**LOCAL STABILITY ANALYSIS ON LOTKA-VOLTERRA
PREDATOR-PREY MODELS**

FUNCTIONAL RESPONSES WITH CONSTANT PREY REFUGE

by

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Bachelor of Science, University of Toronto, 2014

A thesis

presented to Ryerson University

in partial fulfillment of the
requirements for the degree of

Master of Science

in the program of

Applied Mathematics

Toronto, Ontario, Canada, 2018

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Abstract

The dynamical behaviours of the predators and prey can be described by studying the local stability of the planar systems. Type I functional response shows that the rate of consumption per predator is proportional to prey's density while type II functional response is related to the situation that predators would reach satiation as they consumed sufficient amount of prey. We seek out a method of using transformation to reduce the number of parameters of original models and then study the stability analysis of equilibrium points. Under suitable restrictions on the new parameters, we prove that the positive interior equilibrium is a stable node for the system of type I and type II functional responses. Moreover, in the case of type II functional response, the boundary equilibria can have more types of stability other than saddle points.

Acknowledgements

I would first like to express my sincere gratitude to my thesis advisor Dr. Kunquan Lan of the Applied Mathematics at Ryerson University. His continuous and considerable support helped me in all the time of research and writing of this thesis. I greatly improved my knowledge of mathematical biology with his valuable guidance and lectures which contributed to perfecting my thesis contents gradually.

Besides, I would also like to thank my colleagues, Christopher Chow, Marvin Hoti, Phuc Ngo, for helping me to correct some mistakes and giving important feedback. Their advice also enhanced my results of this thesis with more accuracy. Especially, without Christopher Chow and Marvin Hoti's co-works, the results presented in Chapter 4 and Chapter 5 would not be finished in time.

Finally, I would like to thank the members of the examining committee of Applied Mathematics at Ryerson University, Dr. Kunquan Lan, Dr. Silvana Ilie, Dr. Pawal Pralat and Dr. Dzung Minh Ha for their time and consideration to organize the defense of this thesis. I am gratefully indebted to them for their very valuable comments on this thesis.

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Chapter 1

Introduction

According to records of a recently published document, *Ecology System Encyclopedia* in [26], there are approximately 8 million animal species on earth with only less than 25% of them currently identified by scientists. They exist and interact with one another as well as their physical environment around the world. One principal interaction among species is predation, which is considered as a major part of natural rules that preserve ecosystems in a virtuous circle.

Generally, biologists observed that populations of predators and prey keep at a balanced coexistence, that is, neither of them are out of controls or become endangered in most cases[40]. Predators usually drive the populations of prey up and down as they hunt them as foods, whereas the prey holds a stabilized growth under such external effects. Into the bargain, with continuous in-depth research on prey's growth, scientists found that prey was also restricted by environmental capacity which would prevent prey's infinite increase. Prey's population might still reach a limited level despite the lack of its predators, and then decrease to adjust the fixed physical environment. Further, some prey could search for a hiding place to avoid its predators from hunting, which is called prey refuge in predator-prey models.

Systems of two suitable first order ordinary differential equations can be used to model the interaction between predators and their prey. The dynamical behaviors

of the predators and prey can be described by studying the local stability of the planar systems. These dynamical properties provide predication whether the prey and predators will coexist or suffer from mutual extinction. One of the classic predator-prey models is the Lotka-Volterra predator-prey model often used to describe the dynamics of biological systems in which two species interact. Since 1925, a variety of predator-prey models have been proposed by introducing capacity, prey refuge, and functional responses [1].

Through the development of this thesis, we first review and examine some classical models related to predator-prey interaction by focusing on the following questions: How the models were established and gradually improved? What new factors or concepts were added since Lotka-Volterra model was proposed? And how the different types of functional response influence the study of predation? Next, we will investigate how to generalize from the foregoing classical models after classifying functional responses. Moreover, local stability analysis on Lotka-Volterra models will be addressed by incorporating type II functional response into predation and adding a number of parameters to indicate what kinds of factor would affect the predator-prey system. Finally, the main focus of this thesis is what other new results we can obtain by applying transformation theory to solving for equilibria and local stability analysis and how they are different from the original study of the models.

Chapter 2

Preliminaries

In this chapter, we will introduce and present a few basic but essential definitions and lemmas regarding to the knowledge of differential equations, because the core of studying predator-prey models—finding equilibrium points and stability analysis—are heavily dependent on them. The references we selected for this chapter are mostly from [1] and [12]. The former is a mathematical biology textbook and the latter is a fundamental ecology course which included a lecture on predator-prey systems. Besides, the last section of this chapter is about the transformation theory which has been widely employed in various research papers on predator-prey or SIR epidemic models. References of [2, 24, 35] are selected as major sources of transformation theory.

2.1 Ordinary Differential Equation

Definition 2.1.1. An ordinary differential equation of order n is an equation of the form

$$f(x, dx/dt, d^2x/dt^2, \dots, d^nx/dt^n, t) = 0.$$

If this differential equation does not depend on t explicitly, then it is said to be autonomous; otherwise it is nonautonomous.

When discussing one species of predator and one species of its prey, the biological models entail two-dimensional autonomous system of first-order differential equations:

$$\begin{cases} \dot{u}(t) = f(u(t), v(t)), \\ \dot{v}(t) = g(u(t), v(t)), \end{cases} \quad (2.1.1)$$

where $f, g \in C^1(\mathbb{R}^2)$ and $\dot{u}(t) = \frac{d(u(t))}{dt}$, $\dot{v}(t) = \frac{d(v(t))}{dt}$.

$u(t)$ and $v(t)$ denote the density of prey and predator populations at time t , respectively. f, g are functions of $u(t)$ and $v(t)$ with several parameters which have certain biological meanings to affect them such that either increasing or decreasing rates of prey and predators at time t (i.e., $\dot{u}$ and $\dot{v}$) are primarily related to $u(t)$ and $v(t)$ not explicitly dependent on time t .

Definition 2.1.2. $(u, v) \in \mathbb{R}^2$ is an equilibrium of (2.1.1) if it satisfies $f(u, v) = 0$ and $g(u, v) = 0$. An equilibrium point (u, v) is said to be positive if $u, v \geq 0$; to be a positive interior equilibrium if $u, v > 0$.

Equilibrium points are literally population levels at which both predators and prey are stabilized within a specific time period (i.e., $\dot{u}(t) = 0$ and $\dot{v}(t) = 0$). In reality, however, neither of predators nor prey have negative population, which implies that the equilibrium points that are meaningful to mathematical biology studies should be positive.

Definition 2.1.3. Based on the system (2.1.1), we can construct a jacobian matrix of f and g at (u, v) (denoted by $A(u, v)$):

$$A(u, v) = \begin{pmatrix} \frac{\partial f}{\partial u} & \frac{\partial f}{\partial v} \\ \frac{\partial g}{\partial u} & \frac{\partial g}{\partial v} \end{pmatrix}, \quad (2.1.2)$$

$|A(u, v)| = \left(\frac{\partial f}{\partial u}\right)\left(\frac{\partial g}{\partial v}\right) - \left(\frac{\partial f}{\partial v}\right)\left(\frac{\partial g}{\partial u}\right)$ and $\text{tr}(A(u, v)) = \frac{\partial f}{\partial u} + \frac{\partial g}{\partial v}$ represent determinant and trace of (2.1.2), respectively.

The function of jacobian matrix is aimed to serve the local stability analysis (also called as phase portraits or solution behaviour) of each equilibrium point by using $|A(u, v)|$ and $\text{tr}(A(u, v))$. Equilibrium points themselves would not give any further information on how the predator-prey systems would grow in future. In contrast, biologists may be able to predict the development of predator-prey system according to the results of solution behavior (solutions around the equilibrium points). For example, if solutions to the system (2.1.1) are forming in an inward spiral direction to a positive interior equilibrium as time t increases, then it leads to the conclusion that the predator-prey system would not be out of control and the population level of predators and prey are eventually stabilized in a long term period. Nevertheless, if the equilibrium point is $(0, 0)$ instead, the future of this predator-prey system is not optimistic, because solutions toward $(0, 0)$ implies an outcome of extinction confronts both predators and prey.

Definition 2.1.2 and 2.1.3 are basically two major steps of studying a predator-prey model: first and foremost, we need to work out the equilibrium points of a mathematical model in the form of (2.1.1), which is established based on a predator-prey system. Next, we need to employ the jacobian matrix to determine the type of solution behavior around each equilibrium point. We will explain all the types of solution behavior as well as detailed instructions on how to obtain the results of local stability analysis in the subsequent sections.

2.2 First -Order Linear Differential Equation

Definition 2.2.1.

$$\frac{d^n x}{dt^n} + a_1(t) \frac{d^{n-1} x}{dt^{n-1}} + \dots + a_{n-1}(t) \frac{dx}{dt} + a_n(t)x = h(t)$$

The differential equation above is said to be linear if the coefficients a_i , ($i = 1, \dots, n$) and $h(t)$ are either constant or functions of t but not functions of x or any of its derivatives. Otherwise, the differential equation is said to be nonlinear.

Consider the following two-dimensional linear system:

$$\begin{cases} \dot{u} = a_{11}u + a_{12}v, \\ \dot{v} = a_{21}u + a_{22}v. \end{cases} \quad (2.2.1)$$

Jacobian matrix of (2.2.1) by Definition 2.1.3 is

$$A(u, v) = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}. \quad (2.2.2)$$

Clearly, the origin, $(u, v) = (0, 0)$, is an equilibrium point of (2.2.1) with

$$|A(u, v)| = a_{11}a_{22} - a_{12}a_{21} \quad \text{and} \quad \text{tr}(A(u, v)) = a_{11} + a_{22}.$$

In order to obtain eigenvalues, $\lambda_{1,2}$ of matrix (2.2.2), we need

$$|A(u, v) - \lambda I| = \left| \begin{pmatrix} a_{11} - \lambda & a_{12} \\ a_{21} & a_{22} - \lambda \end{pmatrix} \right| = 0. \quad (2.2.3)$$

By solving the characteristic polynomial of the determinant, we have

$$\lambda^2 - (a_{11} + a_{22})\lambda + (a_{11}a_{22} - a_{12}a_{21}) = \lambda^2 - \text{tr}(A(u, v))\lambda + |A(u, v)| = 0$$

$$\lambda_{1,2} = \frac{\text{tr}(A(u, v)) \pm \sqrt{\text{tr}(A(u, v))^2 - 4|A(u, v)|}}{2}.$$

From above expressions for eigenvalues, we can see that the solutions to the system ultimately depend on $|A(u, v)|$ and $\text{tr}(A(u, v))$ of the jacobian matrix, as the solutions are characterized by the eigenvalues and the results of eigenvalues are determined by $|A(u, v)|$ and $\text{tr}(A(u, v))$.

Figure 2.1: Saddle and Stable Node

Definition 2.2.2. According to the different eigenvalues, the behavior of the solutions can be classified as following:

(i) Eigenvalues λ_1 and λ_2 have opposite signs, then the solution behavior is classified as a saddle. Figure 2.1a (Source:[1]) shows the solution behavior around the saddle point.

(ii) Both eigenvalues have the same sign and may be distinct or equal, $\lambda_1 \leq \lambda_2 < 0$ or $0 < \lambda_1 \leq \lambda_2$, then solution behavior can be classified as a node. Figure 2.1b (Source:[1]) shows the example of which the origin is a node.

(iii) If $\lambda_{1,2}$ are complex eigenvalues, (Suppose $\lambda_{1,2} = a \pm ib$), then the solutions are in the form of $e^{at}\cos(bt)$ or $e^{at}\sin(bt)$. If the real part $a < 0$, then the solutions spiral inward, toward the equilibrium points. On the other hand, if $a > 0$, then the solutions spiral outward, away from the equilibrium points. So in the cases of which the eigenvalues have nonzero real part, the equilibrium points are classified as focus

Figure 2.2: Stable Focus and Center

or spiral. If the real part is negative (i.e., $\text{tr}(A(u, v)) < 0$), then (u, v) is stable and if the real part is positive (i.e., $\text{tr}(A(u, v)) > 0$), then (u, v) is unstable. Figure 2.2a (Source:[1]) shows the case of stable focus.

(iv) If eigenvalues are purely imaginary (i.e., $a = 0$, and $\lambda_{1,2} = \pm ib$), then equilibrium points are classified as centre. Figure 2.2b (Source:[1]) shows the solution behavior around the center.

Remark 2.2.1. For instance, an equilibrium point $(0, 0)$ of (2.1.1) means a mutual extinction level for predator-prey system, since population density of both $u(t)$ and $v(t)$ equals to 0. The solution behavior around the equilibrium point $(0, 0)$, however, is more important than simply to consider it as a population level. Because if the stability analysis of the equilibrium shows a saddle (i.e., as described in Definition 2.2.2(iii) and Figure 2.1a), then it implies that solutions around $(0, 0)$ are diffused and avoid to reach $(0, 0)$ as time t passes and therefore, this predator-prey system expands apart from mutual extinction in a long term period.

Models presented in Chapter 3, 4, 5 are not in the form of linear differential equations but they still have an equilibrium of $(0, 0)$ with a saddle phase portrait. The technique used to study such nonlinear models involves linearization and transformation theory, which will be covered in the next two sections.

2.3 Nonlinear Cases and Linearization

Again, we consider the following first-order two dimensional autonomous differential system:

$$\begin{cases} \dot{x}(t) = f(x, y), \\ \dot{y}(t) = g(x, y). \end{cases} \quad (2.3.1)$$

Recall that the equilibria of the system above are solutions $(\bar{x}, \bar{y})$ satisfying $f(\bar{x}, \bar{y}) = 0$ and $g(\bar{x}, \bar{y}) = 0$. The functions f and g are expanded using Taylor formula about the equilibrium, $(\bar{x}, \bar{y})$, where $u = x - \bar{x}$ and $v = y - \bar{y}$. Assume that f and g have continuous second-order partial derivatives in an open set containing the point $(\bar{x}, \bar{y})$.

Then

$$\frac{du}{dt} = f(\bar{x}, \bar{y}) + f_x(\bar{x}, \bar{y})u + f_y(\bar{x}, \bar{y})v + f_{xx}(\bar{x}, \bar{y})\frac{u^2}{2} + f_{xy}(\bar{x}, \bar{y})uv + f_{yy}(\bar{x}, \bar{y})\frac{v^2}{2} + \dots,$$

$$\frac{dv}{dt} = g(\bar{x}, \bar{y}) + g_x(\bar{x}, \bar{y})u + g_y(\bar{x}, \bar{y})v + g_{xx}(\bar{x}, \bar{y})\frac{u^2}{2} + g_{xy}(\bar{x}, \bar{y})uv + g_{yy}(\bar{x}, \bar{y})\frac{v^2}{2} + \dots,$$

where, for example, $f_x(\bar{x}, \bar{y})$ means $\partial f(x, y)/\partial x|_{x=\bar{x}, y=\bar{y}}$. We used the fact that $f(\bar{x}, \bar{y}) = 0$ and $g(\bar{x}, \bar{y}) = 0$.

Definition 2.3.1. The system linearized about the equilibrium $(\bar{x}, \bar{y})$ is

$$\frac{d\vec{X}}{dt} = A\vec{X},$$

where $\vec{X} = (u, v)^T$ and A is the jacobian matrix evaluated at the equilibrium points,

$$A(\bar{x}, \bar{y}) = \begin{pmatrix} f_x(\bar{x}, \bar{y}) & f_y(\bar{x}, \bar{y}) \\ g_x(\bar{x}, \bar{y}) & g_y(\bar{x}, \bar{y}) \end{pmatrix}. \quad (2.3.2)$$

Then, the generalized characteristic polynomial of matrix A is

$$\lambda^2 - \text{tr}(A)\lambda + |A|.$$

We identify the types of equilibria (local stability analysis) for nonlinear systems corresponding to the classification (Definition 2.2.2) mentioned in Section 2.2. However, in some cases, the solution behaviour of the nonlinear system may be different from linear ones:

(i) $|A|=0$. There is at least one zero eigenvalue. In the linear system, the equilibria are not isolated. In the nonlinear system, if there is an isolated equilibrium, it may be a node, spiral, or saddle.

(ii) $\text{tr}(A) = 0$ and $|A| > 0$. The eigenvalues are purely imaginary. The equilibrium is a center in the linear system but may be a center or spiral in the nonlinear system.

(iii) $\text{tr}(A)^2 = 4|A|$. This means the borderline between complex and real eigenvalues. In the nonlinear system the equilibrium could be a node or a spiral.

Figure 2.3: Trace-Determinant Plane

Figure 2.3 (Source:[41]) above shows the stability diagram in the trace-determinant plane. The curves $|A| = 0$, $\text{tr}(A) = 0$ and $|A| > 0$ and $\text{tr}(A)^2 = 4|A|$ are transition regions between two types of behavior.

Further, the following results have been widely employed to study the local stability

and phase portraits for predator-prey models, for example, in [15, 24, 25, 27, 46] and susceptible-infective-removed epidemic models in [11, 20, 28].

