FOOD CHAIN MODEL WITH COMPETITION INTERACTION
IN AN ENVIRONMENT OF A BIOTIC RESOURCE

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ABSTRAK

Persaingan dalam merebut sumber seperti makanan biasanya dikaitkan dengan hubungan interaksi di dalam sesuatu populasi. Kajian ini bertujuan untuk mempelajari sistem permodelan matematik rantaian makanan bagi dua spesis yang menggunakan sumber biotik yang sama. Kaedah seperti analisis kestabilan, bifurkasi dan analisa berangka akan digunakan dalam kajian ini untuk menganalisa dinamik sistem tersebut. Peralihan daripada bermulanya kehidupan sehingga keputusan bagi sesuatu spesis dapat ditentukan dan titik ambang (threshold condition) bagi kestabilan sistem dapat diperolehi. Analisa berangka menunjukkan parameter persaingan interspesifik spesis menentukan keupayaan sesuatu spesis untuk terus hidup berbanding dengan spesis yang lain.
ABSTRACT

Population interactions generally describe the interactions of populations that compete for available food or resources. This research is to study the system of food chain model with competition of two species population with the same biotic resource. Stability, bifurcation and numerical analyses are presented to illustrate the system's dynamical behaviour. The transitions from persistence to extinction of a species are identified and certain threshold conditions are derived. Numerical analysis demonstrates that the inter-specific competition parameters determine the survival of one species over the other.
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<td>$X$</td>
<td>population of species 1</td>
</tr>
<tr>
<td>$Y$</td>
<td>population of species 2</td>
</tr>
<tr>
<td>$t$</td>
<td>time</td>
</tr>
<tr>
<td>$a$</td>
<td>conversion factors for the interaction of species 1 to species 2</td>
</tr>
<tr>
<td>$b$</td>
<td>conversion factors for the interaction of species 2 to species 1</td>
</tr>
<tr>
<td>$a^*$</td>
<td>competitive coefficient of species 1</td>
</tr>
<tr>
<td>$b^*$</td>
<td>competitive coefficient of species 2</td>
</tr>
<tr>
<td>$XY$</td>
<td>interaction among species 1 and species 2</td>
</tr>
<tr>
<td>$r_1$</td>
<td>intrinsic per-capita growth rate for increase of species 1</td>
</tr>
<tr>
<td>$r_2$</td>
<td>intrinsic per-capita growth rate for increase of species 2</td>
</tr>
<tr>
<td>$K_1$</td>
<td>carrying capacity of species 1</td>
</tr>
<tr>
<td>$K_2$</td>
<td>carrying capacity of species 2</td>
</tr>
<tr>
<td>$Z$</td>
<td>biotic resource</td>
</tr>
<tr>
<td>$pZ$</td>
<td>environmental carrying capacity for species $X$</td>
</tr>
<tr>
<td>$qZ$</td>
<td>environmental carrying capacity for species $Y$</td>
</tr>
<tr>
<td>$c$</td>
<td>development rate of the resource $Z$</td>
</tr>
<tr>
<td>$dXZ$</td>
<td>the rate of uptake resource by $X$</td>
</tr>
<tr>
<td>$eYZ$</td>
<td>the rate of uptake resource by $Y$</td>
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Non-dimensional Terms

- \( x \) - population of species \( X \)
- \( y \) - population of species \( Y \)
- \( \tau \) - time
- \( r \) - the ratio of the growth rates of \( y \) to \( x \)
- \( \alpha \) - the ratio of death rate of \( x \) by \( y \) to the consumption rate of resource by \( y \)
- \( \beta \) - the ratio of death rate of \( y \) by \( y \) to the consumption rate of resource by \( x \)
- \( \gamma \) - the ratio of the developmental rate of the resource to the growth rate \( x \)
- \( \gamma_1 \) - the ratio of the developmental rate of the resource to the growth rate \( x \) when \( \gamma_1 = \frac{1}{\alpha} \)
- \( \gamma_2 \) - the ratio of the developmental rate of the resource to the growth rate \( x \) when \( \gamma_2 = \frac{r}{\beta} \)
- \( \mu \) - the ratio of the consumption rate of the resource by \( x \) to the consumption rate of the resource by \( y \) in proportion to their carrying capacities
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CHAPTER 1

INTRODUCTION

1.1 Background

Nowadays, ecology field is one of the major interests in mathematical study. Ecologists tried to understand the behaviour of population dynamics to ensure the ecosystem is sustainable and balance. Manipulating the data becomes more crucial and mathematical modelling is considered as one of the mediums to study the complex system of ecology. Even though formulating a model that could describe all possible factors is quite challenging, yet the idea is to obtain a reasonable good first sight to understand and to analyse the complex systems of a population dynamics.

