ISTANBUL TECHNICAL UNIVERSITY ★ GRADUATE SCHOOL

Analysis of a Prey-Predator Dynamics with a Modified Holling-Tanner Model and Delay Effect

M.Sc. THESIS

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Değiştirilmiş Holling-Tanner Modeli ile Bir Av-Avcı Dinamiği Analizi ve Gecikme Etkisi

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FOREWORD

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ABBREVIATIONS

ODE : Ordinary Differential Equation
DDE : Delay Differential Equation
R-H : Routh-Hurwitz Criterion
MHT : Modified Holling-Tanner Type II Model

SYMBOLS

x	: The population rate of one of the prey species
y	: The population rate of one of the prey species
z	: The population rate of the predator species
r_1	: The intrinsic growth rate of the prey species x
r_2	: The intrinsic growth rate of the prey species y
K_1	: The carrying capacity of the prey species x
K_2	: The carrying capacity of the prey species y
m	: The threshold population value
t	: Time
τ	: Amount of time-delay
a_1	: The time required for the predator z to search and find a prey x
a_2	: The time required for the predator z to search and find a prey y
q_1	: Maximum predation rate of z per capita related with x
q_2	: Maximum predation rate of z per capita related with y
n_1	: The quality of prey x as food for predator z
n_2	: The quality of prey y as food for predator z
s_1	: The intrinsic growth rate of the predator species z related with x
s_2	: The intrinsic growth rate of the predator species z related with y

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Analysis of a Prey-Predator Dynamics with a Modified Holling-Tanner Model and Delay Effect

SUMMARY

The main goal of this thesis is to introduce a new dynamic model in order to achieve a better understanding of the biological relations between prey and predators through a new dynamical system that includes a delay effect. The work here focuses on an interaction mechanism between two preys and one predator species and the suggested new model is proposed upon some modifications on the classical Holling-Tanner Type II model. By analyzing the stability of the modified model, the dynamic response of this system is investigated and stability conditions at the equilibrium points are served for both the non-delayed and delayed model. Furthermore, the specific analysis for a Hopf bifurcation is performed. With the numerical simulations at the end of the work, the results are supported numerically.

In this thesis work, the Modified Holling-Tanner Type II model is considered as

$$\frac{dx}{dt} = r_1 x(1-\frac{x}{K_1})(x-m) - \frac{q_1 x\, z}{x+a_1}, \tag{1a}$$

$$\frac{dy}{dt} = r_2 y(1-\frac{y}{K_2}) - \frac{q_2 y\, z}{y+a_2}, \tag{1b}$$

$$\frac{dz}{dt} = z[s_1(1-\frac{z}{n_1 x}) + s_2(1-\frac{z}{n_2 y})], \tag{1c}$$

where $r_1, K_1, m, q_1, a_1, r_2, K_2, q_2, a_2, s_1, n_1, s_2, n_2$ are non-negative parameters of the dynamical system. State variables of the dynamical systems are x, y, which are preys of the ecological system and z that represents the predator of the ecological system.

The delayed system is considered in the form

$$\frac{dx}{dt} = r_1 x(1-\frac{x}{K_1})(x-m) - \frac{q_1 x\, z(t-\tau)}{x+a_1}, \tag{2a}$$

$$\frac{dy}{dt} = r_2 y(1-\frac{y}{K_2}) - \frac{q_2 y\, z(t-\tau)}{y+a_2}, \tag{2b}$$

$$\frac{dz}{dt} = z[s_1(1-\frac{z(t-\tau)}{n_1 x}) + s_2(1-\frac{z(t-\tau)}{n_2 y})]. \tag{2c}$$

The time delay effect $\tau \geq 0$ introduced to the system stands for the time from birth to maturity level for predation for the predator species. This means that a newborn predator species needs time to grow old enough to predate alone and to be represented in the predation function.

The topics covered in the thesis are listed below.

In Chapter 1, we introduce the model we are considering and we present information on the properties of this system. In Chapter 2, we give some brief information about

stability analysis and delay differential equations. In Section 3.1, we present a stability analysis of the dynamical system in the non-delay case. In Section 3.2, we analyze the stability of the delayed dynamical system and show the conditions and occurrence of the Hopf bifurcation. In Section 3.3, in order to support the theoretical results, plots are represented obtained from numerical simulations. We conclude with a final discussion of the work and possible future extensions.

Değiştirilmiş Holling-Tanner Modeli ile
Bir Av-Avcı Dinamiği Analizi ve Gecikme Etkisi

ÖZET

Doğadaki av ve avcı türler arasındaki ilişkiyi anlamak için uzun yıllardır bir çok matematiksel model ortaya konmuş ve geçtiğimiz yıllarda da bu konu matematiksel ekoloji alanında popülerliğini korumaya devam etmiştir. Araştırmacılar günümüze kadar bir çok model önerip, bunların analizini yaparak doğadaki gerçek ekolojik sistemlere bir açıklama getirmek istemişlerdir ve oluşturdukları bu dinamik sistemler ile av ve avcı nüfusundaki zamanla değişimi göstermeye çalışmışlardır.

Av ve avcı nüfusunun bağımlı değişkenler ile temsil edildiği bu dinamik sistemler bir çok açıdan değişim gösterip, lineer veya non-lineer olabilirler. Belirli değişkenler ile bir çok farklı senaryoyu açıklayıp anlamlandırmaya çalışan bu modeller arasında Holling-Tanner modeli de bu ekolojik dinamikleri anlama açısından gerçekçi bir bakış ortaya koyarak, önemli bir model olduğunu kanıtlamıştır. Model, ilk olarak önerildiği 20.yy'ın ikinci yarısından bu yana araştırmacılar için de ilgi çekici bir konu olmuştur.

Klasik Holling-Tanner modeli

$$\frac{dx}{dt} = rx(1-\frac{x}{K}) - H(x)y, \tag{3a}$$

$$\frac{dy}{dt} = sy(1-\frac{y}{nx}) \tag{3b}$$

şeklinde ifade edilmektedir. Bu modelde x av nüfusunu temsil ederken, y avcı nüfusunu temsil etmektedir. $H(x)$ fonksiyonu ise avlanmadan kaynaklı nüfus değişimini göstermek için seçilen bir fonksiyondur. r ve s türlerin kendi içerisindeki büyümesini gösteren parametrelerken, K av için nüfusun taşıma kapasitesini, n ise avın avcı için besin değeri olarak kalitesini temsil etmektedir.

Bütün bunlar ışığında, bu çalışmada da Klasik Holling-Tanner modelini belirli yönlerden değiştirerek üç türü içeren yeni bir dinamik sistem oluşturulmuştur ve oluşturulan bu yeni model ile iki farklı av türünden ve bir avcı türden oluşan ekolojik bir senaryo açıklanmaya çalışılmıştır. Bu senaryo doğrultusunda, birbirleri ile aralarında bir avlanma ilişkisi olmayan iki av türü ve bu iki avı da besin olarak tercih eden bir avcıdan oluşan bir habitat şekillendirilmeye ve bunun açıklaması yapılmaya çalışılıp bir stabilite analizi ortaya konmuştur. Geliştirdiğimiz bu modelden ise bu çalışma boyunca Değiştirilmiş 2.Tip Holling-Tanner modeli olarak bahsedeceğiz.

Bu çalışmada önerilen, gecikme terimi içermeyen Değiştirilmiş 2.Tip Holling-Tanner modeli

$$\frac{dx}{dt} = r_1 x(1-\frac{x}{K_1})(x-m) - \frac{q_1 x\, z}{x+a_1}, \tag{4a}$$

$$\frac{dy}{dt} = r_2 y(1-\frac{y}{K_2}) - \frac{q_2 y\, z}{y+a_2}, \tag{4b}$$

$$\frac{dz}{dt} = z[s_1(1-\frac{z}{n_1 x}) + s_2(1-\frac{z}{n_2 y})] \tag{4c}$$

şeklindedir. Bu modelde, r_1, K_1, m, q_1, a_1, r_2, K_2, q_2, a_2, s_1, n_1, s_2, n_2 pozitif parametreler olarak alınmıştır. Dinamik sistemin bağımlı değişkenlerinden x ve y av topluluğunu, z ise avcı topluluğunu ifade etmektedir. Bu model kullanılarak yapılan stabilite analizinden sonra bu sistem üzerinde bir gecikme etkisinin sonuçları araştırılmıştır.

Çalışılan bu modelin gecikmeli versiyonu ise,

$$\frac{dx}{dt} = r_1 x(1-\frac{x}{K_1})(x-m) - \frac{q_1 x\, z(t-\tau)}{x+a_1}, \tag{5a}$$

$$\frac{dy}{dt} = r_2 y(1-\frac{y}{K_2}) - \frac{q_2 y\, z(t-\tau)}{y+a_2}, \tag{5b}$$

$$\frac{dz}{dt} = z[s_1(1-\frac{z(t-\tau)}{n_1 x}) + s_2(1-\frac{z(t-\tau)}{n_2 y})] \tag{5c}$$

şeklinde önerilmiştir. Gecikme değişkeni τ ($\tau \geq 0$) ile kontrol edilen gecikme etkisinin açıklamak istediği durum ise yeni doğan bir avcı türün kendi başına avlanabileceği olgunluğa gelene kadarki avlanamadığı dönemin bu av-avcı dinamiğine etkisinin nasıl olacağıdır. Bu gecikme etkisi incelenirken bir Hopf çatallanması da gözlemlenmiştir.

Ortaya konan çalışmadaki amaçlarımız,

- Oluşturduğumuz yeni modelin stabilize analizini yaparak, bunun ön koşullarını belirlemek,
- Bu senaryo altında bir gecikme faktörünün etkisini görmek,
- Gecikmeli durumda bir Hopf çatallanması oluşumunu incelemek ve bunun ön koşullarını ortaya koymaktır.

Bu amaçları gerçekleştirmek adına tez içerisinde, birinci bölümde av-avcı dinamiği araştırmaları açıklanmış ve Holling-Tanner sistemi ile ilgili bilgi verilmiştir. Daha sonra dinamik sistemdeki her bir parçanın işlevi açıklanıp ortaya konulan yeni Değiştirilmiş 2. Tip Holling-Tanner modeli açıklanmıştır. İkinci bölümde çalışma ile ilgili gerekli teorik bilgiler kısaca sunulmuştur. Üçüncü bölümde, bu yeni modelin stabilite analizi yapılmış ve bunun koşulları her bir denge noktası için ortaya konmuştur. Bununla birlikte, olası bir gecikmeli durumda sistemin davranışı incelenmiş ve Hopf çatallanması gözlemlenmiştir. Bu durumun ön koşulları da ortaya konmuştur. Elde edilen teorik sonuçları destekleme amaçlı olarak sayısal simülasyonlar oluşturulmuş, bununla beraber teorik sonuçların elde edilen grafiklerle de uyumlu olduğu gözlemlenmiştir. Dördüncü bölümde sonuçlar ortaya konarak çalışma son kez özetlenmiş ve gelecek çalışmalar için öneriler sunulmuştur.

Sonuç olarak, yeni geliştirilen Değiştirilmiş 2.Tip Holling-Tanner modeli ile bir av-avcı dinamiği açıklanmış ve gecikme etkisi altında dinamik sistemin davranışı incelenmiştir.

