DYNAMICS OF PREDATOR-PREY MODELS

SUFYAN ABAAS WUHAIB

UNIVERSITI SAINS MALAYSIA

2013

DYNAMICS OF PREDATOR-PREY MODELS

by

SUFYAN ABAAS WUHAIB

Thesis submitted in fulfilment of the requirements
for the degree of
Doctor of Philosophy

May 2013

ACKNOWLEDGEMENTS

In the name of **ALLAH ALMIGHTY**, most Gracious, most Compassionate, and Creator of the universe, who indoctrinated the sanctification upon me to complete this thesis.

I am very grateful to my supervisor, Dr. Yahya Abu Hasan, for his invaluable guidance, who was the best help me, and who gave me scientific and moral, I ask God to help him in all areas of his life. I would like to express my special thank to the Dean Prof. Ahmad Izzani Md. Ismail, the staff of the School of Mathematical Sciences, Universiti Sains Malaysia and the staff of the Institute of Postgraduate Studies for their co-operation and assistance. A thanks also goes to the Ministry of Hair Education of Iraq and also to Tikrit University, I extend my thanks to the teachers who provided me assistance from different universities Iraqi, in particular Dr. Saeed Thallab, Dr. Fadhel Subhi, Dr. Raid Naji, Dr. Taha Hamid, Dr. Luma Naj, Dr. Eman Fadhel, Dr.Rajja Al shaheen and Dr. Muhammed Abbas. I am indebted to my father, my mother, my brother (Abdul Majid) and my sister (Nada) in Illiyun, my brothers and sisters for their love and their generous support during these years. Last but not least, I am gratefully acknowledged my wife, Zahana and my kids, Ibtihal, Ayat, Amenah, Saleh and Alhasan. Without their love, support and sacrifices, this work would have been impossible. This thesis is dedicated to them.

Sufyan Abaas Wuhaib

15-05-2013

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Page

LIST OF PUBLICATIONS

Journals:

[1] Wuhaib, S. A and Abu Hasan, Y, *A Prey Predator Model with Vulnerable Infected Prey*, Applied Mathematical Sciences, Vol. **6**, (2012), 5333–5348.

[2] Wuhaib, S. A and Abu Hasan, Y, *Predator-prey interactions with harvesting of predator with prey in refuge*, Communications in Mathematical Biology and Neuroscience, Vol. **2013**, (2013), 1-19.

[3] Wuhaib, S. A and Abu Hasan, Y, *Dynamics of Predator with Stage Structure and Prey with Infection*, World Applied Sciences Journal, Vol. 20, (2012), 1584-1595.

[4] Wuhaib, S. A and Abu Hasan, Y, *Continuous threshold prey harvesting with vulnerable infected prey*, AIP Conf. Proc. 1522, (2013), 561-575.

[5] Wuhaib, S. A and Abu Hasan, Y, *A Predator - Infected Prey Model with Harvesting of Infected prey*, ScienceAsia. ScienceAsia, 39S, 2013,37-41.

[6] Wuhaib, S. A and Abu Hasan, Y, *Dynamics of a Three-Species Food Chain System with Refuge.*, Applied Mathematics and Computation. (submit on 28 January 2013).

[7] Wuhaib, S. A and Abu Hasan, Y, *A Simple Predator-Prey Model with Infective Prey*, World Applied Sciences Journal. (Accepted in 4 June 2013).

Conference Proceeding:

[1] Wuhaib, S. A and Abu Hasan, Y, “A Predator - Infected Prey Model with Harvesting of Infected prey”, International Conference on Computer Engineering and Mathematical Sciences, ICCEMS, Kuala Lumpur, Malaysia, August 2012.

[2] Wuhaib, S. A and Abu Hasan, Y, "*Continuous threshold prey harvesting with vulnerable infected prey*", National Mthemaics of (UKM) , Kuala Lumpur, Malaysia, December 2012.

[3] Wuhaib, S. A and Abu Hasan, Y, "*The Stability and Harvesting in Prey Predator Model Infected Diseases in the Predator*", National Mathematics Symposium, (USM), (submit).

DINAMIK MODEL PEMANGSA-MANGSA

ABSTRAK

Dalam tesis ini, kami mengkaji beberapa sistem pemangsa mangsa yang melibatkan faktor-faktor seperti jangkitan, penuaian, struktur fasa, pelindungan berterusan dan rawak dan pertemuan kerap pemangsa dengan mangsa. Melalui analisis dan perbandingan, kami mendapati kesan jangkitan kepada kewujudan dan kestabilan sistem populasi; kestabilan sistem populasi ini boleh bertukar menjadi tidak stabil dan juga bertukar kepada kebifurkasi mudah Hopf. Selain itu, kajian ini juga didapati bahawa penuaian tidak menjejaskan kewujudan dan kestabilan sistem, tetapi memberi kesan kepada penyakit dan analisis ini juga boleh digunakan untuk mengawal penyakit dengan mengambil kira bahawa penuaian yang berlebihan boleh membawa kepada kehapusan populasi. Kami menggunakan nombor pembiakan asas untuk membina rantai yang mana semua penduduk di kawasan-kawasan ini terus wujud, penyakit teskaeseal dan kesinambungan penuaian terjamin. Kami mencadangkan satu dasar tuaian optimum yang bermula di peringkat awal kehadiran penyakit dan ini memastikan penyakit tes kawalan dan mencegah ia daripada merebak. Faktor lain yang mempengaruhi penyakit adalah struktur peringkat pemangsa. Dalam model ini, mangsa dijangkiti manakala pemangsa dibahagikan kepada dua kumpulan, matang dan belum matang. Apabila penyakit lenyap, model terdiri daripada mangsa sihat, pemangsa tidak matang dan matang dan model ini adalah stabil. Mangsa kadang-kadang menggunakan tempat untuk melarikan diri dari pemangsa dan tempat-tempat ini disebut perlindungan. Perlindungan menjejaskan kestabilan model dan kewujudan populasi. Kami mengkaji pelindungan berterusan dan secara rawak untuk menunjukkan bahawa pelindungan yang berterusan adalah lebih baik, lebih stabil dan memberi peluang yang lebih baik berbanding dengan pelindungan rawak. Model kajian seterusnya adalah rantaian makanan. Melalui kajian, kami mendapati bahawa pertemuan kerap mangsa dengan pemangsa menjejaskan penyelesaian dan dinamik model. Selain kesan perlindungan yang berterusan, model kajian ini juga mempunyai kesan ke atas penyelesaian terbatas dan positif, penyelesaian berkala, saiz penduduk dan kestabilan. Bifurkasi mudah Hopf juga boleh berlaku.

