

EFFECTS OF DISCRETE TIME DELAYS AND PARAMETERS
VARIATION ON DYNAMICAL SYSTEMS

by

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This dissertation is dedicated to my family and friends. Most especially to my late uncle Lassana Coulibaly, for his love of mathematics and for being such a great mentor to me all these years. May his soul rest in peace !

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ABSTRACT

EFFECTS OF DISCRETE TIME DELAYS AND PARAMETERS VARIATION ON DYNAMICAL SYSTEMS

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To understand the effects of discrete time delays and of parameters variation on certain biological system models, we first consider a Delay Differential Equation model of human immunodeficiency virus (HIV). We investigate the effects of the discrete time on the virulence of the HIV strain, and present sufficient and necessary condition for the virulence of the pathogen to change as the time delay changes.

We also consider the same delay differential model for HIV infection, and we investigate analytically and numerically the stability of the endemically infected equilibrium. Our analysis shows that certain key parameters, such as the rate of infection, play a crucial role on how the discrete time may affect the dynamics of the system.

We carry out a bifurcation analysis of systems of delay differential equations. We present general results for one equation with one and two delays and study a specific example of one equation with one delay. We then establish the procedure for n equations with multiple delays and do a specific example for two equations with two delays. We investigate the stability of the steady states as both chosen bifurcation parameters, the discrete time delay τ and a local equation parameter μ , cross critical

values. Our analysis shows that while changes in both parameters can destabilize the steady state, the discrete time delay can cause stability switches of the steady state for certain values of μ , while the effects of the local equation parameter on the steady state do not necessarily depend on the value of τ . While μ may cause the system to go through different type of bifurcations, the discrete time delay can only introduce a Hopf bifurcation for certain values of μ .

We finally consider a delay partial differential equation of a Holling type predator-prey model. It is well known that the distribution of species is generally heterogeneous spatially, and therefore the species will migrate towards regions of lower population density to increase the possibility of survival. Thus, partial differential equations with delay became the subject of a considerable interest in recent years. We consider, simultaneously, time delays and spatial diffusion to model the predator prey model presented in chapter 4. The discrete time delays are introduced in order to consider the time maturation for both the predator and prey populations. We mainly investigate, analytically and numerically, the effects of the spatial diffusion, the time delays and parameters variation on the dynamics of the system.

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CHAPTER 1

INTRODUCTION

To understand the effects of discrete time delays and of parameter variations on certain biological system models, we first consider in chapter 3 a Delay Differential Equation of cell-free viral spread of human immunodeficiency virus (HIV) in a well-mixed compartment such as the bloodstream. A discrete time delay is introduced to take into account the time between infection of a $CD4^+$ T-cell and the emission of viral particles at the cellular level. The time delay is due to reverse transcription, integration, and the production of capsid proteins. We investigate the effects of the discrete time on the virulence of the HIV strain, and present sufficient and necessary condition in theorem 3.5.2 for the virulence of the pathogen to change as the time delay changes.

In chapter 4 we consider the same delay differential model for HIV infection. We investigate analytically and numerically the stability of the endemically infected equilibrium. Our analysis shows that certain key parameters such as the rate of infection play a crucial role on how the discrete time may introduce stability switch of the steady state (or equilibrium) and cause the system to go through a Hopf bifurcation near that steady state (Lemmas 4.3.1 and 4.3.2). This motivates chapter 5.

We carry out in chapter 5 a bifurcation analysis of systems of delay differential equations. We present general results for one equation with one and two delays and study a specific example of one equation with one delay. We then establish the procedure for n equations with multiple delays and do a specific example for

two equations with two delays. We investigate the stability of the steady states as both chosen bifurcation parameters, the discrete time delay τ and a local equation parameter μ , cross critical values. Our analysis shows that while changes in both parameters can destabilize the steady state, the discrete time delay can cause stability switches of the steady state for certain values of μ , while the effects of the local equation parameter on the steady state do not necessarily depend on the value of τ . While μ may cause the system to go through different type of bifurcations, the discrete time delay can only introduce a Hopf bifurcation for certain values of μ .

We finally consider a delay partial differential equation of a Holling type predator-prey model. We investigate the effects of the diffusion, the time delays and parameters variation on the system. We show that the diffusion highly impacts the effects of the time delays on the system. We present both analytical and numerical analysis of the stability and Hopf bifurcation process of the system.

CHAPTER 2

DELAY DIFFERENTIAL EQUATIONS

Most processes take time to complete. While physical processes such as acceleration and deceleration take little time compared to the times needed to travel most distances, the times involved in biological processes such as gestation and maturation can be substantial when compared to the data-collection times in most population studies. Therefore, it is often imperative to explicitly incorporate these process times into mathematical models of population dynamics. These process times are often called delay times, and the models that incorporate such delay times are referred as delay differential equation (DDE) models.

2.1 Delay Differential Equations (DDE's)

DDE's are differential equations in which the derivatives of some unknown functions at present time are dependent on the values of the functions at previous times. Mathematically, a general delay differential equation for $x(t) \in \mathbb{R}^n$ takes the form:

$$\frac{dx}{dt} = f(x(t), x(t - \tau)), \quad (2.1)$$

where $x \in \mathbb{R}^n$, $\tau \geq 0$ is a constant discrete time, $f \in \mathbb{C}^1$ and is assumed to be smooth enough to guarantee existence and uniqueness of solutions to (2.1) under the initial value condition. $f : \mathbb{R}^n \times C \rightarrow \mathbb{R}^n$, where $C = C([- \tau, 0], \mathbb{R}^n)$, with initial condition

$$x(\theta) = \phi(\theta), \quad \theta \in [-\tau, 0].$$

Observe that $x(\theta)$ with $-\tau \leq \theta \leq 0$ represents the solution trajectory in a recent past. The reason of incorporating discrete time delays to model certain dynamical systems

is for the model to be more realistic. However delay differential equations reveal more complex dynamics than ordinary differential equations. A discrete time delay may cause stability changes of the system and also raise Hopf bifurcations, that is a family of periodic solutions. A steady state or equilibrium point for the system (2.1) is any (x^*, x^*) such that $f(x^*, x^*) = 0$. In the following sections we will introduce the notion of stability of such equilibrium and point out the necessary and sufficient conditions for the equilibrium to be stable.

2.2 Stability of an equilibrium of a DDE's system

Similarly to the Ordinary differential equations (ODE'S) systems, the stability of an equilibrium point of a DDE's system is determined by the location of the roots of the characteristic equation. Consider the following system of non-linear delay differential equations:

$$\frac{dx}{dt} = f(x(t), x(t - \tau_1), \dots, x(t - \tau_k)), \quad (2.2)$$

where $x \in \mathbb{R}^n$, $\tau_j \geq 0$, $1 \leq j \leq k$ are constant discrete times. To linearize system (2.2) around the steady state $x^* \in \mathbb{R}^n$, assume that $\bar{x}(t) = x(t) - x^* \in \mathbb{R}^n$ is solution of (2.2). Apply the Taylor formula to the vector function $f(\bar{x}(t) + x^*, \bar{x}(t - \tau_1) + x^*, \dots, \bar{x}(t - \tau_k) + x^*)$. We have

$$\frac{dx}{dt} = \frac{d\bar{x}(t)}{dt} = f(\bar{x}(t) + x^*, \bar{x}(t - \tau_1) + x^*, \dots, \bar{x}(t - \tau_k) + x^*) \quad (2.3)$$

$$= f(x^*, \dots, x^*) + A_0 \bar{x}(t) + \sum_{j=1}^k A_j \bar{x}(t - \tau_j) + O(\|\bar{x}\|^2) \quad (2.4)$$

with

$$f(x^*, \dots, x^*) = 0, \quad A_j = \left. \frac{\partial f}{\partial x_j} \right|_{(x^*, x^*, \dots, x^*)}, \quad j = 0, 1, \dots, k.$$

Therefore the linearization of (2.2) at (x^*, \dots, x^*) has the form (Ruan [1]):

$$\frac{dX}{dt} = A_0 X(t) + \sum_{j=1}^k A_j X(t - \tau_j), \quad (2.5)$$

where $X \in \mathbb{R}^n$, each A_j ($0 \leq j \leq k$) is an $n \times n$ constant matrix defined as above. If $X(t) = Ie^{\lambda t}$ is solution to the system (2.5), where I is the identity matrix of \mathbb{R}^n , then system (2.5) is equivalent to :

$$\lambda I e^{\lambda t} = A_0 e^{\lambda t} + \sum_{j=1}^k A_j e^{-\lambda \tau_j} e^{\lambda t},$$

or

$$\left[\lambda I - A_0 - \sum_{j=1}^k A_j e^{-\lambda \tau_j} \right] e^{\lambda t} = 0$$

then

$$\left[\lambda I - A_0 - \sum_{j=1}^k A_j e^{-\lambda \tau_j} \right] = 0.$$

$(\lambda I - A_0 - \sum_{j=1}^k A_j e^{-\lambda \tau_j})$ is a non invertible matrix, therefore its determinant is zero.

The transcendental equation or characteristic equation associated with system (2.5) is given as :

$$\det \left[\lambda I - A_0 - \sum_{j=1}^k A_j e^{-\lambda \tau_j} \right] = 0 \quad (2.6)$$

Driver et al [2] have shown the following two very important theorems

Theorem 2.2.1.

Given any real number ρ , the characteristic equation (2.6) has at most a finite number of roots λ such that $Re(\lambda) \geq \rho$.

Loosely speaking, the preceding theorem says that most of the roots of the equation (2.6) have negative real part. Furthermore, the roots cannot accumulate except about $Re(\lambda) = -\infty$. In much of our future analysis, we will be interested

in the space $C([- \tau, 0], \mathbb{R})$, representing all initial functions. When endowed with the norm

$$\|\phi\| = \sup_{t \in [-\tau, 0]} |\phi(t)|$$

This is a Banach Space.

Theorem 2.2.2.

If $\operatorname{Re}(\lambda) < \rho$ for every solution of the characteristic equation (2.6), then there exists a constant $M > 0$ such that, for each $\phi \in C([t_0 - \tau, t_0], \mathbb{R})$, the solution to (2.2) satisfies

$$\|x(t, \phi)\| \leq M \|\phi\| e^{\rho(t-t_0)}$$

So the behavior of linear delay differential equations is given an upper bound by the location of the eigenvalue with the largest real part. By combining these two results, we arrive at the following result proposed by J. Forde [3], which forms the foundation of the stability analysis for a DDE's system.

Corollary 2.2.1.

If $\operatorname{Re}(\lambda) < 0$ for every solution of the characteristic equation (2.6), then there exist constants $M, \gamma > 0$ such that, for each $\phi \in C([t_0 - \tau, t_0], \mathbb{R})$, the solution to (2.2) satisfies

$$\|x(t, \phi)\| \leq M \|\phi\| e^{-\gamma(t-t_0)}.$$

In other words, if all of the eigenvalues have negative real part, then solutions to the delay differential equation decay exponentially to 0, exactly as it is the case for ordinary differential equations.

When there are no delays i.e $\tau_1 = \dots = \tau_k = 0$ then the characteristic equation (2.6) is just a polynomial equation of degree n . A nice result known as the Routh-Hurwitz stability criterion present necessary and sufficient conditions for all the roots

of the characteristic equation to have a negative real part ([4], [5], [6]). We present the result for $n = 3$.

Theorem 2.2.3 (Routh-Hurwitz stability criterion).

Let $f(z) = a_3z^3 + a_2z^2 + a_1z + a_0$ be a polynomial with real coefficients. If all the coefficients satisfy $a_i > 0$, $i = 0, \dots, 3$ and $a_2a_1 - a_3a_0 > 0$ then the equation $f(z) = 0$ has all its roots with negative real part.

In our future analysis we investigate how the discrete time delay may introduce stability change of a steady state point. To do so, we consider the eigenvalues of the characteristic equation (2.6) as functions of the discrete time delay. A very important theorem also known as the Rouché's theorem presented by Dieudonne [7] (theorem 9.17.4) is used as the backbone of our analysis. For the proof of the theorem please see Dieudonne [7] (theorem 9.17.4)

Theorem 2.2.4 (Continuity of the roots of an equation as a function of parameters).

Let A be an open set in \mathbb{C} , M a metric space, f a continuous complex valued function in $A \times M$, such that for each $\alpha \in M$, $z \rightarrow f(z, \alpha)$ is analytic in A . Let B be an open subset of A , whose closure $\overline{B} \in \mathbb{C}$ is compact and contained in A , and let $\alpha_0 \in M$ be such that no zero of $f(z, \alpha_0)$ is on the frontier of B . Then there exists a neighborhood W of α_0 such that:

- *for any $\alpha \in W$, $f(z, \alpha)$ has no zeros on the frontier of B ,*
- *for any $\alpha \in W$, the sum of the orders of the zeros of $f(z, \alpha)$ belonging to B is independent of α .*

In other words the Rouché's theorem gives us an idea of the location of the zeros of an analytic function, and also the number of its zeros independently of a parameter that the function may depend on. Using the Rouché's theorem we can now formulate the following important result

Lemma 2.2.1.

Consider the transcendental equation

$$\lambda^n + \sum_{i=1}^n a_{n-i} \lambda^{n-i} + \sum_{i=1}^n b_{n-i} e^{-\lambda\tau} \lambda^{n-i} = 0, \quad (2.7)$$

if there exists a $\tau_c > 0$ such that $\lambda(\tau_c)$ is a purely imaginary eigenvalue of (2.7), then for $\tau > \tau_c$ the transcendental equation (2.7) has at least one eigenvalue with a strictly positive real part.

Before we prove the above lemma, let just first consider a much simpler case.

Consider the analytic function

$$h(\lambda, a) = \lambda + e^{-\lambda\tau} + a,$$

with $\tau \geq 0$, and $a \in \mathbb{R}$.

Then $h(\lambda, 0) = 0$ if and only if

$$\lambda = -e^{-\lambda\tau}. \quad (2.8)$$

Equation (2.8) has purely imaginary roots if and only if $\tau = \tau_c = 2j\pi + \frac{\pi}{2}$, $j = 0, 1, 2, \dots$

The proof of the following lemma can be found in Cooke and Van den Driessche [8]; see also Bellman and Cooke [9].

Lemma 2.2.2.

If $\tau \in [0, \frac{\pi}{2})$, then all roots of equation (2.8) have strictly negative real parts. If $\tau \in (2j\pi + \frac{\pi}{2}, (2j+1)\pi + \frac{\pi}{2}]$, then equation (2.8) has exactly $2j+1$ roots with strictly positive real parts.

We have $h(\lambda, a)$ is an analytic function in λ, a . When $\tau \neq 2j\pi + \frac{\pi}{2}$, the function $h(\lambda, 0)$ has no zeros on the boundary of Ω , where $\Omega = \{\lambda, |Re(\lambda)| \geq 0, |\lambda| \leq \rho\}$. Thus, Rouché's theorem implies that there exists a $\delta > 0$ such that :

- (1) for any $a < \delta$, $h(\lambda, a)$ has no zero on the boundary of Ω
- (2) for any $a < \delta$, $h(\lambda, a)$ and $h(\lambda, 0)$ have the same sum of the orders of zeros belonging to Ω .

It follows from lemma 2.2.2 that when $\tau > \frac{\pi}{2}$, the sum of the orders of the zeros of $h(\lambda, 0)$ belonging to Ω is at least 1. Thus when $\tau > \frac{\pi}{2}$, $\tau \neq 2j\pi + \frac{\pi}{2}$, and $a < \delta$ then $h(\lambda, a)$ has at least a root with strictly positive real part.

Now we can prove the more general form which is lemma 2.2.1

Proof : Consider the analytic function in λ, A

$$h(\lambda, A) = \lambda^n + \sum_{i=1}^n a_{n-i} \lambda^{n-i} + \sum_{i=1}^n b_{n-i} e^{-\lambda\tau} \lambda^{n-i}, \quad (2.9)$$

where $\lambda \in \mathbb{C}$, and $A = (a_{n-1}, \dots, a_1, a_0, b_{n-1}, \dots, b_1) \in \mathbb{R}^{n \times (n-1)}$. Then

$$h(\lambda, A_0) = \lambda^n + b_0 e^{-\lambda\tau}$$

where $A_0 = (0, \dots, 0)$ is the null vector. $h(\lambda, A_0)$ has purely imaginary roots if and only if

$$\tau = \tau_c^j = \frac{2j\pi}{b_0^{1/n}} \quad j = 1, 2, \dots \quad \text{when } n \text{ is even,}$$

or

$$\tau = \tau_c^j = \frac{(4j+1)\pi}{2b_0^{1/n}} \quad j = 0, 1, 2, \dots \quad \text{when } n \text{ is odd,}$$

and here we assume that $b_0 > 0$, otherwise we multiple by a $-$ sign. When $\tau \neq \tau_c^j$ the function $h(\lambda, A_0)$ has no zero on the boundary of Ω , where $\Omega = \{\lambda, |Re(\lambda)| \geq 0, |\lambda| \leq \rho\}$.

Thus, Rouché's theorem implies that there exists a $\delta > 0$ such that :

- (1) when $\|A\|_\infty < \delta$, $h(\lambda, A)$ has no zero on the boundary of Ω
- (2) when $\|A\|_\infty < \delta$, $h(\lambda, A)$ and $h(\lambda, A_0)$ have the same sum of the orders of zeros belonging to Ω .

It follows from lemma 2.2.2 that when $\tau > \tau_c = \frac{2\pi}{b_0^{1/n}}$ and $\tau \neq \frac{2j\pi}{b_0^{1/n}}$ (or $\tau > \tau_c = \frac{1\pi}{2b_0^{1/n}}$ and $\tau \neq \frac{(4j+1)\pi}{2b_0^{1/n}}$), the sum of the orders of the zeros of $h(\lambda, A_0)$ belonging to Ω

is at least 1. Thus when $\tau > \tau_c$, $\tau \neq \tau_c^j$ and $\|A\|_\infty < \delta$ then $h(\lambda, A)$ has at least a root with strictly positive real part. \square

Definition 2.2.1.

In the mathematical theory of bifurcations, a Hopf or Poincare-Andronov-Hopf bifurcation, named after Henri Poincare, Eberhard Hopf, and Aleksandr Andronov, is a local bifurcation in which a fixed point of a dynamical system loses stability as a pair of complex conjugate eigenvalues of the linearization around the fixed point cross the imaginary axis of the complex plane. Under reasonably generic assumptions about the dynamical system, we can expect to see a small-amplitude limit cycle branching from the fixed point. [10], [11]

One of the most important features of DDE's is the notion of Hopf bifurcation. When a discrete time delay causes stability switch of steady state, and if further the transversality condition is satisfied then the delay will cause the system to go through a Hopf bifurcation, near the steady state. Here we formulate the Hopf bifurcation theorem, see Culshaw [12].

2.3 Hopf bifurcation theorem

Consider the 3-dimensional autonomous system of differential equations given by

$$\frac{dx}{dt} = F(x, y, z, \tau), \quad (2.10)$$

$$\frac{dy}{dt} = G(x, y, z, \tau), \quad (2.11)$$

$$\frac{dz}{dt} = H(x, y, z, \tau), \quad (2.12)$$

which depends on the real parameter τ . If

- (i) $F(x^*, y^*, z^*, \tau) = G(x^*, y^*, z^*, \tau) = H(x^*, y^*, z^*, \tau) = 0$ for τ in an open interval containing τ_c , and (x^*, y^*, z^*) is a steady state solution of the system (2.10-2.12),

- (ii) F, G, and H are analytic in x, y, z and τ in a neighbourhood of (x^*, y^*, z^*, τ_c) ,
- (iii) The Jacobian matrix of (2.10-2.12) at (x^*, y^*, z^*, τ_c) has a pair of complex conjugate eigenvalues λ and λ^* such that:

$$\lambda(\tau) = \alpha(\tau) + i\omega(\tau),$$

where

$$\omega(\tau_c) = \omega_c > 0, \quad \alpha(\tau_c) = 0, \quad \left. \frac{d\alpha(\tau)}{d\tau} \right|_{\tau=\tau_c} \neq 0,$$

- (iv) The remaining eigenvalue of the Jacobian matrix at (x^*, y^*, z^*, τ_c) has strictly negative real part, then the system (2.10-2.12) has a family of periodic solutions: there is an $\epsilon_H > 0$ and an analytic function, $\tau^H(\epsilon) = \sum_2^\infty \tau^H(\epsilon^i)$, ($0 < \epsilon < \epsilon_H$) such that for each $\epsilon \in (0, \epsilon_H)$ there exists a periodic solution $p_\epsilon(t)$ occurring for $\tau = \tau^H(\epsilon)$. The period $T^H(\epsilon)$ of $p_\epsilon(t)$ is an analytic function

$$T^H(\epsilon) = \frac{2\pi}{\omega_c} \left(1 + \sum_2^\infty \tau^H(\epsilon^i) \right), \quad (0 < \epsilon < \epsilon_H)$$

2.4 Numerical Methods for DDEs

In this section we discuss few aspects of two main tools for DDE's, a Matlab delay differential equation solver `dde23`, and a stability and bifurcation's analysis tool `DDE-BIFTOOL` for DDE.