Lemma 2.3.1. *Let (u^*, v^*) be an equilibrium of (2.1.1). Then the following assertions hold.*

- (i) *If $|A(u^*, v^*)| < 0$, then (u^*, v^*) is a saddle.*
- (ii) *If $|A(u^*, v^*)| > 0$ and $(\text{tr}(A(u^*, v^*)))^2 - 4|A(u^*, v^*)| \geq 0$, then (u^*, v^*) is a node. It is stable if $\text{tr}(A(u^*, v^*)) < 0$ and unstable if $\text{tr}(A(u^*, v^*)) > 0$.*
- (iii) *If $|A(u^*, v^*)| > 0$ and $(\text{tr}(A(u^*, v^*)))^2 - 4|A(u^*, v^*)| < 0$, then (u^*, v^*) is a focus. It is stable if $\text{tr}(A(u^*, v^*)) < 0$ and unstable if $\text{tr}(A(u^*, v^*)) > 0$.*
- (iv) *Assume that $|A(u^*, v^*)| > 0$. If $\text{tr}(A(u^*, v^*)) < 0$, then (u^*, v^*) is locally asymptotically stable; if $\text{tr}(A(u^*, v^*)) \leq 0$, then it is stable and if $\text{tr}(A(u^*, v^*)) > 0$, then it is unstable.*

2.4 Transformation Theory

We still consider the following autonomous system of first-order differential equations:

$$\begin{cases} \dot{u}(t) = f(u(t), v(t)), \\ \dot{v}(t) = g(u(t), v(t)). \end{cases} \quad (2.4.1)$$

Definition 2.4.1. A map $T : \mathbb{R}^2 \rightarrow \mathbb{R}^2$ defined by $T(u, v) = (f(u, v), g(u, v))$ is said to be regular if T is one to one and onto, T and T^{-1} are continuous and $|A(u, v)| \neq 0$ on $\mathbb{R}^2$. If T is regular, then the following transformation from (2.4.1)

$$\begin{cases} u_1 = f(u, v), \\ v_1 = g(u, v) \end{cases} \quad (2.4.2)$$

is said to be a regular transformation.

If (2.4.1) is changed into another system under suitable regular transformations, then the two systems are said to be equivalent. It is known (for example see [2]) that under regular transformations, the topological structures of solutions of a planar system near equilibria including a variety of dynamics like saddles, topological saddles, nodes, saddle-nodes, focus, centers, or cusps remain unchanged.

We need the following result which was proved in [24, Proposition 3.2].

Lemma 2.4.1. *Let (u^*, v^*) be an equilibrium of (2.4.1). Assume that $|A(u^*, v^*)| = 0$, $\text{tr}(A(u^*, v^*)) \neq 0$ and (2.1.1) is equivalent to the following system*

$$\begin{cases} \dot{u}_1 = p(u_1, v_1), \\ \dot{v}_1 = \varrho v_1 + q(u_1, v_1) \end{cases} \quad (2.4.3)$$

with an isolated equilibrium $(0, 0)$, where $p(u_1, v_1) = \sum_{i+j=2, i, j \geq 0}^{\infty} a_{ij} u_1^i v_1^j$ and $q(u_1, v_1) = \sum_{i+j=2, i, j \geq 0}^{\infty} b_{ij} u_1^i v_1^j$ are convergent power series. If $\varrho \neq 0$ and $a_{20} \neq 0$, then (u^*, v^*) is a saddle-node.

A function $f : \Omega \subset \mathbb{R}^2 \rightarrow \mathbb{R}$ is said to be *analytic* in an open set Ω if it has a convergent Taylor series in some neighborhood of each point in Ω (see [35, p.69]).

When $|A(u^*, v^*)| = \text{tr}(A(u^*, v^*)) = 0$ and $A(u^*, v^*) \neq 0$, under suitable regular transformations, (2.1.1) is equivalent to the following form

$$\begin{cases} \dot{u} = v, \\ \dot{v} = a_k u^k [1 + h(u)] + b_n u^n v [1 + g(u)] + v^2 R(u, v) \end{cases} \quad (2.4.4)$$

with equilibrium $(0, 0)$, where h, g and p are analytic in a neighborhood of $(0, 0)$, $h(0) = g(0) = 0$, $k \geq 2$, $a_k \neq 0$ and $n \in \mathbb{N}$.

Lemma 2.4.2 ([2, 35]). *Let (u^*, v^*) be an equilibrium of (2.4.1) and $|A(u^*, v^*)| = \text{tr}(A(u^*, v^*)) = 0$ and $A(u^*, v^*) \neq 0$. If (2.4.1) is equivalent to (2.4.4), $k = 2m+1 \in \mathbb{N}$ and $a_k > 0$, then (u^*, v^*) is a topological saddle.*

Chapter 3

Classical Predator-Prey Models

In this chapter, we will examine how the knowledge of differential equations discussed in the previous chapter were applied to classical models (i.e., solving for equilibrium first and then analyze the dynamical behaviors of predators and prey systems). Classical models can be sorted into three different categories according to 3 types of functional responses: Type I, Type II and Type III. For type I functional response, we choose Lotka-Volterra typical model, Holling's logistic model, refuge model and a generalized model from Ma's paper[29] that contains all the prior cases. Moreover, we will inspect how the most basic Lotka-Volterra model was expanded and enriched gradually by adding different parameters to become other later type I models. For Type II functional response, we will develop a model based on Holling's conjectures from [18]. Differing between these two types of functional responses is subject to the term at the first equation of models showing the total number of prey killed under predation; Type III functional response is beyond the contents of this thesis, therefore only a few brief explanations for Type III functional response will be displayed at the end of this chapter. We will cover the way of classification and explain in Section 3.4 with more details on why functional responses matter to predator-prey models.

3.1 Lotka-Volterra Predator-Prey Model

Lotka-Volterra predator-prey model, which was originally proposed by two Biological Mathematicians in 1910, Alfred Lotka and Vito Volterra, is one of the most classical and oldest predator-prey model in the history of ecology studies. Many mathematical biology textbooks or ecology courses (see [1, 12, 35, 41]) introduce this model as fundamentals to students. Studying Lotka-Volterra predator-prey model will help us to understand the primary connection between predators and their prey in terms of math formations, based on which our modern knowledge of predator-prey models advanced.

The Lotka-Volterra predator-prey model is formed of a pair equations with first-order nonlinear differential equations:

$$\begin{cases} \dot{x} = rx - cxy, \\ \dot{y} = exy - dy, \end{cases} \quad (3.1.1)$$

where $x(t)$ and $y(t)$ ($\dot{x} = \frac{dx(t)}{dt}$, $\dot{y} = \frac{dy(t)}{dt}$) denote the density of prey and predator populations at time t , respectively; parameter r is the natural growth rate of the prey, while c is the per capita rate of predation of the predator (fraction of the prey population eaten per predator), e is a conversion rate of eaten prey into new predator abundance, d is the per capita death rate of the predator. More specifically, cxy is the number of prey killed by predator and exy is the number new recruitment of predator after consuming prey.

Lotka-Volterra predator-prey model assumes that the ratio between consumption of each predator and prey density is proportional. The parameter e also means the conversion efficiency rate of predator consuming prey. In reality, c and e are different due to energy lost (e.g., eating a rabbit for one fox does not mean that there will be a new baby fox born afterward. That is, not all the energy consumed from prey biomass transfers to predator biomass.)

The following theorem with respect to the Lotka-Volterra predator-prey model was stated in Allen's textbook[1]. The proof given by the textbook applied the transformation method instead of the traditional one. Further, the textbook omitted the details of transformation process, thus we will first show the detailed process and then give another proof using traditional way.

By transformation theory explained in Section 2.4, let $\bar{t} = rt$, $u(\bar{t}) = \frac{ex(t)}{d}$ and $v(\bar{t}) = \frac{cy(t)}{r}$ for (3.1.1). Then, $x(t) = \frac{du(\bar{t})}{e}$ and $y(t) = \frac{rv(\bar{t})}{c}$. Taking derivatives for $x(t)$ and $y(t)$ with respect to t , we have

$$\frac{dx(t)}{dt} = \frac{d\left(\frac{du(\bar{t})}{e}\right)}{d\bar{t}} \frac{d\bar{t}}{dt} = \frac{d\left(\frac{du(\bar{t})}{e}\right)}{d\bar{t}} r = \frac{dr}{e} \frac{d(u(\bar{t}))}{d\bar{t}}$$

and

$$\frac{dy(t)}{dt} = \frac{d\left(\frac{rv(\bar{t})}{c}\right)}{d\bar{t}} \frac{d\bar{t}}{dt} = \frac{d\left(\frac{rv(\bar{t})}{c}\right)}{d\bar{t}} r = \frac{r^2}{c} \frac{d(v(\bar{t}))}{d\bar{t}}.$$

Then, applying the above results back to system (3.1.1), we have the following new equations for $u(\bar{t})$ and $v(\bar{t})$:

$$\begin{aligned} \frac{dx(t)}{dt} &= \frac{dr}{e} \frac{d(u(\bar{t}))}{d\bar{t}} = rx(t) - cx(t)y(t) \quad \Rightarrow \quad \frac{d(u(\bar{t}))}{d\bar{t}} = \frac{ex(t)}{d} - \frac{ecx(t)y(t)}{dr}, \\ \frac{dy(t)}{dt} &= \frac{r^2}{c} \frac{d(v(\bar{t}))}{d\bar{t}} = ex(t)y(t) - dy(t) \quad \Rightarrow \quad \frac{d(v(\bar{t}))}{d\bar{t}} = \frac{d}{r} \left(\frac{ecx(t)y(t)}{rd} - \frac{cy(t)}{r} \right). \end{aligned}$$

Next, replacing $\frac{ex(t)}{d}$ and $\frac{cy(t)}{r}$ by $u(\bar{t})$ and $v(\bar{t})$, respectively, we have the following new equivalent system in terms of time $\bar{t}$, where $\alpha = \frac{d}{r}$:

$$\begin{cases} \dot{u} = u - uv, \\ \dot{v} = \alpha(uv - v). \end{cases} \quad (3.1.2)$$

Theorem 3.1.1. *Assume that $\alpha > 0$, then system (3.1.2) has two positive equilibrium points: $(0, 0)$ and $(1, 1)$, and the origin $(0, 0)$ is a saddle while the other equilibrium point $(1, 1)$ is a centre.*

Proof. By letting $\dot{u} = 0$ and $\dot{v} = 0$, we have $u - uv = 0$ and $\alpha(uv - v) = 0$.

If $v = 0$, then second equation equals to 0, and first equation becomes $u - 0 = 0$. Thus, we have obtained an equilibrium point $(0, 0)$.

If $v \neq 0$, then by $\alpha(uv - v) = \alpha v(u - 1) = 0$, we have $u = 1$. Substituting $u = 1$ into $u - uv = 0$, we have $v = 1$. Therefore, the other equilibrium point is $(1, 1)$.

Now, jacobian matrix of (3.1.2) by (2.1.2) is

$$A(u, v) = \begin{pmatrix} 1 - v & -u \\ \alpha v & \alpha u - \alpha \end{pmatrix}. \quad (3.1.3)$$

Then, at each equilibrium

$$A(0, 0) = \begin{pmatrix} 1 & 0 \\ 0 & -\alpha \end{pmatrix} \quad (3.1.4)$$

and

$$A(1, 1) = \begin{pmatrix} 0 & -1 \\ \alpha & 0 \end{pmatrix}. \quad (3.1.5)$$

From matrix (3.1.4), $|A(0, 0)| = -\alpha$. By Lemma 2.3.1, because $|A(0, 0)| = -\alpha < 0$, we can conclude that the equilibrium point $(0, 0)$ is a saddle.

From matrix (3.1.5), $|A(1, 1)| = \alpha$ and $\text{tr}(A(1, 1)) = 0$. By Lemma 2.3.1 and Definition 2.2.2, we see that the eigenvalues of matrix (3.1.5) are purely imaginary, thus the equilibrium point $(1, 1)$ is a center. $\square$

The following theorem was originally stated in [41] in purpose of explaining the Lotka-Volterra model only. The proof in [41] was simple and some processes (such as how to obtain trace and determinant) were omitted. We will analyze the phase

portraits of the system (3.1.1) in full details and then compare the process with the one showed in [1] (using transformation) to see what differences we could conclude.

Theorem 3.1.2. *Assume that t, r, c, e, d are all positive, then the equilibrium points of (3.1.1) are $(0, 0)$ and $(\frac{d}{e}, \frac{r}{c})$. The origin $(0, 0)$ is a saddle point, while the other equilibrium point $(\frac{d}{e}, \frac{r}{c})$ is a centre.*

Proof. Equilibrium points are obtained by letting

$$\begin{cases} \dot{x} = rx - cxy = 0, \\ \dot{y} = exy - dy = 0. \end{cases} \quad (3.1.6)$$

If $y = 0$, then second equation becomes true for any values of x . Substituting $y = 0$ into first equation, we have $rx = 0$, and we obtained one equilibrium point $(0, 0)$.

If $y \neq 0$, then the second equation becomes $y(ex - d) = 0$. Dividing both sides by y , we have $x = \frac{d}{e}$. Since $x \neq 0$, by dividing both sides of first equation by x , we have $r - cy = 0$, and then $y = \frac{r}{c}$. Thus, the other equilibrium point is $(\frac{d}{e}, \frac{r}{c})$.

As we mentioned in the Lemma 2.3.1, stability of equilibrium points can be studied by analyzing jacobian matrix of (3.1.1). By (2.1.2),

$$A(x, y) = \begin{pmatrix} r - cy & -cx \\ ey & ex - d \end{pmatrix} \quad (3.1.7)$$

and the jacobian matrix at origin $(0, 0)$ is

$$A(0, 0) = \begin{pmatrix} r & 0 \\ 0 & -d \end{pmatrix}. \quad (3.1.8)$$

Then, $|A(0, 0)| = -rd$ and $\text{tr}(A(0, 0)) = r - d$. By referring to Lemma 2.3.1 and Definition 2.2.2, it implies that origin is a saddle point, since $|A(0, 0)| = -rd < 0$.

For the other equilibrium point $(\frac{d}{e}, \frac{r}{c})$, we deploy similar method to analyze the stability. The jacobian matrix at $(\frac{d}{e}, \frac{r}{c})$ is

$$A(\frac{d}{e}, \frac{r}{c}) = \begin{pmatrix} 0 & \frac{-cd}{e} \\ \frac{er}{c} & 0 \end{pmatrix}. \quad (3.1.9)$$

Then, $|A(\frac{d}{e}, \frac{r}{c})| = dr > 0$ and $\text{tr}(A(\frac{d}{e}, \frac{r}{c})) = 0$. By referring to Definition 2.2.2, the equilibrium point $(\frac{d}{e}, \frac{r}{c})$ is a centre, because $|A(\frac{d}{e}, \frac{r}{c})| = dr > 0$ and $\text{tr}(A(\frac{d}{e}, \frac{r}{c})) = 0$, which implies that the eigenvalues are purely imaginary. Simulation evidence of a center for $(\frac{d}{e}, \frac{r}{c})$ will be presented in Section 6.1. $\square$

We see that Theorem 3.1.1 and 3.1.2 have same conclusions in terms of stability analysis, although the expressions of equilibrium points are different. The reason for this occurrence is that α has the same biological meaning as d and r which have been normalized to 1 in (3.1.2) after transformation. Also, $u(\bar{t}) = \frac{ex(t)}{d}$ and $v(\bar{t}) = \frac{cy(t)}{r}$ mean that d and c are proportional to e and r , respectively. d/e is related to the conversion of hunted prey biomass into predator biomass, while c/r is related to the proportion of increased prey that killed by predators. In other words, we normalize c and e (increasing rate of prey and the per capita reduction in prey per predator) to 1 by letting them be proportional to r and d .

Applying transformation wisely would reduce the number of parameters without changing the biological meaning of the original model and therefore, the process of stability analysis would also be more simple. Sometimes using transformation would give more generalized results than the ones obtained from traditional method. (see chapter 4 for the examples of different results of stability analysis between transformation and traditional method.)

3.2 C.S. Holling Logistic Equations

Crawford Stanley Holling (a famous Canadian Ecologist) made some modification to Lotka-Volterra model by adding the logistic equations added to the term of prey's growth in [18]. This improved model indicates population density of prey is restricted by the carrying capacity of its physical environments. We denote by k the carrying capacity in the following model:

$$\begin{cases} \dot{x} = rx(1 - \frac{x}{k}) - cxy, \\ \dot{y} = exy - dy, \end{cases} \quad (3.2.1)$$

where r , c , e and d are all positive parameters and have the same biological meanings as explained in Section 3.1. If the population density of prey becomes too large and exceed the original capacity (e.g., the environmental space, natural resources that are needed for prey to grow up), then the term $(1 - \frac{x}{k})$ eventually starts to be negative and in turn, there must be a decrease in the whole prey population; if x is very small, there would be little competition among the prey and $rx(1 - \frac{x}{k})$ becomes very close back to the previous prey's growth rx .

The following results are sorted out from Holling's research published in [16, 17]. Further, we will give our own proofs to corresponding theorems by applying the lemmas and definitions showed in preliminaries as the original research papers provided less detailed process.

Theorem 3.2.1. *Assume that r , c , e and d are all positive, then the following assertions hold:*

- (i) *If $\frac{d}{e} < k$, then (3.2.1) has 4 positive equilibrium points, which are $(0, 0)$, $(\frac{d}{e}, 0)$, $(k, 0)$ and $(\frac{d}{e}, \frac{r}{c}(1 - \frac{d}{ek}))$.*
- (ii) *If $\frac{d}{e} \geq k$, then (3.2.1) have 2 positive equilibrium points, which are $(0, 0)$, $(k, 0)$.*

Proof. By Definition 2.1.2, the equilibrium points are obtained by solving

$$\begin{cases} rx(1 - \frac{x}{k}) - cxy = 0, \\ exy - dy = 0. \end{cases} \quad (3.2.2)$$

If $y = 0$, from first equation we have, $x = 0$ or $x = k$. So under either condition of (i) and (ii), we both have equilibrium points $(0, 0)$ and $(0, k)$.