Ecology is a branch of science that deals with the study of interactions between living organisms and their physical environment (De and De, 2009; Chapman and Reiss, 1999). The general principle of ecology deals with food webs, nutrient cycling, community interactions, population dynamics and species diversity. Population ecology is the study of population that relates the population to the environment including environmental influences on population density and distribution, age structure, and population size. Population in ecology is defined as a group of (potentially) interbreeding individual occurring together in space and time (Smith and Smith, 1998). Each population is not independent. They interact with each other, inside the population or community, in order to survive or to get resources such as water, food and space.

Food chain can be defined as the fundamental relationship among different producers and consumers in the natural world where the length of the food chain can describes the relationship from primary producers to the top predators (Xiao et al., 2014). While food chain is a route in which energy passes through a community and feeding relations between some of its species
(Beeby and Brennan, 2004). This claim is illustrated in Figure 1.1. Each link in this chain indicates the food for the next link. A food chain always starts with plants and ends with an animal. Plant is a producer because they are able to use light energy from the sun to produce food (sugar) from carbon dioxide and water. Since the animal cannot produce their own food they are called consumers. Generally, there are three groups of consumers. The first group of consumer is herbivore, where they feed on plants. They are defined as primary consumer. Another group of consumer is carnivore, in which it is further divided into two groups; a) secondary consumer, in which they feed on other herbivore animal; and b) tertiary consumer in which the carnivore eats other carnivore animals (specific example are shown in Figure 1.2).

Figure 1.2: A hypothetical food chain typical of a European mixed deciduous oak wood (Chapman and Reiss, 1999).

Since ecology deals with interaction within population, there are several classes of interaction that can be categorized. Krebs (2009) categorized six different interactions among individuals of different species. The first one is based
on competition in which two-species use the same limited resources or fight with each other in order to get the resources. Predation is another type of interaction that can conquer all prey. Herbivore eats the plant species, parasitism is when the two-species of populations live in the same place and only the parasite gains benefit from the host. Disease is an association between a pathogenic, microorganism and host species in which the host suffers physiologically and mutualism is two-species live in close association with one another and benefit both.

![Diagram of interaction between abiotic and biotic factors](image)

**Figure 1.3:** Summary of the complexity of interaction between an organism and the biotic and abiotic components of its environment (Chapman and Reiss, 1999).

There are two types of resources in the ecosystem that is abiotic and biotic. Abiotic and biotic are important factors in determining whether the species can live in the population or not. Abiotic resources are the non-living chemical and physical factors which affect the ability of the population to survive or reproduce, while the biotic resources are the living components in ecosystem. Examples of abiotic resources are water, rain, nutrients, toxic while biotic resources can be determined as any living components in ecosystem such as plants, animals, fungi, bacteria, protists and prokaryotes (monerans) (Fetzer, 2005). The interaction between abiotic and biotic allows the species to grow while other conditions may lead to a species decline or even extinction. The interaction between organism and the abiotic and biotic components is quite complex (Chapman and Reiss, 1999). This interaction can be summarised in Figure 1.3.

Commonly, in biotic environment we can divide into two major types
of interactions which are intra-specific relationships and inter-specific relationships (Chapman and Reiss, 1999; Beeby and Brennan, 2004). Intra-specific relationship can be defined as interaction between individual of the same species while inter-specific relationship interaction that occurs between two or more species.

In some cases, the difference in some of ecological characteristics may reduce the inter-specific competition. Hammen et al. (2013) studied the turbot and brill (Figure 1.4) that are widely distributed in the Northeast Atlantic. Even though they are ecologically similar and closely related; they can sustain themselves at low abundances and avoid the strong inter-specific competition. The study has resulted the difference at size of hatching and the duration of spawning for both species can reduce the inter-specific competition. A spatial overlap of adult stages of turbot and brill during the spawning period, indicates the areas of spawning to overlap. However, the difference in timing of spawning will reduce the potential competition for food between planktonic larvae early demersal stages, although the slightly larger eggs of brill need longer to hatch.

Inter-specific competition takes two forms – interference competition and exploitative competition. Interference competition is where individuals of one species inhibits individuals of another species directly through the consumption of shared resource. Either way, each species controls the abundance of the other species where the outcome depends on how effectively each of the competitors uses the resource. The exploitation competition refers to individuals of one species inhibits individuals of another species indirectly through the consumption of shared resource.

The idea was proven in a laboratory experiment by Gause (1934) where he studied the competition between paramecium aurelia and paramecium caudatum (Figure 1.5). In the case of exploitation competition, the paramecium caudatum was harmed by paramecium aurelia. Thus paramecium caudatum became extinct. This behaviour can be seen in Figure 1.6.

