will first describe the positive equilibrium of the system. Then we will analyze the stability of this equilibrium. In particular, we will show that the differential algebraic system (3.1) exhibits a singularity induced bifurcation as the profit m exceeds 0. This results in the loss of stability of the equilibrium and a Hopf bifurcation occurs. We also analyze this Hopf bifurcation.

3.2 Existence of Equilibrium Solutions

Symbol	Meaning
$x(t)$	is the density of the prey population at time t
$y(t)$	is the density of the predator population at time t
E_1	is the effort applied to harvest the prey species
E_2	is the effort applied to harvest the predator species
q	is the catchability coefficient
m	is the economic profit which is also the bifurcation parameter of system
s	s is the predator death rate in the absence of food
r	is the intrinsic growth rate of prey
k	is the prey's carrying capacity
n	is the constant of capture saturation
a_2	is the maximal number of predator
a_1	is the predation coefficient
p	is the price of each unit harvested biomass
c	is the cost of each unit harvest

Table 1: The meaning of the symbols of the main equation (3.1).

To analyze the system we should find the **fixed point** (x_0, y_0) which makes

$$\frac{dy}{dt} = \frac{dx}{dt} = 0$$

In this thesis, we will concentrate on the case where the harvesting effort for both species is identical.

$$E_1 = E_2 = E$$

We can find this point by using the Mathematica codes:

```
Solve[s y (-1 + a2 x/(n + x)) - q2 e y == 0, x] // Simplify
Solve[(1 - x / k ) r x - a1 x y /(n + x ) - q1 e x == 0, y]
```

We find the fixed point as

$$(x_0, y_0, E_0) = \left(-\frac{n(E_0 q_2 + s)}{E_0 q_2 + s - a_2 s}, \frac{-(n + x_0)(E_0 k q_1 - kr + r x_0)}{a_1 k}, E_0\right) \tag{3.2}$$

where E_0 satisfies the equation

$$E_0 = \frac{m}{q_1(p_1 x_0 - c_1) + q_2(p_2 y_0 - c_2)} \tag{3.3}$$

For this equilibrium point to be **biologically meaningful**, we have to make sure that $x_0 > 0$, $y_0 > 0$, $E_0 > 0$. The conditions which guarantee these are given below

$$c q_2 + s - a_2 s < 0 \qquad E_0 k q_1 - kr + r x_0 < 0 \qquad E_0 > 0 \tag{3.4}$$

Our main goal is to study the stability and bifurcations of this fixed point.

We first show that we can indeed find parameters for which the interior equilibrium X_0 exists. As an example, we choose the parameters as given below.

```
In[6]:= a1 = 5; a2 = 6; c1 = 4; c2 = 5; k = 6; m = 2; n = 4;
p1 = 3; p2 = 3; q1 = 1; q2 = 4; r = 4; s = 2;
x0 = -((n (E0*q2 + s))/(E0*q2 + s - a2*s));
y0 = -(((n + x0) (E0*k*q1 - k*r + r*x0))/(a1*k));
```

```
sol = NSolve[E0 == m/(q1*(p1*x0 - c1) + q2 (p2*y0 - c2)), E0]
E0 = E0 /. sol[[2]];
{x0, y0, E0}
E0 = E0 /. sol[[3]];
{x0, y0, E0}

Out[10]= {{E0 -> -17.9158}, {E0 -> 0.858467}, {E0 -> 0.11288}}

Out[12]= {3.31024, 1.36658, 0.858467}

Out[14]= {1.02698, 3.21975, 0.11288}
```

Thus for the given parameters, there exists three solutions for E_0. One of them is negative and hence not biologically relevant. However, the other two are positive and thus biologically relevant. Thus the system exhibits multiple interior equilibrium.

Although, our main focus will be on the stability and bifurcation behavior of the positive interior fixed point, the system has two other fixed points. The first one is

$$(x_1, y_1, E_1) = (k - \frac{q_1 E_0 k}{r}, 0, E_1) \tag{3.5}$$

Here E_1 can be found by solving the third equation in (3.1). Since it has a complicated form, we omit its expression and give the below code to compute it symbolically.

```
Solve[q1*e*p1*(k - q1*e*k/r) - q1*e*c1 - q2*e*c2 - m == 0 , e]
```

This fixed point represents the disappearance of the predator species.

The third fixed point of the system (3.1) is

$$(x_2, y_2, E_2) = (0, 0, \frac{-m}{q_1 c_1 + q_2 c_2}) \tag{3.6}$$

We note that there is no eqilibrium point of the system of the form $x = 0$ and $y > 0$. The significance of this last fixed point is that it represents the annihilation of both species. From an economic point of view, this equilibrium is meaningless as it assumes that there is still an harvesting activity going on even though there are no prey/predator to harvest. We also note that the last fixed point (3.6) is meaningful, that is $E_2 > 0$ only if $m < 0$, that is there is a net loss due to harvesting.

The main focus is the investigation of the stability of the positive interior equilibrium points given by X_0.