On the other hand, if $y \neq 0$, from second equation we have, $x = \frac{d}{e}$. Re-arranging the first equation, we obtain $r(1 - \frac{x}{k}) - cy = 0$. Substituting x into $r(1 - \frac{x}{k}) - cy = 0$, we have $y = \frac{r}{c}(1 - \frac{d}{ek})$.

(i) If $\frac{d}{e} < k$, then $\frac{d}{ek} < 1$ since all parameters are positive. $y = \frac{r}{c}(1 - \frac{d}{ek}) > 0$ in this case, therefore, $x = \frac{d}{e}$ and $y = \frac{r}{c}(1 - \frac{d}{ek})$ is a positive equilibrium point of (3.2.1).

(ii) If $\frac{d}{e} \geq k$, then $y = \frac{r}{c}(1 - \frac{d}{ek}) \leq 0$. In the case of $y = \frac{r}{c}(1 - \frac{d}{ek}) = 0$, we have $1 - \frac{d}{ek} = 0$, which implies again $x = 0$ or $x = k$; in addition, if $y = \frac{r}{c}(1 - \frac{d}{ek}) < 0$, then (x, y) is not a positive equilibrium point, thus we omit this option.

□

Theorem 3.2.2. *If $\frac{d}{e} < k$, then equilibrium point $(\frac{d}{e}, \frac{r}{c}(1 - \frac{d}{ek}))$ is locally asymptotically stable.*

Proof. We use jacobian matrix of the system (3.2.1) to analyze the stability of equilibrium point:

$$A(x, y) = \begin{pmatrix} r - \frac{2rx}{k} & -cx \\ ey & ex - d \end{pmatrix}. \quad (3.2.3)$$

Then, $A(x, y)$ at $\left(\frac{d}{e}, \frac{r}{c}\left(1 - \frac{d}{ek}\right)\right)$ becomes

$$A\left(\frac{d}{e}, \frac{r}{c}\left(1 - \frac{d}{ek}\right)\right) = \begin{pmatrix} \frac{-rd}{ek} & \frac{-cd}{e} \\ \frac{rek - rd}{ck} & 0 \end{pmatrix}. \quad (3.2.4)$$

By jacobian matrix (3.2.4), we have

$$\left|A\left(\frac{d}{e}, \frac{r}{c}\left(1 - \frac{d}{ek}\right)\right)\right| = \frac{cdr(ek - d)}{eck}$$

and

$$\text{tr}\left[A\left(\frac{d}{e}, \frac{r}{c}\left(1 - \frac{d}{ek}\right)\right)\right] = \frac{-rd}{ek}.$$

Because all parameters are positive and $\frac{d}{e} < k$, we have $ek - d > 0$. Thus,

$$\left|A\left(\frac{d}{e}, \frac{r}{c}\left(1 - \frac{d}{ek}\right)\right)\right| = \frac{cdr(ek - d)}{eck} > 0,$$

$$\text{tr}\left[A\left(\frac{d}{e}, \frac{r}{c}\left(1 - \frac{d}{ek}\right)\right)\right] = \frac{-rd}{ek} < 0.$$

By Lemma 2.3.1 in the Section 2.3, we can conclude that $\left(\frac{d}{e}, \frac{r}{c}\left(1 - \frac{d}{ek}\right)\right)$ is locally asymptotically stable. $\square$

As Morrissey stated in [34], compared with the results of phase portraits we studied in Section 3.1, the solutions in Holling's logistic model illustrate more stabilized cycle, while the Lotka-Volterra model shows that the solutions are just circling around the equilibrium points. The latter results tell us any large proportional decrease happens to prey population may cause the predator-prey system to a disaster. (e.g., the population of prey or predator could be 0 in the end or become extinct.) But in the former results we can conclude that all the solutions spiral towards the equilibrium points, which means in terms of biological meaning that the predator-prey system avoids extinction.

3.3 Prey Refuges

Among the predator-prey interactions, the response of prey to its predator was also considered in the Lotka-Volterra model. Andrew Sih in [40] stated that prey would seek refuges to avoid predators' hunting. Refuges are some places or situations that the risks of being hunted by predators are likely lessened. For instances, small fishes hide in coral reefs (Figure 3.1) or herbivorous animals may try to find caves to keep away from being hunted by their predators.

Figure 3.1: Coral Reef

The use of prey refuges regarding Lotka-Volterra model was primarily explained by Maynard Smith's research in [33]. According to his conjectures, fixed or proportional number of prey could survive from predators by seeking refuges.

Andrew Sih also confirmed a more general case in [40] that included Maynard Smith's conclusion: if relatively large numbers of predators find out the prey's refuges or even break through the protection shielded by refuges (e.g., attacking the group living herbivores), then there must be a chaos in prey population. Constant prey refuges are special cases of Andrew Sih's refuge models.

In this paper, we mainly discuss the case of constant refuge. After incorporating

constant prey refuge denoted by p , the Lotka-Volterra model becomes:

$$\begin{cases} \dot{x} = rx - c(x - p)y, \\ \dot{y} = e(x - p)y - dy, \end{cases} \quad (3.3.1)$$

where $(x - p)$ means some of prey protected in refuges are excluded from being killed by predation. In addition, r , c , e and d are all positive parameters and have the same biological meanings as explained in Section 3.1.

Remark 3.3.1. According to the Andrew Sih's general case in [40], total number of prey killed by predators is a function of proportion of prey in refuges.

$$P_k = P_T(a'S + a(1 - S)) = P_T(a - Sx)$$

where P_k is the total number killed by predators after excluding the survived numbers due to refuge, P_T is the total number of prey killed without refuge, S is the proportion of prey in the safe state.

The model also introduced the attack rate of inside refuge (a') is lower than the attack rate of outside refuge (a). Then, $x = a - a'$ means the per predator advantage of being in a refuge. If the refuge is untouchable for predators, then $a' = 0$ and $x = a$. In addition, if there are no refuges (i.e, $S = 0$), the attack rate is a , but as prey uses more refuges, the attack rate decreases. (The increase in S would result in a decrease of $(a - Sx)$.)

The following theorems and proofs were initially provided by Maynard Smith in his research [33]. Due to lack of detailed proof process for Theorem 3.3.3 in the original paper, we will provide more comprehensive explanation for the proof by using Lemma 3.3.1.

Theorem 3.3.1. *Assume that r , c , e , d and p are all positive, then the positive equilibrium points of system (3.3.1) are $(0, 0)$ and $(\frac{d}{e} + p, \frac{r(d + ep)}{cd})$.*

Proof. By letting equations of (3.3.1) equal to 0, we have:

$$\begin{cases} \dot{x} = rx - c(x - p)y = 0, \\ \dot{y} = e(x - p)y - dy = 0. \end{cases} \quad (3.3.2)$$

If $y = 0$, then the second equation is true for any values of x . And the first equation becomes $rx = 0$, which gives $x = 0$.

If $y \neq 0$, then by the first equation, we have $e(x - p) = d$. And solving for x , we have $x = \frac{d}{e} + p$. Substituting $x = \frac{d}{e} + p$ into the first equation, we obtain $y = \frac{r(d + ep)}{cd}$. $\square$

Theorem 3.3.2. *The origin $(0, 0)$ is a saddle point for system (3.3.1).*

Proof. By Definition 2.2.2 and Lemma 2.3.1, stability of equilibrium points can be studied by analyzing jacobian matrix. By (2.1.2), we set up jacobian matrix of (3.3.1):

$$A(x, y) = \begin{pmatrix} r - cy & -c(x - p) \\ ey & e(x - p) - d \end{pmatrix}. \quad (3.3.3)$$

The jacobian matrix at origin $(0, 0)$ is

$$A(0, 0) = \begin{pmatrix} r & cp \\ 0 & -(ep + d) \end{pmatrix} \quad (3.3.4)$$

with $|A(0, 0)| = -r(ep + d)$ and $\text{tr}(A(0, 0)) = r - (ep + d)$. By referring to Lemma 2.3.1, it implies that origin is a saddle point, since $|A(0, 0)| = -r(ep + d) < 0$. $\square$

Remark 3.3.2. Compared with the stability analysis of the classical Lotka-Volterra model on equilibrium point at origin (see Theorem 3.1.2), we see that both results indicate the origin $(0, 0)$ is a saddle point. Despite the constant prey refuge, the predator-prey system still avoids extinction (i.e., solution behavior of (3.3.1) around origin spreads outward and do not reach the origin). On the other hand, the situation

of positive interior equilibrium point differs significantly between the classical Lotka-Volterra model and constant prey refuge model.

For the positive interior equilibrium point $(\frac{d}{e} + p, \frac{r(d+ep)}{cd})$ of (3.3.1), we deploy similar method to analyze the stability. We first need to find the jacobian matrix at the equilibrium point as well as its trace and determinant.

Jacobian matrix (3.3.3) at point $(\frac{d}{e} + p, \frac{r(d+ep)}{cd})$ is

$$A(\frac{d}{e} + p, \frac{r(d+ep)}{cd}) = \begin{pmatrix} -\frac{rep}{d} & \frac{-cd}{e} \\ \frac{er(d+ep)}{cd} & 0 \end{pmatrix}. \quad (3.3.5)$$

Then, according to Definition 2.1.3, we have

$$|A(\frac{d}{e} + p, \frac{r(d+ep)}{cd})| = r(d+ep)$$

and

$$\text{tr} (A(\frac{d}{e} + p, \frac{r(d+ep)}{cd})) = -\frac{rep}{d}.$$

Notation: Let

$$\sigma(p) = \text{tr}(A(\frac{d}{e} + p, \frac{r(d+ep)}{cd}))^2 - 4|A(\frac{d}{e} + p, \frac{r(d+ep)}{cd})|, \quad$$

$$p_1 = \frac{2d\sqrt{d(d+r)} + 2d^2}{re} \quad \text{and} \quad p_2 = \frac{2d\sqrt{d(d+r)} - 2d^2}{re}.$$

Lemma 3.3.1. *Assume that r, e, c, d are all positive, then the following assertions hold:*

- (i) *If $0 < p < p_1$, then $\sigma(p) < 0$.*
- (ii) *If $p \geq p_1$, then $\sigma(p) \geq 0$.*

Proof. By the jacobian matrix (3.3.5), we have:

$$\begin{aligned}
\sigma(p) &= \text{tr}(A(\frac{d}{e} + p, \frac{r(d+ep)}{cd}))^2 - 4|A(\frac{d}{e} + p, \frac{r(d+ep)}{cd})| \\
&= \left(-\frac{rep}{d}\right)^2 - 4r(d+ep) \\
&= \frac{(rep)^2}{d^2} - 4rep - 4rd \\
&= \frac{(rep)^2}{d^2} - 4rep + 4d^2 - 4d^2 - 4rd \\
&= \left(\frac{rep}{d} - 2d\right)^2 - 4d(d+r) \\
&= \left(\frac{rep}{d} - 2d + 2\sqrt{d(d+r)}\right)\left(\frac{rep}{d} - 2d - 2\sqrt{d(d+r)}\right) \\
&= \frac{(re)^2}{d^2} \left(p + \frac{d(2\sqrt{d(d+r)} - 2d)}{re}\right) \left(p - \frac{d(2\sqrt{d(d+r)} + 2d)}{re}\right) \\
&= \frac{(re)^2}{d^2} (p + p_2)(p - p_1)
\end{aligned}$$

From

$$p_2 = \frac{2d\sqrt{d(d+r)} - 2d^2}{re} = \frac{d(2\sqrt{d(d+r)} - 2d)}{re},$$

we see that $2\sqrt{d(d+r)} - 2d > 0$ with $r, d > 0$, which implies p_2 is always positive.

(i) If $0 < p < p_1$, then $\frac{rep}{d} - 2d < 2\sqrt{d(d+r)}$ and

$$\begin{aligned}
\frac{rep}{d} - 2d - 2\sqrt{d(d+r)} &= \frac{re}{d} \left(p - \frac{d(2\sqrt{d(d+r)} + 2d)}{re}\right) \\
&= \frac{re}{d} (p - p_1) < 0.
\end{aligned}$$

Moreover, from above explanation, we have $p_2 > 0$. Thus,

$$\sigma(p) = \frac{(re)^2}{d^2} (p + p_2)(p - p_1) < 0.$$

(ii) If $p \geq p_1$, then $p - p_1 \geq 0$ and $p - \frac{d(2\sqrt{d(d+r)} + 2d)}{re} \geq 0$. Further, $p_2 > 0$, since $2\sqrt{d(d+r)} > 2d$. Thus, we can conclude that,

$$\sigma(p) = \frac{(re)^2}{d^2}(p + p_2)(p - p_1) \geq 0.$$

□

Lemma 3.3.1 shows the results of $\sigma(p)$ based on the different conditions of p . Finally, we continue to the stability analysis of the equilibrium point $(\frac{d}{e} + p, \frac{r(d + ep)}{cd})$ by applying Lemma 3.3.1.

Theorem 3.3.3. *Assume that r, e, c, d are all positive, then the following assertions hold:*

- (i) *If $0 < p < p_1$, then $(\frac{d}{e} + p, \frac{r(d + ep)}{cd})$ is a stable focus.*
- (ii) *If $p \geq p_1$, then $(\frac{d}{e} + p, \frac{r(d + ep)}{cd})$ is a stable node.*

Proof. Since all parameters are positive, by the jacobian matrix (3.3.5), we have:

$$|A(\frac{d}{e} + p, \frac{r(d + ep)}{cd})| = r(d + ep) > 0,$$

and

$$\text{tr}(A(\frac{d}{e} + p, \frac{r(d + ep)}{cd})) = -\frac{rep}{d} < 0.$$

Next, we need to discuss the result of

$$\sigma(p) = \text{tr}(A(\frac{d}{e} + p, \frac{r(d + ep)}{cd}))^2 - 4|A(\frac{d}{e} + p, \frac{r(d + ep)}{cd})|.$$

By Lemma 3.3.1, $\sigma(p) < 0$, as $0 < p < p_1$; $\sigma(p) \geq 0$, as $p \geq p_1$. Then the results of (i) and (ii) hold by Lemma 2.3.1. □

Remark 3.3.3. If $p = 0$, then (3.3.1) becomes the previous classical Lotka-Volterra model. That is the classical Lotka-Volterra model is a special case for the system (3.3.1) with $p = 0$. By the jacobian matrix (3.3.5) at $(\frac{d}{e} + p, \frac{r(d + ep)}{cd})$, we have $\text{tr}(A(\frac{d}{e} + p, \frac{r(d + ep)}{cd})) = 0$ and $A(\frac{d}{e} + p, \frac{r(d + ep)}{cd}) = dr > 0$, which are exactly

showed same in the Lotka-Volterra model. Thus, $(\frac{d}{e} + p, \frac{r(d + ep)}{cd})$ is a center when $p = 0$ by Lemma 2.3.1. Compared with Theorem 3.3.3, the predator-prey systems are more stabilized with prey refuge. Solutions in prey refuge cases develop towards the stable node or focus, while the solutions are just circling around the equilibrium point if there is no refuge for prey. The former result means that the predator-prey system avoids extinction (no deviation from the equilibrium point), whereas the latter result tells us that a large proportional decrease in prey population is more likely to bring the predator-prey system an extinction rather than develop to equilibrium.

3.4 Functional Responses

Holling's another greatest contribution to predator-prey models was to have introduced the classification of functional responses (see C.S. Holling's research published in [16, 17]) to describe the relationship between the consumption of predators and the density of prey. He categorized the functional responses into three different types: Type I, Type II and Type III.

Figure 3.2: Type I Functional Response

Type I functional response is applied to the cases where the ratio between the

number of prey consumed is proportional to the density of prey (Figure 3.2 (Source:[12])).

It assumes that predators would hunt for foods with a constant increasing rate as the number of prey grows, where the handling time for predators to process prey and time for absorbing the energy after consumption are ignored. But the hunting would not last infinitely, since there is maximum capacity set for prey, which would also cause the prey consumption to reach a maximum value. The models mentioned in the previous sections are all about the examples of type I functional response. The total number of prey killed by predators is either cxy or $c(x - p)$.

The following model was derived from Ma's paper[29], which combined all the factors we mentioned in previous sections,

$$\begin{cases} \dot{x} = rx(1 - \frac{x}{k}) - c(x - p)y, \\ \dot{y} = e(x - p)y - dy, \end{cases} \quad (3.4.1)$$

where r is the natural growth rate of the prey, c is the per capita rate of predation of the predator, e is a conversion rate of eaten prey into new predator abundance, d is the per capita death rate of the predator, p is the constant prey refuge and k is capacity for prey. Intuitively, all the parameters should be positive in order to follow the biological meanings. (For more detailed description of parameters, see the models introduced in Section 3.1-3.3).

All the results of type I functional response may be concluded by investigating this model. In chapter 4, we will use transformation method to reduce the number of parameters of the model and then study the equilibrium points as well as their stability analysis.