2.4.1 DDE's solver `dde23`

A popular approach to solving DDEs is to extend one of the methods used to solve ODEs. Most of the codes are based on explicit Runge-Kutta methods. `dde23`

takes this approach by extending the method of the MATLAB ODE solver ode23, see [13]. For instance consider

$$\frac{dx}{dt} = f(x(t), x(t - \tau)),$$

with given initial condition $\phi : [-\tau, 0] \rightarrow \mathbb{R}^n$. Then the solution on the interval $[0, \tau]$ is given by $\psi(t)$ which is the solution to the inhomogeneous initial value problem

$$\frac{d\psi(t)}{dt} = f(\psi(t), \phi(t - \tau)),$$

with $\psi(0) = \phi(-\tau)$. This can be continued for the successive intervals by using the solution to the previous interval as inhomogeneous term. In practice, the initial value problem is often solved numerically using the numerical tool such as Matlab solver dde23 [13], FORTRAN DDE solver [13], DMRODE [14].

Example: Malthus growth (Allen, 2007)

Consider

$$\frac{dx}{dt} = x(t - 1) + 1$$

with initial condition: $x(t) = 0 = \phi_0(t)$, $t \in [-1, 0]$. First solve from $t = 0$ to $t = 1$ replacing $x(t - 1)$ by $\phi_0(t - 1)$:

$$\frac{dx}{dt} = \phi_0(t - 1) + 1 = 1, \quad x(0) = \phi_0(-1) = 0.$$

The Solution is

$$x(t) = t = \phi_1(t), \quad t \in [0, 1].$$

Step 2 is solve:

$$\frac{dx}{dt} = \phi_1(t - 1) + 1 = t, \quad x(1) = \phi_1(t), \quad t \in [0, 1].$$

The Solution is

$$x(t) = \frac{t^2}{2} + \frac{1}{2} = \phi_2(t), \quad t \in [1, 2].$$

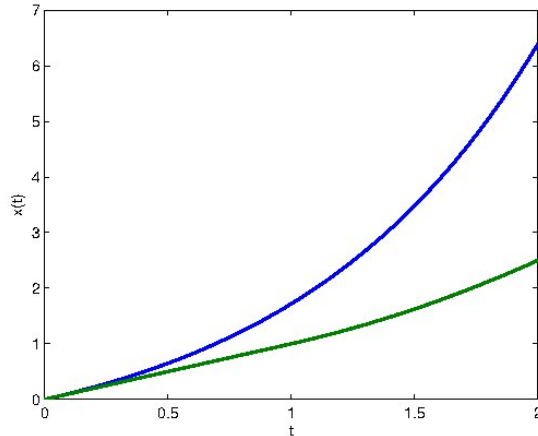


Figure 2.1. Plot of solutions with (green) and without delay (blue)..

2.4.2 DDE-BIFTOOL

DDE-BIFTOOL is a Matlab package for numerical bifurcation analysis of systems of delay differential equations with several fixed, discrete delays. The package implements continuation of steady state solutions and periodic solutions and their stability analysis. It also computes and continues steady state fold and Hopf bifurcations, see [15]. A steady state solution $x^* \in \mathbb{R}^n$ of (2.2) is determined from $(n \times n)$ -dimensional determining system $f(x^*, \dots, x^*) = 0$ using Newton iterations. Once a steady state solution is obtained, stability is determined by computing the rightmost roots of its characteristic equation. These roots are first approximated using a linear multi-step method (LMS-method) applied to (2.5). Please refer to [15] for computation and continuation of the Hopf branches and more details on the package.

2.5 DDE's Model for Human Immunodeficiency Virus (HIV)

Delay differential equations are commonly use to model biological systems such as population models, epidemiological models, infectious models.... One of our main application for DDE's is the mathematical model for the human immunodeficiency virus (HIV). It is well known that HIV targets CD4⁺ T-cells lymphocytes, the most abundant white blood cells of the immune system . A protein called gp120 protein on the viral particle binds to the CD4⁺ receptors on the CD4⁺ T-cell and injects its core. After an intracellular delay associated with reverse transcription, integration, and the production of capsid proteins, the infected cell releases hundreds of virions. These virions can infect other CD4⁺ T-cells. Based on this understanding we write the following DDE's for the infection

$$\frac{dT}{dt} = s - \mu_T T - k_1 VT, \quad (2.13)$$

$$\frac{dI}{dt} = k_2 V(t - \tau) T(t - \tau) - \mu_I I, \quad (2.14)$$

$$\frac{dV}{dt} = N\mu_b I - k_1 VT - \mu_V V, \quad (2.15)$$

under the initial values

$$T(\theta) = T_0, \quad I(\theta) = 0, \quad V(\theta) = V_0, \quad \theta \in [-\tau, 0].$$

Where the discrete time delay τ represent the viral eclipse phase.

The parameter's values and description are given as in Culshaw [12], see table 2.1:

Table 2.1. Variables and parameters for viral spread

Parameters and variables	Description	Values
T	Uninfected $CD4^+$ T-cell population size	1000 mm^{-3}
I	Infected $CD4^+$ T-cell density	0
V	Initial density of HIV RNA	$10^{-3} mm^{-3}$
μ_T	Natural death rate of $CD4^+$ T-cells	0.02 day^{-1}
μ_I	Blanket death rate of infected $CD4^+$ T-cells	0.26 day^{-1}
μ_b	Lytic death rate for infected cells	0.24 day^{-1}
μ_V	Death rate of free virus	2.4 day^{-1}
k_1	Rate of $CD4^+$ T-cell to become infected by virus	$2.4 * 10^{-5} mm^3day^{-1}$
k_2	Rate infected cells become active	$2 * 10^{-5} mm^3day^{-1}$
N	Number of virions produced by infected $CD4^+$ T-cells	Varies
s	Source term for uninfected $CD4^+$ T-cells	10 $day^{-1}mm^{-3}$
τ	Discrete time delay due to viral eclipse phase	Varies

CHAPTER 3

EFFECTS OF DISCRETE TIME DELAY ON THE VIRULENCE

3.1 The Basic Reproduction Number

The basic reproduction number, R_0 , is defined as the expected number of secondary cases produced by a single (typical) infection in a completely susceptible population. It is important to note that R_0 is a dimensionless number and not a rate, which would have units of $time^{-1}$. Some authors incorrectly call R_0 the basic reproductive rate. We can use the fact that R_0 is a dimensionless number to help us in calculating it, see [16].

$$R_0 \propto \left(\frac{infection}{contact} \right) \times \left(\frac{contact}{time} \right) \times \left(\frac{time}{infection} \right).$$

Note that R_0 is a dimensionless quantity. More specifically :

$$R_0 = \gamma \times \bar{c} \times d,$$

where γ is the transmissibility (i.e., probability of infection given contact between a susceptible and infected individual), \bar{c} is the average rate of contact between susceptible and infected individuals, and d is the duration of infectiousness. If $R_0 > 1$ then the disease will propagate, otherwise the disease will eventually die and a fraction of the population will escape infection.

3.2 Next Generation Matrix Method

There are several methods of computing R_0 . The most formal and most popular approach is the next generation matrix approach. Many papers such as Hefferman

et al [17] , and James [16] provide a nice introduction for calculating R_0 using this method. The notation we use here follows their usage. Consider the next generation matrix G . It is comprised of two parts: F and V^{-1} , where

$$F = \left[\frac{\partial F_i(x_0)}{\partial x_j} \right]$$

and

$$V = \left[\frac{\partial V_i(x_0)}{\partial x_j} \right]$$

The F_i are the new infections, while the V_i transfers of infections from one compartment to another. x_0 is the disease-free equilibrium state. R_0 is the dominant eigenvalue of the matrix $G = FV^{-1}$.

3.3 Evolutionary Stable Strategy (ESS) of Virulence

It is instructive to think about epidemics from the pathogen's perspective. Pathogens bear biological information in their nucleic acids. This information varies from one copy of a pathogen to another, and the ability of a pathogen to persist and multiply can be a function of this variability (Jones [16], Baalen et al [18]), known as Virulence. In other word virulence is the pathogen ability to transmit disease to a host .

Note that more copies of a virus (say) means that conditional on contact with an infected individual, the pathogen is more likely to be transmitted. However, more viral copies means the host is sicker, and potentially dead. Dead hosts do not transmit and very sick hosts are less likely to be up and interact with susceptible.

An Evolutionary Stable Strategy (ESS) is a phenotype that can not be invaded by a rare mutant. Loosely speaking, it represents the optimal phenotype. The ESS virulence occurs where the fitness gradient equal zero (Jones [16]), meaning :

$$\frac{dR_0}{dx} = 0,$$

where x denoted the virulence.

3.4 Change in Selective Pressures

Researches (Basu et al [19], Otto and Day [20]) have proved that the direction of virulence evolution around an ESS as selective pressures change will be determined by the sign of the derivative of the fitness gradient with respect to the parameter that is changing. In other word the virulence will increase (decrease) when we increase (decrease) a selected parameter n if :

$$\frac{\partial}{\partial n} \left[\frac{\partial R_0(x, n)}{\partial x} \right] > 0. \quad (< 0)$$

3.5 Effects of Discrete Time Delay on Virulence

Consider a delay differential equation of HIV model:

$$\frac{dT}{dt} = s - \mu_T T - k_1 V T, \quad (3.1)$$

$$\frac{dI}{dt} = k_2 V(t - \tau) T(t - \tau) - \mu_I I, \quad (3.2)$$

$$\frac{dV}{dt} = N \mu_b I - k_1 V T - \mu_V V, \quad (3.3)$$

under the initial values

$$T(\theta) = T_0, \quad I(\theta) = 0, \quad V(\theta) = V_0, \quad \theta \in [-\tau, 0].$$

The parameter values and description are given in table 2.1.

To investigate the effects of the discrete time delay τ on the virulence, we compute the basic reproduction number R_0 (see appendix A):

$$R_0(x, \tau) = \frac{\log r_0(x)\tau}{\tau},$$

where,

$$r_0(x) = \frac{N\mu_b k_2(x)}{\mu_I \mu_V(x)}$$

is the basic reproduction number when there is no delay i.e. $\tau = 0$, and x denoted the virulence. $k_2(x)$, and $\mu_V(x)$ denote the dependence of the rate infected cells become active and the death rate of free virions on the virulence respectively.

Theorem 3.5.1.

The Evolutionary Stable Strategy (ESS) of the virulence is independent of the discrete time delay.

Proof:

The fitness gradient of the system is given by :

$$\frac{\partial R_0(x, \tau)}{\partial x} = \frac{\frac{dk_2(x)}{k_2(x)} - \frac{d\mu_v(x)}{\mu_v(x)}}{\tau}. \quad (3.4)$$

The ESS virulence occurs where

$$\frac{dR_0}{dx} = 0,$$

that is if and only if :

$$\frac{dk_2(x)}{d\mu_v(x)} = \frac{k_2(x^*)}{\mu_v(x^*)}, \quad (3.5)$$

where x^* denoted the ESS of x (virulence).

When there is no delay ($\tau = 0$) the fitness gradient is given by :

$$\frac{dr_0(x)}{dx} = \frac{N\mu_b [\mu_v k_2'(x) - k_2 \mu_v'(x)]}{\mu_I \mu_v}, \quad (3.6)$$

therefore the ESS occurs when

$$\mu_v k_2'(x) - k_2 \mu_v'(x) = 0,$$

which is equivalent to equation (3.5). \square

Equation (3.5) has a nice geometric interpretation. The ESS virulence occurs where a line (L1) is tangent to the curve that relates k_2 to μ_v . This result is known as the Marginal Value Theorem and has applications in economics and ecology as well as epidemiology.

Theorem 3.5.2.

The virulence of the HIV strain of the system (3.1-3.3) increases when we increase the discrete time delay τ due to the viral eclipse if and only if

$$k_2 < \mu_v.$$

Proof: The derivative of the fitness gradient (equation (3.4)) with respect to τ is given as :

$$\frac{\partial}{\partial \tau} \left[\frac{\partial R_0(x, \tau)}{\partial x} \right] = - \frac{\frac{dk_2(x)}{k_2(x)} - \frac{d\mu_v(x)}{\mu_v(x)}}{\tau^2}.$$

And

$$\frac{\partial}{\partial \tau} \left[\frac{\partial R_0(x, \tau)}{\partial x} \right] > 0,$$

if and only

$$\frac{dk_2(x)}{k_2(x)} < \frac{d\mu_v(x)}{\mu_v(x)},$$

take the integral of both side and notice that $k_2(0) = \mu_v(0) = 0$, then we obtain

$$k_2 < \mu_v. \quad \square$$

3.6 Results

To illustrate the effects of the delay on the virulence of the infection, we compute numerically the solution of system (3.1-3.3) using Matlab package dde23. The

parameter values are given in table 2.1. The discrete time delay only introduces a time shift, but has no effect on the number of copy of the $CD4^+$ T-cell as shown on figure 3.1.

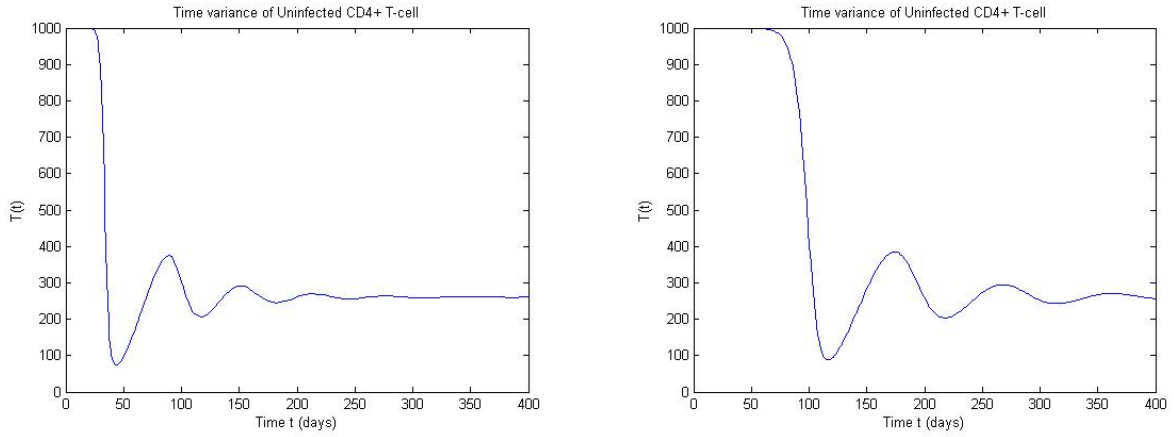


Figure 3.1. Time variance of uninfected $CD4^+$ T-cell without delay (left) and with delay (right) $\tau = 5$ days.

As we increase the delay, the virulence of the disease increases excessively therefore decrease the number of copy of infected $CD4^+$ T-cell see figure 3.2 and the number of copy of free virions see figure 3.3.

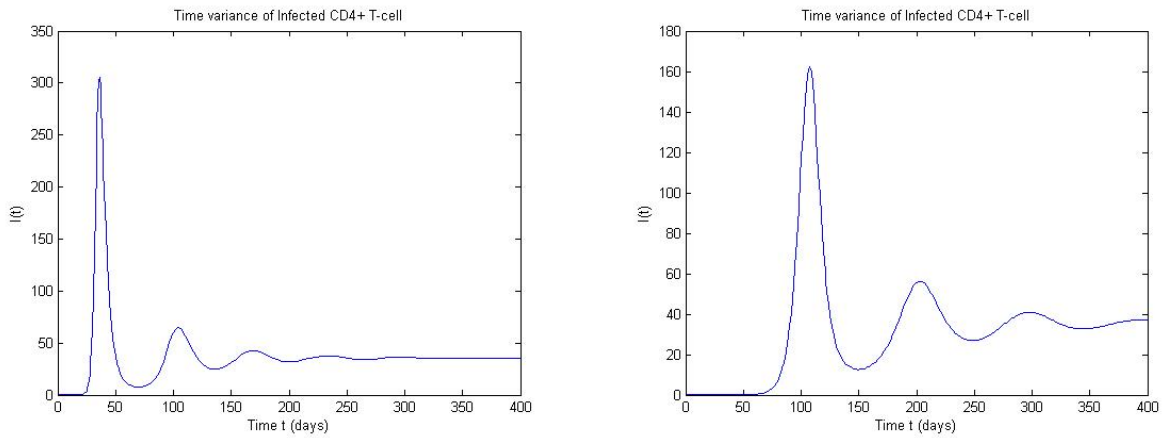


Figure 3.2. Time variance of infected $CD4^+$ T-cell without delay (left) and with delay (right) $\tau = 5$ days.

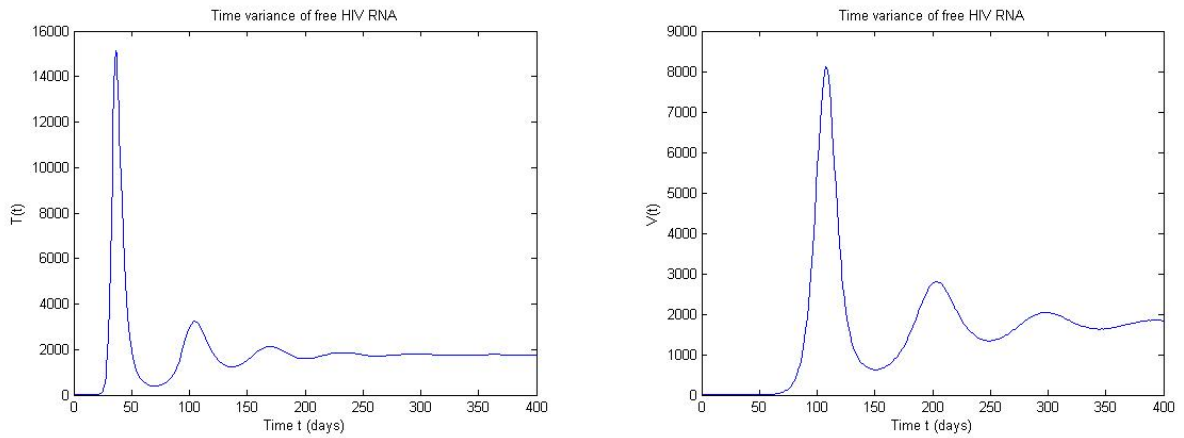


Figure 3.3. Time variance of free HIV virions without delay(left) and with delay (right) $\tau = 5$ days.

CHAPTER 4

EFFECTS OF DISCRETE TIME DELAY ON STABILITY

4.1 Introduction

In this section we investigate the effects of a discrete time delay on the stability of a steady state of a given dynamical system. To do so, we consider the same delay differential equation for a HIV infection (system 3.1- 3.3) as in chapter 1. We first describe the stability of the steady states of the system as there is no delay i.e $\tau = 0$, and then investigate the changes in stability as we introduce the delay. We also point out necessary and sufficient conditions for the delay to affect the stability of the steady states, and to introduce possible Hopf bifurcations.

4.2 Ordinary Differential model for HIV

Assume that all the infected cells are capable of producing virus

$$\frac{dT}{dt} = s - \mu_T T - k_1 VT, \quad (4.1)$$

$$\frac{dI}{dt} = k_2 VT - \mu_I I, \quad (4.2)$$

$$\frac{dV}{dt} = N\mu_b I - k_1 VT - \mu_V V, \quad (4.3)$$

where

- $T(t)$ concentration of healthy $CD4^+$ cells
- $I(t)$ concentration infected $CD4^+$ cells
- $V(t)$ concentration of free HIV cells

All the other parameter descriptions and values are given in table 2.1

Proposition 4.2.1.

i) If $R \leq 1$, then the non-negative steady state of the system (4.1-4.3) is $(T_0^*, I_0^*, V_0^*) = (\frac{s}{\mu_T}, 0, 0)$.

ii) If $R > 1$ and $\beta > 0$ (ie $N > N_{crit} = \frac{\mu_I(k_1s + \mu_v\mu_T)}{\mu_b k_1s}$), then the non-negative steady states are giving as : $(T_0^*, I_0^*, V_0^*) = (\frac{s}{\mu_T}, 0, 0)$, $(T_1^*, I_1^*, V_1^*) = (\frac{\mu_v\mu_I^2}{k_1(R-1)}, \frac{\beta\mu_I}{k_1(R-1)}, \frac{\beta}{k_1\mu_v\mu_I})$

Where

$$R = \frac{N\mu_b}{\mu_I}, \quad \beta = (N\mu_b - \mu_I)k_1s - \mu_v\mu_I\mu_T.$$

Notice that the threshold parameter R could be interpreted as the basic reproductive number. If $R > 1$ then the disease will spread into the system, otherwise if $R \leq 1$ then the disease will eventually die. The parameter N is clearly a bifurcation parameter

4.2.1 Stability Analysis of the equilibria

The Jacobian matrix of the model system evaluated at (T^*, I^*, V^*) is

$$J = \begin{bmatrix} -\mu_T - k_1V^* & 0 & -k_1T^* \\ k_2V^* & -\mu_I & k_2T^* \\ -k_1V^* & N\mu_b & -k_1T^* - \mu_v \end{bmatrix}$$

We will study the stability of our model base on the eigenvalues of the Jacobian matrix.

Proposition 4.2.2.

(i) If $R \leq 1$ and $\beta < 0$ (ie $N < N_{crit} = \frac{\mu_I(k_1s + \mu_v\mu_T)}{\mu_b k_1s}$), then the steady state $(T_0^*, I_0^*, V_0^*) = (\frac{s}{\mu_T}, 0, 0)$ is stable.

(ii) If $R \leq 1$ and $\beta > 0$, then the steady state (T_0^*, I_0^*, V_0^*) is unstable.