1. INTRODUCTION

The main goal of this thesis is to establish a new prey-predator model based on the the classical Holling-Tanner model in order to achieve a better understanding of the biological relations between preys and predators through this new dynamical system that includes delay effect, which is designed to explain an interaction mechanism between two prey species and one predator species. Additional to that goal, a stability analysis of the suggested new model, that is proposed upon some modifications on the classical Holling-Tanner Type II model is performed and a delay effect in order to make a more realistic ecological model is studied within the model.

There are significantly many prey-predator models studied to understand the true relations of the ecological processes between prey and predators in nature. These models are used for explaining the dynamic relations as well as the changes of populations through time. Among many successful models such as Lotka-Volterra [1] or Leslie-Gower, Holling-Tanner model is a very effective one to show the true dynamics of the prey-predator relations and many researchers paid significant attention to this model [2–4]. The origin of the Holling-Tanner [5] is based on the generalized Gauss model. After the functional response suggestions of Holling, who is a biologist, in 1959 and some later modifications by Tanner, the final model is referred to as Holling-Tanner model in the literature. The following model is a two-dimensional dynamical system on the temporal domain where $x(t)$ represents the prey population at time t while $y(t)$ shows the predator population at time t. The classical Holling-Tanner model is

$$\frac{dx}{dt} = rx(1 - \frac{x}{K}) - H(x)y, \tag{1.1a}$$

$$\frac{dy}{dt} = sy(1 - \frac{y}{nx}). \tag{1.1b}$$

In the system (1.1), r and s are the intrinsic growth rate of the prey and predator populations. K is the carrying capacity of the prey population. n is the quality of prey as food for the predator. Meanwhile, $H(x)$ represents a predation functional response

which describes the effect of predation upon the prey population. In the absence of the predator, the equation for $x(t)$,

$$\frac{dx}{dt} = rx(1 - \frac{x}{K}), \tag{1.2}$$

is the well-known logistic differential equation that is used for the evolution of species. The logistic differential equation provides a realistic description of the growth of the population $x(t)$ by putting an upper bound on the rate of change of the population.

A predation function in the dynamical system can be suggested as

$$H(x) = \frac{qx}{x+a}. \tag{1.3}$$

This predation function (1.3), which is also the original suggestion of Holling in 1959, which makes the model Holling-Tanner Type II. Moreover, the model with linear form of predation function is named Holling-Tanner Type I and the models with predation function like $H(x) = \frac{qx^2}{x^2+a^2}$ are called Holling-Tanner Type III. In the predation function (1.3), q is the maximum predation rate per capita and a represents a value to explain the time required for the predator to search and find prey. In Ref [6], the Holling-Tanner model with Allee effect,

$$\frac{dx}{dt} = rx(1 - \frac{x}{K})(x-m) - \frac{qxy}{x+a}, \tag{1.4a}$$

$$\frac{dy}{dt} = sy(1 - \frac{y}{nx}), \tag{1.4b}$$

has been studied. Here the term $(x-m)$ represents the Allee effect. Allee effect is basically a density-dependent phenomenon in biology, which is directly related to population growth, while m stands for the threshold population value. The first description of the Allee effect, that is in the 1930s, belongs to Warder Clyde Allee. To summarise, the Allee effect provides a correlation between population density and individual fitness. Individual fitness is referred to the ability to survive from possible predation, finding mates, cooperation of hunting, or similar biological phenomena [7].

$$g(x) = rx(1 - \frac{x}{K})(x-m) \tag{1.5}$$

is the logistic growth function (1.5) with Allee effect, if the threshold value $m \leq 0$, this results as $g(0) = 0$ and $g'(0) \geq 0$. This case is named as weak Allee effect. However, if $m > 0$, we have $g(0) = 0$ and $g'(0) < 0$. This case is a strong Allee effect [6].

1.1 Related Studies and Literature Review

In this part, we give a brief survey to motivate and clarify the status of our model among the ones available in the current literature.

In Refs. [8–10], researchers studied the ratio-dependent Holling-Tanner predator-prey model, which is

$$\frac{dx}{dt} = rx(1-\frac{x}{K}) - \frac{qxy}{x+ay}, \tag{1.6a}$$

$$\frac{dy}{dt} = sy(1-\frac{y}{nx}). \tag{1.6b}$$

The model above is for understanding relations of one prey represented by x and one predator which is shown by y. On the contrary to the classical Holling-Tanner Type II model, the predation response function $H(x,y)$ contains predator species y in itself.

Another modified Holling-Tanner model in Ref. [11] , which is a Type I model with Allee effect is

$$\frac{dx}{dt} = rx(1-\frac{x}{K})(x-m) - qxy, \tag{1.7a}$$

$$\frac{dy}{dt} = sy(1-\frac{y}{nx+c}). \tag{1.7b}$$

It is easy to see that the predator response function includes a constant term as c unlike the other models above.

Also, in literature, there are systems that contain two preys and one predator, similar to our model, whose stability conditions were analyzed in these studies such as Refs. [12, 13].

Moreover, a three-species dynamical system in Ref. [14] is an interesting case that helps to understand the prey-predator relations in order to create a prey-predator model. This dynamical system is

$$\frac{dx}{dt} = x(1-x) - a_1\frac{xy}{x+b_1} - a_3\frac{xz}{x+b_2}, \tag{1.8a}$$

$$\frac{dy}{dt} = a_2\frac{xy}{x+b_1} - a_5\frac{yz}{y+b_3} - d_1y, \tag{1.8b}$$

$$\frac{dz}{dt} = a_4\frac{xz}{x+b_2} + a_6\frac{yz}{y+b_3} - d_2z. \tag{1.8c}$$

That is a three-species food chain model with Holling type-II functional response for the middle predator-prey interaction and top predator-prey interaction.

Similarly, a three-species interaction study in Ref. [15] modified from classical Holling-Tanner shows how the interaction terms can be used in process of constructing a prey-predator model. The model is

$$\frac{dx_1}{dt} = a_1 x_1 (1 - \frac{x_1}{K_1}) - (\frac{d_1 x_1}{x_1 + \gamma_1}) x_2, \tag{1.9a}$$

$$\frac{dx_2}{dt} = x_2 (a_2 - \frac{x_2}{c_2 x_1}) - (\frac{d_2 x_2}{x_2 + \gamma_2}) x_3, \tag{1.9b}$$

$$\frac{dx_3}{dt} = x_3 (a_3 - \frac{x_3}{c_3 x_2}). \tag{1.9c}$$

In the model above, there is a chain interaction from top predator x_3 to last prey x_1.

In the ecological systems, there are many biological processes, that concern both prey and predators, which can be explained by delays [16]. In literature, single or multiple delay terms are used in prey-predator models [17–19]. Likewise, Holling-Tanner models with delay effect were studied many times in the past as can be shown below.

In Ref. [20], we can see a dynamic system such as

$$\frac{dx}{dt} = rx(1 - \frac{x}{K}) - \frac{\alpha xy}{a + bx + cy}, \tag{1.10a}$$

$$\frac{dy}{dt} = sy(1 - \frac{hy(t-\tau)}{x(t-\tau)}). \tag{1.10b}$$

The time delay parameter τ is used in the only second equation in order to create a negative feedback of the predator density.

In Ref. [21], there is a dynamic system modified from classic Holling-Tanner that includes multiple delays, in the form

$$\frac{du}{dt} = ru(1 - \frac{u}{K}) - \frac{\alpha uv(t-\tau_1)}{1 + bu} - \frac{Auw(t-\tau_1)}{1 + Bu}, \tag{1.11a}$$

$$\frac{dv}{dt} = v(-d + \frac{eu(t-\tau_2)}{1 + bu(t-\tau_2)}), \tag{1.11b}$$

$$\frac{dw}{dt} = w(-D - Gw - \frac{Eu(t-\tau_2)}{1 + Bu(t-\tau_2)}), \tag{1.11c}$$

where $\tau_1 > 0$ represents the time from birth to predation for two competitor species and $\tau_2 > 0$ denotes the intrinsic growth time of prey species which is a time gap from birth to being a predated object.

In addition, a lot of inspiring models were modified from classical Holling-Tanner such as that of Ref. [22] or three-species studies in Refs. [23, 24] to explain different

cases such as disease transmission in prey-predator relations. These studies help us to establish our modified Holling-Tanner model.

After this brief literature review, we can introduce our modified Holling-Tanner model for three species.

1.2 Modified Model

In the following suggested model, $x(t)$ and $y(t)$ represent two different types of prey species and $z(t)$ represents predator species. The Allee effect is only used for just one of the preys, which is $x(t)$. In the following parts of the paper, the model below is named as Modified Holling-Tanner Type II Model (MHT).

The newly established model is

$$\frac{dx}{dt} = r_1 x(1-\frac{x}{K_1})(x-m) - \frac{q_1 x\, z}{x+a_1}, \tag{1.12a}$$

$$\frac{dy}{dt} = r_2 y(1-\frac{y}{K_2}) - \frac{q_2 y\, z}{y+a_2}, \tag{1.12b}$$

$$\frac{dz}{dt} = z[s_1(1-\frac{z}{n_1 x}) + s_2(1-\frac{z}{n_2 y})]. \tag{1.12c}$$

In the model (1.12), all coefficients like growth rates or carrying capacities are assumed to be positive in order to maintain the realistic nature of the ecological model.

As an explanation of the Modified Holling-Tanner Type II model (MHT), let us state that:

- The part $r_1 x(1-\frac{x}{K_1})(x-m)$ is the population logistic growth function of the prey x-species with Allee effect, which are controlled by r_1 and K_1 parameters and m is a threshold value for Allee effect. The population of x grows logistically in the absence of predator.
- The part $\frac{q_1 x}{x+a_1}$ is the predation function which shows the relation of the prey x and predator z. Here q_1 is the maximum predation rate per capita and a_1 represents a value to explain the time required for the predator to search and find prey.
- Similarly, $r_2 x(1-\frac{y}{K_2})$ is the population logistic growth function of the prey y-species and similar to x, the population of y grows logistically in the absence of predator.

- Meanwhile $\frac{q_2 y}{y+a_2}$ is the predation function between y and z with the parameters q_2 and a_2.

- The species z, which is the only predator species of the system controlled by the growth rates s_1 and s_2 as well as relation factors with both preys, in which the relations are controlled by n_1 and n_2.

- The predator z can eat both preys, meantime there is no interaction between x and y.

To observe the effect of a time in this model, added a delay parameter to the predator population in the MHT model. Delay effect here, introduced to the system by the parameter $\tau \geq 0$, is to realize the situation that the predator population needs time from birth to predation. This means that a newborn predator species need time to grow old enough to predate alone and to be represented in the predation function mathematically.

Therefore, the suggested delayed model is

$$\frac{dx}{dt} = r_1 x(1-\frac{x}{K_1})(x-m) - \frac{q_1 x\, z(t-\tau)}{x+a_1}, \tag{1.13a}$$

$$\frac{dy}{dt} = r_2 y(1-\frac{y}{K_2}) - \frac{q_2 y\, z(t-\tau)}{y+a_2}, \tag{1.13b}$$

$$\frac{dz}{dt} = z[s_1(1-\frac{z(t-\tau)}{n_1 x}) + s_2(1-\frac{z(t-\tau)}{n_2 y})]. \tag{1.13c}$$

After this Chapter, we continue with some information about stability analysis and delay differential equations.