In more realistic situations, predators are not hunting for foods all the time if they have enough intake of energy from prey consumption. As May and McLea they described in their book [32], if predators reached a level of satiation for food demands, they needed to process the hunted foods for a while. Holling's disk equation incorporates this time period into Lotka-Vorterra models and replaces the part of prey attacked

by predators with the following, which is called type II functional response:

$$f(x) = \frac{aT(x - p)}{1 + aT'(x - p)}.$$

Precisely, a is the attack rate of predation; T indicates the total periods of time for predators including the handling time (such as capture and consumption) and predators' searching time for prey until next cycle. We specifically denote by T' the handling time. Then, $\frac{aT(x - p)}{1 + aT'(x - p)}$ is the new term showing the total number of prey reduction due to one unit of predator. Clearly, it would cost the majority of time for predators to hunt for foods when there is a shortage of prey, while their time for handling food would increase when the prey is abundant. If the density of prey x is very large, then $f(x)$ reaches a steady level, which means the predators stopped hunting more than saturation and the total decrease in prey is stabilized. (See Figure 3.3 (Source:[12]))

Figure 3.3: Type II Functional Response

Equilibrium points as well as their stability analysis of Lotka-Volterra model with type II functional response will be studied by using transformation in Chapter 5. Based on the expression of type II functional response explained above, the modified

Lotka-Volterra model is:

$$\begin{cases} \dot{x} = rx(1 - \frac{x}{k}) - \frac{c(x-p)y}{1+m(x-p)}, \\ \dot{y} = \frac{e(x-p)y}{1+m(x-p)} - dy, \end{cases} \quad c, m > 0, \quad (3.4.2)$$

where m is the combination of the attack rate a of predation and the handling time T' . Previously, c denotes the per capita rate of predation of the predator. But in type II functional response, c has a more precise meaning as a combination of the attack rate of predation a and the total periods of time T (the time of predators from handling to searching for next prey). Other parameters are consistent with the model (3.4.1) discussed in type I functional response.

Remark 3.4.1. As an aside, the following is how $f(x)$ was derived from Holling's work[17]. Firstly, we set total time $T = T_s + T_h$, where T_s is the time cost in searching and T_h is the time spent on handling. Let F be the total number of prey captured by one predator, and the handling time is considered proportional to the total number of prey hunted. Then, the relationship between F and T_h is $T' = \frac{T_h}{F}$.

Now T' has the meaning of the time for handling each prey. We already denoted by $a(x - R)$ that prey density $(x - R)$ is attacked by predators with the attack rate a . The attack on prey involves the time T_s , therefore F also can be obtained as following in terms of the searching time:

$$F = a(x - R)T_s$$

Substituting $T_s = \frac{F}{a(x - R)}$ and $T_h = FT'$ into $T = T_s + T_h$, we obtain

$$T = \frac{F}{a(x - R)} + FT'.$$

By isolating F ,

$$F = \frac{aT(x - R)}{1 + aT'(x - R)},$$

which is exactly the function of $f(x)$ above.

Type III functional response is taken into account when predators have different response to prey as the density of prey increases. Type III functional response has the form of as following:

$$\frac{cx^2y}{mx^2 + 1}, c, m > 0.$$

In such cases, predators' activities are closely dependent on how much prey they can hunt for. If the population density is low among the prey, then predators are likely to have weak response to prey's existence. As the prey's density increases, predators' start to hunt actively but will reach satiation again just like type II functional response illustrated. (Figure 3.4 (Source:[12]))

Figure 3.4: Type III Functional Response

Hassell in his book[14] stated that Type I and Type II are more typical of invertebrate predators, while Type III is more typical of vertebrates.

Chapter 4

Lotka-Volterra Predator-Prey Model with Type I Functional Response

In this chapter, we will investigate the Lotka-Volterra model incorporating the factors of capacity and refuge. Recent research papers such as [6, 7, 29] have studied similar models and concluded some useful and helpful theorems for future studies. However, we will consider another method that is different from traditional one to keep studying the model by applying transformation theory. In this way, the number of parameters would be reduced and some results of the stability analysis for nonlinear cases also become more accurate.

4.1 Positive Equilibria

In Section 3.1-3.3, we studied the traditional Lotka-Volterra predator-prey systems by consecutively incorporating capacity k and a constant number of prey using refuges p . Ma in his paper[29] proposed a combined model incorporating both factors of capacity and refuge with type I functional response as following:

$$\begin{cases} \dot{x} = rx(1 - \frac{x}{k}) - c(x - p)y, \\ \dot{y} = -dy + e(x - p)y, \end{cases} \quad (4.1.1)$$

where $x(t)$ and $y(t)$ denotes the density of prey and predator populations at time t , respectively; r, k, c, p, e, d are all positive constants. Referring to Section 3.1, 3.2 and 3.3, r is the natural growth rate of the prey, k is capacity for prey's growth, c is the per capita rate of predation of the predator, e is a conversion rate of eaten prey into new predator abundance, d is the per capita death rate of the predator.

Using the transformation theory we discussed in Section 2.4 may simplify the system (4.1.1) by reducing the number of parameters.

Theorem 4.1.1. *Let $\bar{t} = rt$, $u(\bar{t}) = \frac{x(t)}{k}$, $v(\bar{t}) = \frac{cy(t)}{r}$. Then the following system is equivalent to (4.1.1) after applying transformation:*

$$\begin{cases} \dot{u} = u(1 - u) - (u - \alpha)v := f(u, v), \\ \dot{v} = \beta(u - \alpha)v - \gamma v := g(u, v), \end{cases} \quad (4.1.2)$$

where $\alpha = \frac{p}{k}$, $\beta = \frac{ek}{r}$, and $\gamma = \frac{d}{r}$ have same biological meanings as p, e and d respectively.

Proof. Firstly, from $\bar{t} = rt$, $u(\bar{t}) = \frac{x(t)}{k}$, $v(\bar{t}) = \frac{cy(t)}{r}$, we have the following new expressions for $x(t), y(t)$: $x(t) = ku(\bar{t})$; $y(t) = \frac{rv(\bar{t})}{c}$.

Then, taking derivatives of above two equations:

$$\begin{cases} \frac{dx(t)}{dt} = \frac{d[ku(\bar{t})]}{d\bar{t}} \frac{d\bar{t}}{dt} = rk \frac{du(\bar{t})}{d\bar{t}}, \\ \frac{dy(t)}{dt} = \frac{d(\frac{rv(\bar{t})}{c})}{d\bar{t}} \frac{d\bar{t}}{dt} = \frac{r^2}{c} \frac{dv(\bar{t})}{d\bar{t}}. \end{cases} \quad (4.1.3)$$

Replacing $\frac{dx(t)}{dt}$ and $\frac{dy(t)}{dt}$ by $rk \frac{du(\bar{t})}{d\bar{t}}$ and $\frac{r^2}{c} \frac{dv(\bar{t})}{d\bar{t}}$ respectively for the system (4.1.2), we can obtain new differential equations in terms of time $\bar{t}$:

$$\begin{aligned} \frac{dx(t)}{dt} &= rk \frac{du(\bar{t})}{d\bar{t}} = rx(t) \left(1 - \frac{x(t)}{k}\right) - c(x(t) - p)y(t) \\ \frac{du(\bar{t})}{d\bar{t}} &= \frac{x(t)}{k} \left(1 - \frac{x(t)}{k}\right) - \frac{c}{r} \left(\frac{x(t)}{k} - \frac{p}{k}\right) y(t) \\ &= u(\bar{t}) (1 - u(\bar{t})) - v(\bar{t}) (u(\bar{t}) - \alpha), \end{aligned}$$

$$\begin{aligned} \frac{dy(t)}{dt} &= \frac{r^2}{c} \frac{dv(\bar{t})}{d\bar{t}} = -dy(t) + e(x(t) - p)y(t) \\ \frac{dv(\bar{t})}{d\bar{t}} &= \frac{-dcy(t)}{r^2} + \frac{ce}{r^2} (x(t) - p)y(t) \\ &= \frac{-d}{r} \frac{cy(t)}{r} + \frac{ek}{r} \left(\frac{x(t)}{k} - \frac{p}{k}\right) \frac{cy(t)}{r} \\ &= -\gamma v(\bar{t}) + \beta (u(\bar{t}) - \alpha) v(\bar{t}). \end{aligned}$$

The system (4.1.2) is now changed into the following equivalent system:

$$\begin{cases} \dot{u} = u(1 - u) - (u - \alpha)v := f(u, v), \\ \dot{v} = \beta(u - \alpha)v - \gamma v := g(u, v), \end{cases} \quad (4.1.4)$$

where $\alpha = \frac{p}{k}$, $\beta = \frac{ek}{r}$, $\gamma = \frac{d}{r}$. Parameters k and r are normalized to 1 as proportional relationship with p , e and d , respectively. Thus, α , β and γ have same biological

meanings as p , e and d . □

By Definition 2.1.2, it is easy to verify that (u, v) is an equilibrium point of system (4.1.2) if and only if (u, v) satisfies,

$$\begin{cases} u(1 - u) = 0, \\ v = 0 \end{cases} \quad (4.1.5)$$

or

$$\begin{cases} u(1 - u) - (u - \alpha)v = 0, \\ v \neq 0 \quad \text{and} \quad u = \frac{\gamma}{\beta} + \alpha. \end{cases} \quad (4.1.6)$$

Lemma 4.1.1. *Assume that $\alpha \geq 0$, $0 < \beta < \gamma$. If $v=0$ for (4.1.2), then (u, v) of (4.1.5) has two solutions: $(0, 0)$ and $(1, 0)$.*

Proof. If (u, v) is a solution of system (4.1.5), then $v = 0$ is fixed, and by solving $u(1 - u) = 0$, we have $u = 1$, or $u = 0$. □

Lemma 4.1.2. *If $\beta > 0$, $\gamma > 0$, then (4.1.6) has a unique solution (u^*, v^*) , where*

$$u^* = \frac{\gamma + \alpha\beta}{\beta} \quad \text{and} \quad v^* = \frac{(\gamma + \alpha\beta)(\beta - \gamma - \alpha\beta)}{\beta\gamma}.$$

Proof. If (u, v) is a solution of system (4.1.6) then $v \neq 0$ and from $\beta(u - \alpha)v - \gamma v = 0$, u satisfies $u = u^* = \frac{\gamma}{\beta} + \alpha$.

Substituting $u = u^*$ into the first equation of (4.1.6), we have

$$\left(\frac{\gamma}{\beta}\right)v = \left(\frac{\gamma}{\beta} + \alpha\right)\left(1 - \frac{\gamma}{\beta} - \alpha\right).$$

Solving for v ,

$$v = v^* = \frac{(\gamma + \alpha\beta)(\beta - \gamma - \alpha\beta)}{\beta\gamma}.$$

□

Notation: Let

$$u^* = \frac{\gamma + \alpha\beta}{\beta} \quad \text{and} \quad v^* = \frac{(\gamma + \alpha\beta)(\beta - \gamma - \alpha\beta)}{\beta\gamma}.$$

Lemma 4.1.3. *If $\beta > 0$, $\gamma > 0$, then the following assertions hold:*

- (i) *If $\alpha \geq 0$, $0 < \beta < \gamma$, then $u^* > 0$, $v^* < 0$.*
- (ii) *If $\beta > \gamma > 0$, $\alpha > 1 - \frac{\gamma}{\beta}$, then $u^* > 0$, $v^* < 0$.*
- (iii) *If $0 < \gamma \leq \beta$, $\alpha = 1 - \frac{\gamma}{\beta} \geq 0$, then $u^* = 1$, $v^* = 0$.*
- (iv) *If $\beta > \gamma > 0$, $0 \leq \alpha < 1 - \frac{\gamma}{\beta}$, then $u^* > 0$, $v^* > 0$.*

Proof. (i) If $\alpha \geq 0$, $0 < \beta < \gamma$, then $-\alpha\beta \leq 0$, $\beta - \gamma < 0$, it implies that $\beta - \gamma - \alpha\beta < 0$. Thus, $\frac{\gamma + \alpha\beta}{\beta} > 0$ and $\frac{(\gamma + \alpha\beta)(\beta - \gamma - \alpha\beta)}{\beta\gamma} < 0$, which concludes that $u^* > 0$ and $v^* < 0$.

(ii) If $\beta > \gamma > 0$, $\alpha > 1 - \frac{\gamma}{\beta}$, it implies that $\alpha\beta > \beta - \gamma$, $\beta - \gamma - \alpha\beta < 0$. Since $\beta > \gamma > 0$, $\alpha > 1 - \frac{\gamma}{\beta} > 0$, we have $\frac{\gamma + \alpha\beta}{\beta} > 0$ and $\frac{(\gamma + \alpha\beta)(\beta - \gamma - \alpha\beta)}{\beta\gamma} < 0$, which means $u^* > 0$, $v^* < 0$.

(iii) If $0 < \gamma \leq \beta$, $\alpha = 1 - \frac{\gamma}{\beta} \geq 0$, then $\alpha - 1 + \frac{\gamma}{\beta} = 0$. By Multiplying $-\beta$ both sides, we have $\beta - \gamma - \alpha\beta = 0$ and $\beta = \gamma + \alpha\beta$. Then, $\frac{(\gamma + \alpha\beta)(\beta - \gamma - \alpha\beta)}{\beta\gamma} = 0$, $\frac{\gamma + \alpha\beta}{\beta} = 1$. Therefore, $u^* = 1$, $v^* = 0$.

(iv) If $\beta > \gamma > 0$, $0 < \alpha < 1 - \frac{\gamma}{\beta}$, it implies that $1 - \frac{\gamma}{\beta} - \alpha > 0$. By multiplying β both sides, we have $\beta - \gamma - \alpha\beta > 0$. Since $\beta > \gamma > 0$, $0 < \alpha$, we have $\frac{\gamma + \alpha\beta}{\beta} > 0$ and $\frac{(\gamma + \alpha\beta)(\beta - \gamma - \alpha\beta)}{\beta\gamma} > 0$. Therefore, $u^* > 0$, $v^* > 0$. □

Theorem 4.1.2. (i) *If $\alpha \geq 0$, $0 < \beta < \gamma$, or if $\beta \geq \gamma > 0$, $\alpha \geq 1 - \frac{\gamma}{\beta}$, then the system (4.1.2) only has two positive equilibria: $(0, 0)$ and $(1, 0)$.*

(ii) *If $\beta > \gamma > 0$, $0 \leq \alpha < 1 - \frac{\gamma}{\beta}$, then the system (4.1.2) has three positive*

equilibria: $(0, 0)$, $(1, 0)$ and (u^*, v^*) , where

$$u^* = \frac{\gamma + \alpha\beta}{\beta} \quad \text{and} \quad v^* = \frac{(\gamma + \alpha\beta)(\beta - \gamma - \alpha\beta)}{\beta\gamma}$$

are positive interior.

Proof. (i) By Lemma 4.1.1, for any $\beta > 0, \gamma > 0, \alpha \geq 0$ we have two equilibrium points $u = 0, v = 0$ and $u = 0, v = 1$. If $\alpha \geq 0, 0 < \beta < \gamma$, or if $\beta > \gamma > 0, \alpha < 1 - \frac{\gamma}{\beta}$, then by Lemma 4.1.3 (i) and (ii), we have $u^* > 0, v^* < 0$, which implies that u^*, v^* cannot be equilibrium points under the conditions. Further, if $0 < \gamma \leq \beta, \alpha = 1 - \frac{\gamma}{\beta} \geq 0$, then $u^* = 1, v^* = 0$ is a positive equilibrium.

(ii) When $v \neq 0$, the system (4.1.2) can be converted into the system (4.1.6).

By Lemma (4.1.2), if $\beta > 0, \gamma > 0$, we have concluded that (4.1.6) has a unique solution (u^*, v^*) , where

$$u^* = \frac{\gamma + \alpha\beta}{\beta} \quad \text{and} \quad v^* = \frac{(\gamma + \alpha\beta)(\beta - \gamma - \alpha\beta)}{\beta\gamma}.$$

According to Lemma 4.1.3 (iv), we see that if $\beta > \gamma > 0, 0 \leq \alpha < 1 - \frac{\gamma}{\beta}$, then the values of u^* and v^* can be always positively taken. Therefore, under assumption of $\beta > \gamma > 0, 0 < \alpha < 1 - \frac{\gamma}{\beta}$, the system (4.1.2) has a positive interior equilibrium, which is (u^*, v^*) . $\square$

The equilibrium (u^*, v^*) of (4.1.2) was obtained in [29], also see [6, Theorem B]. The number of positive equilibria of (4.1.2) was not discussed in [6, 29].

4.2 Stability and Phase Portraits

In this section, we study the stability and phase portraits of each positive equilibrium of (4.1.2). We have learned from Section 2.2 and 2.3 that the types of equilibria (solution behaviour around the equilibrium points) are determined by $|A(u, v)|$ and

$\text{tr}(A(u, v))$ of the jacobian matrix evaluated at each equilibrium (see Definition 2.2.2 and Lemma 2.3.1). According to the Definition 2.1.3, let $A(u, v)$ be the jacobian matrix of f and g defined in (4.1.2). By (4.1.2) and (2.1.2), we have

$$A(u, v) = \begin{pmatrix} 1 - 2u - v & -(u - \alpha) \\ \beta v & \beta u - (\beta\alpha + \gamma) \end{pmatrix}.$$

Then, by Definition 2.1.3 we obtain $|A(u, v)|$ and $\text{tr}(A(u, v))$ as below:

$$|A(u, v)| = (1 - 2u - v)[\beta u - (\beta\alpha + \gamma)] + \beta v(u - \alpha), \quad (4.2.1)$$

$$\text{tr}(A(u, v)) = 1 - 2u - v + \beta u - (\beta\alpha + \gamma). \quad (4.2.2)$$

Lemma 4.2.1. (i) If $\alpha \geq 0$, $0 < \beta < \gamma$, then $|A(1, 0)| > 0$.

(ii) If $\beta > \gamma > 0$, $\alpha > 1 - \frac{\gamma}{\beta}$, then $|A(1, 0)| > 0$.