Gause (1934) also studied paramecium bursaria (Figure 1.5) with paramecium aurelia where both of the species coexisted in a tube that contains yeast. Paramecium aurelia feed on the yeast in the upper layers of fluid, while paramecium bursaria fed at the bottom layer. In this case, both of the species coexisted.
The example of interference competition was examined by Connell (1961) for Scottish barnacles is *balanus balanoides* and *chthamalus stellatus* (Figure 1.7), where commonly *chthamalus* occurs higher up in the intertidal zone. Young *chthamalus* can survive while competing with *balanus*. When young *chthamalus* moved at lower level intertidal, *balanus* crushed or displaced (through its own growth) the young *chthamalus*. If *balanus* were removed immediately from the area, the young *chthamalus* can survive well in the lower intertidal. This evidence supports at the lower limit of distribution of intertidal organism is mainly determined by the action of abiotic factors such as competition for space, while at the upper limit it is set by physical factors.
1.2 Problem Statement

In this research, we consider the inter-specific competition of a two-species populations. We make use the food chain competition modelling in order to study the system of interaction between two-species populations. Competition interaction can exhibit extinction and coexistence states of the two-species. There are many factors contribute to these dynamics such as the variation of resource or the enrichment of resource in the environment. By introducing a slight difference in the environment, it can alter the behaviour of the system. In this research we investigate the impacts of inter-species interaction between
two-species population and also investigate the impacts of biotic resource incorporate with two-species population of competition model.

1.3 Objective

The aims of this research are to:

1. formulate a mathematical model of two-species populations with competition that share the same biotic resource;
2. analyse the mathematical model of two-species populations with competition interaction via stability and bifurcation analyses;
3. investigate the impacts of biotic resource enrichment on two-species population with competition model.

1.4 Scope of the Study

The scope of this research deals with bifurcation and stability analyses in order to understand the effects of an environment that is enriched by a biotic resource on two-species populations with competition model. The steady-state solutions of the system and the behavior of the system are investigated. Bifurcation diagrams are used to display the steady-state solution branches that exist in the system. All numerical and bifurcation analyses are performed using computer softwares such as MATLAB, MAPLE and XPPAUT.
1.5 Thesis Layout

The aim of this thesis is to analyse the mathematical model of two-species which is modified from classical Lotka–Volterra competition model subject to changing environment. The thesis is organised as follows:

Chapter 1 introduces the background of the research, definitions and some terms in ecology. The problem statement of the research, the objectives of this research and also the scope of the study are discussed.

Chapter 2 introduces the literature review, the brief introduction on carrying capacity and reviews of other research or previous studies which conclude the theoretical aspects and some results from the studies are discussed.

Chapter 3 introduces the methodology, the fundamental idea to modify the system of food chain model with competition. A brief introduction of bifurcation analysis is explained and the mathematical softwares used in this study are listed.

Chapter 4 introduces the results of this study. Analysis, simulation output and comparison between results are explained in this chapter.

Chapter 5 concludes this thesis by summarizing all the main result from the study and also the recommendation for further study.
CHAPTER 2

LITERATURE REVIEW

2.1 Carrying Capacity

Generally, carrying capacity is a maximal abundance of the population in an environment with limited resource. Safuan (2014) has defined carrying capacity as the maximal capacity of the environment to sustain a given species within the restriction of certain biological resources (biotic and/or abiotic). Ayllón et al. (2012) study on carrying capacity dynamics for the conservation and management of territorial salmonids claimed that knowledge of carrying capacity is essential for wildlife conservation since it is intrinsic in determining how much habitat must be conserved to maintain healthy populations. The research proposed the maximum abundance is limited to environmentally induced fluctuating habitat conditions and regulated through territorial behaviour. Carrying capacity is estimated as the amount of habitat available divided by the expected individual territory area for a given life stage.

Carrying capacity is also known as limiting factors. Schmitz (2007) claimed that the factor that limiting the maximum size of population at some location was competition for fixed supplies of resources or space. This consideration had been made the factor that influencing the dynamic of the population were intrinsic to the population itself. This argument however is not always true since the factor actually faces the extrinsic limiting factor where all species in population are embedded in food webs in which they must compete with individual or other species for resource or space. Ayllón et al. (2012) agreed that carrying capacity of the environment is not only determined by the abundance and distribution of limited resources but also by how individuals compete.

A feature of carrying capacity is when the population grows exponentially and its growth starts slowly and become rapidly until it levels off when the
carrying capacity for that species has been reached. Schmitz (2007) explained the connection of population steady-state and equilibrium when facing the intensifying competition with rising population size, as per individual net fitness eventually reduce to the point where per individual birth rate is exactly offset by per individual death rate. Birth rate declines with population density can be caused by fewer resources that are available per-capita basis to be allocated for off-spring production. Mortality rate increases with population density because fewer resources are available to support individual survival. The intersection between the birth rate and mortality line (since birth rate decline and mortality rate increase) represents the point of equilibrium or carrying capacity. What will happen if the population exceeds their carrying capacity? In this case, mortality rate exceeds birth rates and population density declines until a balance between birth and mortality rate is recovered. The rate at which the population declines depends on the difference between mortality rate and birth rate. Thus population that are far exceeding their carrying capacity will crash faster than population that are marginally exceed their carrying capacity.