2. STABILITY ANALYSIS AND DELAY DIFFERENTIAL EQUATIONS

The stability analysis of non-linear systems gives us some information to understand the behavior of a dynamical system at an equilibrium point without solving it. Considering that some dynamical systems are hard to solve by analytical methods, stability analysis is very useful and efficient. In this part, we give some information about stability analysis and delay dynamical systems.

2.1 Linear and Non-Linear Systems

A linear system can be introduced as

$$\dot{x} = Ax \tag{2.1}$$

where $x \in R^n$ and A is an $n \times n$ matrix. The n-dimensional system (2.1) is formed of first-order linear homogeneous equations.

Meantime, a non-linear system can be considered as

$$\dot{x} = f(x), \quad x, f \in R^n \tag{2.2}$$

in which the function f does not depend on the time variable t explicitly, which can be considered as an autonomous system.

In this paper, an autonomous non-linear ODE system is studied. Hence, the following information is related to this.

Assume ϕ_t is the flow of the system (2.2) for $\forall t \in R$. If for all $\varepsilon > 0$ there exists a $\sigma > 0$ such that for all $x \in N_\sigma(x_0)$ and $t \geq 0$ we get

$$\phi_t(x) \in N_\sigma(x_0), \tag{2.3}$$

this equilibrium point x_0 is stable. But, if x_0 is not stable, then it is called an unstable equilibrium point. x_0 is called asymptotically stable when x_0 is stable and a $\sigma > 0$ such that $\forall x \in N_\sigma(x_0)$, so we can have $\lim_{t\to\infty} \phi_t(x) = x_0$, exists.

The first step to analyze a non-linear system is to find the critical points or in other words, the equilibrium points of the system. An equilibrium point x_0 is a solution of $f(x) = 0$ where $\dot{x} = f(x)$, which is a time-independent solution of the system. Later, a characteristic equation $D(\lambda)$ is formed by using the Jacobi matrix $Df(x_0)$ and $\det(Df(x_0) - \lambda I) = 0$ for each equilibrium point to classify every one of them. If the roots of the characteristic equation, the eigenvalues λ_i, all have negative real parts, then the equilibrium point x_0 is asymptotically stable. On the other hand, if one of the eigenvalues has a positive real part, the equilibrium point is unstable.

As a geometrical illustration, this situation can be seen in the phase portraits. The trajectories on the phase portraits are the paths of the solutions of the dynamical system. If the dynamical system is stable at the equilibrium point x_0, the trajectories are getting close to the equilibrium point x_0. However, if the dynamical system has an unstable equilibrium point such as x_0, the behavior of the trajectories is intended to go away from that unstable equilibrium point x_0.

2.2 Routh-Hurwitz Criterion

The purpose of Routh-Hurwitz Criterion (R-H) is to determine the stability of dynamical systems [25]. The R-H conditions present restrictions on the roots of the characteristic equation, i.e., on the eigenvalues of the dynamical system at an equilibrium point. These conditions help to decide whether the dynamical system is stable or unstable at the equilibrium point.

Consider the characteristic equation as a third-order polynomial equation

$$D_1(\lambda) = \lambda^3 + \beta_2\lambda^2 + \beta_1\lambda + \beta_0 = 0. \tag{2.4}$$

Under these circumstances Routh-Hurwitz Criterion can be written as

$$\begin{aligned} &\beta_2 > 0, \\ &\beta_0 > 0, \\ &\beta_2\beta_1 > \beta_0. \end{aligned} \tag{2.5}$$

Satisfying these conditions, it can be ensured that all roots of the characteristic equation (2.4) are on the open left half-plane and they all have negative real parts. Hence,

once satisfied, it proves that the equilibrium point is asymptotically stable under these conditions.

2.3 Stability Analysis of Nonlinear Delay Differential Equations

A delay term can be used to explain the different dynamics of a differential equation caused by a time delay. These equations with one or more delay terms are named delay differential equations (DDE). Moreover, a system of delay differential equations that contain a single constant delay term is expressed as,

$$\dot{x} = f(t, x(t), x(t-\tau)) \tag{2.6}$$

with $x, f \in R^n$.

Analytical solutions of a delay differential equation depend on the value of delay as well as non-linearity or the number of dynamical variables. However, like many other differential equations, a numerical investigation may be necessary to obtain a solution for such systems.

Local stability analysis at the equilibrium points can be sufficient to reach some information about the stability of a DDE, which can be seen by examining whether the trajectories are approaching to or diverging from a specific equilibrium point.

Similar to the non-delay dynamical systems, an equilibrium point x_0 of (2.6) is a specific solution which does not change in time, hence, $x(t) = x(t-\tau) = x_0$ for every t. Naturally, x_0 can be obtained from

$$f(t, x(t) = x_0, x(t-\tau) = x_0) = 0, \qquad x_0 = (x_{01}, x_{02}, ..., x_{0n})^T. \tag{2.7}$$

In order to analyze the stability of a DDE at the equilibrium point, it can be perturbed by varying the solution infinitesimally in the neighborhood of the equilibrium point x_0 via a time-dependent function $\delta x(t)$, which exists over an interval of smallest the values of the longest delay, τ_{max}, considering that there are multiple delays. Recalling that this is an autonomous case and denoting $x = x(t)$ and $x_\tau = x(t-\tau)$, we have

$$x = x_0 + \delta x, \quad x_\tau = x_0 + \delta x_\tau. \tag{2.8}$$

So, we get

$$\dot{x} = \delta\dot{x} = f(x_0 + \delta x, x_0 + \delta x_\tau), \tag{2.9}$$

in which δx's are the infinitesimal displacements from the equilibrium point over the interval $(t_0-\tau,t_0)$. Eq. (2.9) can be linearized at the equilibrium point as

$$\delta\dot{x} = J_0\,\delta x + J_\tau\,\delta x_\tau, \tag{2.10}$$

$$(J_0)_{i,j} = \left(\frac{\partial f_i}{\partial x_j}\right)|_{x_j=x_{0j}} \quad for \quad i,j = 1,2,...,n, \tag{2.11}$$

$$(J_\tau)_{i,j} = \left(\frac{\partial f_i}{\partial x_{\tau j}}\right)|_{x_{\tau j}=x_{0j}} \quad for \quad i,j = 1,2,...,n, \tag{2.12}$$

using the Taylor series expansion, J_0 is the Jacobi matrix with respect to x meanwhile J_τ is the Jacobi matrix with respect to x_τ, which are both evaluated at $x = x_\tau = x_0$. Assuming, $\delta x(t)$ is solved by exponential functions of time along with the exponents given by the eigenvalue of the corresponding Jacobi matrix,

$$\delta x(t) = Ae^{\lambda t} \tag{2.13}$$

where A is a constant column matrix. Substituting the equation (2.13) into the equation (2.10) and collecting the coefficients of $e^{\lambda t}$, one obtains the matrix equation

$$\lambda A = (J_0 + e^{-\lambda\tau}J_\tau)A. \tag{2.14}$$

This equation obviously can be satisfied with a nonzero vector A if

$$|J_0 + e^{-\lambda\tau}J_\tau - \lambda I| = 0, \tag{2.15}$$

where I is the identity matrix.

Furthermore, the non-delay part and the transcendental part form the characteristic equation (2.15) of a DDE system. Similarly, if all eigenvalues of the characteristic equation have negative real parts, the equilibrium point is asymptotically stable. Besides that, if one of the eigenvalues has a positive real part, the equilibrium point is an unstable equilibrium point.

For some cases in which one of the eigenvalues is zero, the stability is undetermined. Therefore, in order to determine the stability of the equilibrium point, it is needed to take into account the higher-order terms in Taylor expansion (2.9). For an n degree polynomial characteristic equations, there are exactly n roots which include counting the repeated ones as well. On the other hand, characteristic equations that have both transcendental terms and polynomials may have an infinite number of roots in the complex plane. Even though it is difficult to obtain these roots, there are some

methodologies that have been developed to decide the stability of the equilibrium points for such the cases of characteristic equations that include transcendental parts.

2.4 Hopf Bifurcation

The term bifurcation, generally, refers to a change in phase portraits against the normal topological structure of the dynamical system, with the variation of the parameters. According to that, Hopf bifurcation occurs at a critical point where the system's stability switches and a periodic solution is observed [26].

Assume that a two-dimensional system has a stable equilibrium point. If a bifurcation occurs at the equilibrium point when a parameter τ varies, its stability switches from stable to unstable. Assume that the equilibrium point is stable, hence λ_1 and λ_2 both have negative real parts and $Re(\lambda) < 0$, there are two possibilities: either the eigenvalues are both real and negative or complex conjugates with negative real parts. If one or both eigenvalues change as τ varies to the one(s) with positive real part, this makes the equilibrium point unstable.

Hopf bifurcation is defined according to the properties of the eigenvalues as follows.

Consider a system

$$\dot{x} = f_\tau(x), \quad x \in R^n, \quad \tau \in R \tag{2.16}$$

where τ is a parameter. Suppose the system has an equilibrium (x_0, τ_0), and $f \in C^\infty$.

Assume that,

- The Jacobi matrix $D_x f_{\tau_0}(x_0)$ has a simple pair of purely imaginary eigenvalues and other eigenvalues have negative real parts.

  Then there is a smooth curve of equilibria $(x(\tau), \tau)$ with $x(\tau_0) = x_0$. The eigenvalues $\lambda(\tau), \bar{\lambda}(\tau)$ of $J(\tau) = D_x f_\tau(x(\tau))$ which are purely imaginary at $\tau = \tau_0$ vary smoothly with τ. Moreover, if

- $\frac{d(Re(\lambda(\tau)))}{d\tau}|_{\tau=\tau_0} \neq 0$

  then there is a Hopf bifurcation. Whether it is supercritical, subcritical, or degenerate depends on the higher order terms in system (2.16) [27, 28].

After this preliminaries part, the study continues with the stability analysis of the Modified Holling-Tanner Type II model in Chapter 3. In Section 3.2, a delay effect on the predation will follow. Later, some numerical examples of the model will be shown to illustrate the dynamic relations. Finally, there is a concluding chapter to summarize all results and to give suggestions for further studies at the end of the thesis.

3. THE ANALYSIS OF MODIFIED HOLLING-TANNER TYPE II MODEL

In this chapter, the stability analysis for both the delayed and non-delayed system is performed.

3.1 Stability Analysis of The Dynamical System Without Delay

In this section, the stability analysis of the Modified Holling-Tanner Type II Model (MHT) is performed. MHT model is,

$$\frac{dx}{dt} = r_1 x(1-\frac{x}{K_1})(x-m) - \frac{q_1 x\, z}{x+a_1}, \tag{3.1a}$$

$$\frac{dy}{dt} = r_2 y(1-\frac{y}{K_2}) - \frac{q_2 y\, z}{y+a_2}, \tag{3.1b}$$

$$\frac{dz}{dt} = z[s_1(1-\frac{z}{n_1 x}) + s_2(1-\frac{z}{n_2 y})]. \tag{3.1c}$$

The dynamical system has three equilibrium points, which are $E_1(K_1, K_2, 0)$, $E_2(m, K_2, 0)$ and $E_3(x^*, y^*, z^*)$.