(iii) If $\beta > \gamma > 0$, $0 \leq \alpha < 1 - \frac{\gamma}{\beta}$, then $|A(1, 0)| < 0$.

(iv) If $0 < \gamma \leq \beta$, $\alpha = 1 - \frac{\gamma}{\beta} \geq 0$, then $|A(1, 0)| = 0$.

Proof. If $u = 1, v = 0$, then by (4.2.1) we have

$$A(1, 0) = \begin{pmatrix} -1 & \alpha - 1 \\ 0 & \beta - \gamma - \alpha\beta \end{pmatrix} \quad (4.2.3)$$

and $|A(1, 0)| = \alpha\beta + \gamma - \beta$.

(i) Since $\alpha \geq 0$, $0 < \beta < \gamma$, $|A(1, 0)| = \alpha\beta + \gamma - \beta > 0$ and then the result follows.

(ii) Since $\beta > \gamma > 0$, $\alpha > 1 - \frac{\gamma}{\beta}$, we have $\alpha\beta > \beta - \gamma$, then $\alpha\beta + \gamma - \beta > 0$, which implies $|A(1, 0)| = \alpha\beta + \gamma - \beta > 0$.

(iii) With conditions of $\beta > \gamma > 0$, $0 \leq \alpha < 1 - \frac{\gamma}{\beta}$, we have $\alpha\beta < \beta - \gamma$, then $\alpha\beta + \gamma - \beta < 0$. Therefore $|A(1, 0)| = \alpha\beta + \gamma - \beta < 0$.

(iv) If $0 < \gamma \leq \beta$, $\alpha = 1 - \frac{\gamma}{\beta} \geq 0$, we have $\alpha\beta = \beta - \gamma$, which implies $\alpha\beta + \gamma - \beta = 0$, therefore $|A(1, 0)| = \alpha\beta + \gamma - \beta = 0$. $\square$

Lemma 4.2.2. (1) If $\beta > \gamma + 1$ and $1 - \frac{\gamma + 1}{\beta} > \alpha \geq 0$, then $\text{tr}(A(1, 0)) > 0$.

(2) If $\beta < \gamma + 1$ and $\alpha \geq 0$, then $\text{tr}(A(1, 0)) < 0$.

(3) If $\beta \geq \gamma + 1$ and $\alpha > 1 - \frac{\gamma + 1}{\beta}$, then $\text{tr}(A(1, 0)) < 0$.

(4) If $\beta > \gamma + 1$ and $\alpha = 1 - \frac{\gamma + 1}{\beta}$, then $\text{tr}(A(1, 0)) = 0$.

Proof. If $u = 1, v = 0$, then by (4.2.2) we have

$$\text{tr}(A(u, v)) = \text{tr}(A(1, 0)) = \beta - \gamma - \alpha\beta - 1.$$

(1) If $\beta > \gamma + 1$ and $1 - \frac{\gamma + 1}{\beta} > \alpha \geq 0$, we have equivalently $\beta - \gamma - 1 - \alpha\beta > 0$.

Therefore $\text{tr}(A(1, 0)) > 0$.

(2) With conditions of $\beta < \gamma + 1$ and $\alpha \geq 0$, we have $\beta - \gamma - 1 < 0$. Since $\alpha\beta > 0$, also $\beta - \gamma - 1 - \alpha\beta < 0$. Therefore $\text{tr}(A(1, 0)) < 0$.

(3) Assuming $\beta \geq \gamma + 1$ and $\alpha > 1 - \frac{\gamma + 1}{\beta}$, we have $\alpha\beta > \beta - \gamma - 1$. It implies that $\beta - \gamma - 1 - \alpha\beta < 0$. Therefore $\text{tr}(A(1, 0)) < 0$.

(4) Assuming $\beta > \gamma + 1$ and $\alpha = 1 - \frac{\gamma + 1}{\beta}$, then we have $\alpha\beta = \beta - \gamma - 1$. Equivalently, $\beta - \gamma - 1 - \alpha\beta = 0$. Therefore $\text{tr}(A(1, 0)) = 0$.

□

Lemma 4.2.3. Assume that $\alpha \geq 0, \beta > 0, \gamma > 0$, then $(\text{tr}(A(1, 0)))^2 - 4|A(1, 0)| \geq 0$.

Proof. By equations (4.2.1) and (4.2.2), we have

$$\begin{aligned} [\text{tr}(A(1, 0))]^2 - 4|A(1, 0)| &= (\beta - \gamma - \alpha\beta - 1)^2 - 4(\alpha\beta + \gamma - \beta) \\ &= (-|A(1, 0)| - 1)^2 - 4|A(1, 0)| \\ &= |A(1, 0)|^2 + 2|A(1, 0)| + 1 - 4|A(1, 0)| \\ &= (|A(1, 0)| - 1)^2 \\ &= (\alpha\beta + \gamma - \beta - 1)^2 \end{aligned}$$

Since $(\alpha\beta + \gamma - \beta - 1)^2 \geq 0$, therefore $(\text{tr}(A(1, 0)))^2 - 4|A(1, 0)| \geq 0$.

□

Theorem 4.2.1. Assume that $\beta > 0, \gamma > 0$, then

- (1) $(0, 0)$ is a saddle point of system (4.1.2).
- (2) $(1, 0)$ is a saddle point of (4.1.2), if $\beta > \gamma$ and $1 - \frac{\gamma}{\beta} > \alpha \geq 0$.
- (3) $(1, 0)$ is a saddle-node of (4.1.2), if $0 < \gamma \leq \beta$, $\alpha = 1 - \frac{\gamma}{\beta} \geq 0$.
- (4) $(1, 0)$ is a stable node of (4.1.2), if
  - (i) $\alpha \geq 0$, $0 < \beta < \gamma$, or
  - (ii) $\beta \geq \gamma + 1$ and $\alpha > 1 - \frac{\gamma}{\beta}$.

Proof. (1) If $\beta > 0, \gamma > 0$, from (4.2.1), and (4.2.2) we have that $|A(0, 0)| = -\alpha\beta - \gamma < 0$ with any positive value of α . According to Lemma 2.3.1(i), we can conclude that $(0, 0)$ is a saddle point.

(2) If $\beta > \gamma$ and $1 - \frac{\gamma}{\beta} > \alpha \geq 0$, then by Lemma 4.2.1 (ii), we have $|A(1, 0)| < 0$. Therefore, $(1, 0)$ is a saddle point of (4.1.2) by Lemma 2.3.1(i).

(3) If $0 < \gamma \leq \beta$, $\alpha = 1 - \frac{\gamma}{\beta} \geq 0$, then $|A(u, v)| = |A(1, 0)| = \beta - \gamma - \alpha\beta = 0$ and $\text{tr}(A(1, 0)) = -(\beta - \gamma - \alpha\beta) - 1 = -1 \neq 0$. Moreover, we apply the transformation theory of Section 2.4 to determine the solution behaviour.

By Definition 2.4.1 and Lemma 2.4.1, we suppose $p := u - 1$ and $q := v$, then $\dot{p} = \dot{u}$ and $\dot{q} = \dot{v}$, since they are both in linear connections. Thus,

$$\begin{cases} \dot{p} = -p(p+1) - (p+1-\alpha)q = -p^2 - p - pq - (1-\alpha)q, \\ \dot{q} = \beta(p+1-\alpha)q - \gamma q = \beta pq. \end{cases} \quad (4.2.4)$$

Next, suppose $p_1 := p + \frac{1-\alpha}{2}q$, $q_1 := q$ and then substitute them into (4.2.4):

$$\begin{aligned} \dot{p}_1 &= \dot{p} + \frac{1-\alpha}{2}\dot{q} \\ &= -(p_1 - \frac{1-\alpha}{2}q_1)^2 - (p_1 - \frac{1-\alpha}{2}q_1) - (p_1 - \frac{1-\alpha}{2}q_1)q_1 - (1-\alpha)q_1 + \frac{1-\alpha}{2}q_1 \\ &= -(p_1 - \frac{1-\alpha}{2}q_1)^2 - p_1 - (p_1 - \frac{1-\alpha}{2}q_1)q_1, \end{aligned}$$

and $\dot{q}_1 = \beta(p_1 - \frac{1-\alpha}{2}q_1)q_1$.

Again, let $p_2 := q_1$ and $q_2 := p_1$. Then we have $\dot{p}_2 = \beta(q_2 - \frac{1-\alpha}{2}p_2)p_2$ and $\dot{q}_2 = -q_2 - (q_2 - \frac{1-\alpha}{2}p_2)^2 - (q_2 - \frac{1-\alpha}{2}p_2)p_2$.

It implies the following system, which is equivalent to (4.1.2):

$$\begin{cases} \dot{p}_2 = \beta q_2 p_2 - \beta \frac{1-\alpha}{2} p_2^2, \\ \dot{q}_2 = -q_2 - (q_2 - \frac{1-\alpha}{2} p_2)^2 - (q_2 - \frac{1-\alpha}{2} p_2) p_2. \end{cases} \quad (4.2.5)$$

Since $\varrho = -1 \neq 0$ and $a_{20} = \frac{-\beta(1-\alpha)}{2} \neq 0$, $(1, 0)$ is a saddle-node of (4.1.2) by Lemma 2.4.1.

(4) (i) By Lemma 4.2.1 (i), if $\alpha \geq 0$, $0 < \beta < \gamma$, then $|A(1, 0)| > 0$. Also by Lemma 4.2.2 (2), we have that if $\alpha \geq 0$, $0 < \beta < \gamma + 1$, then $\text{tr}(A(1, 0)) < 0$. Since $0 < \beta < \gamma + 1$ has a wider range than $0 < \beta < \gamma$, after combining these two ranges, the common area becomes $0 < \beta < \gamma$ and $\alpha \geq 0$. Under this condition, we have $|A(1, 0)| > 0$ and $\text{tr}(A(1, 0)) < 0$. In addition, in accordance with Lemma 4.2.3, we have $(\text{tr}(A(1, 0)))^2 - 4|A(1, 0)| \geq 0$ for any $\alpha \geq 0, \beta \geq 0, \gamma \geq 0$. Therefore, by Lemma 2.3.1(ii), $(1, 0)$ is a stable node of (4.1.2), if $\alpha \geq 0$, $0 < \beta < \gamma$.

(ii) By Lemma 4.2.1 (ii), if $\beta > \gamma$ and $\alpha > 1 - \frac{\gamma}{\beta}$ then $|A(1, 0)| > 0$. Besides, by Lemma 4.2.2 (3), we have if $\beta \geq \gamma + 1$ and $\alpha > 1 - \frac{\gamma+1}{\beta}$, then $\text{tr}(A(1, 0)) < 0$. The common area of $\beta > \gamma$ and $\beta \geq \gamma + 1$ becomes $\beta \geq \gamma + 1$, since $\beta > \gamma$ contains $\beta \geq \gamma + 1$. Moreover, $\alpha > 1 - \frac{\gamma+1}{\beta}$ contains the area of $\alpha > 1 - \frac{\gamma}{\beta}$, thus the common range for α is $\alpha > 1 - \frac{\gamma}{\beta}$. Therefore, under the conditions of $\beta \geq \gamma + 1$ and $\alpha > 1 - \frac{\gamma}{\beta}$, we have that $|A(1, 0)| > 0$ implies $\text{tr}(A(1, 0)) < 0$. Otherwise, we cannot get $|A(1, 0)| > 0$ or $\text{tr}(A(1, 0)) < 0$. In addition, in accordance with Lemma 4.2.3, we have $[\text{tr}(A(1, 0))]^2 - 4|A(1, 0)| \geq 0$. Therefore, by Lemma 2.3.1(ii), $(1, 0)$ is a stable node of (4.1.2), if $\beta \geq \gamma + 1$ and $\alpha > 1 - \frac{\gamma}{\beta}$. That is, $\beta \geq \gamma + 1$ implies $\beta > \gamma$, which implies $\frac{\gamma}{\beta} < 1$, $\Rightarrow 1 - \frac{\gamma}{\beta} > 0$ and $\alpha > 0$. $\square$

Remark 4.2.1. Theorem 4.2.1 shows that the equilibrium $(1, 0)$ can be a saddle, a stable node or a saddle-node for suitable choice of the refuge constant α . However, [7, Theorem 2.3] shows that $(1, 0)$ only is a saddle for each refuge $\alpha \geq 0$ by using a different method.

Lemma 4.2.4. *If $\beta > 0$, $\gamma > 0$, then the following assertions hold:*

- (i) *If $\alpha \geq 0$, $0 < \beta < \gamma$, then $|A(u^*, v^*)| < 0$.*
- (ii) *If $\beta > \gamma > 0$, $\alpha > 1 - \frac{\gamma}{\beta}$, then $|A(u^*, v^*)| < 0$.*
- (iii) *If $0 < \gamma \leq \beta$, $\alpha = 1 - \frac{\gamma}{\beta} \geq 0$, then $|A(u^*, v^*)| = 0$.*
- (iv) *If $\beta > \gamma > 0$, $0 \leq \alpha < 1 - \frac{\gamma}{\beta}$, then $|A(u^*, v^*)| > 0$.*

Proof. Substituting (u^*, v^*) into (4.2.1), we obtain the following expression for $|A(u^*, v^*)|$:

$$\begin{aligned}
|A(u^*, v^*)| &= (1 - 2u^* - v^*)[\beta u^* - (\beta\alpha + \gamma)] + \beta v^*(u^* - \alpha) \\
&= \beta u^* - 2\beta(u^*)^2 - \beta u^* v^* - \beta\alpha + 2\beta\alpha u^* + \beta\alpha v^* - \gamma \\
&\quad + 2\gamma u^* + \gamma v^* + \beta u^* v^* - \alpha\beta v^* \\
&= \beta u^*(1 - 2u^* + 2\alpha) - \beta\alpha - \gamma + 2\gamma u^* + \gamma v^* \\
&= (\gamma + \alpha\beta)(1 - \frac{2(\gamma + \alpha\beta)}{\beta} + 2\alpha) - \beta\alpha - \gamma + 2\gamma(\frac{\gamma + \alpha\beta}{\beta}) + \gamma v^* \\
&= \gamma - 2\gamma(\frac{\gamma + \alpha\beta}{\beta}) + 2\gamma\alpha + \alpha\beta - 2\alpha(\gamma + \alpha\beta) \\
&\quad + 2\alpha^2\beta - \beta\alpha - \gamma + 2\gamma(\frac{\gamma + \alpha\beta}{\beta}) + \gamma v^* \\
&= \gamma v^*
\end{aligned}$$

Since $\gamma > 0$ and $|A(u^*, v^*)| = \gamma v^*$, the results follow by Lemma 4.1.3. $\square$

Theorem 4.2.2. *If $\beta > \gamma > 0$, $0 \leq \alpha < 1 - \frac{\gamma}{\beta}$, then (u^*, v^*) is locally asymptotically stable.*

Proof. Firstly, iff $\beta > \gamma > 0$, $0 \leq \alpha < 1 - \frac{\gamma}{\beta}$, we have positive interior equilibrium point (u^*, v^*) . Besides, with conditions of the theorem, we also have $|A(u^*, v^*)| > 0$

by Lemma 4.2.4. Next, we derive the following expression for $\text{tr}(A(u^*, v^*))$:

$$\begin{aligned}
\text{tr}(A(u^*, v^*)) &= 1 - 2u^* - v^* + \beta u^* - (\beta\alpha + \gamma) \\
&= 1 - 2\left(\frac{\gamma + \alpha\beta}{\beta}\right) - \frac{(\gamma + \alpha\beta)(\beta - \gamma - \alpha\beta)}{\beta\gamma} + (\gamma + \alpha\beta) - \beta\alpha - \gamma \\
&= \frac{\beta\gamma - 2\gamma^2 - 2\alpha\beta\gamma - \gamma\beta + \gamma^2 + \alpha\beta\gamma - \alpha\beta^2 + \alpha\beta\gamma + \alpha^2\beta^2}{\beta\gamma} \\
&= \frac{\alpha^2\beta^2 - \alpha\beta^2 - \gamma^2}{\beta\gamma}
\end{aligned}$$

Finally, we keep the conditions of $\beta > \gamma > 0$, $0 \leq \alpha < 1 - \frac{\gamma}{\beta}$ and discuss the results of $\text{tr}(A(u^*, v^*))$ in two different cases:

1) If $\alpha = 0$, then $\text{tr}(A(u^*, v^*)) = \frac{-\gamma^2}{\beta\gamma} < 0$.

2) If $\alpha \neq 0$, then $0 < \alpha < 1 - \frac{\gamma}{\beta}$, which means $\beta > \gamma > 0$. Besides, since $\beta > \gamma > 0$, it implies $0 < 1 - \frac{\gamma}{\beta} < 1$ and $0 < \alpha < 1$. Then $\alpha^2\beta^2 - \alpha\beta^2 < 0$, and consequently

$$\text{tr}(A(u^*, v^*)) = \frac{\alpha^2\beta^2 - \alpha\beta^2 - \gamma^2}{\beta\gamma} < 0.$$

Thus, by Lemma 2.3.1 we have (u^*, v^*) is locally asymptotically stable. $\square$

Remark 4.2.2. Theorem 4.2.2 provides the conditions on the prey refuge under which the interior equilibrium (u^*, v^*) of (4.1.2) is locally asymptotically stable. Theorem 4.2.2 improves [7, Lemma 2.2 and Theorem 2.5] with $m = 1$, where it is proved that (u^*, v^*) is locally asymptotically stable and globally asymptotically stable, respectively.