DYNAMICS OF PREDATOR-PREY MODELS

ABSTRACT

In this thesis, we studied a number of predator prey system involving factors such as infections, harvesting, phase structure, constant and random refuges and frequent encounters of predator and prey. Through analysis and comparison we found the effect of the infection on the existence and the stability of populations systems; this stability may turn into instability and sometimes into simple Hopf bifurcation. It was also found that harvesting does not affect the existence and stability of systems, but affects the disease, and thus can be used to control the disease, taking into account that excessive harvesting may lead to extinction of communities. We employ the basic reproduction number to construct regions, whereby in these regions all populations survive, disease under control and the continuation of the harvest guaranteed. We propose an optimal harvest policy in that the harvest begins in the initial stages of the presence of disease and this ensures the disease is under control and prevent it from spreading. Another factor affecting disease is the stage structure of the predator. In this model, the prey becomes infected while the predator is divided into two groups, mature and immature. When the disease disappears, the model consists of susceptible prey, immature and mature predator and this model is stable. The prey sometimes uses places to escape from the predator and these places are called refuges. The refuges affect the stability of the models and the existence of populations. We studied constant and random refuges to show that the constant refuges are better than random refuges; they are more stable and offer a better chance of survival than random refuges. We next study models of the food chain. Through the study we found that the frequent encounters of predator and prey affect the solution and the dynamics of the model. In addition to the effect of constant refuge, this also has an effect on bounded and positive solution, periodic solution, size of population and on stability. A simple Hopf bifurcation may occur.

CHAPTER 1

INTRODUCTION

"A thing is right when it tends to preserve the integrity, stability and beauty of the biotic community. It is wrong when it tends otherwise."

Aldo Leopold (American ecologist, 1887-1948)

1.1 Overview

1.1.1 Historical Introduction

In the natural world, we find that species compete, evolve and disperse for the purpose of finding resources to carry on the struggle for existence. These behaviors can be modelled mathematically by predator-prey models. The basic model was first proposed by Lotka and Volterra. However, any form of interactions, be it win-win (Host-bacterial mutualism in the human intestine, F Bäckhed et al. (2005)) or loss-win, within and sometimes outside of ecology can be modelled by these models. Depending on their specific settings of applications, they can take the forms of resource-consumer, plant-herbivore, parasite-host, tumor cells (virus)-immune system, susceptible-infectious interactions, and others.

Historically, the mathematical description of the Lotka-Volterra system goes back 100 years, to the time of the First World War $(1914-1918)$. The Italian scientist, D'Ancona was puzzled by the very large increase in the percentage of selachians (a predatory fish) caught during the war. After the war, the partial restriction on fishing was lifted and there was a decrease of the percentage of selachians. The relative abundance of prey (all other species found on the market) followed the opposite pattern. He was puzzled by the oscillation of populations of both predator and prey species. He turned to the mathematician Volterra for help, and within a few months, Volterra developed a series of models describing interactions of two or even more species. Since then, variations or improvements of the equations were developed and analyzed.

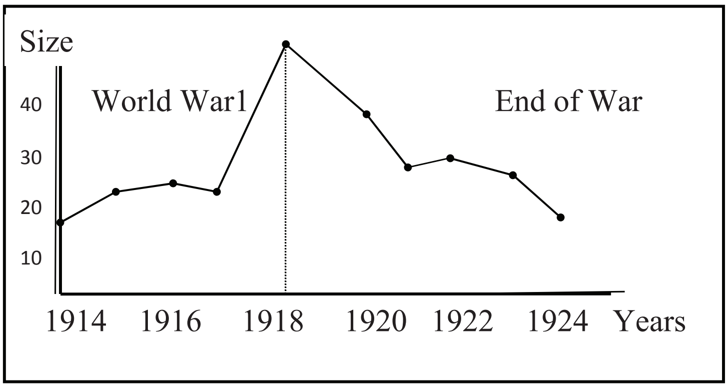

Figure 1.1: The frequency of predatory fish in the farm market during and after WWI.

Although the Lotka-Volterra system is a simple model to represent interactions between species, it consists of two nonlinear first order differential equations that are coupled. Nonlinear systems are very important; this importance comes from of the ability of these systems to describe complex phenomena. Numerous models were developed to understand complex problems such as the coexistence between species or threats to the survival of species as a result of environmental changes or seeking a good environment to ensure the survival of the species and appropriate economic returns. Another problem is to discover the best way to create an environment that is free from diseases or for the disease to be under control, while achieving continued species survival. These and other problems together with the solutions are influenced by a number of factors such as the harvest, stage structure, diseases, and refuges. Therefore there is a need to study all the possibilities for the survival of the species and to ensure a good economic resource.

The properties of these models are analyzed theoretically using tools and ideas from dynamical system theory and numerically solved using the standard Runge-Kutta algorithm or its variants.

Since the 60's, a huge body of knowledge was developed in dynamical system theory. It is an active research area in mathematics used to describe complex dynamical system. Essentially, this theory considers the long-term qualitative behavior of dynamical systems and the studies of the solutions to the systems of equations that describe motion of systems. With regard to numerical solutions, some of the most accurate and robust algorithms have made their way into commercial softwares such as Maple, Matlab and Mathematica. For those who prefer to work in the Fortran or C environment, commercial or open source libraries are available.