Table 3.1 : Equilibrium Points

Points	Case
$E_1(K_1, K_2, 0)$	Absence of predator
$E_2(m, K_2, 0)$	Absence of predator
$E_3(x^*, y^*, z^*)$	Coexistence State

For the equilibrium point E_3, the coordinate y^* is the solution of a polynomial equation of ninth degree, which we do not produce here due to its complexity. Then we describe the coordinates of E_3 as

$$x^* = \frac{n_2 r_2 s_1 y^*(y^*-K_2)(a_2+y^*)}{n_1[a_2 K_2 r_2 s_2 + y^*(-K_2 n_2 q_2(s_1+s_2) - a_2 r_2 s_2 + K_2 r_2 s_2 - r_2 s_2 y^*)]}, \tag{3.2a}$$

$$y^* = y^*, \tag{3.2b}$$

$$z^* = \frac{r_2(a_2+y^*)(K_2-y^*)}{K_2 q_2}. \tag{3.2c}$$

In order to realize a realistic biological model, only non-negative values of x^*, y^* and z^* are considered. Assuming y^* is positive, if the conditions

$$y^* < K_2, \qquad r_2 s_2 (K_2 - y^*)(a_2 + y^*) < y^* K_2 n_2 q_2 (s_1 + s_2) \tag{3.3}$$

are satisfied, then x^*, y^* and z^* are all positive. Hence, $E_3(x^*,y^*,z^*)$ is a positive equilibrium of dynamical system (3.1).

Analyzing the stability of the equilibrium points, we find the Jacobian matrix of the dynamical system as

$$J = \begin{pmatrix} \alpha_{11} & 0 & \alpha_{13} \\ 0 & \alpha_{22} & \alpha_{23} \\ \alpha_{31} & \alpha_{32} & \alpha_{33} \end{pmatrix}, \tag{3.4}$$

where

$$\begin{aligned} &\alpha_{11} = r_1(2x-m) - \frac{r_1}{K_1}(3x^2 - 2mx) - \frac{q_1 a_1 z}{(x+a_1)^2}, \qquad \alpha_{13} = -\frac{q_1 x}{x+a_1}, \\ &\alpha_{22} = r_2(1 - \frac{2y}{K_2}) - \frac{q_2 a_2 z}{(y+a_2)^2}, \qquad \alpha_{23} = -\frac{q_2 y}{y+a_2}, \\ &\alpha_{31} = \frac{s_1 z^2}{n_1 x^2}, \qquad \alpha_{32} = \frac{s_2 z^2}{n_2 y^2}, \qquad \alpha_{33} = s_1(1 - \frac{2z}{n_1 x}) + s_2(1 - \frac{2z}{n_2 y}). \end{aligned} \tag{3.5}$$

The characteristic equation is

$$D(\lambda) = \begin{vmatrix} \alpha_{11} - \lambda & 0 & \alpha_{13} \\ 0 & \alpha_{22} - \lambda & \alpha_{23} \\ \alpha_{31} & \alpha_{32} & \alpha_{33} - \lambda \end{vmatrix} = 0 \tag{3.6}$$

and

$$D(\lambda) = \lambda^3 + \beta_2 \lambda^2 + \beta_1 \lambda + \beta_0 = 0 \tag{3.7}$$

where

$$\begin{aligned} &\beta_2 = -(\alpha_{11} + \alpha_{22} + \alpha_{33}), \\ &\beta_1 = \alpha_{22}\alpha_{33} - \alpha_{23}\alpha_{32} + \alpha_{11}\alpha_{22} + \alpha_{11}\alpha_{33} - \alpha_{13}\alpha_{31}, \\ &\beta_0 = -\alpha_{11}\alpha_{22}\alpha_{33} + \alpha_{11}\alpha_{23}\alpha_{32} + \alpha_{13}\alpha_{31}\alpha_{22}. \end{aligned} \tag{3.8}$$

3.1.1 Investigating $E_1(K_1, K_2, 0)$

At E_1, there is no predator and both prey populations are at the limit of the carrying capacity of the habitat. Substituting coordinates of E_1 into the characteristic equation, it becomes

$$D_1(\lambda) = \lambda^3 + \beta_2 \lambda^2 + \beta_1 \lambda + \beta_0 = 0 \tag{3.9}$$

where

$$\begin{aligned}\beta_2 &= -r_1(m-K_1)+r_2-(s_1+s_2),\\ \beta_1 &= -r_2(s_1+s_2)-r_1r_2(m-K_1)+r_1(m-K_1)(s_1+s_2),\\ \beta_0 &= r_1r_2(m-K_1)(s_1+s_2).\end{aligned} \tag{3.10}$$

Obviously, if $\beta_2 > 0$ and $\beta_0 > 0$, while $\beta_2\beta_1 > \beta_0$, the Routh-Hurwitz criterion holds and Eq. (3.9) have the roots which are on the left-half plane and all have negative real parts. Hence, the equilibrium point E_1 is asymptotically stable under these conditions.

According to that, the conditions are explicitly

$$r_1(m-K_1)+(s_1+s_2) < r_2, \tag{3.11a}$$

$$m > K_1, \tag{3.11b}$$

$$\frac{B-r_2}{Ar_1} - \frac{(B+r_2)(Ar_1+B-r_2)}{Br_2} + 1 < 0, \tag{3.11c}$$

where

$$A = m-K_1 \ \ and \ \ B = s_1+s_2. \tag{3.12}$$

If these conditions are satisfied, the roots of the characteristic equation have negative real parts and the dynamical system is asymptotically stable at E_1.

3.1.2 Investigating $E_2(m,K_2,0)$

Similarly, the system at E_2 is in absence of predator. The population y is at the limit of carrying capacity, whereas the population of x is at the threshold limit of the Allee effect. For E_2, the characteristic equation becomes

$$D_1(\lambda) = \lambda^3+\beta_2\lambda^2+\beta_1\lambda+\beta_0 = 0 \tag{3.13}$$

where

$$\begin{aligned}\beta_2 &= -r_1(m-\frac{m^2}{K_1})+r_2-(s_1+s_2),\\ \beta_1 &= -r_2(s_1+s_2)-r_1r_2(m-\frac{m^2}{K_1})+r_1(m-\frac{m^2}{K_1})(s_1+s_2),\\ \beta_0 &= r_1r_2(m-\frac{m^2}{K_1})(s_1+s_2).\end{aligned} \tag{3.14}$$

Again, if $\beta_2 > 0$ and $\beta_0 > 0$, while $\beta_2\beta_1 > \beta_0$, the Routh-Hurwitz criterion holds and the characteristic equation have the roots which they are on the left-half plane.

Hence, the conditions are

$$r_1(m-\frac{m^2}{K_1})+(s_1+s_2)<r_2, \tag{3.15a}$$

$$m<K_1, \tag{3.15b}$$

$$\frac{B-r_2}{Ar_1}-\frac{(B+r_2)(Ar_1+B-r_2)}{Br_2}+1<0, \tag{3.15c}$$

where

$$A=m-\frac{m^2}{K_1} \ \textit{and} \ B=s_1+s_2.$$

When the above conditions are satisfied, the roots of the characteristic equation have negative real parts. Hence, it means the dynamical system is asymptotically stable at E_2.

3.1.3 Investigating $E_3(x^*,y^*,z^*)$

Now, the system at E_3 is in the coexistence state of the populations. We substitute coordinates of E_3 into the characteristic equation,

$$D_1(\lambda)=\lambda^3+\beta_2\lambda^2+\beta_1\lambda+\beta_0=0 \tag{3.16}$$

where

$$\begin{aligned}
\beta_2&=-(\alpha_{11}+\alpha_{22}+\alpha_{33}),\\
\beta_1&=\alpha_{22}\alpha_{33}-\alpha_{23}\alpha_{32}+\alpha_{11}\alpha_{22}+\alpha_{11}\alpha_{33}-\alpha_{13}\alpha_{31},\\
\beta_0&=-\alpha_{11}\alpha_{22}\alpha_{33}+\alpha_{11}\alpha_{23}\alpha_{32}+\alpha_{13}\alpha_{31}\alpha_{22}
\end{aligned} \tag{3.17}$$

and

$$\begin{aligned}
&\alpha_{11}=r_1(2x^*-m)-\frac{r_1}{K_1}(3(x^*)^2-2mx^*)-\frac{q_1a_1z^*}{(x^*+a_1)^2},\ \alpha_{13}=-\frac{q_1x^*}{x^*+a_1},\\
&\alpha_{22}=r_2(1-\frac{2y^*}{K_2})-\frac{q_2a_2z^*}{(y^*+a_2)^2}, \qquad \alpha_{23}=-\frac{q_2y^*}{y^*+a_2},\\
&\alpha_{31}=\frac{s_1(z^*)^2}{n_1(x^*)^2}, \quad \alpha_{32}=\frac{s_2(z^*)^2}{n_2(y^*)^2}, \quad \alpha_{33}=s_1(1-\frac{2z^*}{n_1x^*})+s_2(1-\frac{2z^*}{n_2y^*}).
\end{aligned} \tag{3.18}$$

According to Routh-Hurwitz Criterion, under the conditions

$$\begin{aligned}
&\beta_2>0,\\
&\beta_0>0,\\
&\beta_2\beta_1>\beta_0
\end{aligned} \tag{3.19}$$

the dynamical system is asymptotically stable at E_3.

This completes the stability analysis in the non-delay case. We proceed to analyse the delay-dynamical system we propose.

3.2 The Delayed Model and Stability

The following analysis of the Modified Holling-Tanner Type II Model is based on a delay modification for the predator population controlled by the parameter τ where $\tau \geq 0$ is to explain the situation caused by the time from birth to predation for the predator species.

The suggested delayed model is

$$\frac{dx}{dt} = r_1 x(1-\frac{x}{K_1})(x-m) - \frac{q_1 x\, z(t-\tau)}{x+a_1}, \tag{3.20a}$$

$$\frac{dy}{dt} = r_2 y(1-\frac{y}{K_2}) - \frac{q_2 y\, z(t-\tau)}{y+a_2}, \tag{3.20b}$$

$$\frac{dz}{dt} = z[s_1(1-\frac{z(t-\tau)}{n_1 x}) + s_2(1-\frac{z(t-\tau)}{n_2 y})]. \tag{3.20c}$$

There is no delay condition at E_1 and E_2. Because there are no predator species at these equilibrium points and the only delay terms here are on the predator-z. Hence, the investigation of E_3 with delay conditions is performed only.