According to the proofs of Lemma 4.2.4 and Theorem 4.2.2, we have obtained $|A(u^*, v^*)|$ and $\text{tr}(A(u^*, v^*))$ in terms of α, β, γ :

$$|A(u^*, v^*)| = \frac{(\gamma + \alpha\beta)(\beta - \gamma - \alpha\beta)}{\beta}, \quad (4.2.6)$$

$$\operatorname{tr}(A(u^*, v^*)) = \frac{\alpha^2 \beta^2 - \alpha \beta^2 - \gamma^2}{\beta \gamma}. \quad (4.2.7)$$

Notation: Let $\alpha_0 = \frac{1}{2} - \frac{\gamma}{\beta}$, $\alpha_1 = \frac{1}{2} + \alpha_0$,

$$\sigma(\alpha) := [\operatorname{tr}(A(u^*, v^*))]^2 - 4|A(u^*, v^*)| \quad (4.2.8)$$

and for $0 < \gamma < \beta$, let

$$\omega(\beta, \gamma) = \beta^2 - 8\beta\gamma^2 + 4\gamma^2. \quad (4.2.9)$$

In the following, we show that under suitable conditions on the parameters, (u^*, v^*) is a stable node of (4.1.2).

Lemma 4.2.5. (1) If $\frac{4\beta^2}{1+4\beta} \leq \gamma < \beta$, then $\sigma(0) \geq 0$.

(2) If $\beta > 0$ and $\gamma > \max\{0, (2\beta - 1)/4\}$, then $\sigma'_\alpha(0) > 0$.

(3) If $0 < \gamma < \beta$ and $0 \leq \alpha < \alpha_1$, then

$$\sigma''(\alpha) = \frac{12\beta^2}{\gamma^2} \left[\left(\alpha - \frac{1}{2} \right)^2 - \frac{\omega(\beta, \gamma)}{12\beta^2} \right]. \quad (4.2.10)$$

Proof. By (4.2.6) and (4.2.7), we have

$$\sigma(\alpha) = \frac{\beta^2}{\gamma^2} \left[\frac{\gamma^2}{\beta^2} - \alpha(\alpha - 1) \right]^2 - 4\beta \left[\frac{1}{4} - (\alpha - \alpha_0)^2 \right] \quad (4.2.11)$$

(1) Since $\sigma(0) = \frac{\gamma^2}{\beta^2} - 4\beta \left[\frac{1}{4} - \alpha_0^2 \right]$ and $\alpha_0 = \frac{1}{2} - \frac{\gamma}{\beta}$, we have

$$\begin{aligned} \sigma(0) &= \frac{\gamma^2}{\beta^2} - \beta + 4\beta \left(\frac{1}{2} - \frac{\gamma}{\beta} \right)^2 \\ &= \frac{\gamma^2}{\beta^2} - 4\gamma + 4\frac{\gamma^2}{\beta^2} \\ &= \frac{\gamma(1+4\beta)}{\beta^2} \left(\gamma - \frac{4\beta^2}{1+4\beta} \right) \end{aligned}$$

Thus, if $\frac{4\beta^2}{1+4\beta} \leq \gamma < \beta$, then $\sigma(0) \geq 0$.

(2) By (4.2.11), we have for $\alpha \geq 0$,

$$\sigma(\alpha) = \frac{\beta^2}{\gamma^2} \left[\frac{\gamma^2}{\beta^2} - \alpha(\alpha - 1) \right]^2 - 4\beta \left[1/4 - (\alpha - \alpha_0)^2 \right] \quad (4.2.12)$$

and

$$\sigma'(\alpha) = \frac{2\beta^2}{\gamma^2} \left[\frac{\gamma^2}{\beta^2} - \alpha(\alpha - 1) \right] (1 - 2\alpha) + 8\beta(\alpha - \alpha_0). \quad (4.2.13)$$

It follows that

$$\begin{aligned} \sigma'(0) &= \frac{2\beta^2}{\gamma^2} \left[\frac{\gamma^2}{\beta^2} - 0 \right] (1 - 0) + 8\beta(0 - \alpha_0) \\ &= 2 - 8\beta\alpha_0 = 2 - 8\beta(1/2 - \gamma/\beta) \\ &= 8 \left[\gamma - \frac{2\beta - 1}{4} \right] > 0. \end{aligned}$$

(3) By (4.2.13), we have for $\alpha \geq 0$,

$$\begin{aligned} \sigma''(\alpha) &= \frac{2\beta^2}{\gamma^2} (2\alpha - 1)^2 - \frac{4}{\gamma^2} [\gamma^2 - \beta^2\alpha(\alpha - 1)] + 8\beta \\ &= \frac{12\beta^2}{\gamma^2} \left[\left(\alpha - \frac{1}{2} \right)^2 - \frac{\beta^2 - 8\beta\gamma^2 + 4\gamma^2}{12\beta^2} \right] \\ &= \frac{12\beta^2}{\gamma^2} \left[\left(\alpha - \frac{1}{2} \right)^2 - \frac{\omega(\beta, \gamma)}{12\beta^2} \right]. \end{aligned}$$

The result (3) holds. □

Lemma 4.2.6. (1) If either $0 < \beta \leq 5/8$ and $0 < \gamma < \beta$ or $\beta > \frac{5}{8}$ and $0 < \gamma < \frac{\beta}{2\sqrt{2\beta-1}}$, then $\omega(\beta, \gamma) > 0$.

(2) If $\beta > \frac{5}{8}$ and $\frac{\beta}{2\sqrt{2\beta-1}} \leq \gamma < \beta$, then $\omega(\beta, \gamma) \leq 0$.

Proof. (1) If $0 < \gamma < \beta \leq 1/2$, then by (4.2.9), $\omega(\beta, \gamma) = \beta^2 + 4\gamma^2(1 - 2\beta) > 0$. If

$\beta > 1/2$, then

$$\omega(\beta, \gamma) = 4(2\beta - 1) \left(\frac{\beta}{2\sqrt{2\beta - 1}} + \gamma \right) \left(\frac{\beta}{2\sqrt{2\beta - 1}} - \gamma \right). \quad (4.2.14)$$

It is easy to verify that if $1/2 < \beta \leq 5/8$, then $\beta \leq \frac{\beta}{2\sqrt{2\beta - 1}}$. If $1/2 < \beta \leq 5/8$ and $0 < \gamma < \beta$ or $\beta > \frac{5}{8}$ and $0 < \gamma < \frac{\beta}{2\sqrt{2\beta - 1}}$, then by (4.2.14), $\omega(\beta, \gamma) > 0$.

(2) Since $\beta > \frac{5}{8}$ and $\frac{\beta}{2\sqrt{2\beta - 1}} \leq \gamma < \beta$, by (4.2.14) we have $\omega(\beta, \gamma) \leq 0$. $\square$

Theorem 4.2.3. *If $\beta > \frac{5}{8}$, $\max\{\frac{4\beta^2}{1 + 4\beta}, \frac{\beta}{2\sqrt{2\beta - 1}}\} \leq \gamma < \beta$ and $\max\{0, \alpha_0\} \leq \alpha < \alpha_1$, then (u^*, v^*) is a stable node of (4.1.2).*

Proof. Since $\beta > \frac{5}{8}$, $\max\{\frac{4\beta^2}{1 + 4\beta}, \frac{\beta}{2\sqrt{2\beta - 1}}\} \leq \gamma < \beta$, by Lemma 4.2.6 (2), $\omega(\beta, \gamma) \leq 0$. Since $\max\{0, \alpha_0\} \leq \alpha < \alpha_1$, by Lemma 4.2.5 (3), $\sigma''(\alpha) \geq 0$. By Lemma 4.2.5 (2),

$$\sigma'(\alpha) \geq \sigma'(0) > 0 \quad \text{for } \alpha \in [\max\{0, \alpha_0\}, \alpha_1].$$

This, together with Lemma 4.2.5 (1), implies

$$\sigma(\alpha) > \sigma(0) \geq 0 \quad \text{for } \alpha \in [\max\{0, \alpha_0\}, \alpha_1]. \quad (4.2.15)$$

Besides, by (4.2.6) and (4.2.7), $|A(u^*, v^*)| > 0$ and $\text{tr}(A(u^*, v^*)) < 0$. The result follows from Lemma 2.3.1 (ii). $\square$

Remark 4.2.3. Theorem 4.2.3 is new that under some suitable conditions the positive interior equilibrium (u^*, v^*) is a stable node of (4.1.2), while [6, 7] did not give specific results of stability analysis regarding to $[\text{tr}(A(u^*, v^*))]^2 - 4|A(u^*, v^*)|$.

Chapter 5

Lotka-Volterra Predator-Prey Model with Type II Functional Response

In Section 3.4, we have briefly introduced how Type II functional Response modified the term that demonstrated the total number of prey killed by predators. Some related research on type II functional response has been studied in paper [8, 13, 15, 22]. In this chapter, we will use transformation method to study the model 3.4.2 and see what results we can develop. Transformation method is different from the traditional one that is widely used in other papers. The process of this chapter is new and may lead to a same or more accurate conclusion compared with the papers mentioned above.

5.1 Transformation and Positive Equilibria

In the preceding chapter, we have studied the Lotka-Volterra predator-prey model with type I functional response:

$$\begin{cases} \dot{x} = rx(1 - \frac{x}{k}) - c(x - p)y, \\ \dot{y} = -dy + e(x - p)y. \end{cases} \quad (5.1.1)$$

Now, consider the following model where $c(x - p)y$ of (5.1.1) is replaced by $\frac{c(x - p)y}{1 + m(x - p)}$:

$$\begin{cases} \dot{x} = rx(1 - \frac{x}{k}) - \frac{c(x - p)y}{1 + m(x - p)}, \\ \dot{y} = \frac{e(x - p)y}{1 + m(x - p)} - dy. \end{cases} \quad (5.1.2)$$

The term $\frac{c(x - p)y}{1 + m(x - p)}$ of (5.1.2) is called type II functional response which involves the factor of time process for predators to hunt and consume their prey. Parameters in both systems have identical biological meanings except m .

As explained in Section 4.1, $x(t)$ and $y(t)$ denotes the density of prey and predator populations at time t , respectively; r is the natural growth rate of the prey, k is capacity for prey's growth, c is the per capita rate of predation of the predator, e is a conversion rate of eaten prey into new predator abundance, d is the per capita death rate of the predator.

Precisely, parameter c is combination of attack rate a and total time used on hunting T in the system (5.1.2) and likewise m is combination of attack rate a and handling time T' . (see Section 3.4 and Remark 3.4.1 for more details about how the time used on hunting T and handling time T' are related to type II functional response.)

The model (5.1.2) was firstly studied by Olivares and Jiliberto in their paper [13]. They showed the stability analysis on positive interior equilibrium points, but they

did not discuss the cases of boundary equilibria. On the other hand, Chen improved the results of [13] and proved the global stability in his paper [8]. However, Chen's paper still did not show the stability of boundary equilibria either.

In this chapter, we will study the model of (5.1.2) by employing transformation method and discuss the equilibrium points as well as their stability analysis. Besides the phase portraits of positive interior equilibria, we will also show the local stability analysis on boundary equilibria. Further, we will compare our results of stability analysis on interior equilibrium points with Chen's conjectures in [8]. Following a similar pattern of Chapter 4, we start with transformation applying to system (5.1.2).

Theorem 5.1.1. *By using the transformation below:*

$$\bar{t} = rt, \quad u(\bar{t}) = x(t)/k \quad \text{and} \quad v(\bar{t}) = cy(t)/r,$$

(5.1.2) can be changed into the following equivalent system:

$$\begin{cases} \dot{u} = u(1 - u) - \frac{(u - \alpha)v}{1 + \rho(u - \alpha)} := f(u, v), \\ \dot{v} = \frac{\beta(u - \alpha)v}{1 + \rho(u - \alpha)} - \gamma v := g(u, v) \end{cases} \quad (5.1.3)$$

where respectively, $\alpha = p/k$, $\beta = ek/r$, $\gamma = d/r$, and $\rho = mk$ have same biological meanings as p , e , d and m .

Proof. From $\bar{t} = rt$, $u(\bar{t}) = \frac{x(t)}{k}$, $v(\bar{t}) = \frac{cy(t)}{r}$, we can derive new expressions for $x(t), y(t)$, which are

$$x(t) = ku(\bar{t}) \quad \text{and} \quad y(t) = \frac{rv(\bar{t})}{c}.$$

Taking derivatives for both above equations, we have

$$\begin{cases} \frac{dx(t)}{dt} = \frac{d[ku(\bar{t})]}{d\bar{t}} \frac{d\bar{t}}{dt} = rk \frac{du(\bar{t})}{d\bar{t}}, \\ \frac{dy(t)}{dt} = \frac{d\left(\frac{rv(\bar{t})}{c}\right)}{d\bar{t}} \frac{d\bar{t}}{dt} = \frac{r^2}{c} \frac{dv(\bar{t})}{d\bar{t}}. \end{cases} \quad (5.1.4)$$

Next, we replace $\frac{dx(t)}{dt}$ and $\frac{dy(t)}{dt}$ by $rk\frac{du(\bar{t})}{d\bar{t}}$ and $\frac{r^2}{c}\frac{dv(\bar{t})}{d\bar{t}}$ respectively for the system 5.1.2 in order to derive new differential equations in terms of time $\bar{t}$:

$$\frac{dx(t)}{dt} = rk\frac{du(\bar{t})}{d\bar{t}} = rx(t)\left(1 - \frac{x(t)}{k}\right) - \frac{c(x(t) - p)y(t)}{1 + m(x - p)}$$

$$\begin{aligned}\frac{du(\bar{t})}{d\bar{t}} &= \frac{x(t)}{k}\left(1 - \frac{x(t)}{k}\right) - \frac{\frac{c}{r}\left(\frac{x(t)}{k} - \frac{p}{k}\right)y(t)}{1 + mk\left(\frac{x(t)}{k} - \frac{p}{k}\right)} \\ &= u(\bar{t})(1 - u(\bar{t})) - \frac{v(\bar{t})(u(\bar{t}) - \alpha)}{1 + \rho(u(\bar{t}) - \alpha)},\end{aligned}$$

$$\frac{dy(t)}{dt} = \frac{r^2}{c}\frac{dv(\bar{t})}{d\bar{t}} = -dy(t) + \frac{e(x(t) - p)y(t)}{1 + m(x(t) - p)}$$

$$\begin{aligned}\frac{dv(\bar{t})}{d\bar{t}} &= \frac{-dcy(t)}{r^2} + \frac{\frac{ce}{r^2}(x(t) - p)y(t)}{1 + m(x(t) - p)} \\ &= \frac{-d}{r}\frac{cy(t)}{r} + \frac{\frac{ek}{r}\left(\frac{x(t)}{k} - \frac{p}{k}\right)\frac{cy(t)}{r}}{1 + mk\left(\frac{x(t)}{k} - \frac{p}{k}\right)} \\ &= -\gamma v(\bar{t}) + \frac{\beta(u(\bar{t}) - \alpha)v(\bar{t})}{1 + \rho(u(\bar{t}) - \alpha)}.\end{aligned}$$

Now, the system (5.1.2) is changed into the following equivalent system in terms of time $\bar{t}$:

$$\begin{cases} \dot{u} = u(1 - u) - \frac{(u - \alpha)v}{1 + \rho(u - \alpha)} := f(u, v), \\ \dot{v} = \frac{\beta(u - \alpha)v}{1 + \rho(u - \alpha)} - \gamma v := g(u, v). \end{cases} \quad (5.1.5)$$

We see that under above transformation, the constants r , k and c in (5.1.3) are normalized to 1. Thus, $\alpha = \frac{p}{k}$, $\beta = \frac{ek}{r}$, $\gamma = \frac{d}{r}$ and $\rho = mk$ have same biological meanings as p , e , d and m . $\square$

Using suitable transformations to reduce the number of parameters in predator-prey models and SIR models has been widely used in [11, 15, 20, 23, 24, 25, 27, 28, 46].

Next, we will study the equilibrium points and stability analysis for model (5.1.3) instead of (5.1.1). By Definition 2.1.2, it is easy to verify that (u, v) is an equilibrium point of system (5.1.3) if and only if (u, v) satisfies:

$$\begin{cases} u(1 - u) = 0, \\ v = 0 \end{cases} \quad (5.1.6)$$

or

$$\begin{cases} (u - u^2)\frac{\beta}{\gamma} - v = 0, \\ v \neq 0 \quad \text{and} \quad u = \frac{\gamma}{\beta - \gamma\rho} + \alpha. \end{cases} \quad (5.1.7)$$

Remark 5.1.1. We see from (5.1.7) that if $\frac{\gamma}{\beta - \gamma\rho} < 0$, then $u < \alpha$. However, the biological meaning of α is prey refuge excluded from the whole prey density u , which implies $u > \alpha$. Thus, we need to keep the condition $\frac{\gamma}{\beta - \gamma\rho} > 0$ for the case of $v \neq 0$ through the whole chapter in order to satisfy $u > \alpha$.

Moreover, we need to discuss what would happen to the model when $\beta - \rho\gamma = 0$. If $\beta - \rho\gamma = 0$, then $\frac{ek}{r} - \frac{d}{r}(mk) = 0$. So we have $ek = adk, e = md$, and substitute back to (5.1.2), we obtain:

$$\dot{y} = \frac{e(x - p)y}{1 + m(x - p)} - dy = \frac{md(x - p)y}{1 + m(x - p)} - dy = yd\left(\frac{m(x - p)}{1 + m(x - p)} - 1\right).$$

As long as $x > p$ (prey density is greater than prey refuge), $0 < \frac{m(x - p)}{1 + m(x - p)} < 1$, which means $\dot{y}$ of (5.1.2) becomes strictly less than 0. Thus, we keep the condition of $\beta - \rho\gamma \neq 0$ through the rest of chapter as well.