1.1.2 Improve Models

Ecosystems are characterized by a wealth of highly complex interdependencies. There is no standard generic model as each phenomenon requires a particular description. However, in describing interactions between species, most models are improvements or variations of the Lotka-Volterra system of equations.

We need various models since the ecosystem is very rich. Looking at a particular habitat or environment, the observed interactions can be different from another habitat even if the same predator and prey are present. This results in the presence of many models in the literature, each describing a different ecological setup.

The modeling process is always evolving so as to gain a deep understanding of the mathematical aspects of the problem. To yield non trivial biological insights, we must carefully construct biologically meaningful and mathematically tractable population models. A realistic and plausible mathematical model has to include carrying capacity, which is the maximum number of prey that the ecosystem can sustain in absence of predator, competition among prey and predators, harvesting of prey or predators and functional responses of predators.

We develop the classical model of predator and prey to determine the effect of the disease on the dynamic of classical model. In order to create an environment free from diseases, we determine the effect of many factors to control disease, such as the harvest, the structure of the stage and refuges. also determine the effect of refuge on the food chain.

We employ several concepts and theorems in this process, as invariant surface and center manifold theorem. The models in this thesis can be represented graphically as follows

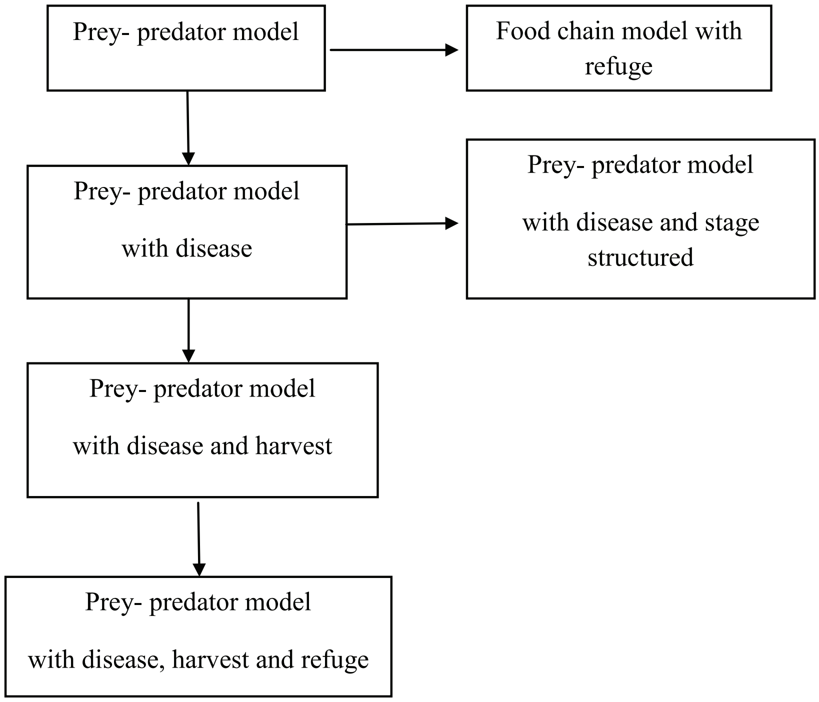

Figure 1.2: Graphically represented of models.

1.2 Research Questions

In this thesis there are many research questions to be addressed as follows

- How does the disease affect the stability and the existence of the populations?
- How to use the harvesting to control disease?
- What is the optimal harvesting policy must be used?
- What is the effect of stage structure on diseases?

- What is effect of the refuge on the stability?
- What is the effect of the refuge on the existences of populations?
- What is the effect of the frequent encounters on dynamic system?
- What is the effect of constant refuge on the dynamic system?
- How to use the basic reproduction number to determine the invariant region?
- Which is better: constant or random refuge?
- Is the disease spread in high level of stage structure?
- Are the hypothesis of persistence of population satisfied?

In this thesis we try to answer these questions using the some basic concepts, definitions, theories, mathematical analysis, some hypotheses and also employing numerical simulation to illustrate some results of these questions.

1.3 Research Objective

Research objectives of research includes

1. To determine the effect of disease on the dynamic system and on the existing populations.
2. To determine the invariant surfaces of the solutions and applied center manifold theorem.
3. To determine the persistence of the populations in food chain systems.
4. To determine the effect of harvesting on the dynamic systems and control disease.
5. To determine the bound and properties of invariant region of harvesting by using the reproduction number.

6. To determine the effect of stage structure on disease.
7. To determine the effect of constant and random refuge on existence and stability of systems.
8. To determine the effect of frequent encounters on the dynamic food chain systems.
9. To determine the Kolmogorov conditions in food chain systems.
10. To determine the effect of constant refuges on dynamic food chain systems.

1.4 Methodology

We discussed several possibilities that would affect the interactions between the populations. In our study, we use mathematical analysis by

1. Setting conditions for solutions to ensure that they are bounded and positive.
2. Find the equilibrium points for each case and thus find out what are the factors that affect on positive points because those points represent the case of the survival of populations.
3. We shall also consider models to create an environment free of diseases and the harvesting processes.
4. We also need to know the factors impacting on the behavior of the solution and the requirements needed to satisfy the local and global stability and why the stability becomes Hopf bifurcation or limit cycle.
5. In some models we try to satisfy conditions of persistence.
6. Using the software Mathematica and Maple, we carry out numerical simulation to describe the models and to see the effect of variables on the dynamic systems

1.5 Contributions

The areas covered by prey and predator models are broad. Although there are many studies dealing with these models, the field of study remains open for researchers to discuss various forms of interaction as we did in this thesis.

In this thesis, we discussed the following problems:

1. The effect of disease on dynamic models.
2. The effect of harvesting on diseases.
3. Influence of the stage structure on disease.
4. Effect of constant and random refuge on the dynamic models.
5. The effect of frequent encounters of predator on the food chain models as well as the impact of constant refuges on those dynamic models.