3.3 Stability of the equilibrium

In this part, we study the linear stability of the equilibrium (3.2). We first carry this equilibrium to the origin by defining new variables as below.

$$y_1(t) = x(t) - x_0, \qquad y_2(t) = y(t) - y_0$$

In the new coordinates, the fixed point $(x, y) = (x_0, y_0)$ is carried to the origin $(y_1, y_2) = (0, 0)$. We get the new system as:

$$f_1 = \frac{dx}{dt} = \frac{d(y_1 + x_0)}{dt} = \frac{dy_1}{dt}$$

$$= r(y_1 + x_0)(1 - \frac{(y_1 + x_0)}{k}) - \frac{a_1(y_1 + x_0)(y_2 + y_0)}{n + y_1 + x_0} - q_1 E(y_1 + x_0)$$

$$f_2 = \frac{dy}{dt} = \frac{d(y_2 + y_0)}{dt} = \frac{dy_2}{dt}$$

$$= s(y_2 + y_0)(-1 + \frac{a_2(y_1 + x_0)}{n + y_1 + x_0}) - q_2 E(y_2 + y_0)$$

The Jacobian matrix at $(y_1, y_2) = (0, 0)$ and $E = E_0$ is

$$Df(0,0) = \begin{bmatrix} A_{11} & A_{12} \\ A_{21} & A_{22} \end{bmatrix}$$

$$A_{11} = -E_0 q_1 + r - \frac{2 r x_0}{k} - \frac{a_1 n y_0}{(n + x_0)^2}$$
$$A_{12} = -\frac{a_1 x_0}{(n + x_0)}$$
$$A_{21} = y_0 \frac{a_2 n s}{(n + x_0)^2}$$
$$A_{22} = -E_0 q_2 + s(-1 + \frac{a_2 x_0}{(n + x_0)})$$

We write this matrix helping Mathematica codes

```
f1 = r (y1 + x0) (1 - (y1 + x0)/k) -
   a1 (y1 + x0) (y2 + y0)/(n + y1 + x0) - q1 e (y1 + x0);
f2 = s (y2 + y0) (-1 + a2 (y1 + x0)/(n + y1 + x0)) - q2 e (y2 + y0);
d = D[{f1, f2}, {{y1, y2}}];
dd = d /. {y1 -> 0, y2 -> 0};
dd // Simplify // MatrixForm
```

The eigenvalues of the Jacobian matrix is given by the following characteristic equation.

$$\lambda^2 - \tau\lambda + \Delta = 0 \tag{3.7}$$

where

$$\tau = \lambda_1 + \lambda_2 = A_{11} + A_{22} \tag{3.8}$$

is the trace and

$$\Delta = \lambda_1 \lambda_2 = A_{11} A_{22} - A_{12} A_{21} \tag{3.9}$$

is the determinant of the Jacobian matrix.

We find that the determinant Δ is always positive.

```
Det[dd] /. x0 -> (-n (e0*q2 + s))/(e0*q2 + s - a2*s) // FullSimplify
```

```
(a1 (e0 q2 + s) (e0 q2 + s - a2 s)^2 y0)/(a2^2 n s^2)
```

According to Figure 1, the equilibrium point can never be saddle. Moreover, it is stable if the trace $\tau < 0$ and unstable if $\tau > 0$.

For the existence of Hopf bifurcation, the requirement on the Jacobian matrix is that its trace is zero and its determinant is positive. That is

$$A_{11} + A_{22} = 0, \qquad A_{11}A_{22} - A_{12}A_{21} > 0 \tag{3.10}$$

3.4 Singularity Induced Bifurcation

In this part we study the singularity induced bifurcation of the system. Our main result is the following theorem.

Theorem. The differential algebraic system (3.1) exhibits a singularity induced bifurcation at the interior equilibrium point X_0 as the critical value of the profit m crosses 0.

The proof of this theorem follows from the general theorem given in the Methods section.

Proof. Let us define.

$$f_1 = rx\left(1 - \frac{x}{k}\right) - \frac{a_1xy}{n+x} - q_1Ex$$

$$f_2 = sy\left(-1 + \frac{a_2x}{n+x}\right) - q_2Ey$$

$$g = q_1E(p_1x - c_1) + q_2E(p_2y - c_2) - m$$

$$T = D_Eg = q_1(-c_1 + p_1x) + q_2(-c_2 + p_2y)$$

Condition I(a). We have to verify that

$$D_Eg = 0 \qquad \text{when } x = x_0,\ y = y_0,\ E = E_0 \text{ and } m = 0.$$

We compute

$$D_Eg|_{(x,y,E,m)=(x_0,y_0,E_0,0)} = q_1(p_1x_0 - c_1) + q_2(p_2y_0 - c_2)$$

By (3.3),

$$D_E g|_{(x,y,E,m)=(x_0,y_0,E_0,0)} = \left.\frac{m}{E_0}\right|_{m=0} = 0$$

Hence the condition I(a) is satisfied.