Beeby and Brennan (2004) explained that carrying capacity is independent from their density for the cases where the resources are abundance and they were closely depended on the long term availability of resources. For example insects can change rapidly according to their number to achieve the equilibrium. Their population number fluctuated wildly every year. But it will be different for large plant or big animal where they grow slowly and live longer. In this situation carrying capacity is meaningful. The prediction is on the size of their body because the mass needs sufficient resource to grow and sustain itself. This is quite common since many large animals or plants can easily extinct especially when their resource is limited.

Without carrying capacity a population growth is out of control. The ecology may collapse due to scarcity of resources; environmental pressure and health issue (Safuan, 2014). In reality, constant carrying capacity is not really practical, especially when modelling the behaviour of population. Therefore, the need of non-constant/variable carrying capacity has to be considered. Yukalov et al. (2012) agreed that the carrying capacity of an environment may vary for different numbers of species and may change over time due to a variety of factors, including food availability, water supply, environmental conditions, living space, and, the most important, population activity. Ayllón et al. (2012) claimed that the carrying capacity is not a fixed number as available resources
and the requirements of a species change over time, and carrying capacity is always changing, across seasons, years and through maturity.

This research investigates and develops a mathematical model to describe the changes in an environment through a variable carrying capacity.

### 2.2 Population Growth

Population growth was first introduced in the 19th century by Pierre–François Verhulst (Bacaër and Nicolas, 2011). He published a growth model in the year of 1838 where this model was utilized for continuous time (adjustment from exponential growth with self-limiting process that should operate when the population becomes too large (Murray, 2002). He claimed that the rate of reproduction is proportional to the existing population and the amount of available resources or will be equal. The equation (known as logistic equation) which is autonomous was published after Verhulst had read Thomas Malthus’ essay on the *Principle of Population*. The classic logistic equation is defined as (Murray, 2002)

\[
\frac{dN(t)}{dt} = rN(t) \left(1 - \frac{N(t)}{K}\right), \quad N(0) = N_0,
\]

where \( r \) and \( K \) are positive constant. \( N(t) \) is size of the population at time, \( t \) and \( r \) is a relative growth rate. In this model the term \( r(t) \left(1 - N(t)/K\right) \) is called per-capita birth rate where it depends on \( N(t) \) (Murray, 2002). The constant \( K \) is the carrying capacity of the environment which represents available sustaining resource and \( N_0 \) represents initial condition.

As shown in Figure 2.1, any positive initial condition given to the logistic equation (2.1) will result the solution to approach the constant carrying capacity, \( K \). If the population starts at a level below of the carrying capacity, \( K \) the population will increase steadily, then rapidly, due to the linear term, until it reaches the inflection point (when the growth rate is maximal). After passing the critical point, the population reproduction rate decreases because of competition for the limited resource. Later, after experiencing the pressure in the environment, the population becomes stabilized. On the other hand, if the population starts above the carrying capacity, \( K \), the population rate will decrease until it reaches the plateau (Safuan, 2014).
When the logistic equation (2.1) is equal to zero, it has two steady-states or equilibria which are $N(t) = 0$ and $N(t) = K$. From equation (2.1), if $N(t)$ is small compared with $K$, then $N(t)/K$ is close to 0 and so $dN(t)/dt \approx rN$. However, if $N(t) \rightarrow K$ (population approaches to carrying capacity) then $N(t)/K \rightarrow 1$, so $dN(t)/dt \rightarrow 0$.

Using separation of variable in equation (2.1), the solution can be expressed as

$$N(t) = \frac{N_0 K}{K e^{-rt} + N_0 (1 - e^{-rt})}, \quad N(0) = N_0. \quad (2.2)$$

Gause (1934) conducted an experiment with the *paramecium aurelia* and *paramecium caudatum*. He began with 50mL of a salt solution buffered to pH8. Each day he added a constant quantity of bacteria, which served as a food. The experiment limited the constant environment and space. He observed the growth for both bacteria and plot the graph (refer Figure 1.6). The logistic equation (2.1) fits the observations reasonably well, thus his experiment supports the equation introduced by Verhulst for logistic growth of the population.