In order to investigate stability of the delayed model (3.20) around the point $E_3(x^*, y^*, z^*)$, the characteristic equation can be obtained by using

$$\left|J_0 + e^{-\lambda\tau} J_\tau - \lambda I\right| = 0. \tag{3.21}$$

In (3.21) , J_0 is the Jacobian of the dynamical system with respect to the non-delay variables and J_τ is the Jacobian with respect to the variables with delay. So,

$$J_0 = \begin{pmatrix} \alpha_{11} & 0 & 0 \\ 0 & \alpha_{22} & 0 \\ \alpha_{31} & \alpha_{32} & \alpha_{33} \end{pmatrix} \tag{3.22}$$

where

$$\begin{aligned} \alpha_{11} &= r_1(2x-m) - \frac{r_1}{K_1}(3x^2-2mx) - \frac{q_1 a_1 z}{(x+a_1)^2}, \\ \alpha_{22} &= r_2(1-\frac{2y}{K_2}) - \frac{q_2 a_2 z}{(y+a_2)^2}, \\ \alpha_{31} &= \frac{s_1 z^2}{n_1 x^2},\ \alpha_{32} = \frac{s_2 z^2}{n_2 y^2},\ \alpha_{33} = s_1(1-\frac{z}{n_1 x}) + s_2(1-\frac{z}{n_2 y}) \end{aligned} \tag{3.23}$$

and

$$J_\tau = \begin{pmatrix} 0 & 0 & \theta_{13} \\ 0 & 0 & \theta_{23} \\ 0 & 0 & \theta_{33} \end{pmatrix} \tag{3.24}$$

where

$$\begin{aligned} \theta_{13} &= -\frac{q_1 x}{x+a_1}, \\ \theta_{23} &= -\frac{q_2 y}{y+a_2}, \\ \theta_{33} &= -z(\frac{s_1}{n_1 x}+\frac{s_2}{n_2 y}). \end{aligned} \tag{3.25}$$

It follows that, the characteristic equation of the delayed system is

$$D_1(\lambda) = \begin{vmatrix} \alpha_{11}-\lambda & 0 & \theta_{13}e^{-\lambda\tau} \\ 0 & \alpha_{22}-\lambda & \theta_{23}e^{-\lambda\tau} \\ \alpha_{31} & \alpha_{32} & \alpha_{33}+\theta_{33}e^{-\lambda\tau}-\lambda \end{vmatrix} = 0 \tag{3.26}$$

and

$$D_1(\lambda) = \lambda^3+\beta_{12}\lambda^2+\beta_{11}\lambda+\beta_{10}+(\beta_{02}\lambda^2+\beta_{01}\lambda+\beta_{00})e^{-\lambda\tau} = 0 \tag{3.27}$$

where

$$\begin{aligned} \beta_{12} &= -(\alpha_{11}+\alpha_{22}+\alpha_{33}), \\ \beta_{11} &= \alpha_{22}\alpha_{33}+\alpha_{11}\alpha_{33}+\alpha_{11}\alpha_{22}, \\ \beta_{10} &= -\alpha_{11}\alpha_{22}\alpha_{33}, \\ \beta_{02} &= -\theta_{33}, \\ \beta_{01} &= (\alpha_{22}+\alpha_{11})\theta_{33}-\alpha_{31}\theta_{13}-\alpha_{32}\theta_{23}, \\ \beta_{00} &= \alpha_{22}\alpha_{31}\theta_{13}+\alpha_{11}\alpha_{32}\theta_{23}-\alpha_{11}\alpha_{22}\theta_{33}. \end{aligned} \tag{3.28}$$

Lemma 1 *Let us consider the exponential polynomial*

$$\begin{aligned} P(\lambda, e^{-\lambda\tau_1}, \ldots, e^{-\lambda\tau_m}) &= \lambda^n + p_1^{(0)}\lambda^{n-1} + \ldots + p_{n-1}^{(0)}\lambda + p_n^{(0)} \\ &+ [p_1^{(1)}\lambda^{n-1} + \ldots + p_{n-1}^{(1)}\lambda + p_n^{(1)}]e^{-\lambda\tau_1} + \ldots \\ &+ [p_1^{(m)}\lambda^{n-1} + \ldots + p_{n-1}^{(m)}\lambda + p_n^{(m)}]e^{-\lambda\tau_m} = 0, \end{aligned} \tag{3.29}$$

where $\tau_i \geq 0$ $(i = 1,2,...,m)$ *and* $p_j^{(i)}$ $(i = 0,1,2,...,m; j = 1,2,...,n)$ *are constants. As* $(\tau_1, \tau_2, ..., \tau_m)$ *vary, the sum of the order of the zeros of* $P(\lambda, e^{-\lambda\tau_1}, ..., e^{-\lambda\tau_m})$ *on the open right half-plane can change only if a zero appears on or crosses the imaginary axis.*

3.2.1 Investigating $E_3(x^*, y^*, z^*)$

To be a starter, recall the characteristic equation (3.27) at E_3

$$D_1(\lambda) = \lambda^3 + \beta_{12}\lambda^2 + \beta_{11}\lambda + \beta_{10} + (\beta_{02}\lambda^2 + \beta_{01}\lambda + \beta_{00})e^{-\lambda\tau} = 0. \tag{3.30}$$

Case 1: When $\tau = 0$, the stability analysis for this case is studied in Section 3.1. To remind that, the characteristic equation for $\tau = 0$ is

$$D_1(\lambda) = \lambda^3 + (\beta_{12} + \beta_{02})\lambda^2 + (\beta_{11} + \beta_{01})\lambda + \beta_{10} + \beta_{00} = 0. \tag{3.31}$$

According to Routh-Hurwitz Criterion, when $\beta_{12} + \beta_{02} > 0$, $\beta_{10} + \beta_{00} > 0$ and $(\beta_{12} + \beta_{02})(\beta_{11} + \beta_{01}) > (\beta_{10} + \beta_{00})$ hold, the dynamical system is asymptotically stable at E_3.

Case 2: If $\tau \neq 0$, assume that $\pm\omega i, (\omega > 0)$ are the roots of the characteristic equation of the delayed system. After substituting $\lambda = \omega i$ into the characteristic equation (3.30), it becomes

$$-i\omega^3 - \beta_{12}\omega^2 + i\beta_{11}\omega + \beta_{10} + (-\beta_{02}\omega^2 + i\beta_{01}\omega + \beta_{00})e^{-i\omega\tau} = 0. \tag{3.32}$$

By using $e^{-i\omega\tau} = \cos\omega\tau - i\sin\omega\tau$ and then separating real and imaginary parts of the equation (3.32), we obtain

$$\omega^3 - \beta_{11}\omega = \beta_{01}\omega\cos\omega\tau + (\beta_{02}\omega^2 - \beta_{00})\sin\omega\tau, \tag{3.33a}$$

$$\beta_{12}\omega^2 - \beta_{10} = \beta_{01}\omega\sin\omega\tau - (\beta_{02}\omega^2 - \beta_{00})\cos\omega\tau. \tag{3.33b}$$

(3.33) gives

$$\omega^6 + (\beta_{12}^2 - 2\beta_{11} - \beta_{02}^2)\omega^4 + (\beta_{11}^2 - 2\beta_{12}\beta_{10} - \beta_{01}^2 + 2\beta_{02}\beta_{00})\omega^2 + \beta_{10}^2 - \beta_{00}^2 = 0. \tag{3.34}$$

Suppose that $u = \omega^2$, then

$$u^3 + p_2u^2 + p_1u + p_0 = 0, \tag{3.35}$$

where

$$\begin{aligned} p_2 &= \beta_{12}^2 - 2\beta_{11} - \beta_{02}^2, \\ p_1 &= \beta_{11}^2 - 2\beta_{12}\beta_{10} - \beta_{01}^2 + 2\beta_{02}\beta_{00}, \\ p_0 &= \beta_{10}^2 - \beta_{00}^2. \end{aligned} \tag{3.36}$$

Let us define

$$h(u) = u^3 + p_2u^2 + p_1u + p_0. \tag{3.37}$$

Definitely, (3.30) has a pure imaginary root $\lambda = i\omega$ if and only if $h(u)$ has at least one positive zero. In what follows we give some conditions to achieve this result with reference to the work [29].

Claim 1 *If $p_0 < 0$, then $h(u)$ in* (3.37) *has at least one positive zero.*

Proof: We have

$$h(u) = u^3 + p_2u^2 + p_1u + p_0. \tag{3.38}$$

It is easy to see that

$$h(0) = p_0 < 0, \qquad \lim_{u\to\infty} h(u) = \infty. \tag{3.39}$$

Hence, there exist a $u_0 \in (0,\infty)$ so that $h(u_0) = 0$. The proof is complete.

Claim 2 *If $p_0 \geq 0$, the necessary condition for $h(u)$ to have real zeros is*

$$\Delta = p_2^2 - 3p_1 \geq 0. \tag{3.40}$$

Proof: We know

$$h'(u) = 3u^2 + 2p_2u + p_1, \tag{3.41}$$

$$3u^2 + 2p_2u + p_1 = 0. \tag{3.42}$$

Hence, the roots of equation (3.42) are

$$u_{1,2} = \frac{-2p_2 \pm \sqrt{4p_2^2 - 12p_1}}{6} = \frac{-p_2 \pm \sqrt{\Delta}}{3}. \tag{3.43}$$

When $\Delta < 0$, $h'(u)$ does not have real zeros, which means $h(u)$ is monotone increasing in u. Together with $h(0) = p_0 \geq 0$, this concludes that $h(u)$ has no positive real zeros. This completes the proof.

In the following, if $\Delta \geq 0$, $u_1 = \dfrac{-p_2 + \sqrt{\Delta}}{3}$ is the local minimum of $h(u)$. Hence, we have the next claim.

Claim 3 *Final claim is that, if $p_0 \geq 0$, then $h(u)$ has at least one zero if and only if $u_1 > 0$ and $h(u_1) \leq 0$.*

Proof: The sufficiency here is clear but we still have to prove the necessity. If $u_1 \leq 0$, since $h(u)$ is increasing for $u \geq u_1$ and $h(0) = p_0 \geq 0$, it follows $h(u)$ has no positive real zeros. If $u_1 > 0$ and $h(u_1) > 0$ since $u_2 = \dfrac{-p_2 - \sqrt{\Delta}}{3}$ is the local maximum value, it follows that $h(u_1) < h(u_2)$. Hence, by $h(0) = p_0 \geq 0$, $h(u)$ does not have positive real zeros. This completes the proof.

To summarize, the following lemma can be obtained.

Lemma 2 *Suppose that u_1 is defined as above.*

(i) If $p_0 < 0$, then $h(u)$ of (3.37) *has at least one positive zero.*

(ii) If $p_0 \geq 0$ and $\Delta = p_2^2 - 3p_1 < 0$, then $h(u)$ has no positive zero.

(iii) If $p_0 \geq 0$, then $h(u)$ has a positive zero if and only if $u_1 = \dfrac{-p_2 + \sqrt{\Delta}}{3}$ and $h(u_1) \leq 0$.

Obviously, if $h(u)$ has at least one positive zero $u_{0,k}$, we then calculate corresponding $\omega_k = \sqrt{u_{0,k}}$, which gives us the pure imaginary eigenvalue $\lambda = i\omega_k$ we are looking for. This pure imaginary eigenvalue occurs for specific values of τ, which are given explicitly as

$$\tau_k^{(j)} = \frac{1}{\omega_k} \arccos \frac{\omega_k^2 \beta_{01}(\omega_k^2 - \beta_{11}) - (\omega_k^2 \beta_{02} - \beta_{00})(\omega_k^2 \beta_{12} - \beta_{10})}{(\omega_k^2 \beta_{02} - \beta_{00})^2 + \omega_k^2 \beta_{01}^2} + \frac{2j\pi}{\omega_k}, \quad (3.44)$$

where $k = 1, 2, 3$, $j = 0, 1, 2, \ldots$. Then, $\pm i\omega_k$ is a pair of purely imaginary roots of the characteristic equation (3.30) with $\tau = \tau_k^{(j)}$, $k = 1, 2, 3$; $j = 0, 1, \ldots$.