We summarize our contributions to the above problems as follows:

1.5.1 The Effect of Disease on the Dynamic of Prey Predator Model

We consider two different cases of disease in the prey predator models; we discussed infection of the disease on the dynamic models and on the sizes of populations, which may cause chaos in the behaviour of the system. In the first model we proved that the system is stable overall, while in second model, effect of disease on the stability. We show that the third model satisfied the invariant surfaces, as we have noted diseases perhaps cannot continue when the predator is strong enough to get rid of diseases.

1.5.2 The Effect of Harvesting on the Disease in Prey Predator Model

In the study on the impact of harvesting on the disease, we show that harvesting affects the dynamic systems and also on the existence of populations. In this study, we determine the invariant regions; we guarantee that in these regions all populations survive. We also discuss the control of disease and the continuation of harvesting. A policy was formulated for optimal harvesting to ensure that all populations survive. This policy is to start harvesting early when disease occurs in population interactions, and does not use excessive harvesting operations.

1.5.3 Influence of the Stage Structure on Disease

In this case we show the stage structure has effects on the dynamic system and on the disease. We could use the stage structure as a way to control the disease and also to eliminate them.

1.5.4 Effect of Constant and Random Refuge on the Dynamic Models

In general, refuges have large effect on the existence of populations and the behaviour dynamism. By studying constant and random refuge, we show that the constant refuge gives an opportunity for populations to coexist. The system is more stable in constant refuge than random refuge. In addition, in constant refuge we do not need any condition to prove the global stability, while in random refuge, we need condition to show the system is globally stable.

1.5.5 The Effect of Frequent Encounters of Predator and Constant Refuges

In a food chain system consisting of prey, intermediate predator and top predator, when the prey is able to use constant refuge, we find that the frequent encounter of the predator effect the dynamic system. We show the effect of these encounters on the existence of periodic orbit and on the stability; we need high frequent encounters to satisfy the stability. Another effect of frequent encounters is that the simple Hopf bifurcation may occur at the critical value.

We employ the Kolmogorov conditions to determine the lower and upper limits, which could results in the growth of the populations. We proved that the food chain satisfy hypotheses of persistence.

1.6 Thesis Structure

This thesis is divided into eight chapters as follows: In chapter one, we discuss in general the setup of our research efforts and what we have achieved.

Some of basic concepts, definitions and theories related to proposed study are given in chapter two.

We discuss three different prey predator models in chapter three. First when the prey become infected and then recovers; however the prey does not have immunity from the disease. In the second model, we studied the same first model but using the functional response type II. In the third model, the prey become infected and do not recover. We study the behavior of the solutions to these three models. We show the effect of the disease on existence of the populations and the stability. Next, we determine the circumstances under which the disease disappears, and what is the difference in the dynamics of the three systems? Further we asked the question: How are the conditions of persistence satisfied in the third system? Finally we describe some results of some numerical simulations. The effects of harvesting on the disease are studied in three different models on chapter four. First, the prey is exposed to the risk of disease and harvesting, second, when predator is exposed to the risk of disease and harvesting, and a harvesting function is used in the third model. In these models, we study the effect of harvesting on the existence and size of all populations, the stability and the size of invariant region. We also show the important role of harvesting in controlling disease. We ask the question, is it possible to design an optimal harvesting policy for the continuation of harvesting and at the same time controlling the disease and preventing it from turning into an epidemic. Can we take advantage of harvesting to preserve the species from extinction?

An important concept in ecology is "stage structure". This concept means that the species exist in two stages, namely immature and mature. Chapter five is devoted to discuss the effect of this idea. When the prey is exposed to disease and predation while the predator is divided into mature and immature classes. Can we use the stage structure to control disease? We study these classes in two cases, first without disease and second with disease.

Another important concept in biology is refuges, which are used by communities to avoid risks, whether those risks are natural as a result of coexistence with other communities or artificial, such as harvesting. Chapter six is devoted to this study. We consider two types of these refuges, constant refuges and random refuges. Through dynamic analysis for both cases, we want to know which provides greater opportunity for the co-existence of communities.

In chapter seven, we study the food chain model. We study two models; the first model consisting prey using refuge, while both prey and intermediate predator using the constant refuge in second model. The predation in this chapter is Beddington-DeAngelis type of functional response. We discuss in first model the effect of frequent encounters of predator on the stability and on periodic orbit. We also prove this model satisfied the conditions of persistence. In the second model we discuss when the conditions of Kolmogorov are satisfied in the subsystem and we prove this subsystem has no non trivial periodic orbit. Lastly, we employ numerical simulations to explain the effect of frequent encounters and constant refuge on system behavior. A simple summary of the results of each chapter of the thesis have been developed in the last chapter of the thesis and Some future studies.

CHAPTER 2

PRELIMINARIES

In this chapter, we shall review some definitions, basic concepts and ideas from dynamical system theory and theoretical ecology. These will be used in subsequent chapters when we analyze a number of models.

2.1 Lotka Volterra Model

One of the well-researched models in theoretical ecology is the Lotka-Volterra system of equations Takeuchi (1996). It describes the interactions between two species. Although it is a simple model, it is able to meet many objectives expected by the ecologist. Among the objectives are explanations of what is currently happening and to forecast future interactions. In ecology simple models can give important description. For example, in population ecology, the simple model gives exponential growth. This needs to be modified, so that there is a limit to growth. However, the simple model can model the initial growth of a population. Another well-known example is the important discovery of the chaos phenomenon by May (1974). He just considered a simple discrete model of population growth and he observed that with certain parameters and initial conditions, chaos ensured. The Lotka Volterra model can be written as follows:

$$\begin{cases} \dfrac{dx}{dt} = rx - bxy, \\ \dfrac{dy}{dt} = -\rho y + cxy, \end{cases} \tag{2.1}$$

where x, y, are prey and predator respectively, r the growth rate of the prey (natural rate of increase), ρ the natural death rate of the predator (in biological individuals have a probability

ρ_1 to die per unit of time) and ρ_2 is a birth rate then, $r = \rho_2 - \rho_1$, Rockwood (2006).