Since the population can alter its carrying capacity by interacting with the environment, the productive and deaths terms of a biotic should be included (Safuan, 2014; Dua et al., 2004). The idea is to modify the system that was
introduced before (equation (2.1)). The carrying capacity, \( K \) was introduced as a variable dependent form. The system can be written in a form of

\[
\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right), \quad (2.3a)
\]

\[
\frac{dK}{dt} = f(N, K), \quad (2.3b)
\]

where \( f(N, K) \) is a function that involves linear or non-linear interaction terms between population, \( N \), and carrying capacity, \( K \). In contrast to non-autonomous equation with time-dependent carrying capacity, a system with variable-dependent capacity can be an autonomous system, thus the system (2.3) can be analysed using standard tools, such linear stability and phase-plane analyses. The dynamic of the system also can be determined by studying the complex interaction terms between the population and its carrying capacity.

### 2.3 Related Works

In this section the previous work on the food chain model of the three species and the two species population-growth models with variable carrying capacities are studied.

Tilman (1977) studied the competition between two species plankton algae which are *Asterionella Formosa* and *Cyclotella Meneghiriana*. The model was based on the functional resource-utilization response of each species to limiting resources. From the research, *Asterionella Formosa* was found to be more competitively dominant when the phosphate is limited, while *Cyclotella Meneghiriana* was more competitive when limited by silicate. Both species can coexist when limited by a different resource.

Chauvet et al. (2002) proposed a three-species model to represent species \( x \), \( y \) and \( z \). The lowest level prey \( x \) is preyed upon by a mid level species \( y \), which in turn, is preyed upon by a top level predator \( z \). The study found that the species \( z \) depends only on the parameter of natural growth rate of prey in the absence of predators, the parameter of effectiveness predation on the prey, the parameter natural death rate of the predator \( z \) in the absence of prey and the parameter efficiency and propagation rate of the predator \( z \) in the presence of prey. The parameters most directly related to species \( y \) does not affect the extinction of species \( z \). It is found that, species \( y \) was acting as a conduit
between the top ($x$) and bottom ($y$) species. As species $x$ persists, species $y$ will not extinct.

Dua et al. (2004) studied the trajectory behaviour of a Lotka–Volterra competition model. In their study of the non-autonomous dynamical system of competition model it was found to satisfy bistability condition which is, there exist a unique solution, bounded above and below by positive constants. They assumed that environmental change can directly affect the model parameter. When the environmental fluctuation is not too large the qualitative character of the model does not change. One species can persist during some periods and also can go extinct during another period because it is affected by the changes in the external environment.

Safuan (2014) studied on the modified predator and prey models where the environmental carrying capacity represents as a biotic resource enrichment. The models were extensions from the model proposed by Leslie (1958), Basener and Ross (2005) and Safuan et al. (2012). In the models, the biotic resource only affects the carrying capacity each species through the intra–specific interaction term. Furthermore, the species can adapt the amount of resource available while interact with each other. The bifurcation parameter of development rate (the enrichment parameter denoted as $\gamma$) was the main bifurcation parameter. In the study, the persistence of each species can be controlled at low enrichment level of the resource. Under certain circumstances, the Hopf bifurcation and bistability can exist in the system.

2.4 Summary

Population growth is the central process in ecology. However, the population does not grow forever, and this will lead to the problem of population regulation. Interaction among species such as competition will affect the population growth (Krebs, 2009). In order to understand the behaviour of the population, one may consider the idea on any of the regulation problem on population mentioned. The variable carrying capacity is one of the major interests in ecology to avoid the population growth out of control. In this research, we focus on the competition interaction as the main system to be discussed.
CHAPTER 3

METHODOLOGY

3.1 Stability Analysis

In ecology, the term of equilibrium is defined as a point or period in time which the state of an ecological system is at climax, wherein it ceases to grow (Kirkpatrick, 2000). In dynamical system, the equilibrium point can be generated by an autonomous system of ordinary differential equations where the solution does not change with time (Izhikevich, 2014). The equilibrium point sometimes refer as fixed point, rest point, critical point or singular point of the dynamical system. According to J.Cronin (2008), the equilibrium of an autonomous system can be defined as definition (3.1).

Definition 3.1 (Equilibrium Point). Given $n$-dimensional autonomous system

$$x'_i = f_i(x_1^0, \ldots, x_i^n) \quad i = 1, \ldots, n.$$ 

If $(x_1^0, \ldots, x_1^n) \in D$ is such that $i = 1, \ldots, n$

$$f_i(x_1^0, \ldots, x_i^n) = 0,$$

then $(x_1^0, \ldots, x_i^n)$ is an equilibrium point (or rest point or critical point or singular point) of system autonomous mentioned above. Note that if $(x_1^0, \ldots, x_1^n)$ is an equilibrium point, and it for all real $t$

$$x_i(t) = x_i^0 \quad i = 1, \ldots, n,$$

then $(x_i(t), \ldots, x_n(t))$ is a solution for given autonomous system.