Clearly,

$$\lim_{j \to \infty} \tau_k^{(j)} = \infty, \qquad k = 1, 2, 3. \quad (3.45)$$

Hence, it can be defined that

$$\tau_0 = \tau_{k_0}^{j_0} = \min_{1 \leq k \leq 3, j \geq 1} \{\tau_k^{(0)}\}, \quad \omega_0 = \omega_{k_0}. \quad (3.46)$$

We therefore obtain the following results.

Lemma 3 *Suppose that $\beta_{12} + \beta_{02} > 0$, $\beta_{10} + \beta_{00} > 0$ and $(\beta_{12} + \beta_{02})(\beta_{11} + \beta_{01}) > (\beta_{10} + \beta_{00})$.*

(i) If $p_0 \geq 0$ and $\Delta = p_2^2 - 3p_1 < 0$, then all roots of the characteristic equation (3.30) *have negative real parts for all $\tau \geq 0$.*

(ii) If $p_0 < 0$ or $p_0 \geq 0$, $u_1 > 0$ and $h(u_1) \leq 0$, then all roots of the characteristic equation (3.30) *have negative real parts when $\tau \in [0, \tau_0)$.*

In order to test the spatially homogeneous Hopf bifurcation conditions, the sufficient transversality condition can be obtained as follow.

Let

$$\lambda(\tau) = \alpha(\tau) + i\omega(\tau) \tag{3.47}$$

be the root of the the characteristic equation (3.30) that satisfying $\alpha(\tau_0) = 0,\ \omega(\tau_0) = \omega_0$.

Lemma 4 *Assume that $h'(u_0) \neq 0$. Then, $\mp i\omega_0$ is a simple (i.e., not multiple) pure imaginary root of the equation when $\tau = \tau_0$. Then, the following transversality condition is satisfied:*

$$\frac{d(\mathrm{Re}\lambda(\tau))}{d\tau}\Big|_{\tau=\tau_0} \neq 0 \tag{3.48}$$

and the sign of $d(\mathrm{Re}\lambda(\tau))/d\tau|_{\tau=\tau_0}$ is consistent with that of $h'(u_0)$.

Proof: Denote

$$R(\lambda) = \lambda^3 + \beta_{12}\lambda^2 + \beta_{11}\lambda + \beta_{10}, \tag{3.49}$$

$$Q(\lambda) = \beta_{02}\lambda^2 + \beta_{01}\lambda + \beta_{00}. \tag{3.50}$$

Then, the equivalent the characteristic equation to (3.30) can be rewritten as

$$R(\lambda) + Q(\lambda)e^{-\lambda\tau} = 0 \tag{3.51}$$

from which we obtain

$$R(i\omega)\bar{R}(i\omega) - Q(i\omega)\bar{Q}(i\omega) = 0. \tag{3.52}$$

Besides, h can be represented as

$$h(\omega^2) = R(i\omega)\bar{R}(i\omega) - Q(i\omega)\bar{Q}(i\omega). \tag{3.53}$$

Differentiating both sides of (3.53), we obtain

$$2\omega h'(\omega^2) = -i\{R\bar{R}' - R'\bar{R} + Q'\bar{Q} - Q\bar{Q}'\}. \tag{3.54}$$

If $i\omega_0$ is not a simple root, i.e., if it is a multiple root, then it must satisfy

$$\frac{d}{d\lambda}[R(\lambda) + Q(\lambda)e^{-\lambda\tau}]|_{\lambda=i\omega_0} = 0, \tag{3.55}$$

that is

$$R'(i\omega_0) + Q'(i\omega_0)e^{-i\omega_0\tau_0} - \tau_0 Q(i\omega_0)e^{-i\omega_0\tau_0} = 0. \tag{3.56}$$

With (3.51), we find

$$\tau_0 = \frac{Q'(i\omega_0)}{Q(i\omega_0)} - \frac{R'(i\omega_0)}{R(i\omega_0)}. \tag{3.57}$$

Thus

$$\begin{aligned}
\mathrm{Im}(\tau_0) &= \mathrm{Im}\left(\frac{Q'(i\omega_0)}{Q(i\omega_0)} - \frac{R'(i\omega_0)}{R(i\omega_0)}\right) \\
&= \mathrm{Im}\left(\frac{Q'(i\omega_0\bar{Q}(i\omega_0)}{Q(i\omega_0)\bar{Q}(i\omega_0)} - \frac{R'(i\omega_0)\bar{R}(i\omega_0)}{R(i\omega_0)\bar{R}(i\omega_0)}\right) \\
&= \mathrm{Im}\left(\frac{Q'(i\omega_0)\bar{Q}(i\omega_0) - R'(i\omega_0)\bar{R}(i\omega_0)}{R(i\omega_0)\bar{R}(i\omega_0)}\right) \\
&= \frac{-i\left(Q'\bar{Q} - R'\bar{R} - \bar{Q}'Q + \bar{R}'R\right)}{2R\bar{R}}\Big|_{\lambda=i\omega_0} \\
&= \frac{\omega_0 h'(\omega_0^2)}{|R(i\omega_0)|^2}.
\end{aligned} \tag{3.58}$$

This yields $h'(\omega_0^2) = 0$, since τ_0 is real and $\mathrm{Im}(\tau_0) = 0$. We have a contradiction to the assumption $h'(\omega_0^2) \neq 0$. This is the proof of the first conclusion.

Now, we need to prove that $\left.\frac{d(\mathrm{Re}(\lambda\tau))}{d\tau}\right|_{\tau=\tau_0,\lambda=i\omega_0} \neq 0$.

Differentiating both sides of (3.51) with respect to τ,

$$\frac{d}{d\tau}[R(\lambda) + Q(\lambda)e^{-\lambda\tau}] = 0. \tag{3.59}$$

Obtaining

$$\frac{d\lambda}{d\tau}[R'(\lambda) + Q'(\lambda)e^{-\lambda\tau} - \tau Q(\lambda)e^{-\lambda\tau}] - \lambda Q(\lambda)e^{-\lambda\tau} = 0, \tag{3.60}$$

which implies

$$\begin{aligned}
\frac{d\lambda}{d\tau} &= \frac{\lambda Q(\lambda)e^{-\lambda\tau}}{R'(\lambda)+Q'(\lambda)e^{-\lambda\tau}-\tau Q(\lambda)e^{-\lambda\tau}} \\
&= \frac{\lambda Q(\lambda)}{R'(\lambda)e^{\lambda\tau}+Q'(\tau)-\tau Q(\lambda)} \\
&= \frac{\lambda Q(\lambda)[\bar{R}'(\lambda)e^{\bar{\lambda}\tau}+\bar{Q}'(\lambda)-\tau\bar{Q}(\lambda)]}{|R'(\lambda)e^{\lambda\tau}+Q'(\lambda)-\tau Q(\lambda)|^2} \\
&= \frac{\lambda[-R(\lambda)\bar{R}'(\lambda)e^{\lambda\tau}e^{\bar{\lambda}\tau}+Q(\lambda)\bar{Q}'(\lambda)-\tau\bar{Q}(\lambda)Q(\lambda)]}{|R'(\lambda)e^{\lambda\tau}+Q'(\lambda)-\tau Q(\lambda)|^2} \\
&= \frac{\lambda[-R(\lambda)\bar{R}'(\lambda)e^{\lambda\tau}e^{\bar{\lambda}\tau}+Q(\lambda)\bar{Q}'(\lambda)-\tau|Q(\lambda)|^2]}{|R'(\lambda)e^{\lambda\tau}+Q'(\lambda)-\tau Q(\lambda)|^2}.
\end{aligned} \tag{3.61}$$

It follows

$$\begin{aligned}
&\frac{d(\mathrm{Re}\lambda(\tau))}{d\tau}\Big|_{\tau=\tau_0,\lambda=i\omega_0} \\
&= \frac{\mathrm{Re}\{\lambda[-R(\lambda)\bar{R}'(\lambda)e^{\lambda\tau}e^{\bar{\lambda}\tau}+Q(\lambda)\bar{Q}'(\lambda)-\tau|Q(\lambda)|^2]\}_{\tau=\tau_0,\lambda=i\omega_0}}{|R'(\lambda)e^{\lambda\tau}+Q'(\lambda)-\tau Q(\lambda)|^2_{\tau=\tau_0,\lambda=i\omega_0}} \\
&= \frac{i\omega_0}{2}\frac{[-R\bar{R}'+Q\bar{Q}'+\bar{R}R'-\bar{Q}Q']_{\lambda=i\omega_0}}{|R'(i\omega_0)e^{i\omega_0\tau_0}+Q'(i\omega_0)-\tau_0 Q(i\omega_0)|^2} \\
&= \frac{i\omega_0}{2}\frac{2\omega_0 h'(\omega_0^2)}{i|R'(i\omega_0)e^{i\omega_0\tau_0}+Q'(i\omega_0)-\tau_0 Q(i\omega_0)|^2} \\
&= \frac{\omega_0^2 h'(\omega_0^2)}{|R'(i\omega_0)e^{i\omega_0\tau_0}+Q'(i\omega_0)-\tau_0 Q(i\omega_0)|^2} \neq 0.
\end{aligned} \tag{3.62}$$

The proof is repeated from Li's studies [30] with some corrections in the thesis work [31]. To complete the analysis, the following Lemma is needed, which is studied and stated clearly by Ruan and Wei [29].

In the light of Lemma 1, Lemma 3 and Lemma 4, the following theorem can be obtained.

Theorem 1 *Consider ω_0, τ_0 and $\lambda(\tau)$ as they are defined above with respect to $u_0 = \omega_0^2$. Suppose that $\beta_{12}+\beta_{02}>0$, $\beta_{10}+\beta_{00}>0$ and $(\beta_{12}+\beta_{02})(\beta_{11}+\beta_{01})>(\beta_{10}+\beta_{00})$.*

(i) If $p_0 \geq 0$ and $\Delta = p_2^2 - 3p_1 < 0$, then all roots of the characteristic equation (3.30) *have negative real parts for all $\tau \geq 0$. Hence, the equilibrium point E_3 is asymptotically stable for all $\tau \geq 0$ in this case.*

(ii) If $p_0 < 0$ or the case where $p_0 \geq 0$, $u_1 > 0$ and $h(u_1) \leq 0$, then all roots of the characteristic equation (3.30) *have negative real parts when $\tau \in [0, \tau_0)$. So, the equilibrium point E_3 is asymptotically stable for $\tau \in [0, \tau_0)$ whereas it behaves unstable for $\tau \in (\tau_0, \tau_1)$.*

(iii) If the conditions of (ii) are satisfied, $\tau = \tau_0$ and $h'(u_0) \neq 0$, then $\pm i\omega_0$ is a pair of simple purely imaginary roots of the characteristic equation (3.30) *and all other roots have negative real parts. Hence, the system undergoes a Hopf-bifurcation at the equilibrium point E_3 when $\tau = \tau_0$.*

Furthermore, the stability and bifurcation conditions are stated clearly in the discussions above. To illustrate these results, some numerical simulations are performed for chosen specific values of parameters, which are in the suitable range required by the related lemmas.

3.3 Numerical Simulations

In this thesis, the stability conditions of a newly established Modified Holling-Tanner Type II Model are discussed and conditions for a Hopf bifurcation to occur in the delayed case are pointed out. Theoretical results show that time delays have a highly significant effect on the system. To support our theoretical results, some simulations based on numerical calculations are performed for the delayed dynamical system on MATLAB by using the dde23 solver.