(iii) If $R > 1$, $\beta > 0$, $a_1 > 0$, $a_4 + a_5 > 0$ and $a_1(a_2 + a_3) - (a_4 + a_5) > 0$ then the steady state $(T_1^*, I_1^*, V_1^*) = (\frac{\mu_v \mu_I^2}{k_1(R-1)}, \frac{\beta \mu_I}{k_1(R-1)}, \frac{\beta}{k_1 \mu_v \mu_I})$ is stable.

where

$$a_1 := k_1(T^* + V^*) + \mu_v + \mu_I - \mu_T \quad (4.4)$$

$$a_2 := (\mu_I + k_1 V^*)k_1 T^* + \mu_I \mu_v \quad (4.5)$$

$$a_3 := N \mu_b k_2 T^* \quad (4.6)$$

$$a_4 := (\mu_T + k_1 V^*)N \mu_b k_1 k_2 T^* V^* \quad (4.7)$$

$$a_5 := (\mu_T + k_1 V^*)[(N \mu_b - k_2 V^* - \mu_I)k_1 T^* - \mu_I \mu_v] \quad (4.8)$$

Proof: we first remark that the characteristic equation of matrix J is given by :

$$\lambda^3 + a_1 \lambda^2 + (a_2 + a_3) \lambda + (a_4 + a_5) = 0. \quad (4.9)$$

(i) In this case, we substitute the steady state (T_0^*, I_0^*, V_0^*) into the equation (4.9) and find:

$$(\lambda + \mu_T)(\lambda^2 + b_1 \lambda + b_2) = 0,$$

where

$$b_1 := \frac{\mu_I \mu_T + k_1 s + \mu_V \mu_T}{\mu_T} \quad \text{and} \quad b_2 := \frac{-\beta}{\mu_T}$$

– If $\beta < 0$ then $\zeta = b_1^2 - 4b_2 \leq 0$ therefore the eigenvalues of J are

$$\lambda_1 = -\mu_T, \lambda_2 = \frac{-b_1}{2} - \frac{\sqrt{\zeta}}{2}i \quad \text{and} \quad \lambda_3 = \frac{-b_1}{2} + \frac{\sqrt{\zeta}}{2}i$$

Thus the steady state is stable.

– If $\beta > 0$ then $\zeta = b_1^2 - 4b_2 > 0$ therefore the eigenvalues of J are:

$$\lambda_1 = -\mu_T < 0, \lambda_2 = \frac{-b_1}{2} - \frac{\sqrt{\zeta}}{2} < 0 \quad \text{and} \quad \lambda_3 = \frac{-b_1}{2} + \frac{\sqrt{\zeta}}{2} > 0$$

Thus the steady state is unstable.

(ii) Since $R > 1$ and $\beta > 0$, the steady state (T_1^*, I_1^*, V_1^*) exists. By the Routh-Hurwitz criterion, it follows that all roots of the characteristic equation have negative real parts if and only if

$$a_1 > 0, a_4 + a_5 > 0 \text{ and } a_1(a_2 + a_3) - (a_4 + a_5) > 0. \quad \square$$

4.3 Delay Differential Equation Model for HIV

Now we consider the system with a time delay to represent the viral eclipse phase. The model is given as follow:

$$\frac{dT}{dt} = s - \mu_T T - k_1 V T, \quad (4.10)$$

$$\frac{dI}{dt} = k_2 V(t - \tau) T(t - \tau) - \mu_I I, \quad (4.11)$$

$$\frac{dV}{dt} = N \mu_b I - k_1 V T - \mu_V V, \quad (4.12)$$

under the initial values

$$T(\theta) = T_0, \quad I(0) = 0, \quad V(\theta) = V_0, \quad \theta \in [-\tau, 0].$$

Noticed that the delay system has the same steady states as the ODE model.

To study the stability of those steady states, let us define solution of the delay system of the form:

$$\begin{bmatrix} T' \\ I' \\ V' \end{bmatrix} = e^{-\lambda\tau} \begin{bmatrix} T \\ I \\ V \end{bmatrix}$$

then the Jacobian of the system is given by :

$$M = \begin{bmatrix} -\mu_T - k_1 V^* & 0 & -k_1 T^* \\ e^{-\lambda\tau} k_2 V^* & -\mu_I & e^{-\lambda\tau} k_2 T^* \\ -k_1 V^* & N\mu_b & -k_1 T^* - \mu_v \end{bmatrix}$$

the characteristic equation of the DDE model is given by :

$$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3e^{-\lambda\tau}\lambda + a_4e^{-\lambda\tau} + a_5 = 0, \quad (4.13)$$

where $a_i, i = 1, \dots, 5$ are defined as in equations (4.4) to (4.8).

Proposition 4.3.1.

The stability of the non infected steady state does not depend on the delay. Therefore the steady state (T_0^, I_0^*, V_0^*) stability conditions remain the same as of proposition 4.2.2*

Proof: Notice that when consider (T_0^*, I_0^*, V_0^*) , then the coefficients $a_3 = a_4 = 0$ and the characteristic equation of the DDE system becomes $(\lambda + \mu_T)(\lambda^2 + b_1\lambda + b_2) = 0$, and this for all $\tau > 0$. \square

Recall that for the ODE model the steady state (T_1^*, I_1^*, V_1^*) is stable for the parameter values satisfying conditions in proposition 3.2.1(ii). Here, we are interested in determining whether there exists a critical delay $\tau_c > 0$ so that $Re(\lambda) > 0$ for $\tau > \tau_c$. In other words, τ_c is the value of τ s.t $Re(\lambda) = 0$, at which the transition from stability to instability occurs.

For the steady state (T_1^*, I_1^*, V_1^*) , if we let $\lambda(\tau) = \alpha(\tau) + i\omega(\tau)$, where α and ω are real, then we have $\alpha(0) < 0$. Suppose $\alpha(\tau_c) = 0$ for some $\tau_c > 0$, then by the continuity in τ of α , $\alpha(\tau) < 0$ for values of τ such that $0 \leq \tau < \tau_c$. Therefore the steady state remains stable for these values of τ .

If such $\tau_c > 0$ exists, with $\alpha(\tau_c) = 0$ and $\alpha(\tau) < 0$ for $0 \leq \tau < \tau_c$, then by Rouché's Theorem (Dieudonne[7], Theorem 9.17.4) the steady state will lose stability at $\tau = \tau_c$. In fact such τ_c exists if and only there exists $\omega(\tau_c) > 0$ such that $\lambda(\tau_c) = i\omega(\tau_c) = i\omega_c$ is a root of the characteristic equation (4.13), and that is :

$$-i\omega_c^3 - a_1\omega_c^2 + a_2i\omega_c + a_5 + (a_4 + a_3i\omega_c)(\cos \omega_c\tau_c - i \sin \omega_c\tau_c) = 0.$$

Equating real parts and imaginary parts of the equation to zero, one obtains:

$$a_1\omega_c^2 - a_5 = a_4 \cos \omega_c\tau_c + a_3\omega_c \sin \omega_c\tau_c, \quad (4.14)$$

$$-\omega_c^3 + a_2\omega_c = a_4 \sin \omega_c\tau_c - a_3\omega_c \cos \omega_c\tau_c. \quad (4.15)$$

Adding up the square of equations (4.14) and (4.15), one obtains

$$u(\omega_c) := \omega_c^6 + (a_1^2 - 2a_2)\omega_c^4 + (a_2^2 - 2a_1a_5 - a_3^2)\omega_c^2 + a_5^2 - a_4^2 = 0. \quad (4.16)$$

For simplification, we introduce the quantities

$$z := \omega_c^2, \quad p := a_1^2 - 2a_2, \quad q := a_2^2 - 2a_1a_5 - a_3^2, \quad r := a_5^2 - a_4^2$$

Then equation (4.16) reduces to

$$K(z) := z^3 + pz^2 + qz + r = 0. \quad (4.17)$$

Lemma 4.3.1.

Suppose that equation (4.17) has no positive roots. Then , all the roots of the characteristic equation have negative real parts for all $\tau > 0$.

We present conditions that ensure that equation (4.17) has a positive root or has no positive roots. Consider

$$K'(z) = 3z^2 + 2pz + q$$

and

$$3z^2 + 2pz + q = 0,$$

has the roots:

$$Z_0 := \frac{-p + \sqrt{p^2 - 3q}}{3}, \quad Z_1 := \frac{-p - \sqrt{p^2 - 3q}}{3}$$

Lemma 4.3.2.

- i) If either (a) $r < 0$, or (b) $r \geq 0$, $p^2 - 3q > 0$, $p < 0$ and $K(Z_0) < 0$, then equation (4.17) has a positive root.*
- ii) If $r \geq 0$ and $p^2 - 3q < 0$, then equation (4.17) has no positive roots.*

Proof:

- (i) Suppose that condition (a) holds, that is, $r < 0$. Then we have $K(0) = r < 0$.

On the other hand, since

$$\lim_{z \rightarrow +\infty} K(z) = \infty,$$

by the intermediate value theorem, then equation (4.17) must have a positive root z_0 , that is, $K(z_0) = 0$. Now suppose that condition (b) holds. Since $r \geq 0$, $p < 0$, and $p^2 - 3q > 0$, we find that Z_0 is real and $Z_0 > 0$. Since $K(0) = r \geq 0$ and $k(Z_0) < 0$, again by the intermediate value theorem, K has a zero between the origin and Z_0 .

- (ii) Since $p^2 - 3q < 0$, both zeros Z_0 and Z_1 are not real. That is, $K'(z) = 0$ has no real root. Noting that

$$K'(0) = q > \frac{p^2}{3} \geq 0$$

We conclude that the quadratic polynomial K' is strictly positive on the real numbers. This implies that K is increasing on the real numbers. Moreover, since

$K(0) = r \geq 0$, we observe that $K(z)$ does not vanish for $z > 0$ and thus, equation (4.17) has no positive roots.

Noticed that, Lemma 4.3.2(ii) implies that there is no positive ω such that $i\omega$ is a solution of the characteristic equation (4.13). Therefore the real parts of all the eigenvalues of (4.13) are negative for all delay $\tau \geq 0$. \square

Next, we will provide the conditions on the parameters to ensure that Hopf bifurcation occurs. Suppose conditions in Lemma 4.3.2(i) hold, then equation (4.17) has a positive root. We denote, without loss of generality the positive roots of (4.17) by m_j , $j \in \{0, 1, 2\}$ depending on the number of positive roots (4.17) has. Equation (4.16), therefore has at most six roots, $\pm\sqrt{m_j}$ for $j = 0, 1, 2$.

If the solution of equation (4.16) exists, it is among these $\pm\sqrt{m_j}$ for $j = 0, 1, 2$. If $\lambda = i\omega$ is a root of equation (4.13) so is $-i\omega$.

Substituting ω_j into equations (4.14) and (4.15) and solving for τ , we obtain

$$\tau_j^{(n)} = \frac{1}{\omega_j} \arccos \frac{a_3\omega_j^4 + (a_1a_4 - a_2a_3)\omega_j^2 - a_4a_5}{a_4^2 + a_3^2\omega_j^2} + \frac{2n\pi}{\omega_j},$$

where

$$j = 0, 1, 2 \quad \text{and} \quad n = 0, 1, 2, \dots$$

Now, let $\tau_c > 0$ be the smallest of such τ for which $\alpha(\tau_c) = 0$. Thus,

$$\tau_c = \min \tau_j^{(n)} > 0, \quad 0 \leq j \leq 2, n \geq 1, \quad \omega_c = \omega_{jc} \quad (4.18)$$

Theorem 4.3.1.

For the time lag τ , let the critical time lag τ_c and ω_c be defined as in (4.18), and suppose that $(E_2E_3 - E_1E_4) \sin \omega_c\tau_c - (E_2E_4 + E_1E_3) \cos \omega_c\tau_c \neq 0$ then the system of delay differential equations (4.10-4.12) exhibits a Hopf bifurcation at the steady state (T_1^, I_1^*, V_1^*) . Whith*

$$E_1 := a_3 \sin \omega_c\tau_c - 2a_1\omega_c, \quad E_2 := a_3 \cos \omega_c\tau_c + a_2 - 3\omega_c^2,$$

$$E_3 := a_4\omega_c, \quad E_4 := a_3\omega_c^2.$$

Proof. We will show that

$$\frac{d\alpha(\tau)}{d\tau}\Big|_{\tau=\tau_c} \neq 0,$$

which guarantees that the Hopf bifurcation occurs. First we equate real parts and imaginary parts of the characteristic equation to zero:

$$\alpha^3 - 3\alpha\omega^2 + a_1\alpha^2 - a_1\omega^2 + a_2\alpha + a_5 + e^{-\alpha\tau}[(\alpha \cos \omega\tau + \omega \sin \omega\tau)a_3 + a_4 \cos \omega\tau] = 0, \quad (4.19)$$

$$3\alpha^2\omega - \omega^3 + 2a_1\alpha\omega + a_2\omega + e^{-\alpha\tau}[(\omega \cos \omega\tau - \alpha \sin \omega\tau)a_3 - a_4 \sin \omega\tau] = 0 \quad (4.20)$$

We differentiate equations (4.19) and (4.20) with respect to τ and evaluate at $\tau = \tau_c$ for which $\alpha(\tau_c) = 0$ and $\omega(\tau_c) = \omega_c$. We then obtain

$$E_1 \frac{d\omega(\tau)}{d\tau}\Big|_{\tau=\tau_c} + E_2 \frac{d\alpha(\tau)}{d\tau}\Big|_{\tau=\tau_c} = E_3 \sin \omega_c\tau_c - E_4 \cos \omega_c\tau_c, \quad (4.21)$$

$$E_2 \frac{d\omega(\tau)}{d\tau}\Big|_{\tau=\tau_c} - E_1 \frac{d\alpha(\tau)}{d\tau}\Big|_{\tau=\tau_c} = E_3 \cos \omega_c\tau_c + E_4 \sin \omega_c\tau_c. \quad (4.22)$$

By solving equations (4.21) and (4.22), we therefore obtain

$$\frac{d\alpha(\tau)}{d\tau}\Big|_{\tau=\tau_c} = \frac{(E_2E_3 - E_1E_4) \sin \omega_c\tau_c - (E_2E_4 + E_1E_3) \cos \omega_c\tau_c}{E_1^2 + E_2^2} \neq 0.$$

Hence, the Hopf bifurcation occurs when τ passes through the critical value τ_c .

4.4 Numerical Methods for HIV

Using the DDE-BIFTOOL we will examine the stability and the bifurcation process of the steady state $(T_1^*, I_1^*, V_1^*) = \left(\frac{\mu_v\mu_I^2}{k_1(R-1)}, \frac{\beta\mu_I}{k_1(R-1)}, \frac{\beta}{k_1\mu_v\mu_I}\right)$.

We compute the eigenvalues of the characteristic equation (4.13), and display their real parts versus imaginary parts as shown on the figure 4.1.

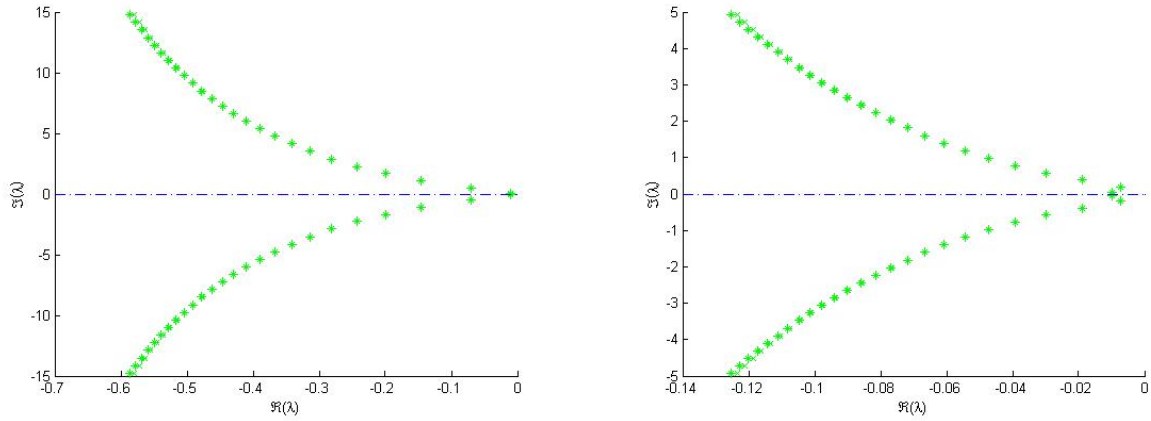


Figure 4.1. Roots of the characteristic equation (4.13) with $\tau = 10$ days (left) and $\tau = 15$ days (right).

All eigenvalues have negative real part , therefore the steady state (T_1^*, I_1^*, V_1^*) is stable for those values of τ . But as we increase the delay, we obtain

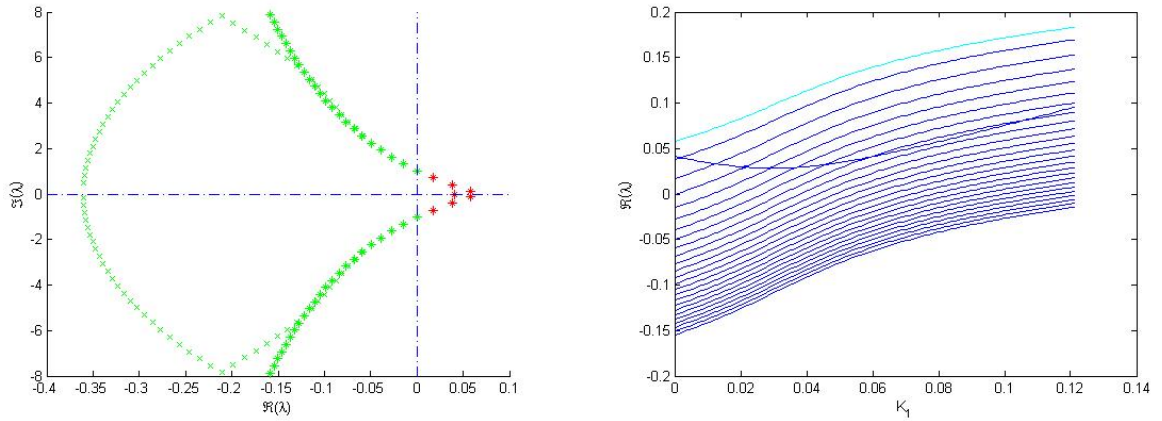


Figure 4.2. Roots of the characteristic equation (4.13) with $\tau = 20$ days (left), and Real part Vs k_1 (right).

We see that there exists a critical delay τ_c such that the steady state is destabilizes (some of the eigenvalues of the characteristic equation (4.13) have strictly positive real parts) as τ passes through τ_c .

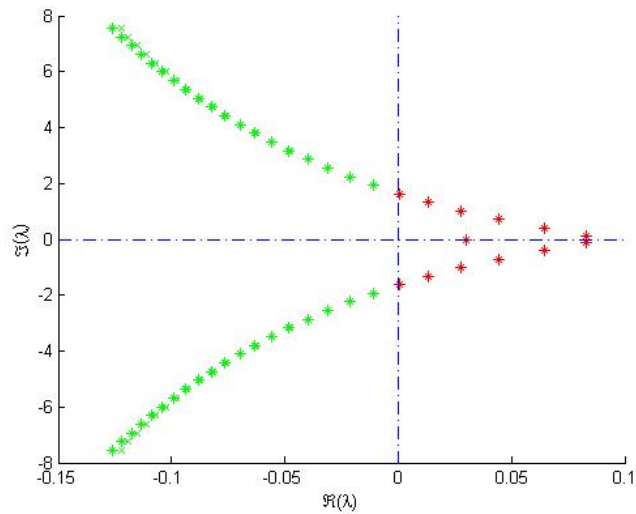


Figure 4.3. A pair of pure eigenvalues is clearly visible (Hopf bifurcation) and also a real eigenvalue (returning point or Hold bifurcation).

One can plot the time lag τ versus the rate of infection of the $CD4^+$ T-cells with free virus, and notice that as τ passes through the critical delay τ_c the steady state is destabilized through a second Hopf bifurcation branch.

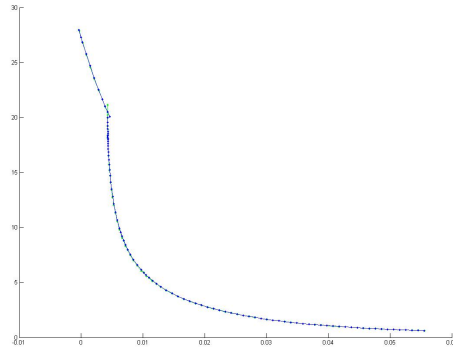


Figure 4.4. Hopf bifurcation branches: τ vs k_1 .