In the absence of predator, prey growth is exponential according to $\frac{dx}{dt} = rx$ with solution $x(t) = x(0)e^{rt}$, and in the absence of prey, the predator will decrease exponentially. The predation is taken into account in the form of a mass action xy term with b and c some constants. The solution of the system (2.1) is seen in figure (2.1).

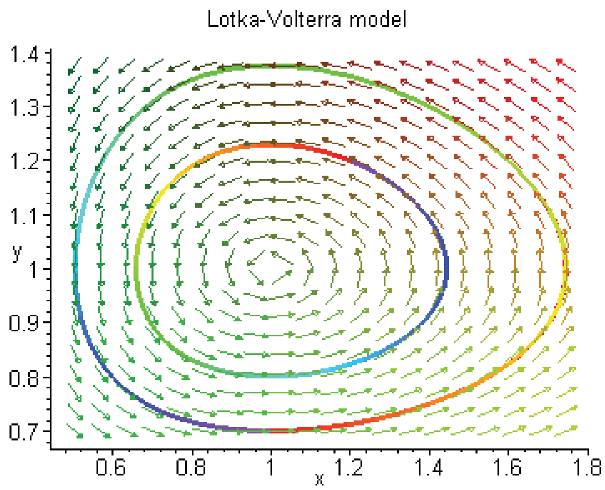

Figure 2.1: Solution to the two species prey predator model.

2.2 Tools

For the analysis of predator prey models we need a number of basic concepts, definitions and theories that enable us to analyze those models. By using these concepts, definitions and theories we can describe the behaviour the solution of these models and thus to predict the behaviour of solution in the future. As example, we need to use Routh Hurwitz theorem show the stability of equilibrium points, and by Dulac's Criterion to show the periodic solution and so on.

Below are some tools that have been used in this thesis:

2.2.1 The Behaviour of Solutions

Sánchez (1979) consider, the solutions of the linear equation

$$L(P)z = z^n + a_1 z^{n-1} + ... + a_n z = 0, \tag{2.2}$$

where $a_1, a_2, ..., a_n$ are constants. defined on $-\infty < t < \infty$. In many problems and applications, we are interested in the behaviour of the solutions as t approaches infinity. This behaviour is related to the nature of the roots of the characteristic polynomial $L(P)$ of Eq. (2.2).

Theorem 2.1 *Sánchez (1979), if all the roots of the characteristic polynomial $L(P)$ of Eq. (2.2) have negative real parts, then given any solution $z(t)$ of Eq. (2.2) there exist positive numbers a and M such that*

$$|z(t)| \leq Me^{-at} \text{ with } t \geq 0.$$

Hence $\lim |z(t) = 0|$ *as* $t \to \infty$.

2.2.2 Equilibrium Point

Assume the system of differential equations describing the interactions between n species as:

$$\left.\begin{array}{l} \dfrac{dX_1}{dt} = F_1(X_1, X_2, ..., X_n), \\ \dfrac{dX_2}{dt} = F_2(X_1, X_2, ..., X_n), \\ . \\ . \\ . \\ \dfrac{dX_n}{dt} = F_n(X_1, X_2, ..., X_n), \end{array}\right\} \Rightarrow \frac{dX}{dt} = F(X), \tag{2.3}$$

May (1974), then the equilibrium point (fixed point) denoted by X^*, is

$X^* = (X_1^*, X_2^*, ..., X_n^*)$, if it satisfied the equations $\frac{dX_i}{dt} = 0$, $\forall i = 1, 2, .., n$

2.2.3 Stability

The equilibrium point X^* of system (2.3) is stable if for each $\varepsilon > 0$ there exists $\delta > 0$ such that

$\|X(0) - X^*\| < \delta \rightarrow \|X(t) - X^*\| < \varepsilon \ \ \forall t > 0$,

where $X : [0, \infty) \rightarrow R^n$ is a solution of system (2.3). Stuart and Humphries (1998) the equilibrium point X^* is asymptotically stable if it is stable and $\delta > 0$ can be chosen such that

$\|X(0) - X^*\| < \delta \rightarrow \lim \|X(t) - X^*\| = 0$.

If the equilibrium point is not stable then it is unstable. If the equilibrium point is asymptotically stable for all $X(0) \in R^n$, then the point in this case is globally stable.

To investigate the dynamical behaviour of the system (2.3) near equilibrium point X^*, define a small perturbation or disturbance from equilibrium, then the solutions $X_i(t), i = 1, 2, ..., n$ is written as follows:

$$\begin{cases} X_1(t) = X_1^*(t) + \gamma_1(t), \\ X_2(t) = X_2^*(t) + \gamma_2(t), \\ . \\ . \\ . \\ X_n(t) = X_n^*(t) + \gamma_n(t), \end{cases} \tag{2.4}$$

where the small perturbation is $\gamma(t) = \gamma_1(t), \gamma_2(t), ..., \gamma_n(t)$ of the original solution. Then by Taylor's theorem, linearizing the differential equation near equilibrium, yields

$$
\begin{cases}
\dfrac{d\gamma_1(t)}{dt} = \dfrac{\partial F_1}{\partial X_1} |_{X^*} \gamma_1 + \dfrac{\partial F_1}{\partial X_2} |_{X^*} \gamma_2 + ... + \dfrac{\partial F_1}{\partial X_n} |_{X^*} \gamma_n, \\
\dfrac{d\gamma_2(t)}{dt} = \dfrac{\partial F_2}{\partial X_1} |_{X^*} \gamma_1 + \dfrac{\partial F_2}{\partial X_2} |_{X^*} \gamma_2 + ... + \dfrac{\partial F_2}{\partial X_n} |_{X^*} \gamma_n, \\
. \\
. \\
. \\
. \\
\dfrac{d\gamma_n(t)}{dt} = \dfrac{\partial F_n}{\partial X_1} |_{X^*} \gamma_1 + \dfrac{\partial F_n}{\partial X_2} |_{X^*} \gamma_2 + ... + \dfrac{\partial F_n}{\partial X_n} |_{X^*} \gamma_n.
\end{cases}
\tag{2.5}
$$