In other words, to find the equilibrium we have to solve $f(x) = 0$ for continuous system.
However, not all equilibrium points are the same. Sometimes, it can be defined as stable equilibrium or unstable equilibrium points. Figure 3.1 shows the examples of three types of equilibrium. The types of equilibrium points of the system are stable, marginally stable or unstable. Stable equilibrium is when we have initial condition \( x_0 \) near equilibrium \( \hat{x} \), the system not only stay near \( \hat{x} \) but also \( x(t) \to \hat{x} \) as \( t \to \infty \). Precisely, for every positive number \( \epsilon \), one can find the positive number \( \delta \) with the property of if \( x_0 \) is within the distance \( \delta \) of \( \hat{x} \), then \( x(t) \) is within distance \( \epsilon \) of \( \hat{x} \) of all \( t \geq 0 \). Marginally stable is where all the starting values \( x_0 \) near \( \hat{x} \), the system stays near \( \hat{x} \) but does not converge to \( \hat{x} \). This means there is a positive number \( \delta \) so that for any \( x_0 \) within distance \( \delta \) of \( \hat{x} \) the following is true: For every \( \epsilon > 0 \) there is a \( T > 0 \) so that if \( t \geq T \), then \( x(t) \) is within distance \( \epsilon \) of \( \hat{x} \). Hence, the third equilibrium is called unstable when it is neither stable nor marginally stable. In other words, if there is the starting values \( x_0 \) very near \( \hat{x} \), it will moves away from \( \hat{x} \) (Scheinerman, 1996).

![Figure 3.1: Examples of equilibrium points with three types of stability. (a) stable equilibrium; (b) marginally stable equilibrium; (c) unstable equilibrium (Scheinerman, 1996).](image)

In sense of Liapunov stability, the system is said to be stable if equilibrium point \( \hat{x} \) for every neighbourhood \( N \) of \( \hat{x} \), there is a smaller neighbourhood \( \tilde{N} \subseteq N \) of \( \hat{x} \) such that every trajectory which passes through \( \tilde{N} \) remains in \( N \) as \( t \) increases. Equilibrium point \( \hat{x} \) said to be asymptotically stable if it is stable and there is a neighbourhood \( N \) of \( \hat{x} \) such that every trajectory passing \( N \) approaches \( \hat{x} \) as \( t \) tends to infinity (Arrowsmith and Place, 2005). Figure 3.2 shows the schematic illustration of the equilibrium behaviour by Liapunov.

There are many definitions of stability. The terms also describe the different behaviour of the equilibrium point (which not be discuss detail in this study). For our conclusion on this matter, it was found that the definition on
stable equilibrium defined by Scheinerman (1996) is similar with Liapunov definition on asymptotically stable of equilibrium, that is any point in the system will approach the equilibrium point as $t \to \infty$. For simplicity in our discussion, we will use the term stable instead of asymptotically stable.

3.1.1 Routh-Hurwitz criteria

The Routh-Hurwitz criteria is one of tool that can give the necessary and sufficient conditions for all of the roots of the characteristics polynomial (with real coefficients) to lie in the half of complex plane. This criteria is useful in order to determine local asymptotic stability of an equilibrium for nonlinear systems of differential equation (Linda, 2007).

Theorem 3.2. Routh-Hurwitz Criteria

\[ P(\lambda) = \lambda^n + a_1\lambda^{n-1} + \cdots + a_{n-1}\lambda + \lambda^n, \]

where the coefficients $a_i$ are real constants, $i = 1, 2 \ldots, n$, define the $n$ Hurwitz matrices using the coefficients $a_i$ of the characteristics polynomial:

\[ H_1 = \begin{pmatrix} a_1 \end{pmatrix}, \]
\[ H_2 = \begin{pmatrix} a_1 & 1 \\ a_3 & a_2 \end{pmatrix}, \]

\[ H_3 = \begin{pmatrix} a_1 & 1 & 0 \\ a_3 & a_2 & a_1 \\ a_5 & a_4 & a_3 \end{pmatrix}, \]

\[ H_n = \begin{pmatrix} a_1 & 1 & 0 & 0 & \cdots & 0 \\ a_3 & a_2 & a_1 & 1 & \cdots & 0 \\ a_5 & a_4 & a_3 & a_2 & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & 0 & 0 & \cdots & a_n \end{pmatrix}, \]

where \( a_j = 0 \) if \( j > n \). All of the roots of the polynomial \( P(\lambda) \) are negative or have negative real parts iff the determinants of all Hurwitz matrices are positive:

\[ |H_j| > 0, \quad j = 1, 2, \ldots, n. \]

For polynomials of degree \( n = 2, 3 \) and 4, the Routh-Hurwitz criteria can be summarize as

\[ n = 2: a_1 > 0 \quad \text{and} \quad a_2 > 0. \]
\[ n = 3: a_1 > 0, a_3 > 0 \quad \text{and} \quad a_1a_2 > a_3. \]
\[ n = 4: a_1 > 0, a_3 > 0, a_4 > 0 \quad \text{and} \quad a_1a_2a_3 > a_3^2 + a_1^2a_4. \]
This condition is necessary for the roots of the polynomial $P(\lambda)$ to lie in the left of half of the complex plane but is not sufficient enough. Therefore, we introduce the corollary to fulfill the condition.