CHAPTER 5

EFFECTS OF DELAY AND PARAMETERS VARIATION

5.1 Introduction

It is well known, that the values of the parameters play a crucial role in the behavior of dynamical systems and that changes in the values can change the behavior significantly. It has been shown that there is a need to incorporate discrete time delays in dynamical systems (biological systems, physical systems,...) as studied by many researchers (Perelson[21],Allen[22],Bellen[23]). Published papers have shown that the incorporation of discrete time delays can highly impact the dynamics of the system, since they can switch the stability of a steady state point, and also cause the system to go through a Hopf bifurcation near that steady state point (Culshaw[12], Bellen[23]). In our study we consider a system of n delay differential equations (DDE's) with one parameter μ as the bifurcation parameter and also with one or more discrete time delays, τ , which can also behave as bifurcation parameters. We are interested in investigating how the parameters μ and τ affect the stability of the steady state points of the system, and, more important, how their effects on the system are correlated to each other. We present general results in the one dimensional case for necessary and sufficient conditions for a stability switch and present a specific example to illustrate these conditions. For the n dimensional case ($n \geq 2$) we establish the main ideas, but as there are multiple possible cases, we consider only a specific example. We present a non-Kolmogorov type of predator-prey model similar to the model presented by Ruan [1]. In this model we introduce two delays, $\tau_1 > 0$ and $\tau_2 > 0$, to represent the time lag in the growth to maturity of the prey, and the time lag in the growth

to maturity of the predator respectively. We show how the dynamics of the system change depending on certain conditions on τ_1 and on another bifurcation parameter R . We also point out conditions for the system to go through stability changes when both delays τ_1 and τ_2 are non-zero. We present necessary conditions for the system to go through a Hopf bifurcation for $\tau_1 > 0$ and $\tau_2 = 0$. Finally we show numerical results illustrating the theoretical results.

5.2 One Dimensional Field

5.2.1 One Equation with One Delay

Consider the one dimensional delay differential equation with the time delay τ , and the parameter μ as bifurcation parameters:

$$\frac{dX}{dt} = f(X(t), X(t - \tau), \mu), \quad (5.1)$$

where f is assumed to be smooth enough to guarantee the existence and uniqueness of solutions to (5.1) under the initial condition (R. Bellman and K. L. Cooke [9])

$$X(\theta) = \phi(\theta), \quad \theta \in [-\tau, 0].$$

We rewrite equation (5.1) as :

$$\frac{dX}{dt} = f_1(X(t), \mu) + f_2(X(t - \tau), \mu). \quad (5.2)$$

We choose to write the delay equation in this form for analytical reasons and also because many population dynamical models involving delays are of this form. The DDE (5.2) may or may not have equilibrium points (or steady states) and these will depend on the value of μ . Let μ^* be a value for which the DDE has an equilibrium point X^* , i.e., $f(X^*, X^*, \mu^*) = 0$. We are interested in studying the stability of such equilibrium point. In particular, in studying the effect of the parameter μ^* and of

the discrete time τ on its stability. To do this we linearize the DDE around the equilibrium point. The characteristic equation is (Culshaw [12]):

$$\lambda - \frac{df_1}{dX}|_{(X^*, \mu^*)} - \frac{df_2}{dX}|_{(X^*, \mu^*)} e^{-\lambda\tau} = 0, \quad (5.3)$$

and the stability of the equilibrium point (X^*, μ^*) is determined by the sign of the real part of the eigenvalues λ of equation (5.3).

5.2.1.1 Stability of the Steady State

If $\tau = 0$ then the characteristic equation (5.3) becomes

$$\lambda - \frac{df_1}{dX}|_{(X^*, \mu^*)} - \frac{df_2}{dX}|_{(X^*, \mu^*)} = 0.$$

The stability of the steady state then depends only on the value of μ^* . We have two cases:

- (a) The steady state (X^*, μ^*) is stable if $\frac{df_1}{dX}|_{(X^*, \mu^*)} + \frac{df_2}{dX}|_{(X^*, \mu^*)} < 0$.
- (b) The steady state (X^*, μ^*) is unstable if $\frac{df_1}{dX}|_{(X^*, \mu^*)} + \frac{df_2}{dX}|_{(X^*, \mu^*)} > 0$.

Assume that condition (a) holds, namely the steady state (X^*, μ^*) is stable when there is no delay ($\tau = 0$). We want to know if there exists $\tau > 0$ for which the steady state will lose stability. So for $\tau \geq 0$, let $\lambda(\tau) = \alpha(\tau) + i\omega(\tau)$. The characteristic equation (5.3) becomes:

$$\alpha + i\omega = \frac{df_1}{dX}|_{(X^*, \mu^*)} + \frac{df_2}{dX}|_{(X^*, \mu^*)} e^{-\alpha\tau} \cos\omega\tau + i \frac{df_2}{dX}|_{(X^*, \mu^*)} e^{-\alpha\tau} \sin\omega\tau, \quad (5.4)$$

where for clarity in the notation we have not explicitly shown the dependence on τ . Separating the real and imaginary parts, we have:

$$\alpha = \frac{df_1}{dX}|_{(X^*, \mu^*)} + \frac{df_2}{dX}|_{(X^*, \mu^*)} e^{-\alpha\tau} \cos\omega\tau, \quad (5.5)$$

$$\omega = \frac{df_2}{dX}|_{(X^*, \mu^*)} e^{-\alpha\tau} \sin\omega\tau. \quad (5.6)$$

The steady state will lose stability when the real part of the eigenvalue λ crosses the zero axis from negative to positive as τ passes a critical value. By Rouché's Theorem (Dieudonné[7], Theorem 9.17.4) and by the continuity in τ , the transcendental equation (5.3) has roots with positive real parts if and only if it has pure imaginary roots. Therefore, we look at when the real part of the eigenvalue λ becomes zero. In other words, we want to find if there exists a $\tau_c > 0$ such that $\alpha(\tau_c) = 0$. Since

$$\alpha(0) = \frac{df_1}{dX}|_{(X^*, \mu^*)} + \frac{df_2}{dX}|_{(X^*, \mu^*)},$$

and $\alpha(0) < 0$ by assumption (a), therefore if $\tau_c > 0$ exists such that $\alpha(\tau_c) = 0$ then by the continuity (Michael Y. Li and Hogenyng Shu [24]) of α we have:

- $\alpha(\tau) < 0$ for any $0 \leq \tau < \tau_c$,
- $\alpha(\tau) > 0$ for any $\tau > \tau_c$.

Namely the steady state (X^*, μ^*) will lose stability as the delay parameter τ crosses a critical value τ_c . Such τ_c exists if and only if $\alpha(\tau_c) = 0$ and $\omega(\tau_c) = \omega_c$ satisfies :

$$\frac{df_1}{dX}|_{(X^*, \mu^*)} = -\frac{df_2}{dX}|_{(X^*, \mu^*)} \cos\omega_c\tau_c \quad (5.7)$$

$$\omega_c = \frac{df_2}{dX}|_{(X^*, \mu^*)} \sin\omega_c\tau_c. \quad (5.8)$$

Squaring equations (5.7) and (5.8), and adding them up, we obtain:

$$\omega_c^2 = \left[\frac{df_2}{dX}|_{(X^*, \mu^*)} \right]^2 - \left[\frac{df_1}{dX}|_{(X^*, \mu^*)} \right]^2. \quad (5.9)$$

If equation (5.9) has at least a positive root ω_c , then there exists a $\tau_c > 0$ such that $\alpha(\tau) > 0$ whenever $\tau > \tau_c$. An important question we want to address is, since equation (5.9) depends on the bifurcation parameter μ^* , can one chose μ^* so that equation (5.9) does not have a positive root ω_c ? That is, are there values of μ such that the delay does not have any effect on the stability of the steady state (X^*, μ^*) . This question motivates the following propositions.

Proposition 5.2.1.

Consider the one dimensional delay differential equation

$$\frac{dX}{dt} = f_1(X(t), \mu) + f_2(X(t - \tau), \mu).$$

And assume that the steady state (X^, μ^*) is stable for $\tau = 0$ then we have*

- (i) If $\frac{df_1}{dX}|_{(X^*, \mu^*)} < 0$ and $\frac{df_2}{dX}|_{(X^*, \mu^*)} > 0$ then the steady state (X^*, μ^*) remains stable for all $\tau \geq 0$.*
- (ii) If $\frac{df_1}{dX}|_{(X^*, \mu^*)} > 0$ and $\frac{df_2}{dX}|_{(X^*, \mu^*)} < 0$ then there exists a critical value of the delay such that the steady state loses stability as the delay crosses its critical value.*
- (iii) If $\frac{df_1}{dX}|_{(X^*, \mu^*)} < 0$ and $\frac{df_2}{dX}|_{(X^*, \mu^*)} < 0$ then:*
 - (a) the steady state remains stable for all $\tau \geq 0$ if*

$$\left| \frac{df_2}{dX}|_{(X^*, \mu^*)} \right| < \left| \frac{df_1}{dX}|_{(X^*, \mu^*)} \right|,$$

- (b) there exists a $\tau_c > 0$ such that the steady state becomes unstable for all $\tau > \tau_c$ if*

$$\left| \frac{df_2}{dX}|_{(X^*, \mu^*)} \right| > \left| \frac{df_1}{dX}|_{(X^*, \mu^*)} \right|.$$

Proof: We already have the characteristic equation of the one dimensional DDE given by (5.3) and because the steady state is assumed to be stable at $\tau = 0$ then

$$\alpha(0) = \frac{df_1}{dX}|_{(X^*, \mu^*)} + \frac{df_2}{dX}|_{(X^*, \mu^*)} < 0. \quad (5.10)$$

If (i) holds then equation (5.10) implies $|\frac{df_2}{dX}|_{(X^*, \mu^*)}| < |\frac{df_1}{dX}|_{(X^*, \mu^*)}|$ therefore equation (5.9) has no positive root meaning the steady state remains stable for all $\tau \geq 0$.

If (ii) holds then equation (5.10) implies $|\frac{df_2}{dX}|_{(X^*, \mu^*)}| > |\frac{df_1}{dX}|_{(X^*, \mu^*)}|$ therefore equation (5.9) has a positive root then there exists a $\tau_c > 0$ such that $\alpha(\tau) > 0$ whenever $\tau > \tau_c$.

If (iii)(a) holds then again equation (5.9) has no solution therefore $\alpha(\tau) < 0$ for all $\tau \geq 0$ meaning the steady state remains stable.

If (iii)(b) holds then equation (5.9) has a positive root then there exists a $\tau_c > 0$ such that $\alpha(\tau) > 0$ whenever $\tau > \tau_c$. \square

Proposition 5.2.2.

Consider the one dimensional delay differential equation

$$\frac{dX}{dt} = f_1(X(t), \mu) + f_2(X(t - \tau), \mu).$$

And assume that the steady state (X^, μ^*) is stable for $\tau = 0$, that conditions of Proposition 5.2.1 (iii) hold, and that further more we have:*

$$\frac{df_1}{dX}|_{(X^*, \mu^*)} \simeq g(X^*)\mu^*, \quad \frac{df_2}{dX}|_{(X^*, \mu^*)} \simeq \frac{h(X^*)}{\mu^*},$$

then there exists a critical value for μ^* such that the steady state (X^*, μ^*) will stay stable for all $\tau \geq 0$ when $\mu^* > \mu_c^*$.

Proof: If conditions of Proposition 5.2.1(iii)(a) hold then there is nothing to prove. Assume that conditions of Proposition 5.2.1(iii)(b) hold then equation (5.9) has a positive solution, therefore the delay can affect the stability of the equilibrium point. But if we do have the extra condition

$$\frac{df_1}{dX}|_{(X^*, \mu^*)} \simeq g(X^*)\mu^*$$

and

$$\frac{df_2}{dX}|_{(X^*, \mu^*)} \simeq \frac{h(X^*)}{\mu^*},$$

then one can rewrite equation (5.9) as

$$\omega_c^2 = \left[\frac{h(X^*)}{\mu^*} \right]^2 - [g(X^*)\mu^*]^2.$$

Then there exists a critical value μ_c^* of μ^* such that

$$\frac{h(X^*)}{\mu^*} \approx 0 \quad \text{as} \quad \mu^* \rightarrow \mu_c^*.$$

Therefore the equation (5.9) becomes

$$\omega_c^2 = -[g(X^*)\mu_c^*]^2 < 0,$$

which has no real positive root ω_c , therefore $\alpha(\tau) < 0$ for all $\tau \geq 0$. This implies the delay does not have any effect on the stability of the equilibrium point when $\mu^* > \mu_c^*$.

□

5.2.1.2 Example

Consider the one dimensional DDE

$$\begin{cases} \frac{dY}{dt} = \mu \frac{Y(t)}{Y(t)+1} - \frac{1}{\mu} Y(t-\tau)^2, & \text{if } \mu \neq 0 \\ Y(t) = 0, & \text{if } \mu = 0 \end{cases}$$

where μ is a bifurcation parameter and $\tau \geq 0$ is a discrete time delay. The equation has two non-negative equilibrium points: the trivial one $Y_0^* = 0$, and the positive equilibrium point $Y_1^* = \frac{-1+\sqrt{1+4\mu^2}}{2}$. The characteristic equation is given as

$$\lambda - \mu \frac{1}{(Y^* + 1)^2} - \frac{2}{\mu} Y^* e^{-\lambda\tau} = 0. \quad (5.11)$$

- For the trivial equilibrium point $Y^* = 0$, its stability only depends on μ since equation (5.11) evaluated at $Y^* = 0$ becomes $\lambda = \mu$.

The trivial equilibrium is unstable for $\mu > 0$ and all $\tau \geq 0$.

The trivial equilibrium is stable for $\mu < 0$ and all $\tau \geq 0$.

- At $Y_1^* = \frac{-1+\sqrt{1+4\mu^2}}{2}$, equation (5.11) becomes:

$$\lambda - \frac{4\mu}{(1 + \sqrt{1 + 4\mu^2})^2} + \frac{\sqrt{1 + 4\mu^2} - 1}{\mu} e^{-\lambda\tau} = 0, \quad (5.12)$$

then the stability of Y_1^* depends on both μ and τ .

- 1) If $\tau = 0$ then equation (5.12) becomes

$$\lambda = -\frac{4\mu\sqrt{1 + 4\mu^2}}{(1 + \sqrt{1 + 4\mu^2})^2}$$

then

$\lambda < 0$ if $\mu > 0$, therefore the equilibrium Y_1^* is stable (Fig 5.2)

$\lambda > 0$ if $\mu < 0$, therefore the equilibrium Y_1^* is unstable (Fig 5.2).

Remark: To better understand the situation, the stability of both equilibria when there is no delay is shown in the following table:

Table 5.1. Stability regions

Case	$Y_0^* = 0$	$Y_1^* = \frac{-1 + \sqrt{1 + 4\mu^2}}{2}$
$\mu < 0$	stable	unstable
$\mu = 0$	stable	stable
$\mu > 0$	unstable	stable

At the equilibrium $(Y, \mu) = (0, 0)$, there is an exchange of stability. This is a *transcritical bifurcation* (Rohan[?]). Geometrically, there are two curves of equilibria which intersect at the origin and lie on both sides of $\mu = 0$. Stability of the equilibrium changes along either curve on passing through $\mu = 0$.

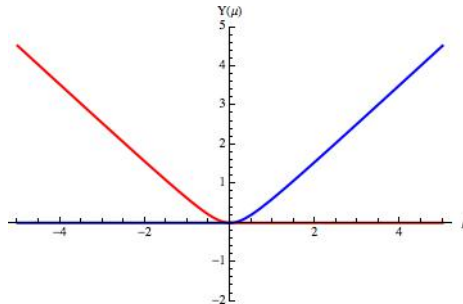


Figure 5.1. Transcritical bifurcation around $\mu = 0$. Unstable equilibrium, red and Stable equilibrium, blue.

- 2) If $\tau > 0$ and $\lambda(\tau) = \alpha(\tau) + i\omega(\tau)$, there exists a critical τ_c such that $\alpha(\tau_c) = 0$ and $\lambda(\tau_c) = \pm i\omega(\tau_c) = \pm i\omega_c$ (a pair of pure imaginary eigenvalues) is solution of equation (5.11) if and only if

$$\omega_c^2 = \frac{16 \left[\mu^2(1 + \sqrt{1 + 4\mu^2})^2 - 1 \right]}{(1 + \sqrt{1 + 4\mu^2})^4}$$

has a positive root ω_c , and that is the case if and only if

$$\mu^2(1 + \sqrt{1 + 4\mu^2})^2 - 1 > 0.$$

- (2a) If $\mu \geq \frac{1}{2}$ then $\mu^2(1 + \sqrt{1 + 4\mu^2})^2 - 1 > 0$ therefore there exists $\tau_c > 0$ such that the equilibrium loses stability whenever $\tau > \tau_c$ (Fig 5.3 left).
- (2b) If $\mu \leq -\frac{1}{2}$ then $\mu^2(1 + \sqrt{1 + 4\mu^2})^2 - 1 > 0$ therefore there exists $\tau_c > 0$ such that the equilibrium gains stability whenever $\tau > \tau_c$.
- (2c) If $-\frac{1}{2} < \mu < \frac{1}{2}$ then $\mu^2(1 + \sqrt{1 + 4\mu^2})^2 - 1 < 0$ therefore the delay has no effect on the stability of the equilibrium.

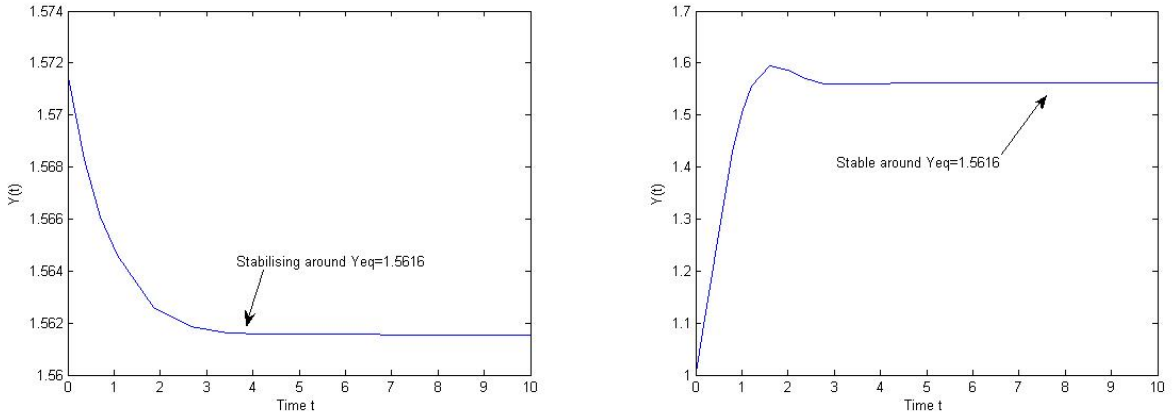


Figure 5.2. The positive equilibrium is stable for $\tau = 0$ and $\mu = 2$, left graph. The equilibrium still remains stable for $\tau = 0.4$ ($\tau < \tau_c = 0.55$) and $\mu = 2$, right graph .

For $\mu \geq \frac{1}{2}$, the equilibrium is unstable for all $\tau > 0.55$, and for $0 < \mu < \frac{1}{2}$ the equilibrium remains stable for all τ .

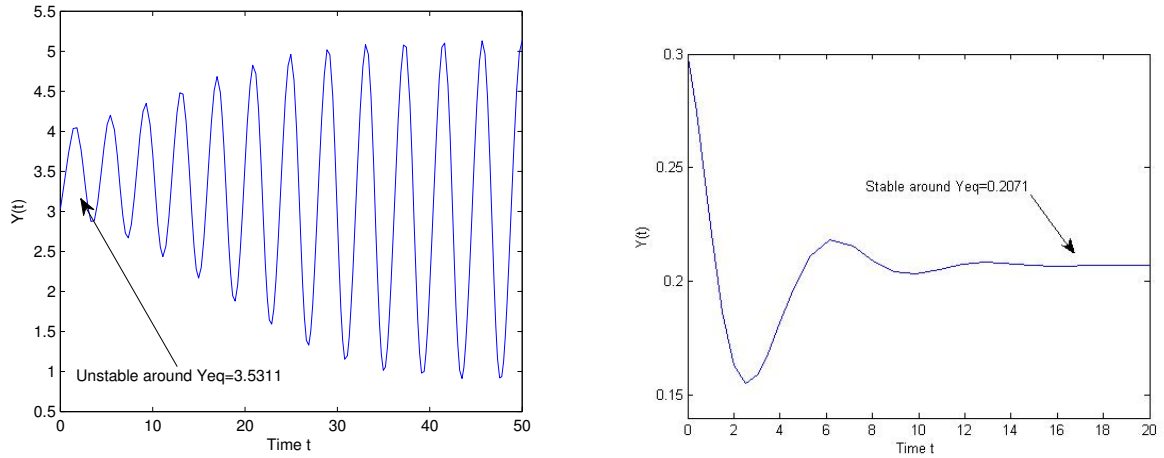


Figure 5.3. For $\mu = 4$ and $\tau = 0.9$ the equilibrium is unstable, left graph. For $\mu = 0.2$ and $\tau = 1$ the equilibrium is stable, right graph.