This is a set of linear constant coefficient equations, which can be written in the form

$$
\begin{pmatrix} \acute{\gamma}_1 \\ \acute{\gamma}_2 \\ . \\ . \\ . \\ \acute{\gamma}_n \end{pmatrix}
=
\begin{pmatrix}
\frac{\partial F_1}{X_1} & \frac{\partial F_1}{\partial X_2} & . & . & . & \frac{\partial F_1}{\partial X_n} \\
\frac{\partial F_2}{\partial X_1} & \frac{\partial F_2}{\partial X_2} & . & . & . & \frac{\partial F_2}{\partial X_n} \\
. & . & . & . & . & . \\
. & . & . & . & . & . \\
. & . & . & . & . & . \\
\frac{\partial F_n}{\partial X_1} & \frac{\partial F_n}{\partial X_2} & . & . & . & \frac{\partial F_n}{\partial X_n}
\end{pmatrix}_{X^*}
\begin{pmatrix} \gamma_1 \\ \gamma_1 \\ . \\ . \\ . \\ \gamma_n \end{pmatrix}.
\tag{2.6}
$$

Rewriting the system (2.6) in matrix form gives

$$
\acute{\gamma} = V\gamma(t), \tag{2.7}
$$

where V is the variational matrix (Jacobian matrix) at the equilibrium point X^*. So the equilibrium point will be locally stable if the real parts of each eigenvalues of V are negative. The characteristic equation for the Jacobian matrix is computed as

$$
P_n(\lambda) = det(V - \lambda I) = \lambda^n + a_1\lambda^{n-1} + a_2\lambda^{n-2} + ... + a_n = 0. \tag{2.8}
$$

Then an application of Routh-Hurwitz criterion, gives number of constraints on the coefficients $a_1, a_2, ...a_n$ which are necessary and sufficient to ensure all eigenvalues lie in left half complex plane. Therefore, if Routh-Hurwitz criterion constraints are simultaneously satisfied, then the system will be asymptotically stable at this equilibrium point. If one of these eigenvalues does not satisfied these conditions, then this point is unstable May (1974).

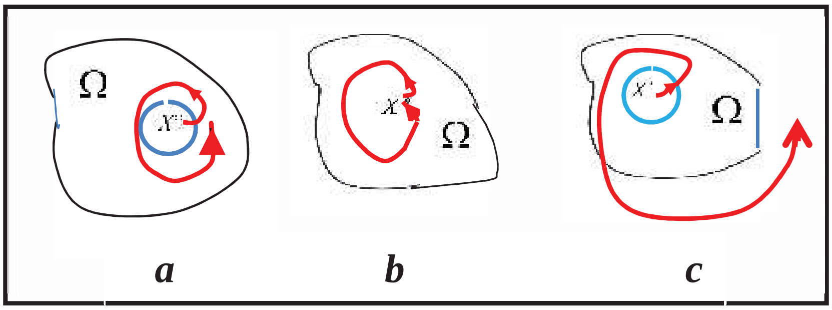

Figure 2.2: (a) stable, (b) asymptotically stable and (c) unstable equilibrium.

2.2.4 Routh-Hurwitz Stability

Given Eq. (2.8) with $a_i, i = 1, 2, ..., n$ real, let $D_1 = a_1$ and for $k = 2, ..., n$ let

$$D_k = det \begin{pmatrix} a_1 & a_3 & a_5 & . & . & . & . & a_{2k-1} \\ 1 & a_2 & a_4 & . & . & . & . & a_{2k-2} \\ 0 & a_1 & a_3 & . & . & . & . & a_{2k-3} \\ 0 & 1 & a_2 & . & . & . & . & a_{2k-4} \\ . & . & 0 & . & . & . & . & . \\ . & . & 0 & . & . & . & . & . \\ . & . & . & . & . & . & . & . \\ 0 & 0 & 0 & . & . & . & . & a_k \end{pmatrix}.$$

where $a_i = 0$ if $i > n$. Then the roots of $P_n(\lambda)$ have negative real parts if and only if $D_k > 0$, for $k = 1, ..., n$.

By applying this criterion when $n = 2$, we get $P_2(\lambda) = \lambda^2 + a_1\lambda + a_2 = 0$, then

$D_1 = a_1$, $D_2 = a_1a_2$. Thus in this case the necessary and sufficient conditions for having negative real part roots are $a_1 > 0$ and $a_2 > 0$. In the case of $n = 3$, we have $P_3(\lambda) = \lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0$, and $D_1 = a_1$, $D_2 = a_1a_2 - a_3$, $D_3 = (a_1a_2 - a_3)a_3$, so the necessary and sufficient conditions for having negative real part roots are $a_1 > 0, a_3 > 0$ and $a_1a_2 > a_3$.

The Routh Hurwitz criterion gives number of constraints on the coefficients , which are necessary and sufficient to ensure all the eigenvalues lie in the half complex plane.

Hence, if the Routh Hurwitz constraints are simultaneously satisfied, then the system (2.3) will be asymptotically stable at X^*. However, violation of any one of these conditions implies unstable point, Anderson and May (1978).

2.2.5 Lyapunov Stability Theorem

Theorem 2.2 *Let X^* be an equilibrium point of (2.3) and $\Omega \subset R^n$.*

If $V : \Omega \to R$ is a C^1 function defined on some neighborhood Ω of $X^*(\Omega \subseteq R^n)$ such that

$$V(X^*) = 0$$

$$V(X) > 0 \qquad \forall X \in \Omega \backslash X^*$$

$$\frac{dV(X^*)}{dt} \leq 0 \qquad \forall X \in \Omega,$$

then $X^*$is stable. Furthermore, if X^* is stable and $\frac{dV(X)}{dt} < 0 \; \forall X \in \Omega \setminus X*$ then X^* is asymptotically stable.