**Corollary 3.3.** Suppose the coefficient of the characteristic polynomial are real. If all of the roots of the characteristic polynomial are negative or have negative real parts, then the coefficients $a_i > 0$ for $i = 1, 2, \ldots, n$.

Thus, this corollary follows that if any coefficient is zero in the characteristic polynomial, then at least one eigenvalue is either zero, is purely imaginary, or lies in the right half of the complex plane.

### 3.1.2 Linearization

The stability criteria depend on the eigenvalues of the Jacobian matrix evaluated at $\bar{X}$, $J(\bar{X})$. If all the eigenvalues have negative real parts, then the equilibrium is asymptotically stable (stable). The eigenvalues can be determined by finding the roots of the characteristic equation where the Routh-Hurwitz criteria can be applied (Linda, 2007).

**Theorem 3.4.** Suppose $\frac{dX}{dt} = F(X)$ is a nonlinear first-order autonomous system with an equilibrium $\bar{X}$, Denote the Jacobian matrix of $F$ evaluated at $\bar{X}$ as $J(\bar{X})$,

$$\lambda^n + a_1\lambda^{n-1} + \cdots + a_{n-1}\lambda + a_n = 0,$$

satisfies the conditions of Routh-Hurwitz criteria in Theorem 3.2, that is, the determinants of all the Hurwitz matrices are positive, $|H_j| > 0, j = 1, 2, \ldots, n$, then the equilibrium $\bar{X}$ is locally asymptotically stable. If $|H_j| < 0$, for some $j = 1, 2, \ldots, n$, then the equilibrium $\bar{X}$ is unstable.

Let $T$ be a transformation that maps a region $S$ in $x, y, z$-space onto a region $\mathcal{R}$ in $f, g, h$-space by means of the equations

$$\frac{dx}{dt} = f(x, y, z),$$

$$\frac{dy}{dt} = g(x, y, z),$$

$$\frac{dz}{dt} = h(x, y, z),$$
where $f, g$ and $h$ are continuously differentiable, then the stability of an equilibrium $(x_0, y_0, z_0)$ often can be determined by the stability $(x_0, y_0, z_0)$ in the associated linearized system

$$\frac{dx}{dt} = \frac{\partial f}{\partial x} x + \frac{\partial f}{\partial y} y + \frac{\partial f}{\partial z} z,$$

$$\frac{dy}{dt} = \frac{\partial g}{\partial x} x + \frac{\partial g}{\partial y} y + \frac{\partial g}{\partial z} z,$$

$$\frac{dz}{dt} = \frac{\partial h}{\partial x} x + \frac{\partial h}{\partial y} y + \frac{\partial h}{\partial z} z,$$

where all partials will be evaluated at $(x_0, y_0, z_0)$. Then the behaviour of the linearized system can be determined by Jacobian matrix:

$$J_{(x,y,z)} = \begin{pmatrix}
\frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} & \frac{\partial f}{\partial z} \\
\frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} & \frac{\partial g}{\partial z} \\
\frac{\partial h}{\partial x} & \frac{\partial h}{\partial y} & \frac{\partial h}{\partial z}
\end{pmatrix}$$

evaluated at $(x_0, y_0, z_0)$ (Stewart, 1999; Linda, 2007).

If we denoted $J_{(x,y,z)} = A_n$, then we can found the characteristics polynomials is given by

$$|A_n - \lambda I|.$$

In order to find the eigenvalues for $A_n$, the following conditions must satisfy (Aris et al., 1994).

$$|A_n - \lambda I| = 0.$$

The classification of equilibrium point $\hat{x}$ based on eigenvalues of Jacobian matrix can be summarize as

<table>
<thead>
<tr>
<th>Eigenvalues of Jacobian matrix at $\hat{x}$</th>
<th>Stability of equilibrium point</th>
</tr>
</thead>
<tbody>
<tr>
<td>All $\mathbb{R}$ $\lambda &lt; 0$</td>
<td>stable</td>
</tr>
<tr>
<td>Some $\mathbb{R}$ $\lambda &gt; 0$</td>
<td>unstable</td>
</tr>
<tr>
<td>All $\mathbb{R}$ $\lambda \leq 0$, some $\mathbb{R}$ $\lambda = 0$</td>
<td>test fails</td>
</tr>
</tbody>
</table>

**Table 3.1**: Linearization test for multidimensional nonlinear system (Scheinerman, 1996).
For the case of linearization test fails, one may consider the Liapunov function which is this method is quite complicated and not to be discussed in this study.