For the numerical simulations, the system and the parameters are considered as

$$\frac{dx}{dt} = 1.7x(1 - \frac{x}{4.7})(x - 7.2) - \frac{0.7x\,z(t-\tau)}{x + 1.5}, \tag{3.63a}$$

$$\frac{dy}{dt} = 1.1y(1 - \frac{y}{5.2}) - \frac{1.1y\,z(t-\tau)}{y + 0.9}, \tag{3.63b}$$

$$\frac{dz}{dt} = z[1.9(1 - \frac{z(t-\tau)}{1.4x}) + 4.3(1 - \frac{z(t-\tau)}{1.2y})], \tag{3.63c}$$

where $r_1 = 1.7, r_2 = 1.1, K_1 = 4.7, K_2 = 5.2, m = 7.2, q_1 = 0.7, q_2 = 1.1, a_1 = 1.5, a_2 = 0.9, s_1 = 1.9, s_2 = 4.3, n_1 = 1.4, n_2 = 1.2$.

For this selected system, there are two positive equilibrium points as $E_{3a}(7.05705, 0.902744, 1.48978)$ and $E_{3b}(4.89752, 0.931502, 1.50342)$. E_{3a} is a stable equilibrium point meanwhile E_{3b} is an unstable one when $\tau = 0$. When

$\tau = 0$, for the stable equilibrium point, the eigenvalues are $-5.38623 \pm 0.1216i$ and -0.714414.

The critical value of τ for E_{3a} is calculated as $\tau_0 = 0.229892$. In that case, the pure imaginary eigenvalue is $6.22658i$. In addition, $h'(\omega_0^2) = 5122.67 > 0$. For $\tau = 0.23 > \tau_0 = 0,229892$, there is an eigenvalue $3.8507 + 4.92275 * 10^{-19}$. This shows that the behavior of the dynamical system is unstable for a specific τ value greater than τ_0.

The following plots show the delay effect for different delays τ, chosen to be less than, equal to and greater than the critical value.

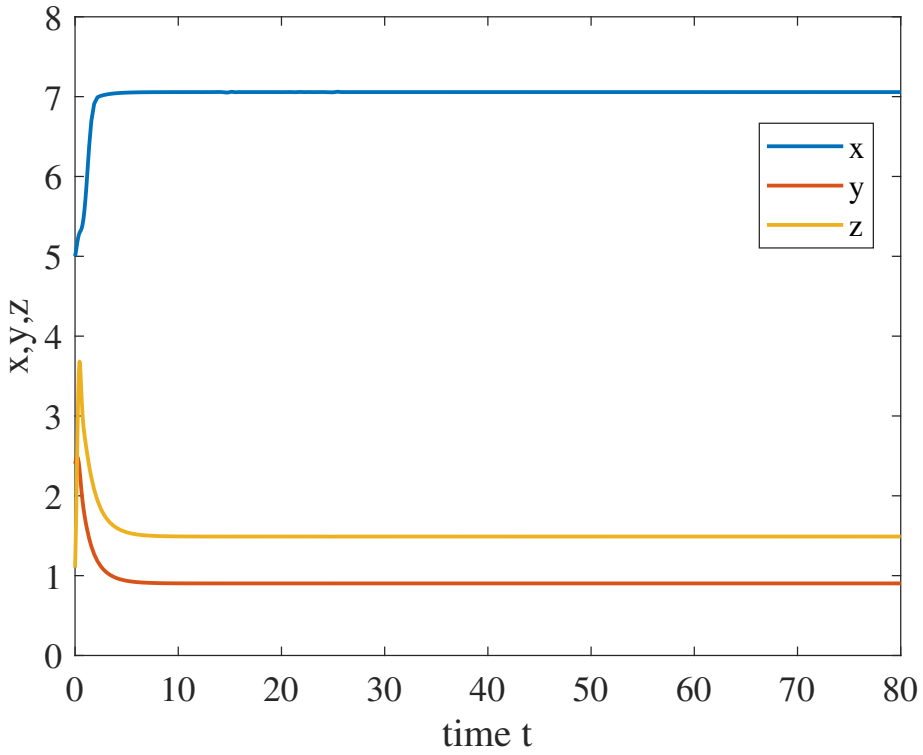


Figure 3.1 : The behavior of the dynamical system for $\tau = 0.1 < \tau_0 = 0.229892$

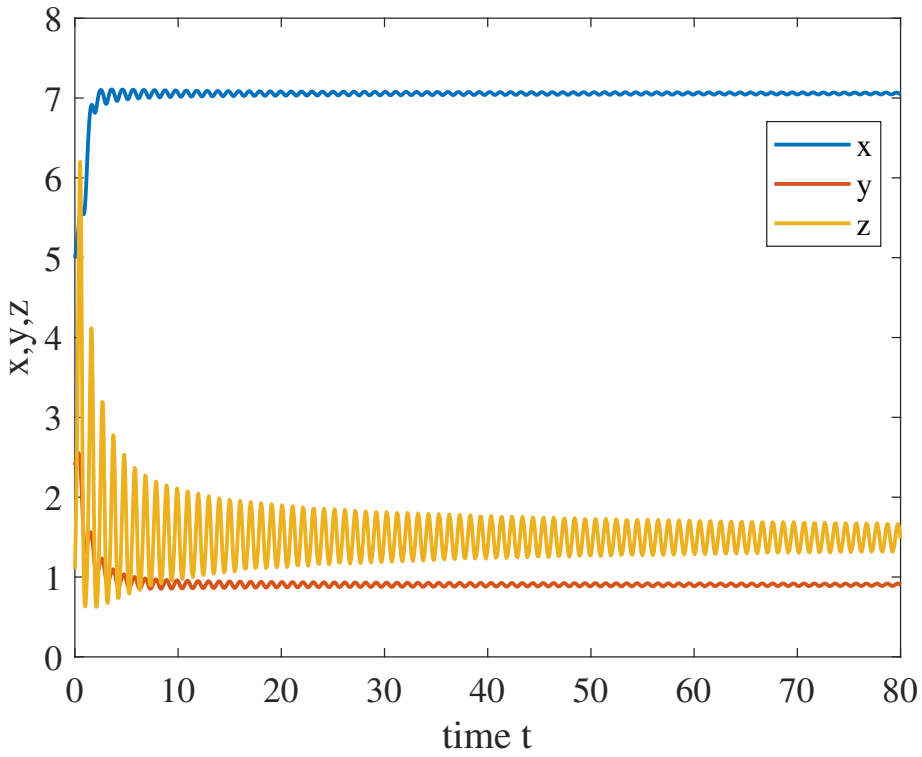


Figure 3.2 : The behavior of the dynamical system for critical value of $\tau_0 = 0.229892$

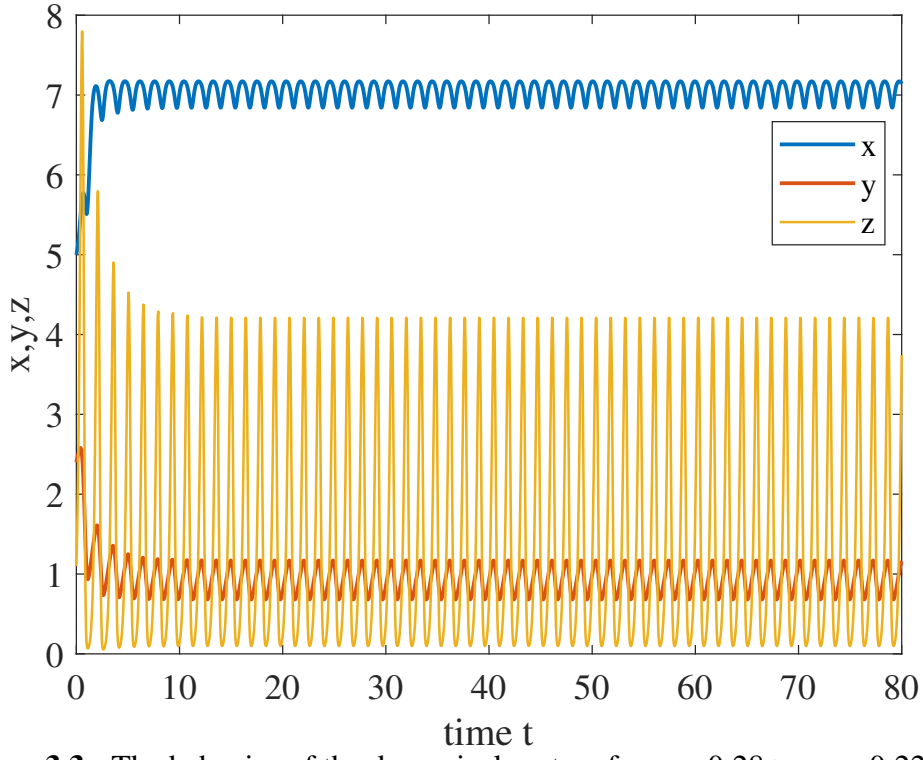


Figure 3.3 : The behavior of the dynamical system for $\tau = 0.28 > \tau_0 = 0.229892$

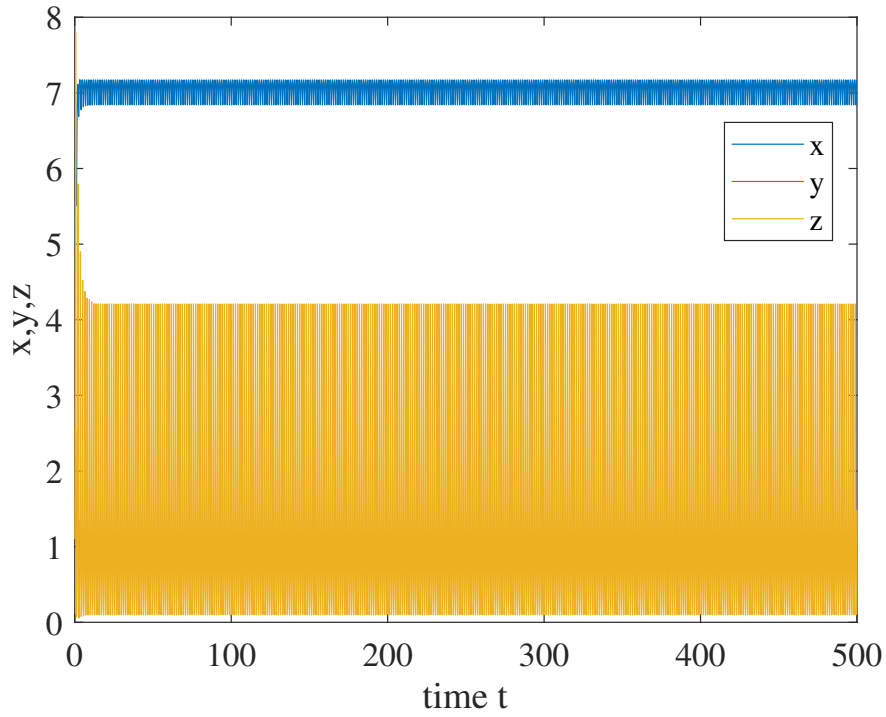
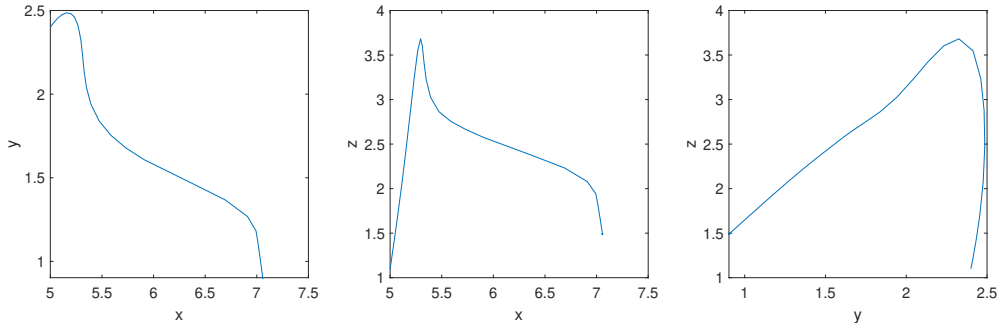