The function V that satisfied these conditions for stability is called a Lyapunov function.

2.2.6 The Center Manifold Theorem

Let $f \in C^r(E)$, where E is an open subset of R^n containing the origin and $r > 1$. Suppose that $f(0) = 0$ and that $Df(0)$ has k eigenvalues with negative real part, j eigenvalues with positive real part, and $m = n - k - j$ eigenvalues with zero real part, then there exists an $m-$ dimensional center manifold $W^C(0)$ of class C^r tangent to the center subspace E^C at 0 of system

$$\frac{dx}{dt} = Ax.$$

Example 2.3 *Let the system*

$$\frac{dx_1}{dt} = x_1^2,$$
$$\frac{dx_2}{dt} = -x_2.$$

Any solution curve of the system in above example, to the left of the origin patched together with positive $x-$ axis at the origin gives a one dimensional center manifold of class C^∞ which is tangent to E^c at the origin. This shows that, in general, the center manifold $W^C(0)$ is not unique; however, in this example there is only one analytic center manifold, namely the $x-$ axis, Perko (2000).

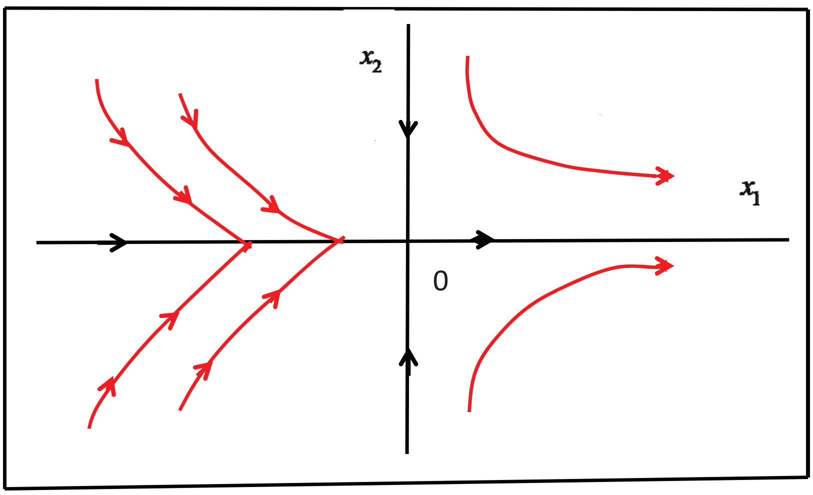

Figure 2.3: The phase portrait for the system in Example (2.3).

2.2.7 Dulac's Criterion

Theorem 2.4 *Recall that a region R of the plane is said to be simply connected if every closed loop within R can be shrunk to a point without leaving R. Dulac's criterion gives sufficient conditions for the non-existence of periodic orbits of dynamical systems in simply connected regions of the plane. The downside of this method is that it depends on the choice of an appropriate multiplier, which might be hard to find. In other ward if f and g are at least C^1. Let H be a function on simply connected region $D \subset R^2$.*
If $\frac{\partial(Hf)}{\partial x} + \frac{\partial(Hg)}{\partial y}$ is not identically zero and does not change sing in D, then the system has no closed orbits lying entirely in D.

2.2.8 Hopf Bifurcation

Assume that equilibrium point X^* depends smoothly on some parameter γ in open interval I in R. If there exists $\gamma \in I$ such that:

1. A simple pair of complex eigenvalues of Jacobian matrix $J(X^*)$ at the equilibrium point X^* exists, say $\alpha(\gamma \pm i\beta(\gamma))$, such that they become purely imaginary at $\gamma = \gamma^*$, whereas all the other eigenvalues remain real and negative.

2. $\left(\frac{d\alpha}{d\gamma}\right)_{\gamma=\gamma^*} \neq 0$ then at γ^* we have simple Hopf bifurcation. According to this definition the traditional simple Hopf bifurcation criterion is started in terms of the properties of eigenvalues. Since the computations of eigenvalues are sometimes difficult, it is ideal to have a criterion stated in terms of the coefficients of the characteristic equations. Liu (1994) derived a criterion for simple Hopf bifurcation using the properties of coefficients of characteristic equations instead of those of eigenvalues; it is related to Routh-Hurwitz criterion and is convenient in many applications. The Liu's criterion is stated in the

following theorem.

Theorem 2.5 *Assume there is a smooth curve of equilibria* $(x(\gamma),\gamma)$ *with* $x(\gamma^*)=x^*$ *for system* $\frac{dx}{dt}=f_\gamma(x)$ *where* $x\in R^n,\gamma\in R$.

Then conditions (1) *and* (2) *for simple Hopf Bifurcation are equivalent to the following conditions on the coefficients of the characteristic polynomial:*

$P_n(\lambda,\gamma)=\lambda^n+a_1(\gamma)\lambda^{n-1}+a_2(\gamma)\lambda^{n-2}+....+a_{n-1}(\gamma)\lambda+a_n(\gamma)$.

1. $a_n(\gamma^*)>0$, $D_1(\gamma^*)=a_1(\gamma^*)>0$,

$$D_2(\gamma^*)=det\begin{bmatrix} a_1(\gamma^*) & a_3(\gamma^*) \\ 1 & a_2(\gamma^*)\end{bmatrix}>0.$$

2. $\frac{dD_{n-1}}{d\gamma}\mid_{\gamma=\gamma^*}\neq 0$.