Notation: Let $\alpha_0 = \frac{1}{2} - \frac{\gamma}{\beta - \gamma\rho}$ and define

$$\delta(\alpha) := \frac{(\gamma + \alpha\beta - \gamma\rho)(\beta - \gamma\rho - \gamma - \alpha\beta + \alpha\gamma\rho)}{(\beta - \gamma\rho)^2}.$$

$\delta(\alpha)$ is derived from (5.1.7) by calculating $u(1 - u)$ with the substitution $u = \frac{\gamma}{\beta - \gamma\rho} + \alpha$. For $\beta > 0$, $\alpha \geq 0$ and $\rho \geq 0$, below are other equivalent expressions of $\delta(\alpha)$:

$$\delta(\alpha) = u(1 - u) = \left(\alpha + \frac{\gamma}{\beta - \gamma\rho}\right)\left(1 - \frac{\gamma}{\beta - \gamma\rho} - \alpha\right) \quad (5.1.8)$$

and

$$\delta(\alpha) = 1/4 - (u - 1/2)^2 = 1/4 - \left(\alpha - 1/2 + \frac{\gamma}{\beta - \gamma\rho}\right)^2. \quad (5.1.9)$$

The following lemma provides the solutions of (5.1.6). Its proof is straightforward and we omit it.

Lemma 5.1.1. *Assume that $v=0$ for (5.1.3), then (u, v) of (5.1.6) has two solutions: $(0, 0)$ and $(1, 0)$.*

Lemma 5.1.2. (1) *Assume one of the following conditions holds:*

- (i) $0 < \gamma < \beta$, $0 \leq \rho < \frac{\beta}{\gamma} - 1$ and $0 \leq \alpha < 1 - \frac{\gamma}{\beta - \gamma\rho}$;
- (ii) $\beta > 0$, $\gamma > 0$, $\rho > \frac{\beta}{\gamma}$ and $\frac{\gamma}{\gamma\rho - \beta} < \alpha < 1 + \frac{\gamma}{\gamma\rho - \beta}$,

then $\delta(\alpha) > 0$.

(2) *Assume one of the following conditions holds:*

- (i) $0 < \gamma < \beta$, $0 \leq \rho < \frac{\beta}{\gamma} - 1$ and $\alpha \geq 1 - \frac{\gamma}{\beta - \gamma\rho}$;
- (ii) $0 < \gamma < \beta$, $\frac{\beta}{\gamma} - 1 \leq \rho < \frac{\beta}{\gamma}$ and $\alpha \geq 1 - \frac{\gamma}{\beta - \gamma\rho}$;
- (iii) $0 < \gamma \leq \beta$, $0 \leq \rho < \frac{\beta}{\gamma}$ and $\alpha \geq 1 - \frac{\gamma}{\beta - \gamma\rho}$;
- (iv) $\beta > 0$, $\gamma > 0$, $\rho > \frac{\beta}{\gamma}$ and $0 \leq \alpha \leq 1 + \frac{\gamma}{\gamma\rho - \beta}$;
- (v) $\beta > 0$, $\gamma > 0$, $\rho < \frac{\beta}{\gamma}$ and $0 \leq \alpha \leq \frac{\gamma}{\gamma\rho - \beta}$,

then $\delta(\alpha) \leq 0$

Proof. (1) From (5.1.8), if $\delta(\alpha) = 1/4 - \left(\alpha - 1/2 + \frac{\gamma}{\beta - \gamma\rho}\right)^2 > 0$, then

$$\begin{aligned} 1/4 - \left[\alpha - 1/2 + \frac{\gamma}{\beta - \gamma\rho}\right]^2 &> 0 \\ \left[\alpha - 1/2 + \frac{\gamma}{\beta - \gamma\rho}\right]^2 &< 1/4 \\ -1/2 < \alpha - 1/2 + \frac{\gamma}{\beta - \gamma\rho} &< 1/2 \\ 0 < \alpha + \frac{\gamma}{\beta - \gamma\rho} &< 1. \end{aligned}$$

(1)(i) If $0 < \gamma < \beta$, $0 \leq \rho < \frac{\beta}{\gamma} - 1$, then

$$0 \leq \rho < \frac{\beta}{\gamma} - 1 \Rightarrow \beta - \gamma\rho > \gamma > 0 \Rightarrow \frac{\gamma}{\beta - \gamma\rho} < 1.$$

Besides, since $0 \leq \alpha < 1 - \frac{\gamma}{\beta - \gamma\rho}$, we have $0 < \alpha + \frac{\gamma}{\beta - \gamma\rho} < 1$. Thus,

$$\begin{aligned} 0 < \alpha + \frac{\gamma}{\beta - \gamma\rho} < 1 &\Leftrightarrow \\ -1/2 < \alpha - 1/2 + \frac{\gamma}{\beta - \gamma\rho} < 1/2 &\Leftrightarrow \\ \left(\alpha - 1/2 + \frac{\gamma}{\beta - \gamma\rho}\right)^2 < 1/4 &\Leftrightarrow \\ 1/4 - \left(\alpha - 1/2 + \frac{\gamma}{\beta - \gamma\rho}\right)^2 > 0 &\Leftrightarrow \\ \delta(\alpha) > 0 &\Leftarrow \text{By (5.1.9).} \end{aligned}$$

Conditions under (i) are based on $\beta - \gamma\rho > 0$. On the other hand, (1)(ii) is concluded based on $\beta - \gamma\rho < 0$. That is for α , we need to satisfy the following in order to let $\delta(\alpha) > 0$:

$$\begin{aligned} 0 < \alpha + \frac{\gamma}{\beta - \gamma\rho} < 1 \\ \frac{\gamma}{\gamma\rho - \beta} < \alpha < 1 + \frac{\gamma}{\gamma\rho - \beta}. \end{aligned}$$

For (2), if we need $\delta(\alpha) = 1/4 - [\alpha - 1/2 + \frac{\gamma}{\beta - \gamma\rho}]^2 \leq 0$, then the following conditions are required:

$$\begin{aligned} 1/4 - [\alpha - 1/2 + \frac{\gamma}{\beta - \gamma\rho}]^2 &\leq 0 \\ [\alpha - 1/2 + \frac{\gamma}{\beta - \gamma\rho}]^2 &\geq 1/4 \\ \alpha - 1/2 + \frac{\gamma}{\beta - \gamma\rho} &\geq 1/2 \\ &\text{or} \\ \alpha - 1/2 + \frac{\gamma}{\beta - \gamma\rho} &\leq -1/2. \end{aligned}$$

After re-arranging the above two final inequalities, we obtain the conditions for $\alpha + \frac{\gamma}{\beta - \gamma\rho}$ as below:

$$\alpha + \frac{\gamma}{\beta - \gamma\rho} \geq 1 \text{ or } \alpha + \frac{\gamma}{\beta - \gamma\rho} \leq 0.$$

From (2)(i) – (iv), we can conclude $\alpha + \frac{\gamma}{\beta - \gamma\rho} \geq 1$; from (2)(v), we can conclude $\alpha + \frac{\gamma}{\beta - \gamma\rho} \leq 0$. □

Theorem 5.1.2. Assume that $\beta > 0$, $\gamma > 0$, $\rho \geq 0$, and $\alpha \geq 0$.

(i) If one of Lemma 5.1.2 (2) holds, then (5.1.3) has two positive equilibrium points, which are $(0, 0)$ and $(1, 0)$.

(ii) If $0 < \gamma < \beta$, $0 \leq \rho < \frac{\beta}{\gamma} - 1$, $0 \leq \alpha < 1 - \frac{\gamma}{\beta - \gamma\rho}$, then there are three equilibria for (5.1.3): $(0, 0)$, $(1, 0)$ and (u^*, v^*) satisfying $u^* > \alpha$ and $v^* > 0$, where (u^*, v^*) is the positive interior equilibrium with

$$u^* = \alpha + \frac{\gamma}{\beta - \gamma\rho} \quad \text{and} \quad v^* = \frac{\beta}{\gamma} \delta(\alpha). \quad (5.1.10)$$

Proof. From equation (5.1.7), if we substitute $u^* = \alpha + \frac{\gamma}{\beta - \gamma\rho}$ into first equation we get $v^* = \frac{\beta}{\gamma} \delta(\alpha)$. The following process shows how to develop the above results:

By (5.1.3), setting $g(u^*, v^*) = 0$, we have

$$\begin{aligned}\frac{(u^* - \alpha)}{1 + \rho(u^* - \alpha)} &= \frac{\gamma}{\beta} \\ \beta(u^* - \alpha) &= \gamma + \gamma\rho(u^* - \alpha) \\ u^* &= \frac{\gamma}{\beta - \gamma\rho} + \alpha.\end{aligned}\tag{5.1.11}$$

By setting $f(u^*, v^*) = 0$, we have

$$\begin{aligned}v^* &= (u^* - (u^*)^2) \frac{\beta}{\gamma} \\ &= \left(\frac{\gamma}{\beta - \gamma\rho} + \alpha - \left[\frac{\gamma}{\beta - \gamma\rho} + \alpha \right]^2 \right) \frac{\beta}{\gamma} \\ &= \left[\frac{\gamma + \alpha(\beta - \gamma\rho)}{\beta - \gamma\rho} - \frac{(\gamma + \alpha(\beta - \gamma\rho))^2}{(\beta - \gamma\rho)^2} \right] \frac{\beta}{\gamma} \\ &= \left[\frac{(\gamma + \alpha(\beta - \gamma\rho))(\beta - \gamma\rho) - (\gamma + \alpha(\beta - \gamma\rho))^2}{(\beta - \gamma\rho)^2} \right] \frac{\beta}{\gamma} \\ &= \left[\frac{(\gamma + \alpha\beta - \alpha\gamma\rho)(\beta - \gamma\rho) - (\gamma + \alpha\beta - \gamma\rho)^2}{(\beta - \gamma\rho)^2} \right] \frac{\beta}{\gamma} \\ &= \left[\frac{(\gamma + \alpha\beta - \alpha\gamma\rho)(\beta - \gamma\rho - \gamma - \alpha\beta + \alpha\gamma\rho)}{(\beta - \gamma\rho)^2} \right] \frac{\beta}{\gamma} \\ &= \left(\frac{\beta}{\gamma} \right) \delta(\alpha).\end{aligned}$$

(i) If one of the Lemma 5.1.2 (2) holds, then $\delta(\alpha) \leq 0$, which implies $v^* = \left(\frac{\beta}{\gamma} \right) \delta(\alpha) \leq 0$. Thus, (u^*, v^*) is not a positive interior equilibrium under any conditions of Lemma 5.1.2 (2). In addition, $v^* = \left(\frac{\beta}{\gamma} \right) \delta(\alpha) = 0$, then u^* becomes either 0 or 1 by (5.1.8) with $u = u^*$.

(ii) By Lemma 5.1.2 (1)(i), we see that if $0 < \gamma < \beta$, $0 \leq \rho < \frac{\beta}{\gamma} - 1$, $0 \leq \alpha < 1 - \frac{\gamma}{\beta - \gamma\rho}$, then $\delta(\alpha) > 0$, which implies $v^* = \left(\frac{\beta}{\gamma} \right) \delta(\alpha) > 0$. Also we need $u^* > \alpha$ due to less prey refuge than the whole prey density. That is, we must have $u^* = \frac{\gamma}{\beta - \gamma\rho} + \alpha > \alpha$. Thus, $\frac{\gamma}{\beta - \gamma\rho} \Rightarrow \beta - \gamma\rho > 0$.

If we apply the conditions of Lemma 5.1.2 (1)(ii), then $\beta - \gamma\rho < 0$, which implies

$u^* < \alpha$. Thus, we omit the positive interior equilibrium (u^*, v^*) under these conditions although $u^* > 0$ and $v^* > 0$. $\square$

Corollary 5.1.1. *Assume that $\rho = 0$ for (5.1.3), then the following assertions hold:*

(i) *If $\alpha \geq 0$, $0 < \beta < \gamma$, or if $\beta \geq \gamma > 0$, $\alpha \geq 1 - \frac{\gamma}{\beta}$, then the system (5.1.3) has two equilibria: $(0, 0)$ and $(1, 0)$.*

(ii) *If $\beta > \gamma > 0$, $0 \leq \alpha < 1 - \frac{\gamma}{\beta}$, then the system (5.1.3) has three positive equilibria: $(0, 0)$, $(1, 0)$ and (u^*, v^*) , where*

$$u^* = \frac{\gamma + \alpha\beta}{\beta} \quad \text{and} \quad v^* = \frac{(\gamma + \alpha\beta)(\beta - \gamma - \alpha\beta)}{\beta\gamma}.$$

Proof. If $\rho = 0$ for (5.1.3), then the model becomes (4.1.2) discussed in chapter 4. By Theorem 5.1.2 we can conclude the results of (i) and (ii) with $\rho = 0$ and corresponding conditions for α, β, γ . $\square$

5.2 Local stability analysis

Now, we use the theoretical results introduced in Section 2.3 to study phase portraits near each of the positive equilibria of (5.1.3) obtained in Section 5.1. Let $A(u, v)$ be the jacobian matrix of f and g defined in (5.1.3). By (5.1.3) and Definition 2.1.3, we have

$$A(u, v) = \begin{pmatrix} 1 - 2u - \left[\frac{v}{(1 + \rho(u - \alpha))^2} \right] & -\frac{u - \alpha}{1 + \rho(u - \alpha)} \\ \frac{\beta v}{(1 + \rho(u - \alpha))^2} & \left[\frac{\beta(u - \alpha)}{1 + \rho(u - \alpha)} \right] - \gamma \end{pmatrix}, \quad (5.2.1)$$

$$\begin{aligned} |A(u, v)| &= \left(1 - 2u - \left[\frac{v}{(1 + \rho(u - \alpha))^2} \right] \right) \left(\left[\frac{\beta(u - \alpha)}{1 + \rho(u - \alpha)} \right] - \gamma \right) \\ &\quad + \frac{\beta v(u - \alpha)}{(1 + \rho(u - \alpha))^3} \end{aligned} \quad (5.2.2)$$

and

$$\text{tr}(A(u, v)) = 1 - 2u - \left[\frac{v}{(1 + \rho(u - \alpha))^2} \right] + \left[\frac{\beta(u - \alpha)}{(1 + \rho(u - \alpha))} \right] - \gamma. \quad (5.2.3)$$

The following Lemma will be used to study the stability analysis on equilibrium $(0, 0)$.

Lemma 5.2.1. *Assume that $\beta > 0$, $\gamma > 0$, then the following assertions hold:*

- (1) *If $\rho = 0$ and $\alpha \geq 0$ or $\rho > 0$ and $0 \leq \alpha < 1/\rho$, then $|A(0, 0)| < 0$.*
- (2) *If $0 < \rho \leq \frac{\beta}{\gamma}$ and $\alpha > 1/\rho$, then $|A(0, 0)| > 0$.*
- (3) *If $\rho > \frac{\beta}{\gamma}$ and $\frac{1}{\rho} < \alpha \leq \frac{\gamma}{\gamma\rho - \beta}$, then $|A(0, 0)| \geq 0$.*
- (4) *If $\rho > \frac{\beta}{\gamma}$ and $\alpha > \frac{\gamma}{\gamma\rho - \beta}$, then $|A(0, 0)| < 0$.*

Proof. By (5.2.1), the jacobian matrix of (5.1.3) at $(0, 0)$ is

$$A(0, 0) = \begin{pmatrix} 1 & \frac{\alpha}{1 - \alpha\rho} \\ 0 & \frac{-\alpha\beta}{1 - \alpha\rho} - \gamma \end{pmatrix}. \quad (5.2.4)$$

Then,

$$\begin{aligned} |A(0, 0)| &= \frac{-\alpha\beta}{1 - \alpha\rho} - \gamma = \frac{-\alpha\beta - \gamma(1 - \alpha\rho)}{1 - \alpha\rho}. \\ &= \frac{-\alpha\beta - \gamma + \alpha\rho\gamma}{1 - \alpha\rho} \\ &= \frac{\alpha(\gamma\rho - \beta) - \gamma}{1 - \alpha\rho}. \end{aligned}$$

(1) If $\rho = 0, \alpha \geq 0$ or $\rho > 0, \alpha = 0$, we have either $|A(0, 0)| = -\gamma < 0$ or $|A(0, 0)| = -\alpha\beta - \gamma < 0$, since $\beta > 0, \gamma > 0$. Further, if $\rho > 0$ and $0 \leq \alpha < 1/\rho$, then $1 - \alpha\rho > 0$. Suppose $\rho = \frac{\beta}{\gamma} > 0$, then $\gamma\rho - \beta = 0$, and

$$|A(0, 0)| = \frac{\alpha(\gamma\rho - \beta) - \gamma}{1 - \alpha\rho} = \frac{-\gamma}{1 - \alpha\rho} < 0.$$

On the other hand, suppose $\rho \neq \frac{\beta}{\gamma}$, $\rho > 0$, then by $0 \leq \alpha < \frac{1}{\rho}$, we also have $\alpha < \frac{1}{\rho} < \frac{\gamma}{\gamma\rho - \beta}$, since $\frac{\beta}{\gamma} > 0$. That is, $\alpha < \frac{\gamma}{\gamma\rho - \beta}$ and $\alpha(\gamma\rho - \beta) < \gamma$, which implies $|A(0, 0)| = \frac{\alpha(\gamma\rho - \beta) - \gamma}{1 - \alpha\rho} < 0$.