5.2.2 One Equation with Multiple Delays

Consider the one dimensional delay differential equation with the time lags τ_k , $k = 1, 2, \dots$, and μ as bifurcation parameters:

$$\frac{dX}{dt} = f_1(X(t), \mu) + f_2(X(t - \tau_1), X(t - \tau_2), \dots, X(t - \tau_k), \mu). \quad (5.13)$$

Let $(X^*, \mu^*) = (X^*, X^*, \dots, X^*, \mu^*)$ be the steady state of equation (5.13), i.e., $f_1(X^*, \mu^*) + f_2(X^*, X^*, \dots, X^*, \mu^*) = 0$. To study the stability of the steady state we compute the characteristic equation:

$$\lambda - \frac{df_1}{dX}|_{(X^*, \mu^*)} - \sum_{j=1}^k \frac{df_2}{dX}|_{(X^*, \mu^*)} e^{-\lambda \tau_j} = 0. \quad (5.14)$$

For clarity of the presentation we consider the case of only two delays. Therefore the characteristic equation is written as

$$\lambda - \frac{df_1}{dX}|_{(X^*, \mu^*)} - \frac{df_2}{dX}|_{(X^*, \mu^*)}(e^{-\lambda\tau_1} + e^{-\lambda\tau_2}) = 0. \quad (5.15)$$

Note that if $\tau_1 = \tau_2 = \tau$ or $\tau_1 = 0$ or $\tau_2 = 0$ then we are back to the previous case of one equation with one delay. We will assume that τ_1 is in its stable domain, i.e., $0 < \tau_1 < \tau_{1c}$ and $\tau_2 > 0$. We now examine how variation of τ_2 and μ^* affects the stability of the steady state. Consider $\lambda(\tau_2) = \alpha(\tau_2) + i\omega(\tau_2)$ as solution of equation (5.15). We look for a critical value τ_{2c} of τ_2 such that $\alpha(\tau_{2c}) = 0$ and $\lambda(\tau_{2c}) = i\omega(\tau_{2c}) = i\omega_{2c}$ is solution of equation (5.15). Such τ_{2c} exists if and only if:

$$i\omega_{2c} - \frac{df_1}{dX}|_{(X^*, \mu^*)} - \frac{df_2}{dX}|_{(X^*, \mu^*)}(\cos \omega_{2c}\tau_1 - i \sin \omega_{2c}\tau_1 + \cos \omega_{2c}\tau_{2c} - i \sin \omega_{2c}\tau_{2c})$$

Separate real and imaginary parts:

$$-\frac{df_2}{dX}|_{(X^*, \mu^*)} \cos \omega_{2c}\tau_{2c} = \frac{df_1}{dX}|_{(X^*, \mu^*)} + \frac{df_2}{dX}|_{(X^*, \mu^*)} \cos \omega_{2c}\tau_1, \quad (5.16)$$

$$\frac{df_2}{dX}|_{(X^*, \mu^*)} \sin \omega_{2c}\tau_{2c} = -\omega_{2c} - \frac{df_2}{dX}|_{(X^*, \mu^*)} \sin \omega_{2c}\tau_1. \quad (5.17)$$

Adding the square of (5.16) and (5.17) we have

$$\left[\frac{df_2}{dX}|_{(X^*, \mu^*)} \right]^2 = \left[\omega_{2c} + \frac{df_2}{dX}|_{(X^*, \mu^*)} \sin \omega_{2c}\tau_1 \right]^2 + \left[\frac{df_1}{dX}|_{(X^*, \mu^*)} + \frac{df_2}{dX}|_{(X^*, \mu^*)} \sin \omega_{2c}\tau_1 \right]^2$$

Clearly τ_{2c} exists if and only the function:

$$H(\omega_{2c}) = \left[\omega_{2c} + \frac{df_2}{dX}|_{(X^*, \mu^*)} \sin \omega_{2c}\tau_1 \right]^2 + \left[\frac{df_1}{dX}|_{(X^*, \mu^*)} + \frac{df_2}{dX}|_{(X^*, \mu^*)} \cos \omega_{2c}\tau_1 \right]^2 - \left[\frac{df_2}{dX}|_{(X^*, \mu^*)} \right]^2$$

has at least a positive root.

Proposition 5.2.3.

Consider the one dimensional delay differential equation with the time lag τ_1 , τ_2 , and μ as bifurcation parameters:

$$\frac{dX}{dt} = f_1(X(t), \mu) + f_2(X(t - \tau_1), X(t - \tau_2), \mu). \quad (5.18)$$

Assume that the steady state $(X^*, \mu^*) = (X^*, X^*, \mu^*)$ of (5.18) is stable for $0 < \tau_1 < \tau_{1c}$. If $\frac{df_2}{dX}|_{(X^*, \mu^*)} > 0$ and $\frac{df_1}{dX}|_{(X^*, \mu^*)} < 0$, then there exists a critical value $\tau_{2c} > 0$ for τ_2 such that (X^*, μ^*) loses stability as τ_2 crosses τ_{2c} .

Proof: Such τ_{2c} exists if and only if equation $H(\omega_{2c}) = 0$ has at least a positive root. Or If $\frac{df_2}{dX}|_{(X^*, \mu^*)} > 0$ and $\frac{df_1}{dX}|_{(X^*, \mu^*)} < 0$ then

$$H(0) = \left[\frac{df_1}{dX}|_{(X^*, \mu^*)} + \frac{df_2}{dX}|_{(X^*, \mu^*)} \right]^2 - \left[\frac{df_2}{dX}|_{(X^*, \mu^*)} \right]^2 < 0.$$

And also $H(\omega_{2c}) \rightarrow \infty$ as $\omega_{2c} \rightarrow \infty$. Then the intermediate value theorem assures that equation $H(\omega_{2c}) = 0$ has at least a positive root. \square

We now extend our analysis to a system of n-delay differential equations with multiple discrete time delays $\tau_1, \tau_2, \dots, \tau_k$, and a local bifurcation parameter μ .

5.3 n Dimensional Field

Consider the following system non-linear delay differential equations:

$$\frac{dx}{dt} = f(x(t), x(t - \tau_1), \dots, x(t - \tau_k), \mu), \quad (5.19)$$

where $x \in \mathbb{R}^n$, $\tau_j \geq 0, 1 \leq j \leq k$ are constant discrete times,

$f : \mathbb{R}^{n+1} \times C^k \rightarrow \mathbb{R}^n$ is assumed to be smooth enough to guarantee existence and uniqueness of solutions to (5.19) under the initial value condition (R. Bellman and K. L. Cooke [9] and J. K. Hale and S. M. Verduyn Lunel [25])

$$x(\theta) = \phi(\theta), \quad \theta \in [-\tau, 0],$$

where $C = C([- \tau, 0], \mathbb{R}^n)$, $\tau = \max_{1 \leq j \leq k} \tau_j$.

Suppose $f(x^*, x^*, \dots, x^*, \mu^*) = 0$, that is, (x^*, μ^*) is a steady state of system (5.19).

We are interested in studying the stability of such equilibrium point. In particular

studying the effect of the parameter μ^* and the discrete time delays $\tau_1, \tau_2, \dots, \tau_k$ on its stability. The linearization of (5.19) at (x^*, μ^*) has the form (Ruan [1]):

$$\frac{dX}{dt} = A_0(\mu^*)X(t) + \sum_{j=1}^k A_j(\mu^*)X(t - \tau_j), \quad (5.20)$$

where $X \in \mathbb{R}^n$, each $A_j(\mu^*)$ ($0 \leq j \leq k$) is an $n \times n$ constant matrix that depends on μ^* . The transcendental equation associated with system (5.19) is given as :

$$\det \left[\lambda I - A_0(\mu^*) - \sum_{j=1}^k A_j(\mu^*)e^{-\lambda\tau_j} \right] = 0. \quad (5.21)$$

Equation (5.21) has been studied by many researchers

(Ruan [1], R. Bellman and K. L. Cooke [9] and J. K. Hale and S. M. Verduyn Lunel [25]). The following result, which was proved by Chin [26] for $k = 1$ and by Datko [27] and Hale et al. [25] for $k \geq 1$, gives a necessary and sufficient condition for the absolute stability of system (5.20).

Lemma 5.3.1.

System (5.20) is stable for all delays τ_j ($1 \leq j \leq k$) if and only if

- (i) $Re\lambda(\sum_{j=0}^k A_j(\mu^*)) < 0$;
- (ii) $\det \left[i\omega I - A_0(\mu^*) - \sum_{j=1}^k A_j(\mu^*)e^{-i\omega\tau_j} \right] \neq 0$ for all $\omega > 0$

Clearly, the stability of the steady state (x^*, μ^*) and the effects of the discrete times τ_j on its stability depend on values of μ^* . To further investigate the effects of μ^* , and the discrete time delays τ_j on the stability of (x^*, μ^*) , the exact entries of the matrices $A_j(\mu^*)$ are needed to avoid doing a large number of cases. Note that the difficulty of the analysis is not due to the number of delays but to the number of equations. Even in the case of two equations with one delay, one needs to consider:

$$\det [\lambda I - A_0(\mu^*) - A_1(\mu^*)e^{\lambda\tau} = 0],$$

where

$$A_i(\mu^*) = \frac{\partial f}{\partial X_i} \Big|_{(X^*, \mu^*)}, \quad i = 0, 1.$$

So the stability depends on all the entries of the A_i , $i = 0, 1$, we have many different cases.

Therefore to present the ideas we consider a specific example with $n = 2$, $k = 2$, that is a two dimensional delay differential equations with two discrete time delays, and a local bifurcation parameter.

5.3.1 Two Dimensional Field Example

Consider the non-Kolmogorov type (Holling) predator-prey model

$$\frac{dx}{dt} = r_1 x(t - \tau_1) - a_1 \frac{x(t)y(t)}{x(t) + 1}, \quad (5.22)$$

$$\frac{dy}{dt} = -r_2 y(t) + a_2 \frac{x(t - \tau_2)y(t - \tau_2)}{x(t - \tau_2) + 1}, \quad (5.23)$$

where the parameters are described in the following table:

Table 5.2. Parameter values

Parameters	Description	Values
$x(t)$	the prey population	
$y(t)$	the predator population	
r_1	the growth rate of the prey in the absence of predators	0.5
r_2	the death rate of predators in the absence of the prey	0.5
a_1	the predation rate of the prey by the predators	0.5
a_2	the conversion rate for the predators	5
τ_1	the time lag in the growth to maturity of the prey	varies
τ_2	the time lag in the growth to maturity of the predators	varies

Note that $r_1 > 0$, $r_2 > 0$, $a_1 > 0$, $a_2 > 0$, $\tau_1 > 0$, $\tau_2 > 0$.

Proposition 5.3.1.

If the basic reproductive ratio (Ameh[28]) $R > 1$, the system has two non-negative steady states:

$$(x_0^*, y_0^*) = (0, 0), \text{ and } (x_1^*, y_1^*) = \left(\frac{1}{R-1}, \frac{RR'}{R-1}\right),$$

where

$$R = \frac{a_2}{r_2}, \quad R' = \frac{a_1}{r_1}.$$

We consider R , τ_1 and τ_2 as the bifurcation parameters for the system (5.22-5.23) since changes of them may affect the existence and stability of the equilibrium points.

5.3.2 Stability Analysis

Proposition 5.3.2.

There exists a critical value for τ_1 such that

- (i) *The steady state (x_0^*, y_0^*) is unstable for $0 \leq \tau_1 < \tau_{1c}$, and all $\tau_2 \geq 0$.*
- (ii) *The steady state (x_0^*, y_0^*) is stable for $\tau_1 \geq \tau_{1c}$, and all $\tau_2 \geq 0$.*

Proof: The Jacobian matrix of the system (5.22-5.23) is given by :

$$J = \begin{bmatrix} r_1 e^{-\lambda \tau_1} - \frac{a_1 y^*}{(x^*+1)^2} & -\frac{a_1 x^*}{x^*+1} \\ \frac{a_2 y^*}{(x^*+1)^2} e^{-\lambda \tau_2} & -r_2 + \frac{a_2 x^*}{x^*+1} e^{-\lambda \tau_2} \end{bmatrix}$$

Evaluating at $(x^*, y^*) = (0, 0)$, the characteristic equation is given as

$$(\lambda - r_1 e^{-\lambda \tau_1})(\lambda + r_2) = 0.$$

We note that the stability of $(x^*, y^*) = (0, 0)$ depends only on τ_1 .

- If $\tau_1 = 0$ then the eigenvalues are :

$\lambda = r_1 > 0$ and $\lambda = -r_2 < 0$. Therefore the $(0, 0)$ is unstable.

- If $\tau_1 > 0$, we have $\lambda = r_1 e^{-\lambda \tau_1}$, let $\lambda(\tau) = \alpha(\tau) + i\omega(\tau)$ then we have

$$\lambda = r_1 e^{-\alpha \tau_1} (\cos \omega \tau_1 - i \sin \omega \tau_1).$$

One can choose $\omega_c \tau_{1c} = \frac{\pi(2n+1)}{2}$ ($n=0,1,2,\dots$) or $\tau_{1c} = \frac{\pi(2n+1)}{2\omega_c}$ such that the real part of $\lambda(\tau) = \alpha(\tau) + i\omega(\tau)$ at τ_{1c} is zero ($\alpha(\tau_{1c}) = 0$) and $\lambda(\tau_{1c}) = i\omega(\tau_{1c}) = i\omega_c$

is a solution of the characteristic equation.

Then by the continuity of α we have :

- $\alpha(\tau) > 0$ for $\tau_1 < \tau_{1c}$,
- $\alpha(\tau) < 0$ for $\tau_1 > \tau_{1c}$. \square

Proposition 5.3.3.

If $[(b - d)^2 - r_1^2 - 2a_1f] < 0$ and

$\Lambda = [(b - d)^2 - r_1^2 - 2a_1f]^2 - 4a_1^2f^2 \geq 0$ then there exists a critical τ'_{1c} such that

- (i) The steady state $(x_1^*, y_1^*) = (\frac{1}{R-1}, \frac{RR'}{R-1})$ is unstable for $0 \leq \tau_1 < \tau'_{1c}$ and $\tau_2 = 0$.
- (ii) The steady state (x_1^*, y_1^*) is stable for $\tau_1 > \tau'_{1c}$ and $\tau_2 = 0$.

Proof: The characteristic equation of the system evaluating at (x_1^*, y_1^*) is given by

$$\lambda^2 + (b - r_1e^{-\lambda\tau_1} - r_2e^{-\lambda\tau_2})\lambda + (f - f_1e^{-\lambda\tau_1} + (a_1 - 1)fe^{-\lambda\tau_2} + f_1e^{-\lambda(\tau_1+\tau_2)}) = 0, \quad (5.24)$$

where

$$b = r_2 + \frac{r_1}{x_1^* + 1}, \quad f = \frac{r_1r_2}{x_1^* + 1}, \quad f_1 = r_1r_2.$$

- If $\tau_1 = \tau_2 = 0$ we have:

$$\lambda^2 + (b - r_1 - r_2)\lambda + a_1f = 0$$

with

$$b - r_1 - r_2 = -\frac{r_1}{R} < 0, \quad \text{and} \quad a_1f > 0.$$

Then the characteristic equation has at least a positive eigenvalue

(if the eigenvalues are real) $\lambda = \frac{r_1}{2R} + \frac{\sqrt{\delta}}{2}$ where

$$\delta = (b - r_1 - d)^2 - 4a_1f,$$

or, all its eigenvalues (if complex) have a positive real part ($\frac{r_1}{2R}$). Therefore the steady state (x_1^*, y_1^*) is unstable.

- If $\tau_1 > 0$ and $\tau_2 = 0$ Then the characteristic equation becomes:

$$\lambda^2 + (b - r_2)\lambda - r_1 e^{-\lambda\tau_1}\lambda + a_1 f = 0.$$

Since we know that the steady state is unstable when $\tau_1 = \tau_2 = 0$, the question becomes: does there exist a τ'_{1c} such that the steady state stabilizes as τ_1 crosses τ'_{1c} ? In other words if $\lambda(\tau_1) = \alpha(\tau_1) + i\omega(\tau_1)$, does there exist τ'_{1c} such that $\alpha(\tau'_{1c}) = 0$ and $\omega(\tau'_{1c}) = \omega'_c$ which satisfies

$$-\omega_c'^2 + i(b - r_2)\omega'_c - ir_1\omega'_c(\cos\omega'_c\tau'_{1c} - i\sin\omega'_c\tau'_{1c}) + a_1 f = 0.$$

Setting the real and imaginary parts equal zero, we obtain:

$$-\omega_c'^2 + a_1 f = r_1\omega'_c \sin\omega'_c\tau'_{1c} \quad (5.25)$$

$$(b - r_2)\omega'_c = r_1\omega'_c \cos\omega'_c\tau'_{1c}. \quad (5.26)$$

Adding the square of both equations, we obtain:

$$\omega_c'^4 + [(b - r_2)^2 - r_1^2 - 2a_1 f]\omega_c'^2 + a_1^2 f^2 = 0. \quad (5.27)$$

Such τ'_{1c} exists if and only if the above equation has at least a positive root ω'_c .

Let $M = \omega_c'^2$, then we have the quadratic equation:

$$M^2 + [(b - r_2)^2 - r_1^2 - 2a_1 f]M + a_1^2 f^2 = 0 \quad (5.28)$$

which has at least a positive root if:

$$C(0) : [(b - r_2)^2 - r_1^2 - 2a_1 f] < 0 \quad \text{and} \quad \Delta = [(b - r_2)^2 - r_1^2 - 2a_1 f]^2 - 4a_1^2 f^2 \geq 0,$$

consequently, equation (5.27) has at least a positive root ω'_c . Which implies there exist a $\tau'_{1c} > 0$ such that the steady state changes stability as τ_1 crosses τ'_{1c} for $\tau_2 = 0$. In fact τ'_{1c} is the smallest of :

$$\tau'_{1c}{}^j = \frac{1}{\omega'_c} \arccos \frac{b - r_2}{r_1} + \frac{2\pi j}{\omega'_c}, \quad j = 1, 2, \dots \quad \square$$

Note that τ_1 affects the stability of the positive equilibrium only for values of R such that conditions $C(0)$ are satisfied.

Remark: For our parameter values, we have

$$\begin{aligned} [(b - r_2)^2 - r_1^2 - 2a_1f] &= -0.9475 < 0 \quad \text{and} \\ \Lambda &= [(b - r_2)^2 - r_1^2 - 2a_1f]^2 - 4a_1^2f^2 = 0.0878 > 0. \end{aligned}$$

Proposition 5.3.4.

Consider system (5.22-5.23) with τ_1 in its unstable interval ($0 \leq \tau_1 < \tau'_{1c}$). If $a_1 \geq 2$, then there exists a critical $\tau_{2c} > 0$, such that the positive equilibrium becomes stable for $\tau_2 > \tau_{2c}$.

Proof: We consider system (5.22-5.23) with τ_1 in its unstable interval ($0 \leq \tau_1 < \tau'_{1c}$). Regarding τ_2 as a parameter, consider $\lambda(\tau_2) = \alpha(\tau_2) + i\omega(\tau_2)$. does there exist a τ_{2c} such that $\alpha(\tau_{2c}) = 0$ and $\lambda(\tau_{2c}) = i\omega_{2c}$ is solution of equation (5.24)? Such τ_{2c} exists if and only if:

$$\omega_{2c}^4 + k_1\omega_{2c}^3 + k_2\omega_{2c}^2 + k_3\omega_{2c} + k_4 = 0, \quad (5.29)$$

has at least a positive root ω_{2c} , with

$$\begin{aligned} k_1 &= 2r_1(\sin \omega_{2c}\tau_1 + b \cos^2 \omega_{2c}\tau_1), \\ k_2 &= b^2 + r_1^2 \sin^2 \omega_{2c}\tau_1 - 2(f - f_1 \cos \omega_{2c}\tau_1) - r_2, \\ k_3 &= 2bf_1^2 \sin^2 \omega_{2c}\tau_1 - 2r_1(f - f_1 \cos \omega_{2c}\tau_1) + 2r_2f_1 \sin \omega_{2c}\tau_1, \\ k_4 &= (f - f_1 \cos \omega_{2c}\tau_1)^2 - (a_1 - 1)^2 f^2 - f_1^2 - 2(a_1 - 1)ff_1 \cos \omega_{2c}\tau_1. \end{aligned}$$

Denote

$$H(\omega_{2c}) = \omega_{2c}^4 + k_1\omega_{2c}^3 + k_2\omega_{2c}^2 + k_3\omega_{2c} + k_4.$$

It is easy to check that $H(0) < 0$ if $a_1 \geq 2$ and $\lim_{\omega_{2c} \rightarrow +\infty} H(\omega_{2c}) = +\infty$. Therefore by the mean value theorem equation (5.29) has at least a positive root ω_{2c} . \square

Note that the effect of τ_2 on the stability of the positive equilibrium does not depend on the values of R .