Figure 3.4 : The periodic solutions of the dynamical system continues in a longer time period for $\tau = 0.28$

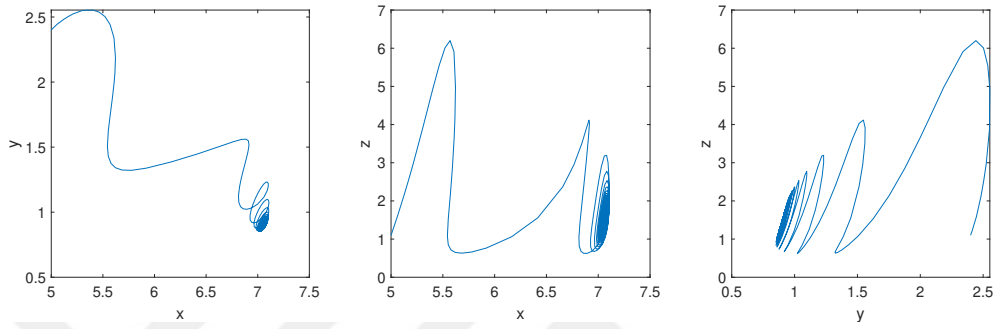
In the Figures above, it is shown clearly that

- Biologically, all three species come to the equilibrium after a time period in Figure 3.1.
- The equilibrium E_{3a} is asymptotically stable when $\tau = 0.1 < \tau_0$.
- The system exhibits a Hopf bifurcation at the equilibrium point E_{3a} when $\tau = \tau_0 = 0.229892$.
- When the delay value $\tau = 0.28 > \tau_0$, periodic solutions bifurcating around the equilibrium point E_{3a} are clearly observed. The bifurcation in this situation is a supercritical bifurcation as bifurcating periodic solutions surrounds an unstable equilibrium point.

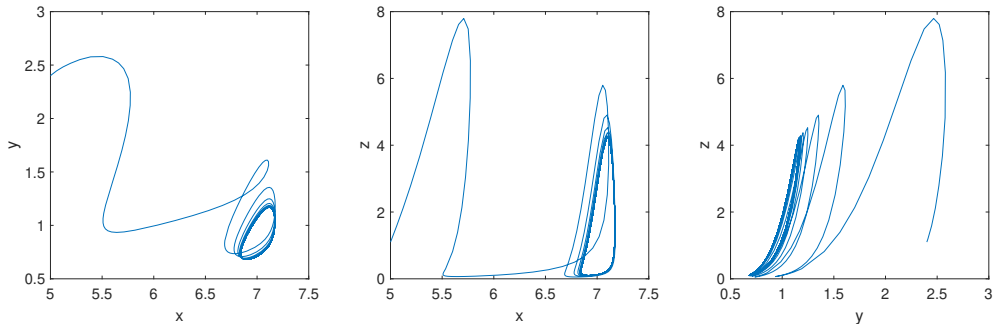
Additionally, there are two and three dimensional phase portrait below for each τ values.



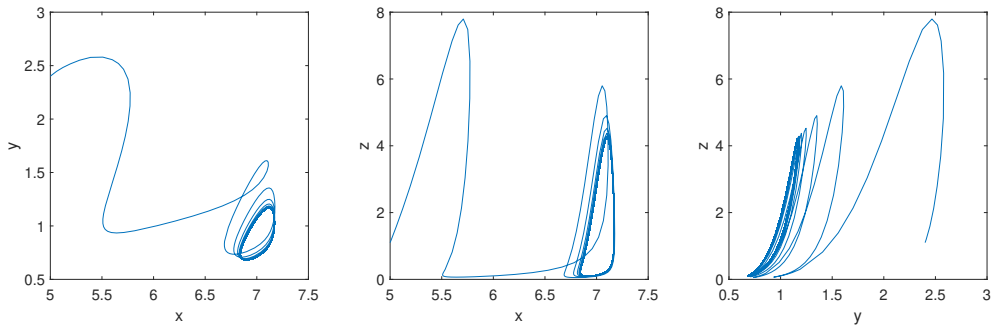
(a)



(b)



(c)



(d)

Figure 3.5 : Two dimensional phase portraits for (a) $\tau = 0.1$, (b) $\tau = 0.229892$, (c) $\tau = 0.28$, (d) $\tau = 0.28$ in a long time period

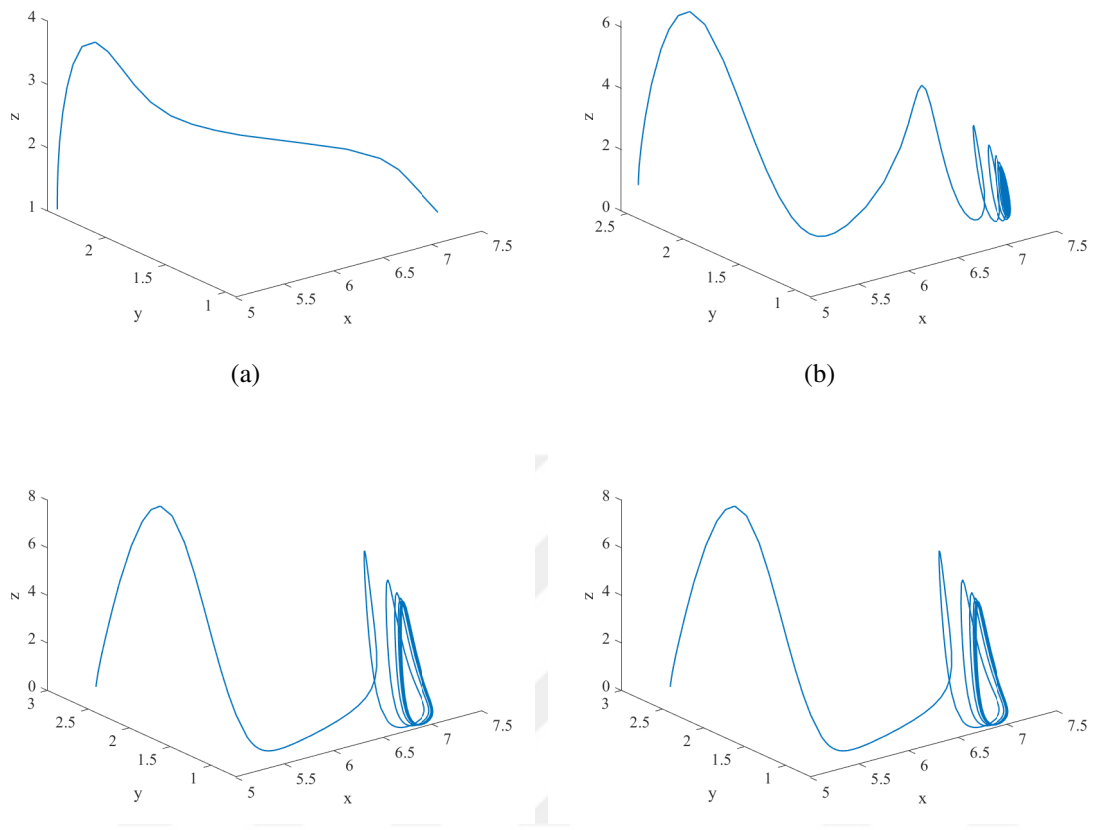


Figure 3.6 : Three dimensional phase portraits for (a) $\tau = 0.1$, (b) $\tau = 0.229892$, (c) $\tau = 0.28$, (d) $\tau = 0.28$ in a long time period

To summarize, all results obtained from numerical simulations matched with the theoretical results in Section 3.2.

4. CONCLUSION

To sum up, in this work, a new prey-predator model is presented and explained to make an understanding of a three-species ecological system, that contains two preys and one predator. Basically, we have established our model on the classical Holling-Tanner model and its variants available in the existing literature. The model proposed and analysed in this study has been named the Modified Holling-Tanner Type II (MHT) and MHT is

$$\frac{dx}{dt} = r_1 x(1-\frac{x}{K_1})(x-m) - \frac{q_1 x\, z}{x+a_1}, \tag{4.1a}$$

$$\frac{dy}{dt} = r_2 y(1-\frac{y}{K_2}) - \frac{q_2 y\, z}{y+a_2}, \tag{4.1b}$$

$$\frac{dz}{dt} = z[s_1(1-\frac{z}{n_1 x}) + s_2(1-\frac{z}{n_2 y})]. \tag{4.1c}$$

Firstly, the stability conditions and the dynamic biological behaviors of this new prey-predator system are studied at three different equilibrium points, that are $E_1(K_1,K_2,0)$, $E_2(m,K_2,0)$ and $E_3(x^*,y^*,z^*)$. The conditions for the system to be stable system at these equilibrium points are obtained and listed by using Routh-Hurwitz criterion.

Based on this model, we proposed a delayed variant in the form

$$\frac{dx}{dt} = r_1 x(1-\frac{x}{K_1})(x-m) - \frac{q_1 x\, z(t-\tau)}{x+a_1}, \tag{4.2a}$$

$$\frac{dy}{dt} = r_2 y(1-\frac{y}{K_2}) - \frac{q_2 y\, z(t-\tau)}{y+a_2}, \tag{4.2b}$$

$$\frac{dz}{dt} = z[s_1(1-\frac{z(t-\tau)}{n_1 x}) + s_2(1-\frac{z(t-\tau)}{n_2 y})] \tag{4.2c}$$

in which the delay term τ is for taking into account the case that the members of the predator species need time from birth to predation for being active predators. Analyzing the stability of the delayed system at the equilibrium point $E_3(x^*,y^*,z^*)$, a Hopf bifurcation is observed while time delay parameter τ changes. When time delay parameter τ passes a critical value τ_0, the system experiences a Hopf bifurcation and the stability of the system at the positive equilibrium $E_3(x^*,y^*,z^*)$ changes from stable

to unstable. There is no need to analyze the delay case at the other two equilibrium $E_1(K_1, K_2, 0)$ and $E_2(m, K_2, 0)$ because of the absence of predator which has the only delay terms in the dynamical system.

Some numerical simulations are performed for different values of τ to support the theoretical results. These simulations matched well with our results in Sections 3.1 and 3.2 of Chapter 3.

We would like to finalize by some recommendations which could be useful for further research that may originate from this thesis work. The newly established prey-predator model has proved itself to explain a case where there are two prey species and one predator species. As a future work, the model can be modified for four species or three species but with different interactions among them. Together with these modifications, different delay-dynamical models beyond the one we have considered in this work could be studied.

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