Condition I(b). As the next condition, we have to verify that

$$\mathrm{trace}(D_E f \,\mathrm{adj}(D_E g) D_X g)_{X_0} \neq 0$$

Here

$$(D_E f)_{(x_0,y_0,E_0)} = \begin{bmatrix} -q_1 x_0 \\ -q_2 y_0 \end{bmatrix}, \qquad (D_X g)_{(x_0,y_0,E_0)} = \begin{bmatrix} q_1 E_0 p_1 & q_2 p_2 E_0 \end{bmatrix}, \qquad \mathrm{adj}(D_E g) = 1$$

Here the adjugate operator is defined as $A\,\mathrm{adj}(A) = \det(A)$. The adjugate of a 1×1 non-zero matrix is always 1 and $D_E g$ is a 1×1 matrix (a number).

$$\mathrm{trace}(D_E f \,\mathrm{adj}(D_E g) D_X g)_{X_0} = -q_1^2 E_0 x_0 p_1 - q_2^2 E_0 y_0 p_2 < 0$$

So the condition I(b) is satisfied.

Condition II. The next condition is

$$\det \begin{bmatrix} D_X f & D_E f \\ D_X g & D_E g \end{bmatrix} \neq 0$$

To show this condition, let

$$L = \begin{bmatrix} D_X f & D_E f \\ D_X g & D_E g \end{bmatrix} = \begin{bmatrix} D_x f_1 & D_y f_1 & D_E f_1 \\ D_x f_2 & D_y f_2 & D_E f_2 \\ D_x g & D_y g & D_E g \end{bmatrix}$$

$$L_{11} = -Eq_1 - \frac{rx}{k} + r(1 - \frac{x}{k}) - \frac{a_1 ny}{(n+x)^2}$$

$$L_{12} = -\frac{a_1 x}{(n+x)}$$

$$L_{13} = -q_1 x$$

$$L_{21} = sy(\frac{a_2 n}{(n+x)^2})$$

$$L_{22} = -Eq_2 + s(-1 + \frac{a_2 x}{(n+x)})$$

$$L_{23} = -q_2 y$$

$$L_{31} = Ep_1 q_1$$

$$L_{32} = Ep_2 q_2$$

$$L_{33} = q_1(-c_1 + p_1 x) + q_2(-c_2 + p_2 y)$$

We can compute L easily using the following codes.

```
f1 = r*(1 - x/k)*x - a1*y*x/(x+n) - q1*x*e
f2 = s*y (-1 + (a2*x)/(n + x)) - q2*e*y
g = q1*e*(p1*x - c1) + q2*e*(p2*y - c2) - m
L11 = D[f1, x]
L12 = D[f1, y]
L13 = D[f1, e]
L21 = D[f2, x]
L22 = D[f2, y]
L23 = D[f2, e]
L31 = D[g, x]
L32 = D[g, y]
L33 = D[g, e]
L = {{L11, L12, L13}, {L21, L22, L23}, {L31, L32, L33}};
Det[L] /. {x -> x0, y -> y0, e -> e0}
```

The result of the above code is as follows.

$$\det(L) = E_0p_1q_1(-E_0q_1q_2x_0 - q_1sx_0 + \frac{x_0^2a_2q_1s}{n+x_0} + \frac{x_0y_0a_1q_2}{n+x_0})$$
$$- E_0p_2q_2(E_0q_1q_2y_0 - q_2ry_0 + \frac{x_0y_02q_2r}{k} - \frac{x_0^2a_2q_1sy_0}{(n+x_0)^2} + \frac{x_0a_2q_1sy_0}{n+x_0} - \frac{x_0a_1q_2y_0^2}{(n+x_0)^2} + \frac{a_1q_2y_0^2}{n+x_0})$$
$$+ (E_0^2q_1q_2 - E_0q_2r + E_0q_1s - rs + \frac{x_02q_2rE_0}{k} + \frac{x_02rs}{k})(q_1(-c_1+p_1x_0) + q_2(-c_2+p_2y_0))$$
$$+ (-\frac{x_0a_2E_0q_1s}{n+x_0} + \frac{a_2rsx_0}{n+x_0} - \frac{2a_2rsx_0^2}{(n+x_0)k})(q_1(-c_1+p_1x_0) + q_2(-c_2+p_2y_0))$$
$$+ (-\frac{x_0a_1E_0q_2y_0}{(n+x_0)^2} - \frac{x_0a_1sy_0}{(n+x_0)^2} + \frac{a_1q_2y_0E_0}{n+x_0} + \frac{a_1sy_0}{n+x_0})(q_1(-c_1+p_1x_0) + q_2(-c_2+p_2y_0))$$

This expression is generically non-zero. That is for an arbitrary choice of parameters it will be non-zero. Hence this conditions is also satisfied.