5.3.3 Hopf Bifurcation Analysis

According to the Hopf Bifurcation Theorem (Culshaw [12]), the discrete time delay τ_1 will cause the system to go through a Hopf bifurcation near the steady state (x_1^*, y_1^*) , if the following transversality condition is satisfied:

$$\left. \frac{d\alpha(\tau_1)}{d\tau_1} \right|_{\tau_1=\tau_{1c}} \neq 0. \quad (5.30)$$

To check this condition we recall that the characteristic equation of the system at (x_1^*, y_1^*) when $\tau_2 = 0$ is given as :

$$\lambda^2 + (b - r_2)\lambda - r_1 e^{-\lambda\tau_1} \lambda + a_1 f = 0. \quad (5.31)$$

Substituting $\lambda(\tau_1) = \alpha(\tau_1) + i\omega(\tau_1)$ in equation (5.31), we have :

$$\alpha^2 - \omega^2 + 2\alpha\omega i + (b - r_2)\alpha + (b - r_2)\omega i - r_1 e^{\alpha\tau_1} (\cos \omega\tau_1 - i \sin \omega\tau_1)(\alpha + i\omega) + a_1 f = 0.$$

We equate the real and the imaginary parts to zero, and we have :

$$\alpha^2 - \omega^2 + (b - r_2)\alpha + a_1 f + r_1 e^{\alpha\tau_1} (\alpha \cos \omega\tau_1 + \omega \sin \omega\tau_1) = 0, \quad (5.32)$$

$$2\alpha\omega + (b - r_2)\omega - r_1 e^{\alpha\tau_1} (\omega \cos \omega\tau_1 - \alpha \sin \omega\tau_1) = 0. \quad (5.33)$$

We differentiate equations (5.32) and (5.33) with respect to τ_1 and evaluate at $\tau_1 = \tau'_{1c}$ for which $\alpha(\tau'_{1c}) = 0$ and $\omega(\tau'_{1c}) = \omega'_c$. We obtain

$$A \frac{d\omega(\tau_1)}{d\tau_1} \Big|_{\tau_1=\tau'_{1c}} - B \frac{d\alpha(\tau_1)}{d\tau_1} \Big|_{\tau_1=\tau'_{1c}} = C \cos \omega'_c \tau'_{1c} + D \sin \omega'_c \tau'_{1c}, \quad (5.34)$$

$$B \frac{d\omega(\tau_1)}{d\tau_1} \Big|_{\tau_1=\tau'_{1c}} + A \frac{d\alpha(\tau_1)}{d\tau_1} \Big|_{\tau_1=\tau'_{1c}} = C \sin \omega'_c \tau'_{1c} - D \cos \omega'_c \tau'_{1c}, \quad (5.35)$$

where

$$\begin{aligned} A &:= 2\omega'_c - r_1 \tau'_{1c} \sin \omega'_c \tau'_{1c}, & B &:= (b - r_2) + r_1 \tau'_{1c} \cos \omega'_c \tau'_{1c} \\ C &:= r_1 \tau'_{1c} (\omega_c'^2 + \omega'_c \tau'_{1c}), & D &:= r_1 \tau'_{1c} \omega'_c \sin \omega'_c \tau'_{1c}. \end{aligned}$$

By solving equations (5.34) and (5.35) we have:

$$\frac{d\alpha(\tau_1)}{d\tau_1} \Big|_{\tau_1=\tau'_{1c}} = \frac{(AC - BD) \sin \omega'_c \tau'_{1c} - (AD + BC) \cos \omega'_c \tau'_{1c}}{A^2 + B^2}. \quad (5.36)$$

The system goes through a Hopf bifurcation near (x_1^*, y_1^*) if:

$$(AC - BD) \sin \omega'_c \tau'_{1c} - (AD + BC) \cos \omega'_c \tau'_{1c} \neq 0.$$

5.3.4 Numerical Results

To illustrate the effect of the parameter R and the discrete time delay on the stability of the steady state (x^*, y^*) , and to support the theoretical predictions discussed above, we conducted numerical simulations for the system (5.22-5.23). We

used DDE-BIFTOOL (Engelborghs[15]) for the stability and bifurcation analysis and also used the Matlab solver ode23 and dde23 (Shampine[?],Shampine[29]) to see the behavior of the predator and prey population through time. All the parameter values are given in Table 5.2.

For the given parameters values we have $R = 10 > 1$, and a positive equilibrium exists and is given as $(x_1^*, y_1^*) = (0.111, 1.111)$. When there is no delay the prey and predator populations variation through time is shown on Figure 5.4.

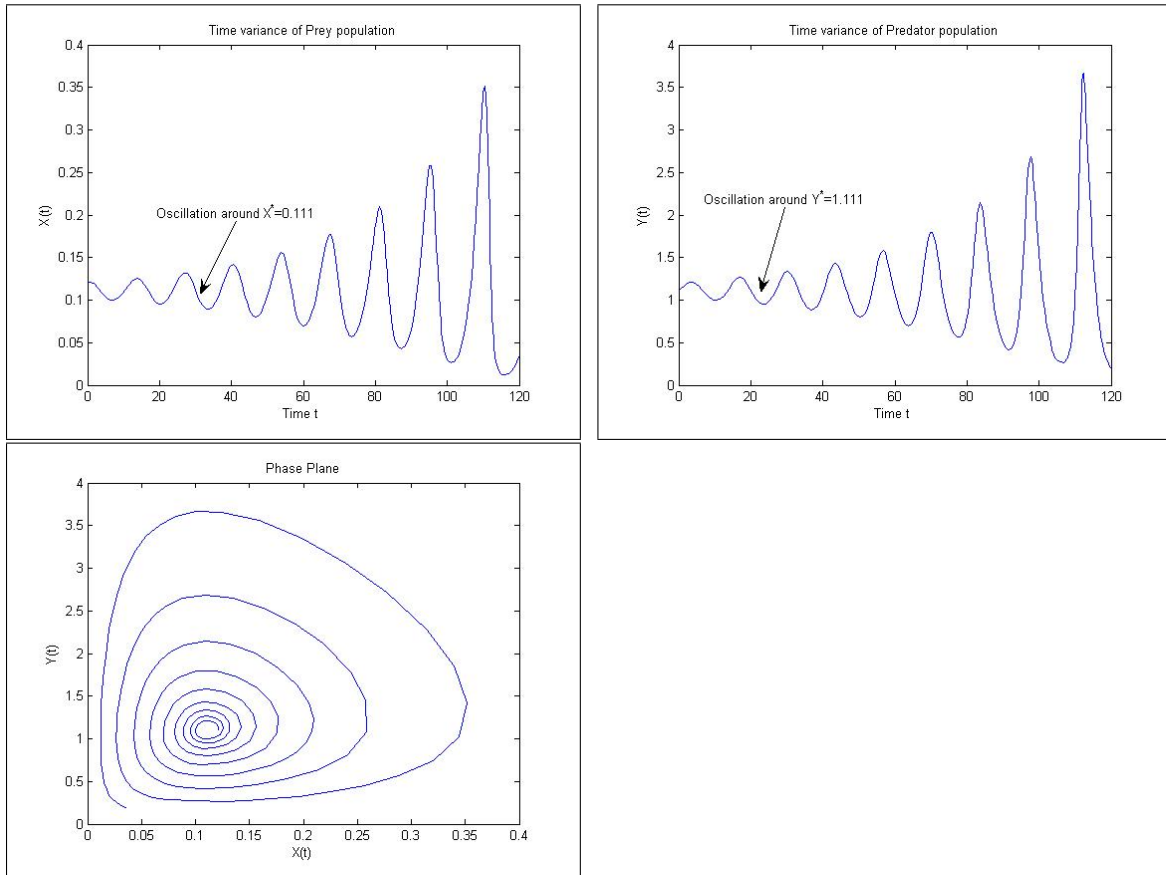


Figure 5.4. The positive equilibrium is unstable for $\tau_1 = \tau_2 = 0$ and $R = 10 > 1$.The system exhibits a spiral out from the equilibrium $(x_1^*, y_1^*) = (0.111, 1.111)$..

For our parameter values we have:

$$[(b - d)^2 - r_1^2 - 4f] = -0.9475 < 0 \quad \text{and}$$

$$\Lambda = [(b - d)^2 - r_1^2 - 4f]^2 - 16f^2 = 0.0878 > 0.$$

Then there exists a $\tau_{1c} = 6$ such that the steady state remains unstable for $0 \leq \tau_1 < \tau_{1c}$ and $\tau_2 = 0$ (see Figure 5.5), it becomes stable as τ_1 crosses τ_{1c} and $\tau_2 = 0$ as shown on Figure 5.6.

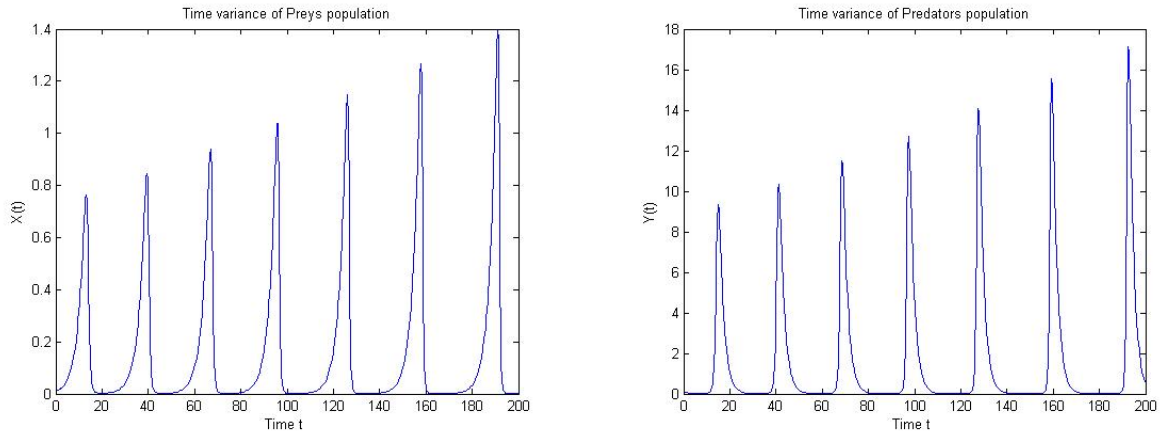


Figure 5.5. The positive equilibrium remains unstable for $\tau_1 = 1 < \tau_{1c} = 6$ and $\tau_2 = 0$.

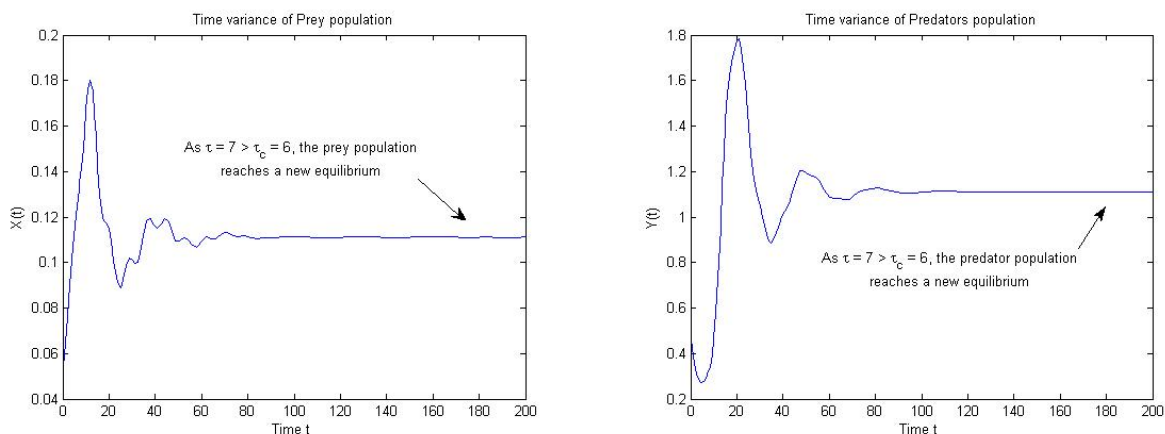


Figure 5.6. The positive equilibrium is stable for $\tau_1 = 7 > \tau_{1c} = 6$ and $\tau_2 = 0$.

We examine closely the stability switch introduced by τ_1 . We use DDE-BIFTOOL to compute the eigenvalues of the characteristic equation (5.24) for $\tau_2 = 0$ and $0 \leq \tau_1 \leq 10$. In Figure 5.7 we plot the real parts versus the imaginary parts of these eigenvalues.

We see that the equilibrium (x_1^*, y_1^*) stabilizes as τ_1 crosses the critical value $\tau'_{1c} = 6$. We also plot in Figure 5.7 the eigenvalues of equation (5.24) for $\tau_1 = \tau'_{1c} = 6$ and observe a pair of two pure imaginary eigenvalues.

The system goes through a Hopf bifurcation as τ_1 crosses τ'_{1c} . We compute the Hopf bifurcation branches using Matlab and show them in Figure 5.8.

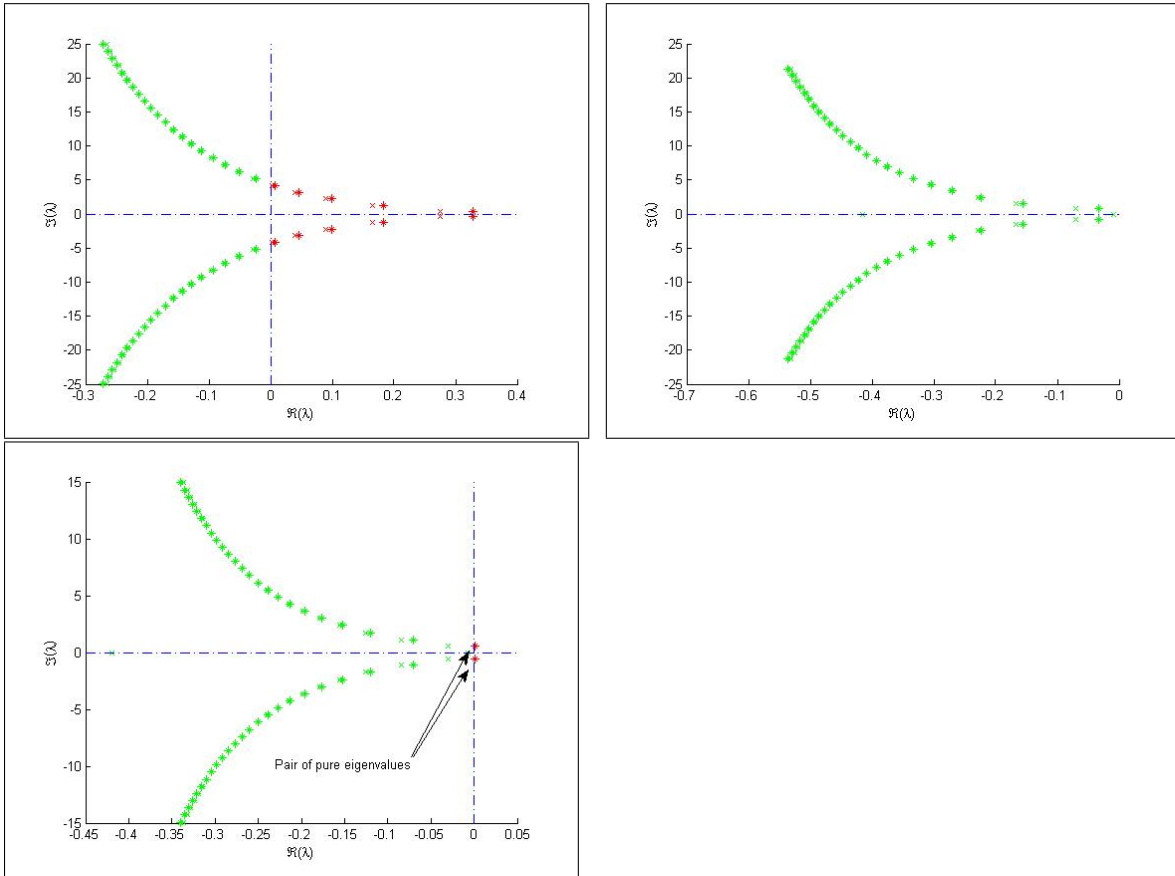


Figure 5.7. The eigenvalues of the characteristic equation (5.24) for $\tau_1 = 3$ (left) and $\tau_1 = 8$ (center) with $\tau_2 = 0$. At $\tau_1 = \tau'_{1c} = 6$ we can clearly observe a pair of 2 pure imaginary eigenvalues (right)..

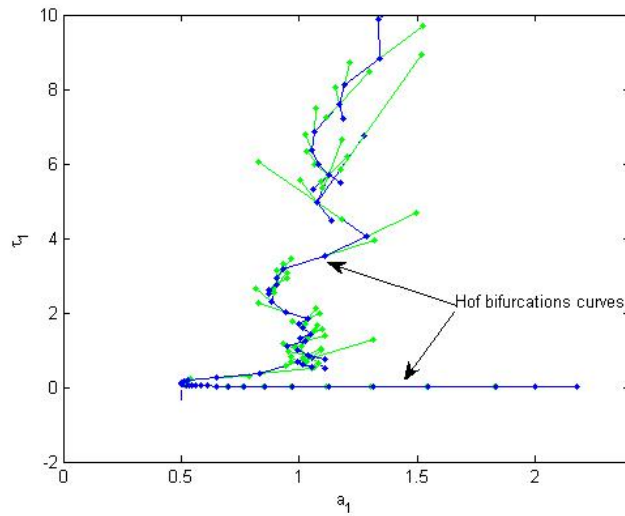


Figure 5.8. Global Hopf bifurcations branches as we vary τ_1 and a_1 (same as varying R)..

For the case of two non-zero delays, we use Matlab to compute numerical simulations illustrating the effects of the two delays. The analysis is summarized in Table 5.3

Table 5.3. Stability regions in case of two non-zero delays

Unstable	Stable	Stable	Unstable
$\begin{cases} 0 \leq \tau_1 < \tau'_{1c}, \\ 0 \leq \tau_2 < \tau_{2c} \end{cases}$	$\begin{cases} \tau_1 > \tau'_{1c}, \\ 0 \leq \tau_2 < \tau_{2c} \end{cases}$	$\begin{cases} 0 \leq \tau_1 < \tau'_{1c}, \\ \tau_2 > \tau_{2c} \end{cases}$	$\begin{cases} \tau_1 > \tau'_{1c}, \\ \tau_2 > \tau_{2c} \end{cases}$
see Fig 5.4 and Fig5.9	see Fig5.6 and Fig5.10	see Fig5.11	see Fig5.12

Note $\tau'_{1c} = 6$ and $\tau_{2c} = 2.5$

For $\tau_1 = 2$ and $\tau_2 = 0.5$ the equilibrium is unstable as shown in Figure 5.9.

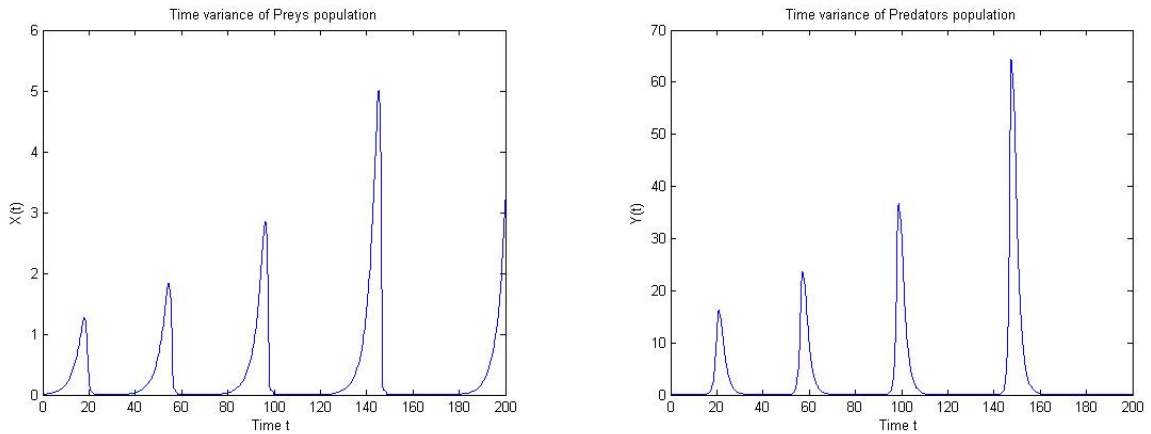


Figure 5.9. The positive equilibrium is unstable for $\tau_1 = 2$ and $\tau_2 = 0.5$.

For $\tau_1 = 7$ and $\tau_2 = 1.2$ the equilibrium becomes stable as shown in Figure 5.10.

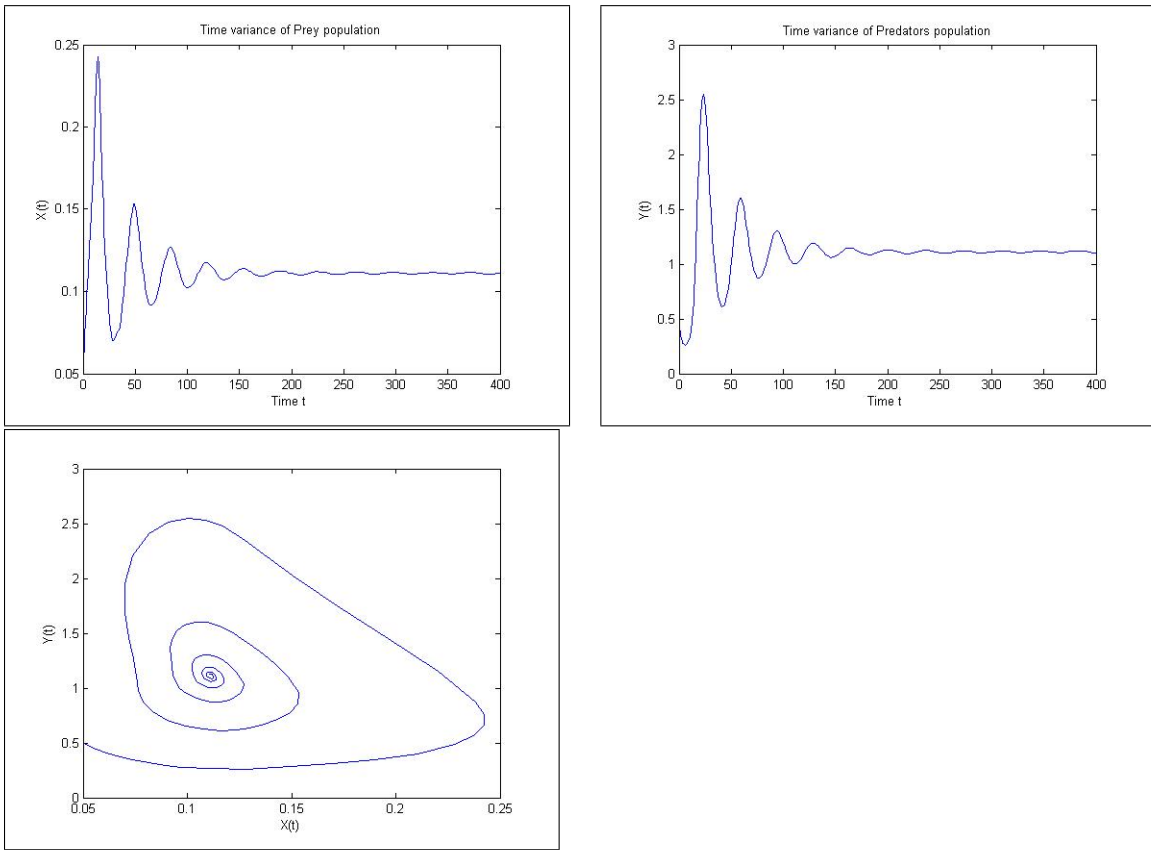


Figure 5.10. The positive equilibrium is stable for $\tau_1 = 7$ and $\tau_2 = 1.2$. The system exhibits a spiral in toward the equilibrium $(x_1^*, y_1^*) = (0.111, 1.111)$.