### 3.2 Bifurcation Analysis

If there is a non-linear autonomous differential equation that is too complicated to solved explicitly by integration, studying the equilibrium analysis is a better way to find the appropriate solution. Bifurcation is one of the analyses of equilibrium. There are many types of bifurcation in dynamical system such as saddle node and transcritical (Strogatz, 1994). If the parameter in the system is vary, the dynamics of differential system may change (Linda, 2007). The equilibrium may be unstable after a periodic solution appears. In addition, new equilibrium appears to be stable and periodic solution may be affected and becomes unstable. Consider one dimensional system in a form

\[
\frac{dx}{dt} = f(x, \gamma),
\]

where \(x\) is state-variable and \(\gamma\) the parameter to be varied (Safuan, 2014). This parameter \(\gamma\) is vary and called as bifurcation parameter. The bifurcation diagram allows us to understand the dynamic of the system involved.

#### 3.2.1 Transcritical Bifurcation

In this equilibrium situation, there are two steady–states for which one is stable and the other one is unstable. When the bifurcation point is passed through, there is an exchange of stability where the stable steady–state becomes unstable and the unstable steady–state becomes stable. This situation can be explained graphically as shown in Figure 3.3. The stability changes occur at the branch \(\gamma = 0\). One of the steady–states is stable before bifurcation parameter, \(\gamma\) less than zero then become unstable after bifurcation parameter, \(\gamma\) greater than zero.

### 3.3 Software Packages

These are the software packages that will be used to solving the system involved in this thesis.
3.3.1 MATLAB®

MATLAB® (MathWorks, 2008) is high level language which has the capabilities to compute numerically, data analysis and visualization, program and algorithm deviation and also application and development and deployment. Most of the plots in this research are produced using Matlab.

MATLAB® ODE solver routines that will be used are ODE15s, ODE23 and ODE45. ODE45 is based on fourth/fifth order Runge-Kutta formula. This will be used first before trying other solvers. ODE23 uses second and third Runge-Kutta formulas. The accuracy can be achieved using ODE45. ODE15s is a multisteps solver that solved stiff ODE system.

3.3.2 MAPLE

MAPLE (Maplesoft, 2008) is one of the mathematical softwares that is capable to solve computation symbolically, compute numerically, visualization, programming and capable to combine multiple tools in a project. In this research, most analytical work will make use of this package besides MATLAB®.

3.3.3 XPPAUT

XPPAUT (Ermentrout, 2011) is a freeware tool for analysing and simulating the dynamical system. This package is useful in order to obtain the steady-state
and periodic solution. Using XPPAUT’s inbuilt AUTO program which allows for path-following and bifurcation analysis, one can simulate the dynamical behaviour of a system by varying the bifurcation parameters.

3.4 Summary

Bifurcation is one of the analyses that is useful in order to understand the behaviour of the system which it can provide models of transitions and instabilities as some control parameter is varied (Strogatz, 1994). Generally, the nonlinear equation systems are quite impossible to solve analytically. Thus, computer softwares will be used in this research in order to find the solution and to simulate the results.
CHAPTER 4

RESULTS AND DISCUSSION

4.1 Competition Model of Two-Species Competition Interaction

Vito Volterra (1860-1940) is an Italian mathematician and physicist that had contributed many of his research on mathematical biology. Alfred James Lotka (1880-1949) is an American mathematician physical chemist, a statistician, and his famous work was on population dynamics (Cleveland et al., 2006). Both of them, together, had independently derived mass action equation (extensions of logistic equation to determine the outcome of competition). This idea was from the logistic equation of predator and prey system that had been widely used in the population dynamics. First, we will consider the model introduced by Lotka–Volterra competition of two-species. Consider the system as follow (Murray, 2002)

\[
\frac{dX}{dt} = r_1 X \left( \frac{K_1 - X}{K_1} \right), \quad (4.1a)
\]

\[
\frac{dY}{dt} = r_2 Y \left( \frac{K_2 - Y}{K_2} \right), \quad (4.1b)
\]

where \( X \) is the population of species 1, \( t \) is the time, \( r_1 \) is intrinsic capacity per-capita growth rate for increase of species 1 and \( K_1 \) is the carrying capacity for species 1. The variable is also similarly defined the species 2 for equation (4.1b). Krebs (2009) visualized the idea on the resource consumed by both species as in Figure 4.1 shows how each of the species try to use the resource. Species 1 uses the resource and the environment will hold \( K_1 \) individual of the species (shown as block number 1) when all the resources are being monopolized. Furthermore, some of this resource can be used by species 2 (shown as block number 2). As illustrated in this example, the resource can support more individual for species 2 rather than species 1. Hence, to support the equality of the resource that
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