Condition III. The last condition to verify is

$$\det\begin{bmatrix} D_Xf & D_Ef & D_mf \\ D_Xg & D_Eg & D_mg \\ D_XT & D_ET & D_mT \end{bmatrix} \neq 0$$

For this purpose, let us define,

$$M = \begin{bmatrix} D_Xf & D_Ef & D_mf \\ D_Xg & D_Eg & D_mg \\ D_XT & D_ET & D_mT \end{bmatrix} = \begin{bmatrix} D_xf_1 & D_yf_1 & D_Ef_1 & D_mf_1 \\ D_xf_2 & D_yf_2 & D_Ef_2 & D_mf_2 \\ D_xg & D_yg & D_Eg & D_mg \\ D_xT & D_yT & D_ET & D_mT \end{bmatrix}$$

$$M_{11} = -Eq_1 - \frac{rx}{k} + r(1 - \frac{x}{k}) - \frac{a_1 ny}{(n+x)^2}$$

$$M_{12} = -\frac{a_1 x}{(n+x)}$$

$$M_{13} = -q_1 x$$

$$M_{14} = 0$$

$$M_{21} = sy(\frac{a_2 n}{(n+x)^2})$$

$$M_{22} = -Eq_2 + s(-1 + \frac{a_2 x}{(n+x)})$$

$$M_{23} = -q_2 y$$

$$M_{24} = 0$$

$$M_{31} = Ep_1 q_1$$

$$M_{23} = Ep_2 q_2$$

$$M_{33} = q_1(-c_1 + p_1 x) + q_2(-c_2 + p_2 y)$$

$$M_{34} = -1$$

$$M_{41} = p_1 q_1$$

$$M_{42} = p_2 q_2$$

$$M_{43} = 0$$

$$M_{44} = 0$$

We compute the matrix M and its determinant using the following code.

```
f1 = x*(1 - x/k)*r - a1*y*x/(x+n) - q1*x*e

f2 = s*y (-1 + (a2*x)/(n + x)) - q2*e*y

g = q1*e*(p1*x - c1) + q2*e*(p2*y - c2) - m

t = q1*(-c1 + p1*x) + q2*(-c2 + p2*y)

M11 = D[f1, x]

M12 = D[f1, y]

M13 = D[f1, e]

M14 = D[f1, m]

M21 = D[f2, x]
```

```
M22 = D[f2, y]
M23 = D[f2, e]
M24 = D[f2, m]
M31 = D[g, x]
M32 = D[g, y]
M33 = D[g, e]
M34 = D[g, m]
M41 = D[t, x]
M42 = D[t, y]
M43 = D[t, e]
M44 = D[t, m]
M = {{M11, M12, M13, M14}, {M21, M22, M23, M24}, {M31, M32, M33,
M34} , {M41, M42, M43, M44}};
Det[M] /. {x -> x0, y -> y0, e -> e0}
M // Simplify // MatrixForm
```

The result is as follows.

$$\begin{aligned}\det(M) = &-E_0 p_1 q_1^2 q_2 x_0 - p_1 q_1^2 x_0 s - E_0 p_2 q_1 q_2^2 y_0 + p_2 q_2^2 r y_0 \\ &- \frac{2 r x_0 y_0 q_2^2 p_2}{k} + \frac{a_2 x_0^2 s p_1 q_1^2}{n + x_0} + \frac{a_1 p_1 q_1 q_2 y_0 x_0}{n + x_0} \\ &- \frac{a_2 p_2 q_1 q_2 s x_0 y_0}{n + x_0} - \frac{a_1 y_0^2 q_2^2 p_2}{n + x_0} + \frac{a_2 p_2 q_1 q_2 s x_0^2 y_0}{(n + x_0)^2} + \frac{a_1 p_2 q_2^2 x_0 y_0^2}{(n + x_0)^2}\end{aligned}$$

This determinant is also generically non-zero.

Finally, we look at some special cases. We observe the following:

- Condition I(a) is satisfied for any q_1, q_2.
- Condition I(b) is satisfied for all (q_1, q_2) except for $(q_1, q_2) = (0, 0)$.

- In the case $q_2 = 0$ we find that

$$\det L = \det M = 0$$

and both condition II and condition III are invalid.

- When $q_2 \neq 0$ but $q_1 = 0$, we still have

$$\det L \neq 0, \qquad \det M \neq 0$$

and the third condition of the singularity induced bifurcation theorem is satisfied.

3.5 Hopf Bifurcation

In the previous part, we have demonstrated that the interior equilibrium X_0 exhibits a bifurcation at $m = 0$. In this part we will analyze the Hopf bifurcation occurring at this interior equilibrium point $(x, y, E) = (x_0, y_0, E_0)$. The conditions for the existence of the Hopf bifurcation was mentioned earlier in (3.10). In this section, our goal is to obtain the normal form of the Hopf bifurcation.

General Formula

$$\begin{aligned}
\dot{y_1} &= f_{1,y_1}(m,\overline{X})y_1 + f_{1,y_2}(m,\overline{X})y_2 + \frac{1}{2}f_{1,y_1y_1}(m,\overline{X})y_1^2 \\
&+ f_{1,y_1y_2}(m,\overline{X})y_1y_2 + \frac{1}{2}f_{1,y_2y_2}(m,\overline{X})y_2^2 + \frac{1}{6}f_{1,y_1y_1y_1}(m,\overline{X})y_1^3 + \frac{1}{2}f_{1,y_1y_1y_2}(m,\overline{X})y_1^2y_2 \\
&+ \frac{1}{2}f_{1,y_1y_2y_2}(m,\overline{X})y_1y_2^2 + \frac{1}{6}f_{1,y_2y_2y_2}(m,\overline{X})y_2^3 + o(Y^4)
\end{aligned}$$