Accordingly, an application of this theorem, three dimensional system can be stated as follows:

1. $a_3(\gamma^*)>0,\ D_1(\gamma^*)=a_1(\gamma^*)>0,$

$$D_2(\gamma^*)=det\begin{bmatrix} a_1(\gamma^*) & a_3(\gamma^*) \\ 1 & a_2(\gamma^*)\end{bmatrix}=a_1(\gamma^*)a_2(\gamma^*)-a_3(\gamma^*)=0.$$

2. $\frac{dD_2}{d\gamma}\mid_{\gamma=\gamma^*}\neq 0.$

2.2.9 Persistence

Persistence of a species means the continued existence in the deterministic sense. Analytically, this means that $\liminf x(t) > 0$ as $t \to \infty$ for each population $x(t)$ which $x(0) > 0$. Geometrically, it means that each trajectory of the modeling system of differential equations is eventually bounded away from the coordinate planes (Freedman and Waltman, 1984; Freedman and Hongshun, 1988). Moreover, a system is said to persist if each component population persists. In this thesis, the abstract theorem for persistence as given by Freedman and Waltman (1984) is used. Consider the general ecological model of three interacting prey predator populations defined as:

$$\begin{aligned} \frac{dx}{dt} &= xG_1(x,y,z), x(0) \geq 0, \\ \frac{dy}{dt} &= yG_2(x,y,z), y(0) \geq 0, \\ \frac{dz}{dt} &= zG_3(x,y,z), z(0) \geq 0, \end{aligned} \tag{2.9}$$

where x represent to prey population, y,z are the intermediate and top predator.

Accordingly, the following hypotheses are made by Freedman and Waltman (1984)

1. The trivial equilibrium point $P(0,0,0)$ is unstable in $x-$ direction and asymptotically stable in $z-$ direction.

2. There exists a unique boundary equilibrium point $P(K,0,0)$ on $x-$ direction, which is asymptotically stable in this direction.

3. No equilibrium point on the positive $z-$ plane.

4. There may or may not exist an equilibrium point of the type $P(0,\bar{y},0)$. If it is exists it is assumed to be unique and asymptotically stable in $y-$ direction and trivial equilibrium point is assumed to be unstable in $y-$ direction.

If $P(0,\bar{y},0)$ fails to exist, trivial point is assumed to be asymptotically stable in the $y-$ direction. Therefore, the abstract theorem for persistence of three species interacting system state as follows:

Theorem 2.6 *In addition to the above hypotheses on equilibria, let the following hold:*

1. *G_1, G_2, G_3 are in C^1 in (x,y,z).*
2. *All solutions of the system (2.9) with non-negative initial conditions are bounded in forward time.*
3. *$P(K,0,0)$and $P(0,\bar{y},0)$ (if it exists) are hyperbolic saddle points.*
4. *Interior to each positive coordinate plane there is at most one equilibrium point, which if it exists is unstable in the positive direction orthogonal to that plane, and around which there are no periodic orbits.*

2.2.10 Kolmogorov Analysis

Consider the two-dimensional autonomous system represented by the prey predator equations as written originally by Anderson and May (1978):

$$\begin{cases} \dfrac{dx}{dt} = xF_1(x,y), \\ \dfrac{dy}{dt} = yF_2(x,y). \end{cases} \tag{2.10}$$

Specifically, Kolmogorov's theorem says, prey- predator systems of the form (2.10) have rather a stable equilibrium point or a stable limit cycle, provided that F_1 and F_2 are continuous functions of x and y, with continuous first derivatives, throughout the domain $x \geq 0, y \geq 0$. And that

1. $\frac{\partial F_1}{\partial y} < 0.$

2. $x(\frac{\partial F_1}{\partial x}) + y(\frac{\partial F_1}{\partial y}) < 0.$

3. $\frac{\partial F_2}{\partial y} < 0.$

4. $x(\frac{\partial F_2}{\partial x}) + y(\frac{\partial F_2}{\partial y}) > 0.$

5. $F_1(0,0) > 0.$

It is also required that there exist quantities A, B and C such that

1. $F_1(0,A) = 0,$ with $A > 0.$

2. $F_1(B,0) = 0,$ with $B > 0.$

3. $F_2(C,0) = 0,$ with $C > 0.$

4. $B > C$

The proof follows Minorsky (1962) straight forwardly and from the Poincare-bendixson theorem. May et al. (1981) suggest that the theorem also usually gives when certain of its conditions are equalities $(=)$ rather than inequalities $(< or >)$. He also gave the biological interpretation for the Kolmogorov's conditions.

2.2.11 Functional Response

Functional responses are used to describe the relationship between an individual's rate of consumption and food density. A predator functional response to prey is the change in the density of prey attack per unit of time per predator as the prey density changes, Holling (1959). In general there are three types of these functions as follows:

1. Functional response Holling type I: This function is a linear increase in consumption rate as food densities rise, until reached a maximum interactions, and some invertebrate predator prey interactions. It can be described as $y = ax + b$.

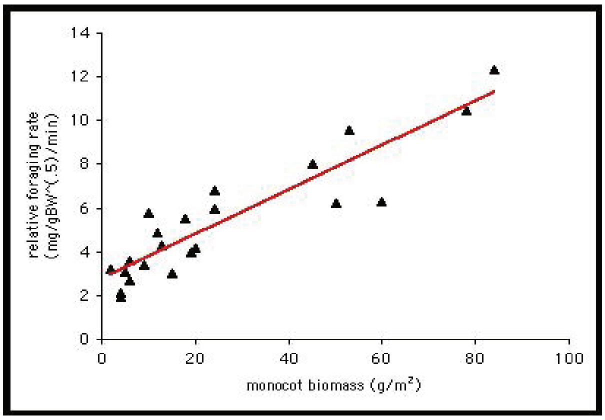

Figure 2.4: The relative foraging rate was calculated by dividing the absolute foraging rate (mg/min) by the square root of body weight $gBW.5$.

2. Functional response Holling type II: In this function the rate of prey consumption by predator rises as prey density increases, eventually levels off at a plateau (or asymptote) at which the rate of consumption remains constant regardless of increases in density of prey. The form of this function as:

   $f(x) = \frac{ax}{1+ahx}$, where f denotes intake rate and x denotes the prey density. The rate at which the consumer encounters food items per unit of food density is called the attack rate a. Average time spent on processing a food item is called the handling time h, Figure (2.5)