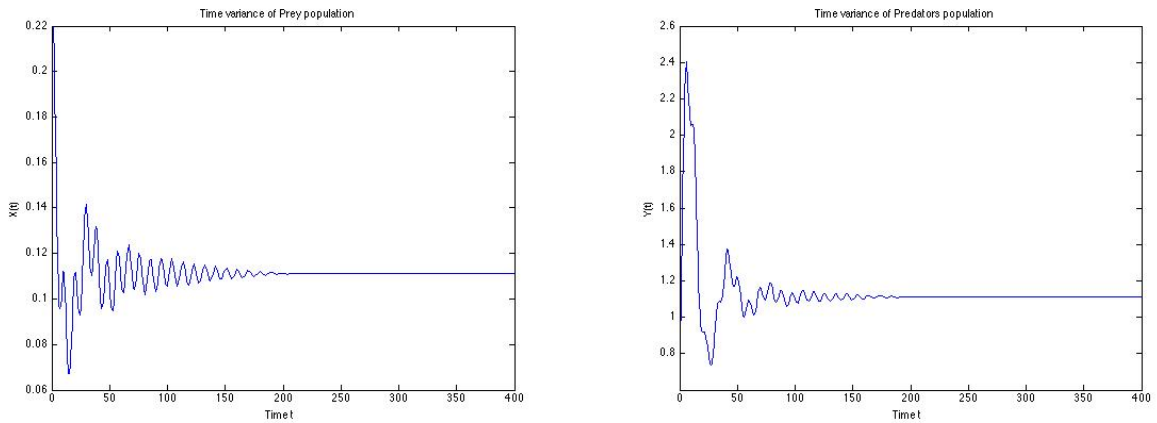


Figure 5.11. The positive equilibrium is stable for $\tau_1 = 0.7$ and $\tau_2 = 8$.

For $\tau_1 = 7$ and $\tau_2 = 3.1$ the equilibrium becomes unstable again as shown in Figure 5.12.

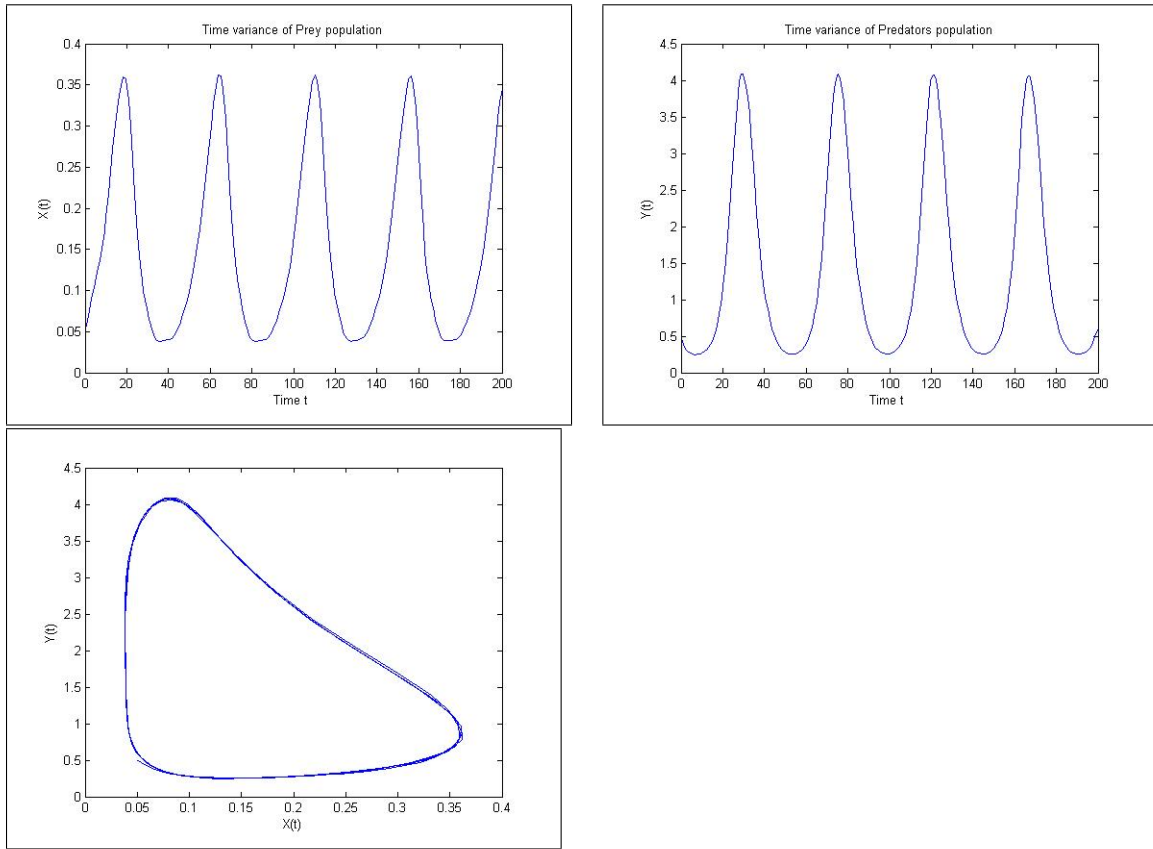


Figure 5.12. The positive equilibrium is unstable for $\tau_1 = 7$ and $\tau_2 = 3.1$.The system exhibits an unstable periodic solutions..

5.4 Conclusions and Discussion

It is well known that changes in the parameters play a crucial role in understanding dynamical systems. There is a need to incorporate discrete time delays in dynamical systems (Biological systems, physical systems,...) as has been shown and studied by many researchers (Perelson[21],Bellen[23],...). Published papers have shown that the incorporation of discrete time delays can highly impact the dynamics of the system, since they can cause stability switches of a steady state point, and can

also cause the system to go through a Hopf bifurcation near that steady state point (Culshaw[12], Bellen[23],...). To understand the effects of discrete time delays and parameter variations on certain biological system models, we carried out a bifurcation analysis of a system of delay differential equations in detail for $n=1$ with specific examples, gave the procedure for higher n , and did a concrete example for $n=2$. We investigated the stability of the steady states as both bifurcation parameters, the discrete time delay τ and a local bifurcation parameter μ , cross critical values. Our analysis shows that while both parameters can destabilize the steady state, the discrete time delay can cause stability switches of the steady state only upon certain values of μ . The local bifurcation parameter effects on the stability of the steady state do not depend on the value of τ . We also showed that both parameters act differently in term of bifurcation. While the discrete time delay may only introduce a Hopf bifurcation, the parameter μ can introduce other type of bifurcations.

CHAPTER 6

DELAY PARTIAL DIFFERENTIAL EQUATIONS OF A HOLLING TYPE PREDATOR-PREY MODEL

6.1 Introduction

It is well known that the distribution of species is generally heterogeneous spatially, and therefore the species will migrate towards regions of lower population density to add the possibility of survival. Thus, partial differential equations with delay became the subject of a considerable interest in recent years. In this section we consider simultaneously time delays and spatial diffusion to model the predator prey model presented in chapter 4. Our main focus is to investigate analytically and numerically the effects of the spatial diffusion, the time delays and parameters variation on the dynamic of the system.

6.2 Delay PDE's Model

The growth dynamics of two species with spatial diffusion corresponding to system (5.22-5.23) can be described by the following diffusion system with delays:

$$\frac{\partial u(t, x)}{\partial t} = d_1 \Delta u(t, x) + r_1 u(t - \tau_1, x) - a_1 \frac{u(t, x)w(t, x)}{u(t, x) + 1}, \quad t > 0, \quad x \in (0, \pi), \quad (6.1)$$

$$\frac{\partial w(t, x)}{\partial t} = d_2 \Delta w(t, x) - r_2 w(t, x) + a_2 \frac{u(t - \tau_2, x)w(t - \tau_2, x)}{u(t - \tau_2, x) + 1}, \quad t > 0, \quad x \in (0, \pi) \quad (6.2)$$

with Neumann boundary conditions:

$$\frac{\partial u(t, x)}{\partial x} = \frac{\partial w(t, x)}{\partial x} = 0, \quad t \geq 0, \quad x = 0, \pi,$$

and history functions:

$$u(t, x) = \phi(t, x) \geq 0, \quad w(t, x) = \psi(t, x) \geq 0, \quad (t, x) \in [-\tau, 0] \times (0, \pi), \quad \tau = \max \{ \tau_1, \tau_2 \}.$$

Where $u(t, x)$ and $w(t, x)$ can be interpreted as the densities of prey and predator populations at time t and space x , respectively; $d_1 > 0$, $d_2 > 0$ denote the diffusion coefficients of prey and predator species, respectively; Δ is the Laplacian operator. Neumann boundary conditions imply that the two species have zero flux across the domain boundary, meaning no individuals can enter or leave the enclosed area $[0, \pi]$. $(\phi, \psi) \in \mathbb{C} = C([-\tau, 0], X)$, and X is defined by :

$$X = \left\{ (u, w) : u, w \in V^{2,2}(0, \pi) : \frac{du}{dx} = \frac{dw}{dx} = 0, \quad x = 0, \pi \right\}$$

with the inner product $\langle \cdot, \cdot \rangle$.

In the remaining part of this section, we focus on the system (6.1-6.2). The main purpose is to investigate the effects of the diffusion and the time delays on the dynamics of the system (6.1-6.2) under parameter variation. To do so, we investigate the stability of the positive spatially homogeneous steady state. We prove that when there is no diffusion and no time delays the steady state point is globally unstable just as in chapter 5. When the species diffuse and both maturation times are zero, then the steady state becomes stable for all parameter values. We also prove that when there is diffusion and the maturation time for the predator is zero, then the maturation time for the prey population has no effect on the dynamic of the system, namely the steady state remains stable. Finally when both species diffuse and the time delays are both positive, then the steady state can be destabilize for a small diffusivity and

a large maturation's time for the predator population. This stability changes may cause a Hopf bifurcation near the steady state depending on the parameter values.

6.3 Stability and Hopf Bifurcation Analysis

It is relatively easy to see that the system (6.1-6.2) has :

- only the trivial steady state $E_0(0, 0)$ and the non-zero spatially heterogeneous steady state $E_1(\varphi \cos \frac{\sqrt{r_1 d_1}}{d_1} x, 0)$ when $R < 1$, with $R = \frac{a_2}{r_2}$ and $\varphi \in \mathbb{R}$.
- the trivial steady state $E_0(0, 0)$, the non-zero spatially heterogeneous steady state $E_1(\varphi \cos \frac{\sqrt{r_1 d_1}}{d_1} x, 0)$, and the positive spatially homogeneous steady state $E^*(u^*, w^*)$ when $R > 1$, with

$$u^* = \frac{1}{R-1}, \quad w^* = \frac{RR'}{R-1}, \quad R = \frac{a_2}{r_2}, \quad R' = \frac{a_1}{r_1}.$$

We will focus on the positive spatially homogeneous steady state $E^*(u^*, w^*)$. Let $\bar{u}(t, x) = u(t, x) - u^*$, and $\bar{w}(t, x) = w(t, x) - w^*$, replace this in system (6.1-6.2) and only consider the terms linear in $\bar{u}(t, x)$ and $\bar{w}(t, x)$ we can write the linearized matrix form of system (6.1-6.2) as (Zhang [30]):

$$\frac{\partial U(t, x)}{\partial t} = d\Delta U(t, x) + L(U^*)U(t, x), \quad (6.3)$$

For convenience of notation, we have replaced $\bar{U}(t, x)$ by $U(t, x)$ in the above equation.

where

$$U(t, x) = (u(t, x), w(t, x))^T, \quad d = (d_1, d_2)^T, \quad \Delta = \begin{pmatrix} \frac{\partial}{\partial x^2} & 0 \\ 0 & \frac{\partial}{\partial x^2} \end{pmatrix},$$

and

$$L(U^*) = \begin{bmatrix} r_1 e^{-\lambda\tau_1} - \frac{a_1 w^*}{(u^*+1)^2} & -\frac{a_1 u^*}{u^*+1} \\ \frac{a_2 w^*}{(u^*+1)^2} e^{-\lambda\tau_2} & -r_2 + \frac{a_2 u^*}{u^*+1} e^{-\lambda\tau_2} \end{bmatrix}.$$

Equation (6.3) has characteristic equation :

$$\det [\lambda I - d\Delta\lambda - L(U^*)] = 0.$$

It is well known that the linear operator Δ on $(0, \pi)$ with homogeneous Neumann boundary conditions has the eigenvalues $-k^2$ ($k \in \mathbb{N}_0 = \{0, 1, 2, \dots\}$) and the corresponding eigenfunctions are :

$$\beta_k^1 = \begin{pmatrix} \gamma_k \\ 0 \end{pmatrix}, \quad \beta_k^2 = \begin{pmatrix} 0 \\ \gamma_k \end{pmatrix}, \quad \gamma_k = \frac{\cos kx}{\|\cos kx\|_{2,2}}, \quad k \in \mathbb{N}_0.$$

The characteristic equation is therefore equivalent to :

$$\det \left[\begin{pmatrix} \lambda + d_1 k^2 & 0 \\ 0 & \lambda + d_2 k^2 \end{pmatrix} - \begin{pmatrix} r_1 e^{-\lambda\tau_1} - \frac{a_1 w^*}{(u^*+1)^2} & -\frac{a_1 u^*}{u^*+1} \\ \frac{a_2 w^*}{(u^*+1)^2} e^{-\lambda\tau_2} & -r_2 + \frac{a_2 u^*}{u^*+1} e^{-\lambda\tau_2} \end{pmatrix} \right] = 0,$$

which can be rewrite as :

$$\begin{aligned} 0 = & \lambda^2 + [b - r_1 e^{-\lambda\tau_1} - r_2 e^{-\lambda\tau_2} + (d_1 + d_2)k^2] \lambda \\ & + (f + A_k - (f_1 + B_k)e^{-\lambda\tau_1} + ((a_1 - 1)f + C_k)e^{-\lambda\tau_2} + f_1 e^{-\lambda(\tau_1 + \tau_2)}), \end{aligned} \quad (6.4)$$

where

$$\begin{aligned} b &= r_2 + \frac{r_1}{u^* + 1}, \quad f = \frac{r_1 r_2}{u^* + 1}, \quad f_1 = r_1 r_2, \\ A_k &= d_1 d_2 k^4 - d_1 r_2 k^2 - d_2 (b - r_2) k^2, \\ B_k &= d_2 r_1 k^2, \quad C_k = d_1 r_2 k^2, \quad k \in \mathbb{N}_0. \end{aligned}$$

Proposition 6.3.1.

If the wave number $k = 0$ (that is neither specie diffuse), and the discrete time delays $\tau_1 = \tau_2 = 0$, then the equilibrium (u^, w^*) is unstable.*

Proof: when $k = 0$, and $\tau_1 = \tau_2 = 0$ we are in the case of proposition 9 and the equilibrium (u^*, w^*) has been shown to be unstable. \square

Proposition 6.3.2.

If the wave number $k \in \mathbb{N} = \{1, 2, \dots\}$, the discrete time delays $\tau_1 = \tau_2 = 0$, and $A_k - B_k + C_k > 0$ then the equilibrium (u^*, w^*) becomes stable.

Proof: If $\tau_1 = \tau_2 = 0$ and $k > 0$, the characteristic equation (6.4) becomes

$$\lambda^2 + [(b - r_1 - r_2) + (d_1 + d_2)k^2] \lambda + a_1 f + A_k - B_k + C_k = 0. \quad (6.5)$$

Notice that $b - r_1 - r_2 = -\frac{r_1}{R} < 0$ is relatively very small compare to $(d_1 + d_2)k^2$, also $a_1 f > 0$, and by assumption $A_k - B_k + C_k > 0$. Therefore all the roots of equation (6.6) have strictly negative real parts. \square

Remark: In general for large wave number k ,

$$A_k + C_k - B_k = d_1 d_2 k^4 - d_2 (b - r_2 + r_1) k^2 > 0.$$

For our parameter values :

$$A_k + C_k - B_k = 2k^4 - 1.9k^2 > 0, \quad k \in \mathbb{N} = \{1, 2, \dots\}.$$

Proposition 6.3.3.

if the wave number $k \in \mathbb{N} = \{1, 2, \dots\}$, the discrete time delay $\tau_2 = 0$, and $A_k - B_k + C_k > 0$ then the equilibrium (u^*, w^*) remains stable for all $\tau_1 \geq 0$.

Proof: Assume that $k \geq 1$, $A_k - B_k + C_k > 0$, and $\tau_2 = 0$. We want to check if there exist $\tau_{1c} > 0$ such that $\lambda(\tau_{1c}) = i\omega(\tau_{1c}) = i\omega_{1c}$ is solution of the characteristic equation (6.4). That is the case if and only if there exists a $\omega_{1c} > 0$ such that:

$$\begin{aligned} 0 = & -\omega_{1c}^2 + [(b - r_2) + (d_1 + d_2)k^2] i\omega_{1c} - (\cos \omega_{1c}\tau_{1c} - \sin \omega_{1c}\tau_{1c}) i r_1 \omega_{1c} \\ & - (\cos \omega_{1c}\tau_{1c} - \sin \omega_{1c}\tau_{1c}) B_k + a_1 f + A_k + C_k. \end{aligned} \quad (6.6)$$

Separating the real and imaginary parts, we have :

$$-\omega_{1c}^2 + a_1 f + A_k + C_k = r_1 \omega_{1c} \sin \omega_{1c} \tau_{1c} + B_k \cos \omega_{1c} \tau_{1c} \quad (6.7)$$

$$[(b - r_2) + (d_1 + d_2)k^2] \omega_{1c} = r_1 \omega_{1c} \cos \omega_{1c} \tau_{1c} - B_k \sin \omega_{1c} \tau_{1c}. \quad (6.8)$$

Square both equations (6.7) and (6.8) and add them up, we have :

$$\omega_{1c}^4 + m_k \omega_{1c}^2 + l_k = 0, \quad (6.9)$$

with

$$m_k = d_1 d_2 k^4 + [d_1 + d_2 - d_2(b - r_2)]k^4 - (a_1 f - r_1^2 + r_2 - b), \quad k = 1, 2, \dots$$

$$l_k = (a_1 f + A_k + C_k)^2 - B_k, \quad k = 1, 2, \dots$$

and equation (6.9) has no positive root since

$$m_k = 2k^4 + 2.1k^2 + 0.58 > 0, \quad \text{for } k = 1, 2, \dots$$

and

$$l_k = (2k^4 - 0.9k^2 + 0.112)^2 - k^4 > 0, \quad \text{for } k = 1, 2, \dots$$

therefore there exists no critical $\tau_{1c} > 0$ such that $\lambda(\tau_{1c}) = i\omega_{1c}$ is solution of the characteristic equation (6.9). Which means the equilibrium (u^*, w^*) remains stable for all $\tau_1 > 0$. \square

Proposition 6.3.4.

if the wave number $k \in \mathbb{N} = \{1, 2, \dots\}$, the discrete time delay $\tau_1 > 0$, and $A_k - B_k + C_k > 0$ then there exists a critical $\tau_{2c} > 0$ such that the equilibrium (u^, w^*) becomes unstable when τ_2 crosses τ_{2c} .*

Proof: Assume that $k \geq 1$, $A_k - B_k + C_k > 0$, and $\tau_1 > 0$. Let $\lambda(\tau_2) = \alpha(\tau_2) + i\omega(\tau_2)$ be solution of the characteristic equation (6.9). We know by proposition 13 that when $\tau_2 = 0$, then $\alpha(0) < 0$. We want to check if there exist $\tau_{2c} > 0$ such that $\alpha(\tau_{2c}) = 0$ or in other word $\lambda(\tau_{2c}) = i\omega(\tau_{2c}) = i\omega_{2c}$ is solution of the characteristic equation (6.4). If such τ_{2c} exists, then by continuity of α on τ_2 , and by the Rouché's theorem the equilibrium (u^*, w^*) loses stability when $\tau_2 > \tau_{2c}$. Such τ_{2c} exists if and only if there exists a $\omega_{2c} > 0$ such that:

$$\begin{aligned}
0 &= -\omega_{2c}^2 + [b + (d_1 + d_2)k^2] i\omega_{2c} - (r_1 \cos \omega_{2c}\tau_1 + r_2 \cos \omega_{2c}\tau_{2c})i\omega_{2c} - (r_1 \sin \omega_{2c}\tau_1 + r_2 \sin \omega_{2c}\tau_{2c})\omega_{2c} \\
&\quad - (f_1 + B_k) \cos \omega_{2c}\tau_1 + (f_1 + B_k)i \sin \omega_{2c}\tau_1 + [(a_1 - 1)f + C_k] \cos \omega_{2c}\tau_{2c} \\
&\quad - i[(a_1 - 1)f + C_k] \sin \omega_{2c}\tau_{2c} + f_1 \cos(\tau_1 + \tau_{2c})\omega_{2c} - if_1 \sin(\tau_1 + \tau_{2c})\omega_{2c} + f + A_k.
\end{aligned} \tag{6.10}$$