$$\begin{aligned}
\dot{y_2} &= f_{2,y_1}(m,\overline{X})y_1 + f_{2,y_2}(m,\overline{X})y_2 + \frac{1}{2}f_{2,y_1y_1}(m,\overline{X})y_1^2 \\
&+ f_{2,y_1y_2}(m,\overline{X})y_1y_2 + \frac{1}{2}f_{2,y_2y_2}(m,\overline{X})y_2^2 + \frac{1}{6}f_{2,y_1y_1y_1}(m,\overline{X})y_1^3 + \frac{1}{2}f_{2,y_1y_1y_2}(m,\overline{X})y_1^2y_2 \\
&+ \frac{1}{2}f_{2,y_1y_2y_2}(m,\overline{X})y_1y_2^2 + \frac{1}{6}f_{2,y_2y_2y_2}(m,\overline{X})y_2^3 + o(Y^4)
\end{aligned}$$

In this case, we examine the Hopf bifurcation of the system.

$$f_1 = r(y_1 + x_0)(1 - \frac{(y_1 + x_0)}{k}) - \frac{a_1(y_1 + x_0)(y_2 + y_0)}{n + y_1 + x_0} - q_1 E(y_1 + x_0)$$

$$f_{1,y_1} = (r\frac{k - 2x_0}{k} - \frac{a_1 y_0 n}{(n + x_0)^2} - Eq_1)$$

$$f_{1,y_2} = (-\frac{a_1 x_0}{n + x_0})$$

$$\frac{1}{2} f_{1,y_1 y_1} = -(\frac{r}{k} + \frac{a_1 y_0 n}{(n + x_0)^3})$$

$$f_{1,y_1 y_2} = (\frac{a_1 n}{(n + x_0)^2})$$

$$\frac{1}{2} f_{1,y_2 y_2} = 0$$

$$\frac{1}{6} f_{1,y_1 y_1 y_1} = (-\frac{a_1 n y_0}{(n + x_0)^4})$$

$$\frac{1}{2} f_{1,y_1 y_1 y_2} = (\frac{a_1 n}{(n + x_0)^3})$$

$$\frac{1}{2} f_{1,y_1 y_2 y_2} = 0$$

$$\frac{1}{6} f_{1,y_2 y_2 y_2} = 0$$

```
with using mathematica codes
f1 = r*(y1 + x0)*(1 - (y1 + x0)/k) -
  a1*(y1 + x0)*(y2 + y0)/(n + y1 + x0) - q1*e*(y1 + x0)
D[f1, y1] /. {y1 -> 0, y2 -> 0}
D[f1, y2] /. {y1 -> 0, y2 -> 0}
1/2*D[f1, y1, y1] /. {y1 -> 0, y2 -> 0}
D[f1, y1, y2] /. {y1 -> 0, y2 -> 0}
1/2*D[f1, y2, y2] /. {y1 -> 0, y2 -> 0}
1/6*D[f1, y1, y1, y1] /. {y1 -> 0, y2 -> 0}
1/2*D[f1, y1, y1, y2] /. {y1 -> 0, y2 -> 0}
1/2*D[f1, y1, y2, y2] /. {y1 -> 0, y2 -> 0}
```

```
1/6*D[f1, y2, y2, y2] /. {y1 -> 0, y2 -> 0}
```

$$f_2 = s(y_2 + y_0)(-1 + \frac{a_2(y_1 + x_0)}{n + y_1 + x_0}) - q_2 E(y_2 + y_0)$$

$$f_{2,y_1} = \frac{a_2 sny_0}{(n + x_0)^2}$$

$$f_{2,y_2} = -Eq_2$$

$$\frac{1}{2} f_{2,y_1 y_1} = -\frac{a_2 sny_0}{(n + x_0)^3}$$

$$f_{2,y_1 y_2} = \frac{a_2 sn}{(n + x_0)^2}$$

$$\frac{1}{2} f_{2,y_2 y_2} = 0$$

$$\frac{1}{6} f_{2,y_1 y_1 y_1} = \frac{a_2 ny_0 s}{(n + x_0)^4}$$

$$\frac{1}{2} f_{2,y_1 y_1 y_2} = \frac{-a_2 ns}{(n + x_0)^3}$$

$$\frac{1}{2} f_{2,y_1 y_2 y_2} = 0$$

$$\frac{1}{6} f_{2,y_2 y_2 y_2} = 0$$

with using Mathematica codes

```
f2 = s*(y2 + y0)*(-1 + a2*(y1 + x0)/(n + y1 + x0)) - q2*e*(y2 + y0)
D[f2, y1] /. {y1 -> 0, y2 -> 0}
D[f2, y2] /. {y1 -> 0, y2 -> 0, x0 -> n/(a2 - 1)}
1/2*D[f2, y1, y1] /. {y1 -> 0, y2 -> 0}
D[f2, y1, y2] /. {y1 -> 0, y2 -> 0}
1/2*D[f2, y2, y2] /. {y1 -> 0, y2 -> 0}
1/6*D[f2, y1, y1, y1] /. {y1 -> 0, y2 -> 0}
1/2*D[f2, y1, y1, y2] /. {y1 -> 0, y2 -> 0}
1/2*D[f2, y1, y2, y2] /. {y1 -> 0, y2 -> 0}
1/6*D[f2, y2, y2, y2] /. {y1 -> 0, y2 -> 0}
```

Finally, we obtain the ODE system describing the Hopf bifurcation.

$$\dot{y_1} = (r\frac{k-2x_0}{k} - \frac{a_1 y_0 n}{(n+x_0)^2} - Eq_1)y_1 + (-\frac{a_1 x_0}{n+x_0})y_2 + -(\frac{r}{k} + \frac{a_1 y_0 n}{(n+x_0)^3})y_1^2$$
$$+ (\frac{a_1 n}{(n+x_0)^2})y_1 y_2 + (-\frac{a_1 n y_0}{(n+x_0)^4})y_1^3 + (\frac{a_1 n}{(n+x_0)^3})y_1^2 y_2 + o(Y^4)$$

$$\dot{y_2} = \frac{a_2 s n y_0}{(n+x_0)^2}y_1 + -Eq_2 y_2 + -\frac{a_2 s n y_0}{(n+x_0)^3}y_1^2 + \frac{a_2 s n}{(n+x_0)^2}y_1 y_2 + \frac{a_2 n y_0 s}{(n+x_0)^4}y_1^3$$
$$+ \frac{-a_2 n s}{(n+x_0)^3}y_1^2 y_2 + o(Y^4)$$

3.6 Numerical Results

In this part, we will demonstrate some numerical results regarding our theoretical findings. We will fix our parameters as follows.

```
a1 = 5; a2 = 6; c1 = 4; c2 = 5; k = 6; n = 4;
p1 = 3; p2 = 3; q1 = 1; q2 = 4; r = 4; s = 2;
```

We first investigate the role of the profit m on the dynamics of the system.

```
x0 := -((n (E0*q2 + s))/(E0*q2 + s - a2*s));
y0 := -(((n + x0) (E0*k*q1 - k*r + r*x0))/(a1*k));
sol = E0 /. NSolve[E0 == m/(q1*(p1*x0 - c1) + q2 (p2*y0 - c2)), E0];
E01 = sol[[1]];
E02 = sol[[2]];
E03 = sol[[3]];
Plot[Chop[E01], {m, -11, 10}]
Plot[Chop[E02], {m, -5, 5}]
Plot[Chop[E03], {m, -2, 2}]
In[54]:= x0 // Simplify

Out[54]= (4 + 8 E0)/(5 - 2 E0)
In[55]:= y0 // Simplify
```

```
Out[55]= (8 (52 - 55 E0 + 6 E0^2))/(5 (5 - 2 E0)^2)
```

```
In[56]:= NSolve[y0 == 0, E0]
```

```
Out[56]= {{E0 -> 1.07046}, {E0 -> 8.09621}}
```

For the existence of the interior positive fixed point (x_0, y_0, E_0), we find that $x_0 > 0$ if $0 < E_0 < 5/2$ and $y_0 > 0$ if $0 < E_0 < 1.07$. Let us denote the three solutions of E_0 by E_1, E_2 and E_3. Our analysis shows that $0 < E_1 < 1.070$ if $-11.5 < m < 6$, $E_2 < 0$ for $-11.5 < m < 6$. Finally $E_3 < 0$ if $m < 0$ and $E_3 > 0$ for $m > 0$. Thus for $-11.5 < m < 0$ only the fixed point (x_1, y_1, E_1) exist. For $0 < m < 6$, two positive fixed points (x_1, y_1, E_1) and (x_3, y_3, E_3) both exist. Finally for $m > 7$ there are no fixed points of the system.

Next we explore the stability of the positive fixed points. The trace τ of the Jacobian matrix is positive for $0 < E_0 < 0.073$ and negative for $E_0 > 0.073$. Hence,

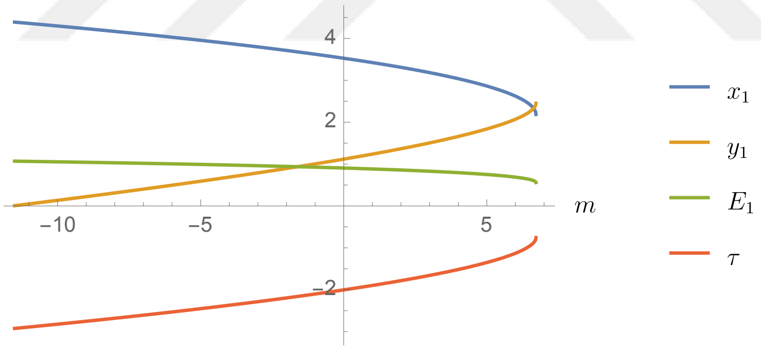

Figure 6: The figure shows the results on the existence and stability of the fixed point (x_1, y_1, E_1). The figure shows that this equilibrium is always exists and is stable for the given m interval $-11.5 < m < 7$ since the trace $\tau < 0$.