Setting real and imaginary parts to zero we have :

$$\begin{aligned}
-\omega_{2c}^2 + f + A_k &= (r_1 \sin \omega_{2c}\tau_1 + r_2 \sin \omega_{2c}\tau_{2c})\omega_{2c} + (f_1 + B_k) \cos \omega_{2c}\tau_1 - f_1 \cos(\tau_1 + \tau_{2c})\omega_{2c} \\
&\quad - [(a_1 - 1)f + C_k] \cos \omega_{2c}\tau_{2c}
\end{aligned} \tag{6.11}$$

$$\begin{aligned}
[b + (d_1 + d_2)k^2] i\omega_{2c} &= (r_1 \cos \omega_{2c}\tau_1 + r_2 \cos \omega_{2c}\tau_{2c})\omega_{2c} + [(a_1 - 1)f + C_k] \sin \omega_{2c}\tau_{2c} \\
&\quad + f_1 \sin(\tau_1 + \tau_{2c})\omega_{2c} - (f_1 + B_k) \sin \omega_{2c}\tau_1
\end{aligned} \tag{6.12}$$

Square both equations (6.11) and (6.12), add them up and apply some basic trigonometric identities :

$$\omega_{2c}^4 + P_k \omega_{2c}^2 - Q_k = 0,$$

with

$$P_k = [b + (d_1 + d_2)k^2]^2 + (r_1^2 + r_2^2) - 2(f + A_k + r_1 r_2 \cos(\tau_1 - \tau_{2c})\omega_{2c},$$

$$Q_k = (f_1 + B_k)^2 + f_1^2 + [(a_1 - 1)f + C_k]^2.$$

Let set

$$H(\omega_{2c}) = \omega_{2c}^4 + P_k \omega_{2c}^2 - Q_k,$$

then $H(0) = -Q_k < 0$ and $H(\omega_{2c}) \rightarrow \infty$ when $\omega_{2c} \rightarrow \infty$. Therefore the Intermediate Value Theorem assures that $H(\omega_{2c})$ has a positive zero. In conclusion there exists

a τ_{2c} such that the positive equilibrium loses stability when τ_2 crosses τ_{2c} . Solving equation (6.11) for τ_{2c} , then we obtain that τ_{2c} is the minimum of :

$$\tau_{2c}^j = \tau_1 - \left[\arccos \frac{\omega_{2c}^4 - (Q_k + M_k)}{2r_1 r_2 \omega_{2c}^3} + 2\pi j \right], \quad j = 0, 1, 2 \dots$$

with

$$M_k = [2(f + A_k) - [b + (d_1 + d_2)k^2]^2 - (r_1^2 + r_2^2)]. \quad \square$$

Let

$$\lambda(\tau_2) = \alpha(\tau_2) + i\omega(\tau_2),$$

be a root of the characteristic equation (6.4) with $k \in \mathbb{N} = \{1, 2, \dots\}$, near $\tau_2 = \tau_{2c}^j$ satisfying $\alpha(\tau_{2c}^j) = 0$, $\omega(\tau_{2c}^j) = \omega_{2c}$, $j \in \mathbb{N}_0$. Then the following result holds

Lemma 6.3.1.

The following transversality conditions hold :

$$\frac{d\alpha(\tau_2)}{d\tau_2} \Big|_{\tau_2 = \tau_{2c}^j} > 0, \quad j \in \mathbb{N}_0.$$

From the previous discussion we have the following theorem on the stability of the positive spatially homogenous steady state (u^*, w^*) of the system (6.1-6.2) and the existence of Hopf bifurcation near (u^*, w^*) .

Theorem 6.3.1.

Assume that $A_k - B_k + C_k > 0$, then

- *If $k = 0$, $\tau_1 = \tau_2 = 0$, the positive constant steady state (u^*, w^*) is unstable;*
- *if $k \geq 1$, $\tau_1 = \tau_2 = 0$, the positive constant steady state (u^*, w^*) is asymptotically stable;*
- *if $k \geq 1$, $\tau_2 = 0$, the positive constant steady state (u^*, w^*) remains stable for all $\tau_1 \geq 0$;*

- $k \geq 1$, $\tau_1 > 0$, the positive constant steady state (u^*, w^*) is unstable when $\tau_2 > \tau_{2c}^j$;
- The system undergoes through Hopf bifurcations near (u^*, w^*) , and $\tau_2 = \tau_{2c}^j$ are the Hopf bifurcation values of system (6.1-6.2).

6.4 Numerical Methods

The most often applied numerical techniques for delay partial differential equations are composed of two consecutive steps:

- discretization in the variable x ,
- integration in t .

In the first step, the partial derivatives with respect to x are replaced by some approximations. To do so, we applied the finite difference method, namely we replace the partial derivative with respect to x by the approximating operator:

$$\frac{\partial^2 u(t, x_i)}{\partial x^2} \approx \frac{u(t, x_{i-1}) - 2u(t, x_i) + u(t, x_{i+1}))}{h^2},$$

$$\frac{\partial^2 w(t, x_i)}{\partial x^2} \approx \frac{w(t, x_{i-1}) - 2w(t, x_i) + w(t, x_{i+1}))}{h^2}.$$

Here, h is a step-size in x -direction and x_i are grid-points defined by:

$$x_i = ih, \quad i = 0, 1, 2, \dots, n, \quad h = \frac{\pi}{n}.$$

This discretization in x results in the following system of ordinary delay differential equations:

$$\frac{du(t, x_i)}{dt} = d_1 \left[\frac{u(t, x_{i-1}) - 2u(t, x_i) + u(t, x_{i+1})}{h^2} \right] + r_1 u(t - \tau_1, x_i) - a_1 \frac{u(t, x_i)w(t, x_i)}{u(t, x_i) + 1},$$

(6.13)

$$\frac{dw(t, x_i)}{dt} = d_2 \left[\frac{w(t, x_{i-1}) - 2w(t, x_i) + w(t, x_{i+1})}{h^2} \right] - r_2 w(t, x_i) + a_2 \frac{u(t - \tau_2, x_i)w(t - \tau_2, x_i)}{u(t - \tau_2, x_i) + 1},$$

(6.14)

when

$$t > 0, \quad x_i \in (x_{i-1}, x_{i+1}), \quad i = 1, \dots, n - 1.$$

and history functions:

$$u(t, x_i) = \phi(t, x_i) \geq 0, \quad w(t, x_i) = \psi(t, x_i) \geq 0, \quad (t, x_i) \in [-\tau, 0] \times (x_{i-1}, x_{i+1}), \quad \tau = \max \{ \tau_1, \tau_2 \}.$$

Notice that $u(t, x_0)$, $w(t, x_0)$, and $u(t, x_n)$, $w(t, x_n)$ are determined from the Neumann boundary conditions, where $x_0 = 0$, and $x_n = \pi$.

We investigate the system numerically with the parameters value given in table 5.2 and $d_1 = 1$, and $d_2 = 2$. We use the Matlab solvers dde-23 and pde-23 to display the following graphs.

The propagation of both species through time and space when there is no delay, that is $\tau_1 = \tau_2 = 0$ is shown on fig 6.1

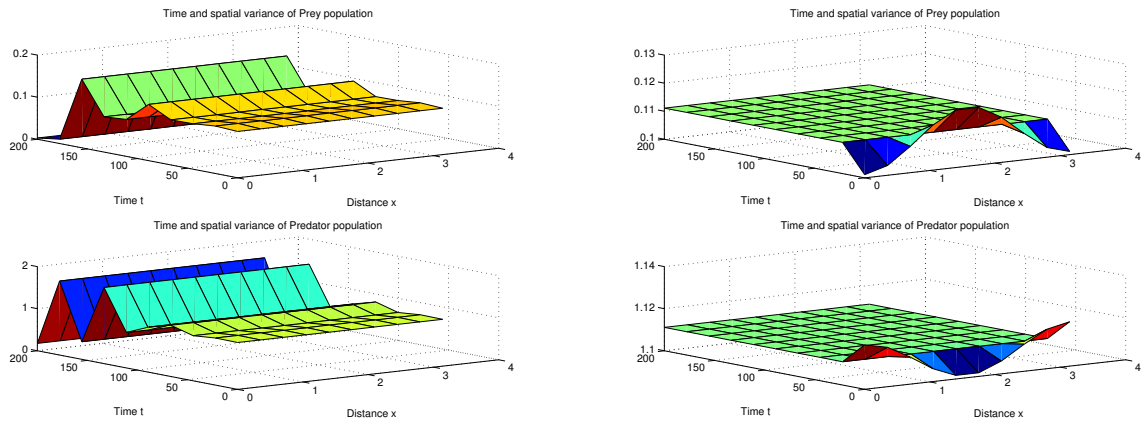


Figure 6.1. The system is unstable when there is no diffusion, and stabilize around the positive equilibrium $(u^*, w^*) = (0.111, 1.111)$ when both species diffuse for $\tau_1 = \tau_2 = 0$.

When we keep the time lag $\tau_2 = 0$, and let both species diffuse then the positive equilibrium (u^*, v^*) remains stable for all $\tau_1 > 0$ as shown on fig 6.2 and fig 6.3.

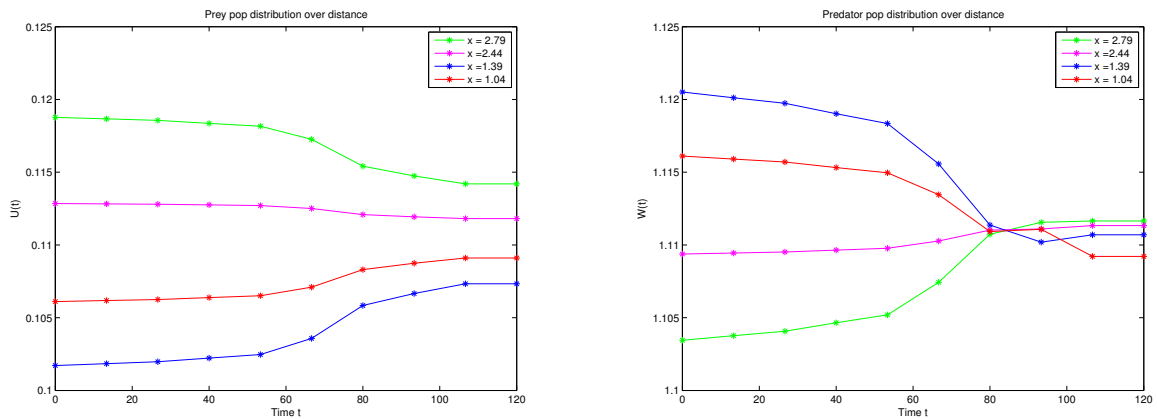


Figure 6.2. The system remains stable through time around the positive equilibrium $(u^*, w^*) = (0.111, 1.111)$ when both species diffuse for $\tau_2 = 0$ and $\tau_1 = 10$.

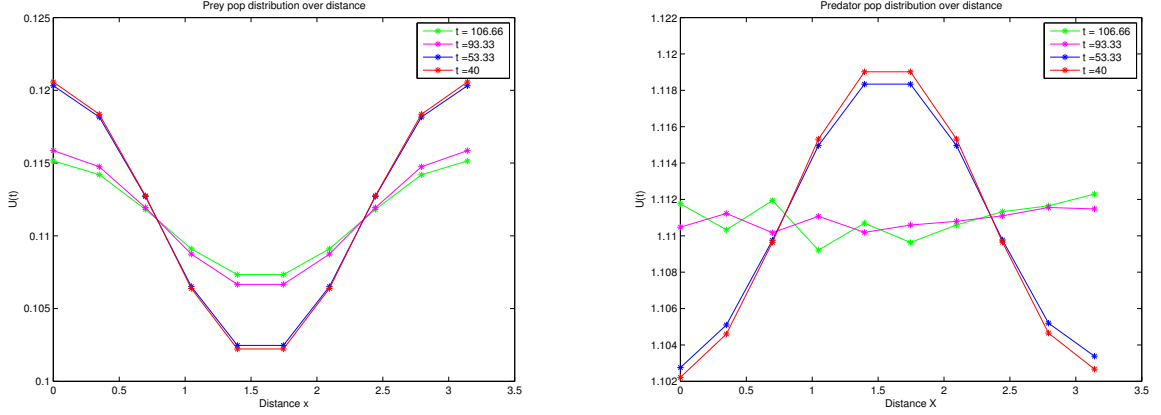


Figure 6.3. The system remains stable through space around the positive equilibrium $(u^*, w^*) = (0.111, 1.111)$ when both species diffuse for $\tau_2 = 0$ and $\tau_1 = 10$.

We finally destabilize the positive equilibrium when both species diffuse, and have time of maturations $\tau_1 = 10$, and $\tau_2 = 6$, as shown on figure 6.4 and 6.5

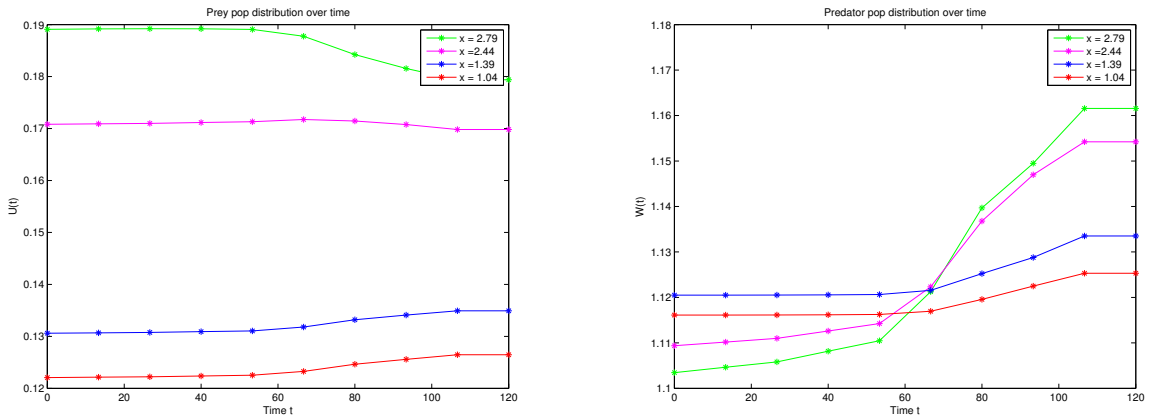


Figure 6.4. Prey and predator distribution over time for $\tau_1 = 10$ and $\tau_2 = 6$. The positive equilibrium $(u^*, w^*) = (0.111, 1.111)$ is unstable.

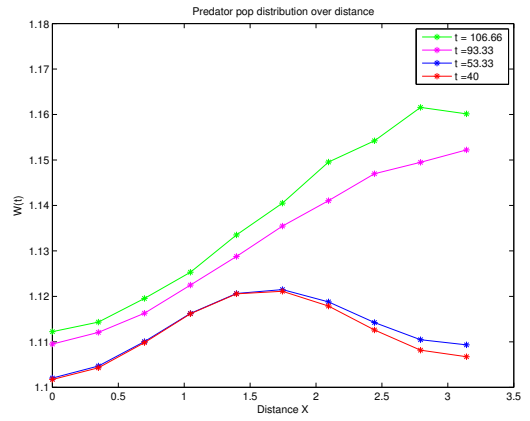
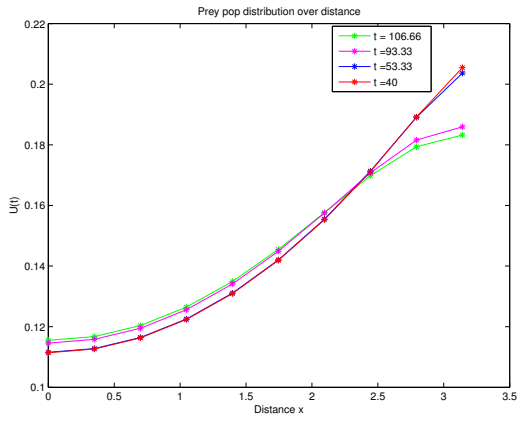


Figure 6.5. Prey and predator distribution over space for $\tau_1 = 10$ and $\tau_1 = 6$. The positive equilibrium $(u^*, w^*) = (0.111, 1.111)$ is unstable.

CHAPTER 7

CONCLUSIONS AND DISCUSSIONS

The use of delay differential equations in the modeling of biological phenomena has become more prevalent in recent years ([31], [32], [33]). Many works have been done in terms of the effects of discrete time delays on the dynamic of a delay system ([12], [1], [23]). In this dissertation we focused on the relationship between parameters variation and the effects of the discrete time delays on such delayed systems. We first considered, in chapter 3, a Delay Differential Equation model of human immunodeficiency virus (HIV). We investigated the effects of the discrete time on the virulence of the HIV strain, and presented sufficient and necessary condition for the virulence of the pathogen to change as the time delay changes. We showed that the delay affects the virulence of the pathogen only upon certain values of the rate at which infected $CD4^+$ T- cells become infected.

In chapter 4, we also investigated analytically and numerically the stability of the endemically infected equilibrium of the same delay model for HIV. Our analysis showed that certain key parameters, such as the rate of infection, play a crucial role on how the discrete time may affect the dynamic of the system. The effects of the delay on the stability of the system were shown to be conditional to certain parameters values.

This motivated chapter 5, where we carried out a bifurcation analysis of systems of delay differential equations. We presented general results for one equation with one and two delays and study a specific example of one equation with one delay. We then established the procedure for n equations with multiple delays and did a specific

example for two equations with two delays. We investigated the stability of the steady states as both chosen bifurcation parameters, the discrete time delay τ and a local equation parameter μ , crossed critical values. Our analysis shows that while changes in both parameters can destabilize the steady state, the discrete time delay can cause stability switches of the steady state for certain values of μ , while the effects of the local equation parameter on the steady state do not necessarily depend on the value of τ . While μ may cause the system to go through different types of bifurcations, the discrete time delay can only introduce a Hopf bifurcation for certain values of μ .

We finally considered a delay partial differential equation of a Holling type predator-prey model. We considered, simultaneously, time delays and spatial diffusion to model the predator prey model presented in chapter 5. The discrete time delays were introduced in order to consider the time maturation for both the predator and prey populations. We mainly investigated, analytically and numerically, the effects of the spatial diffusion, the time delays, and parameters variation on the dynamic of the system. Once again the effects of the delays were proven to be related to parameters values, but also to the diffusion term. In conclusion, for one to understand the effects of discrete time delays on dynamical systems, a rigorous parameter's sensitivity analysis is necessary. Since delayed systems are very complicated to analyze analytically for bigger dimension, numerical tools are crucial to understand the dynamics of delayed systems.

APPENDIX A
COMPUTATION OF R_0

In this appendix we compute the basic reproductive number by the method of next generation matrix.

System (3.1-3.3) has matrix of newly raised infections

$$F = \begin{bmatrix} 0 & k_2 e^{-\lambda\tau} \\ 0 & 0 \end{bmatrix} \quad (\text{A.1})$$

and the matrix of transferred infections :

$$V = \begin{bmatrix} \mu_1 & 0 \\ -N\mu_b & \mu_v \end{bmatrix}. \quad (\text{A.2})$$

The next generation matrix is

$$FV^{-1} = \begin{bmatrix} e^{-\lambda\tau} \frac{k_2 N \mu_b}{\mu_1 \mu_v} & e^{-\lambda\tau} \frac{k_2}{\mu_v} \\ 0 & 0 \end{bmatrix}, \quad (\text{A.3})$$

which has characteristic equation:

$$\lambda \left(\lambda - e^{-\lambda\tau} \frac{k_2 N \mu_b}{\mu_1 \mu_v} \right) = 0. \quad (\text{A.4})$$

If $\tau = 0$, then the dominant eigenvalue is

$$r_0 = \frac{k_2 N \mu_b}{\mu_1 \mu_v} \quad (\text{A.5})$$

If $\tau > 0$, then he dominant eigenvalue is

$$R_0 = \frac{\ln r_0 \tau}{\tau}. \quad (\text{A.6})$$

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BIOGRAPHICAL STATEMENT

Ibrahim Diakite was born in Mali, West Africa, where he graduated from "Lycee Technique de Bamako" the only math and engineering high school of the country. Subsequently he benefited from a Malian/Moroccan cooperation fellowship which led him to Morocco for his undergraduate studies, where he graduated with a B.S in applied Mathematics from Cadi Ayyad University. He came to the United States in 2007, where he first attended the University of Houston language center for intensive English training. In 2009, he began his graduate studies at the University of Texas at Arlington, where he completed a M.S in mathematics in 2011. His current research lies on mathematical analysis of dynamical systems, more specially on biological systems.