For Figure 6, Figure 7 and Figure 8, we used the below code.

```
ResourceFunction["MaTeXInstall"][]
<< MaTeX`
f1 = r (y1 + x0) (1 - (y1 + x0)/k) -
  a1 (y1 + x0) (y2 + y0)/(n + y1 + x0) - q1 E0 (y1 + x0);
```

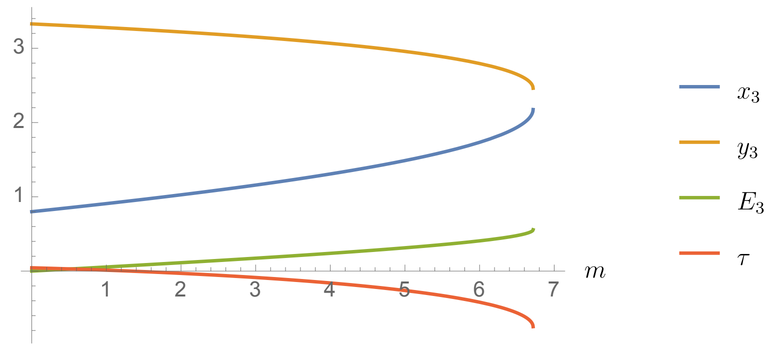

Figure 7: The figure shows the results on the existence and stability of the fixed point (x_3, y_3, E_3). This fixed point exists and is stable for $1.3 < m < 7$. However it is unstable for $0 < m < 1.3$, see Figure 8.

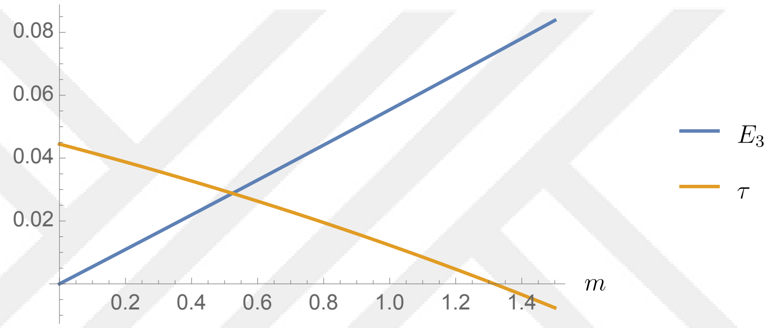

Figure 8: The figure shows the results on the existence and stability of the fixed point (x_3, y_3, E_3). This fixed point exists and is unstable for $0 < m < 1.3$.

```
f2 = s (y2 + y0) (-1 + a2 (y1 + x0)/(n + y1 + x0)) - q2 E0 (y2 + y0);

d = D[{f1, f2}, {{y1, y2}}];

dd = d /. {y1 -> 0, y2 -> 0};

tt = Tr[dd] // Simplify;

Plot[{Chop[x0 /. E0 -> E01], Chop[y0 /. E0 -> E01], Chop[E01],

  Chop[tt /. E0 -> E01]}, {m, -11.5, 7},

 AxesLabel -> {MaTeX["m"], None},

 PlotLegends ->

  Placed[{MaTeX["x_1"], MaTeX["y_1"], MaTeX["E_1"],

    MaTeX["\\tau"]}, {1.1, 0.5}]]

Plot[{Chop[x0 /. E0 -> E03], Chop[y0 /. E0 -> E03], Chop[E03],

  Chop[tt /. E0 -> E03]}, {m, 0, 7}, AxesLabel -> {MaTeX["m"], None},
```

```
 PlotLegends ->
  Placed[{MaTeX["x_3"], MaTeX["y_3"], MaTeX["E_3"],
    MaTeX["\\tau"]}, {1.1, 0.5}]]
Plot[{Chop[E03], Chop[tt /. E0 -> E03]}, {m, 0, 1.5},
 AxesLabel -> {MaTeX["m"], None},
 PlotLegends -> Placed[{MaTeX["E_3"], MaTeX["\\tau"]}, {1.1, 0.5}]]
```

Finally we directly simulate the ODE to show the existence and stability of these fixed point. For the stability of the equilibrium solutions, our results are given below in Figure 10 and Figure 9. The stability of the periodic solution is presented in Figure 11.

We simulate the solution via the following code.

```
Tmax = 30; (*time interval*)
sol2 =
 NDSolve[{x'[t] ==
     r*x[t] (1 - x[t]/k) - (a1*x[t]*y[t])/(n + x[t]) - q1*x[t]*e[t] &&
     y'[t] == s*y[t] (-1 + (a2*x[t])/(n + x[t])) - q2*y[t]*e[t] &&
    e[t] == m/(q1*(p1*x[t] - c1) + q2*(p2*y[t] - c2)) && x[0] == 2 &&
    y[0] == .1}, {x[t], y[t]}, {t, 0, Tmax}]
Plot[{x[t] /. sol2, y[t] /. sol2}, {t, 0, Tmax},
 PlotLabels -> {"x(t)", "y(t)"}]
```

Finally, we show the existence of a periodic solution in

For $m > 0$, we observe that the solution blows up in finite time.

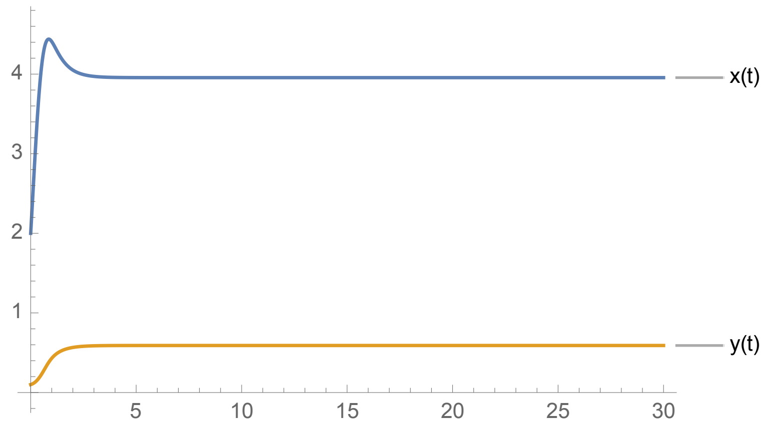

Figure 9: When $m = -5$.

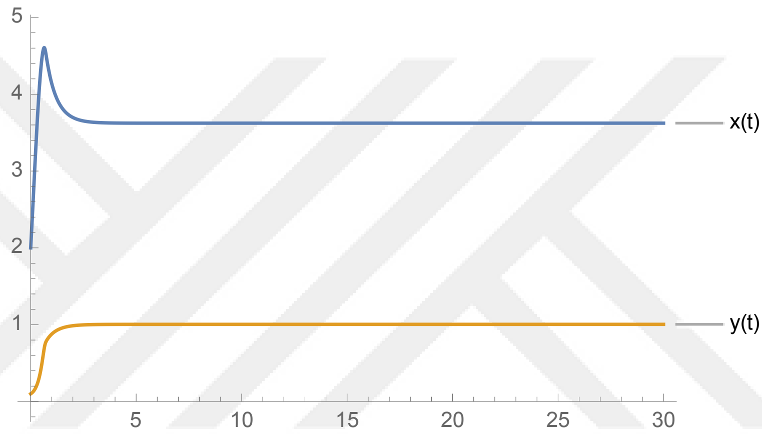

Figure 10: When $m = -1$.

4 CONCLUSIONS

In this thesis, we examined the dynamics of prey-predator population using the tools of dynamical systems theory. In the first chapter, we present some of the ideas about the mathematical biology problems and give a review of the recent studies related to this one. In chapter 2, after introducing the tools of the dynamical systems theory, we give the applications of this theory on basic prey-predator population models. Our main problem is investigated in chapter 3. The main problem we consider is a prey-predator population model with a nonlinear prey-predator interaction coupled with harvesting and economic profit. We consider a linear harvesting on both the prey and predator species. Moreover, the economic balance between cost, revenue and profit is taken into account. This results in a differential algebraic

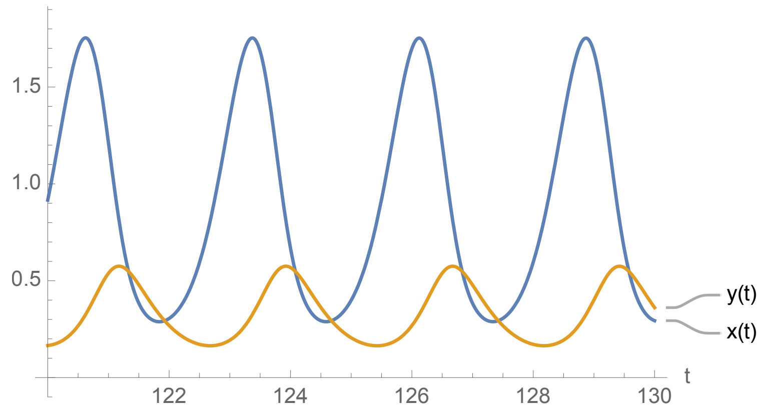

Figure 11: The existence of a periodic solution.

system consisting of two ordinary differential equations describing the time evolution of the prey and predator species and a single algebraic equation describing the economic balance. To the best of our knowledge, this model has not been considered elsewhere.

We first investigate the conditions on the existence and stability of the equilibrium points of the system. We show that several positive equilibria of the system may exist simultaneously. Later, we focus on the singularity induced bifurcation of the system. In particular, we show that the differential algebraic system exhibits a singularity induced bifurcation at the interior equilibrium as the profit turns from negative to positive. Then we show that the system exhibits a Hopf bifurcation and find the normal form of the Hopf bifurcation. Finally, in the numerical results section, we consider particular cases of the main equations we consider and numerically verify that system either converges to an equilibrium or a periodic solution when the net profit is negative. However, our results show that when the net profit is positive, the system displays a finite-time blowup. This aspect of the dynamics requires more analysis.

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Resume

Merve Aygöl was born in 1992 in Erdek. She graduated from Bandırma Primary School in 2007, Bandırma Anatolian Teacher High School in 2011 and Boğaziçi University Faculty of Science and Literature in 2017. In the Fall Semester of the 2017-2018 academic year, she started her master's degree in Marmara University, Institute of Science, Department of Mathematics.