(2) If $\alpha > \frac{1}{\rho}$, then $1 - \alpha\rho < 0$. Besides, as we analyzed in (1) above, if $\rho = \frac{\beta}{\gamma} > 0$, then $\gamma\rho - \beta = 0$. Thus,

$$|A(0, 0)| = \frac{\alpha(\gamma\rho - \beta) - \gamma}{1 - \alpha\rho} = \frac{-\gamma}{1 - \alpha\rho} > 0.$$

For $0 < \rho < \frac{\beta}{\gamma}$, we have $\gamma\rho - \beta < 0$. Then, $\alpha(\gamma\rho - \beta) - \gamma < 0$. Therefore, $|A(0, 0)| = \frac{\alpha(\gamma\rho - \beta) - \gamma}{1 - \alpha\rho} > 0$.

(3) For $\frac{1}{\rho} < \alpha \leq \frac{\gamma}{\gamma\rho - \beta}$, we have $1 - \alpha\rho < 0$ from the first half inequality. Since $\rho > \frac{\beta}{\gamma} \Rightarrow \gamma\rho - \beta > 0$, it implies $\gamma\rho - \beta \neq 0$ and therefore

$$\frac{1}{\rho} < \frac{1}{\rho - (\frac{\beta}{\gamma})} = \frac{\gamma}{\gamma\rho - \beta}.$$

If $\alpha \leq \frac{\gamma}{\gamma\rho - \beta}$, then $\alpha(\gamma\rho - \beta) - \gamma \leq 0$. Thus,

$$|A(0, 0)| = \frac{\alpha(\gamma\rho - \beta) - \gamma}{1 - \alpha\rho} \geq 0.$$

(4) If $\rho > \frac{\beta}{\gamma}$, then we obtain again $\gamma\rho - \beta > 0$. And we already know from (2) that $\frac{1}{\rho} < \frac{\gamma}{\gamma\rho - \beta}$, which implies $\alpha > \frac{\gamma}{\gamma\rho - \beta} > \frac{1}{\rho}$ from the condition. Then, we have $1 - \alpha\rho < 0$ and $\alpha(\gamma\rho - \beta) - \gamma > 0$. Finally, $|A(0, 0)| = \frac{\alpha(\gamma\rho - \beta) - \gamma}{1 - \alpha\rho} < 0$ $\square$

Theorem 5.2.1. Assume that $\beta > 0$, $\gamma > 0$, then the following assertions hold:

(1) If one of the following holds:

(i) $\rho = 0$ and $\alpha \geq 0$;

- (ii) $\rho > 0$ and $0 \leq \alpha < 1/\rho$;
 (iii) $\rho > \frac{\beta}{\gamma}$ and $\alpha > \frac{\gamma}{\gamma\rho - \beta}$,
 then $(0, 0)$ is a saddle for (5.1.3).
 (2) If $\rho > \frac{\beta}{\gamma}$ and $\frac{1}{\rho} < \alpha = \frac{\gamma}{\gamma\rho - \beta}$, then $(0, 0)$ is a saddle-node for (5.1.3).
 (3) If $0 < \rho \leq \frac{\beta}{\gamma}$ and $\alpha > 1/\rho$ or $\rho > \frac{\beta}{\gamma}$ and $\frac{1}{\rho} < \alpha < \frac{\gamma}{\gamma\rho - \beta}$, then $(0, 0)$ is an unstable node for (5.1.3).

Proof. By Lemma 5.2.1 (1) and (4), we see that $|A(0, 0)| < 0$ under conditions of (1)(i) – (iii). Therefore, the results follow by Lemma 2.3.1.

(2) If $\rho > \frac{\beta}{\gamma}$ and $\frac{1}{\rho} < \alpha = \frac{\gamma}{\gamma\rho - \beta}$, then $|A(0, 0)| = 0$ by Lemma 5.2.1 (3). By (5.2.4), we have

$$\text{tr}(A(0, 0)) = \frac{-\alpha\beta}{1 - \alpha\rho} - \gamma + 1 = |A(0, 0)| + 1 = 1 \neq 0.$$

Moreover, the isolated equilibrium origin $(0, 0)$ has been already obtained, we can conclude a saddle-node for (5.1.3) by Lemma 2.4.1 without applying transformation.

(3) If $0 < \rho \leq \frac{\beta}{\gamma}$ and $\alpha > 1/\rho$ or $\rho > \frac{\beta}{\gamma}$ and $\frac{1}{\rho} < \alpha < \frac{\gamma}{\gamma\rho - \beta}$, then $|A(0, 0)| > 0$. Since by Lemma 5.2.4, we have

$$\text{tr}(A(0, 0)) = \frac{-\alpha\beta}{1 - \alpha\rho} - \gamma + 1 = |A(0, 0)| + 1$$

and $\text{tr}(A(0, 0)) > 0$ as well. Then

$$[\text{tr}(A(0, 0))]^2 - 4|A(0, 0)| = [|A(0, 0)| + 1]^2 - 4|A(0, 0)| = [|A(0, 0)| - 1]^2,$$

which implies $[\text{tr}(A(0, 0))]^2 - 4|A(0, 0)| \geq 0$. Therefore, by Lemma 2.3.1, we can conclude that $(0, 0)$ is a unstable node under the conditions of (3). $\square$

Remark 5.2.1. If $\rho = 0$, then (5.1.3) becomes the model (4.1.2) which we have studied in previous chapter. The results of the Theorem 4.2.1 in Section 4.2 are

special cases of Theorem 5.2.1 at $\rho = 0$. With type II functional response (adding the parameter ρ , whose biological meaning is handling time for predators), we see that the stability results of model (5.1.3) at equilibrium $(0, 0)$ have more situations than the ones of model 4.1.2. The former system shows that under some conditions for ρ , the boundary equilibrium $(0, 0)$ has unstable possibility and saddle-node rather than only classified as a saddle point. In other words, incorporating the handling time for predators enhanced the predator-prey system since the unstable node of $(0, 0)$ also implies both predators and prey are trying to avoid extinction in the long term period.

When we study the stability of another equilibrium point $(1, 0)$, α should be less than $u = 1$ because α as a prey refuge cannot exceed the number of prey density u . Therefore, the following Lemma and Theorem will only consider $0 \leq \alpha < 1$.

Lemma 5.2.2. (1) If $0 < \gamma \leq \beta$, $0 \leq \rho \leq \frac{\beta}{\gamma} - 1$ and $1 - \frac{\gamma}{\beta - \gamma\rho} \leq \alpha < 1$, then $|A(1, 0)| \geq 0$.
(2) If $\max\{0, \frac{\beta}{\gamma} - 1\} < \rho \leq \frac{\beta}{\gamma}$ and $0 \leq \alpha < 1$, then $|A(1, 0)| > 0$.
(3) If $\beta > 0$, $\gamma > 0$, $\rho > \frac{\beta}{\gamma}$, and $0 \leq \alpha \leq 1$, then $|A(1, 0)| > 0$.
(4) If $0 < \gamma < \beta$, $\rho < \frac{\beta}{\gamma} - 1$, and $0 \leq \alpha < 1 - \frac{\gamma}{\beta - \gamma\rho}$, then $|A(1, 0)| < 0$.

Proof. By (5.2.2), the jacobian matrix of (5.1.3) at equilibrium point $(1, 0)$ is

$$A(1, 0) = \begin{pmatrix} -1 & \frac{\alpha - 1}{1 + \rho(1 - \alpha)} \\ 0 & \frac{\beta(1 - \alpha)}{1 + \rho(1 - \alpha)} - \gamma \end{pmatrix}. \quad (5.2.5)$$

Then, $|A(1, 0)| = \gamma - \frac{\beta(1 - \alpha)}{1 + \rho(1 - \alpha)}$. More precisely,

$$\begin{aligned} |A(1, 0)| &= \gamma - \frac{\beta(1 - \alpha)}{1 + \rho(1 - \alpha)} = \frac{\gamma(1 + \rho(1 - \alpha)) - \beta(1 - \alpha)}{1 + \rho(1 - \alpha)} \\ &= \frac{\gamma + \gamma\rho(1 - \alpha) - \beta(1 - \alpha)}{1 + \rho(1 - \alpha)} = \frac{(1 - \alpha)(\gamma\rho - \beta) + \gamma}{1 + \rho(1 - \alpha)}. \end{aligned}$$

(1) If $0 < \gamma \leq \beta$, $0 \leq \rho \leq \frac{\beta}{\gamma} - 1$ and $1 - \frac{\gamma}{\beta - \gamma\rho} \leq \alpha < 1$, then we first have $1 - \alpha > 0$ and $\beta - \gamma\rho \geq \gamma > 0$. Besides, $1 - \frac{\gamma}{\beta - \gamma\rho} \leq \alpha$ implies $(1 - \alpha)(\beta - \gamma\rho) - \gamma \leq 0$. Multiplying -1 both sides, we obtain $(1 - \alpha)(\gamma\rho - \beta) + \gamma \geq 0$. Therefore,

$$|A(1, 0)| = \frac{(1 - \alpha)(\gamma\rho - \beta) + \gamma}{1 + \rho(1 - \alpha)} \geq 0.$$

(2) If $\max\{0, \frac{\beta}{\gamma} - 1\} < \rho \leq \frac{\beta}{\gamma}$, then $\beta - \gamma\rho > 0$ and $\rho > \frac{\beta}{\gamma} - 1$. In addition,

$$\frac{\beta}{\gamma} - 1 < \rho \Rightarrow \beta - \gamma < \gamma\rho \Rightarrow 1 - \frac{\gamma}{\beta - \gamma\rho} < 0.$$

Since $0 \leq \alpha < 1$, then $1 - \frac{\gamma}{\beta - \gamma\rho} < \alpha$, which implies

$$(1 - \alpha)(\beta - \gamma\rho) - \gamma < 0 \Rightarrow (1 - \alpha)(\gamma\rho - \beta) + \gamma > 0.$$

Therefore, by $1 - \frac{\gamma}{\beta - \gamma\rho} \leq 0 < \alpha < 1$, we have

$$|A(1, 0)| = \frac{(1 - \alpha)(\gamma\rho - \beta) + \gamma}{1 + \rho(1 - \alpha)} > 0.$$

(3) $\rho > \frac{\beta}{\gamma}$ implies $\gamma\rho - \beta > 0$. And $0 \leq \alpha < 1$ gives $1 - \alpha > 0$. Thus,

$$(1 - \alpha)(\gamma\rho - \beta) + \gamma > 0,$$

from which we can conclude that

$$|A(1, 0)| = \frac{(1 - \alpha)(\gamma\rho - \beta) + \gamma}{1 + \rho(1 - \alpha)} > 0.$$

(4) From $|A(1, 0)| = \frac{(1 - \alpha)(\gamma\rho - \beta) + \gamma}{1 + \rho(1 - \alpha)}$, we see that the only option for $\gamma\rho - \beta$ is less than 0 if we wish $|A(1, 0)| < 0$. Then,

$$\begin{aligned} |A(1, 0)| &= \frac{(1 - \alpha)(\gamma\rho - \beta) + \gamma}{1 + \rho(1 - \alpha)} < 0 \\ &\Leftrightarrow (1 - \alpha)(\gamma\rho - \beta) + \gamma < 0 \quad \Leftrightarrow (\text{Since } 1 + \rho(1 - \alpha) > 0) \\ &\Leftrightarrow (1 - \alpha)(\gamma\rho - \beta) < -\gamma \\ &\Leftrightarrow (1 - \alpha) > \frac{-\gamma}{\gamma\rho - \beta} \quad \Leftrightarrow (\text{Since } \gamma\rho - \beta < 0) \\ &\Leftrightarrow 0 \leq \alpha < 1 - \frac{\gamma}{\beta - \gamma\rho}. \end{aligned}$$

Moreover,

$$1 - \frac{\gamma}{\beta - \gamma\rho} > 0 \quad \Leftrightarrow \quad \rho < \frac{\beta}{\gamma} - 1$$

and

$$\rho < \frac{\beta}{\gamma} - 1 \quad \Rightarrow \quad \frac{\beta}{\gamma} - 1 > 0 \quad \Leftrightarrow \quad 0 < \gamma < \beta.$$

Therefore, under conditions of (4), $|A(1, 0)| < 0$. □

Theorem 5.2.2. (1) If $0 < \gamma < \beta$, $\rho < \frac{\beta}{\gamma} - 1$ and $0 \leq \alpha < 1 - \frac{\gamma}{\beta - \gamma\rho}$,

then the equilibrium point $(1, 0)$ is a saddle for (5.1.3).

(2) If $0 < \gamma \leq \beta$, $0 \leq \rho \leq \frac{\beta}{\gamma} - 1$ and $1 - \frac{\gamma}{\beta - \gamma\rho} = \alpha < 1$,

then the equilibrium point $(1, 0)$ is a saddle-node for (5.1.3).

(3) If one of the following holds:

(i) $0 < \gamma \leq \beta$, $0 \leq \rho \leq \frac{\beta}{\gamma} - 1$ and $1 - \frac{\gamma}{\beta - \gamma\rho} < \alpha < 1$;

(ii) $\max\{0, \frac{\beta}{\gamma} - 1\} < \rho \leq \frac{\beta}{\gamma}$ and $0 \leq \alpha < 1$;

(iii) $\beta > 0$, $\gamma > 0$, $\rho > \frac{\beta}{\gamma}$, and $0 \leq \alpha \leq 1$,

then the equilibrium point $(1, 0)$ is a stable node for (5.1.3).

Proof. First, we need derive $\text{tr}(A(1, 0))$ from jacobian matrix (5.2.5):

$$\text{tr}(A(1, 0)) = \frac{\beta(1 - \alpha)}{1 + \rho(1 - \alpha)} - \gamma - 1 = -|A(1, 0)| - 1$$

(1) If $0 < \gamma < \beta$, $\rho < \frac{\beta}{\gamma} - 1$, and $0 \leq \alpha < 1 - \frac{\gamma}{\beta - \gamma\rho}$, then by Lemma 5.2.2 we have $|A(1, 0)| < 0$. Thus, $(1, 0)$ is a saddle for (5.1.3) by Lemma 2.3.1.

(2) By (5.2.5), if $0 < \gamma \leq \beta$, $0 \leq \rho \leq \frac{\beta}{\gamma} - 1$ and $1 - \frac{\gamma}{\beta - \gamma\rho} = \alpha < 1$, then

$$|A(1, 0)| = \frac{(1 - \alpha)(\gamma\rho - \beta) + \gamma}{1 + \rho(1 - \alpha)} = 0.$$

In addition, since $\text{tr}(A(1, 0)) = -|A(1, 0)| - 1 = -1 \neq 0$, we now apply transformation theory to system (5.1.3) according to Lemma 2.4.1:

Suppose $u_1 = u - 1$, $v_1 = v$ and we choose another time period for u_1 : $d\hat{t} = [1 + \rho(u - \alpha)]d\bar{t}$. Then, substituting above three new expressions into the original system (5.1.3), we have:

$$\begin{aligned} \dot{u}_1 &= [1 + \rho(u_1 + 1 - \alpha)][(u_1 + 1)(1 - u_1 - 1)] - (u_1 + 1 - \alpha)v_1 \\ &= [1 + \rho(u_1 + 1 - \alpha)](-u_1^2 - u_1) - u_1v_1 - (1 - \alpha)v_1 \\ &= -u_1^2 - u_1^2\rho(u_1 + 1 - \alpha) - u_1 - u_1\rho(u_1 + 1 - \alpha) - u_1v_1 - (1 - \alpha)v_1 \\ &= -u_1^2 - u_1^3\rho - u_1^2\rho + u_1^2\rho\alpha - u_1^2\rho - u_1\rho + u_1\rho\alpha - u_1 - u_1v_1 - (1 - \alpha)v_1 \\ &= -\rho u_1^3 - (2\rho - \rho\alpha + 1)u_1^2 - (\rho - \rho\alpha + 1)u_1 - u_1v_1 - (1 - \alpha)v_1 \end{aligned}$$

$$\begin{aligned} \dot{v}_1 &= \beta(u_1 + 1 - \alpha)v_1 - \gamma v_1[1 + \rho(u_1 + 1 - \alpha)] \\ &= \beta u_1 v_1 + \beta v_1 - \alpha \beta v_1 - \gamma v_1 - \gamma \rho u_1 v_1 - \gamma \rho v_1 + \alpha \gamma \rho v_1 \\ &= (\beta - \gamma \rho)u_1 v_1 + (\beta - \alpha \beta - \gamma - \gamma \rho + \alpha \gamma \rho)v_1 \end{aligned}$$

We denote $\zeta = \beta - \alpha\beta - \gamma - \gamma\rho + \alpha\gamma\rho$, $\zeta_1 = \beta - \gamma\rho$, $\zeta_2 = 1 - \alpha$, $\zeta_3 = \rho\zeta_2 + 1$ and $\zeta_4 = \rho(\zeta_3 + 1)$. Using this regular transformation, (5.1.3) is equivalent to the following system:

$$\begin{cases} \dot{u}_1 = -\rho u_1^3 - \zeta_4 u_1^2 - u_1 v_1 - (\zeta_3 u_1 + \zeta_2 v_1), \\ \dot{v}_1 = \zeta_1 u_1 v_1 + \zeta v_1 \end{cases} \quad (5.2.6)$$

Because (5.2.6) still have the term $\zeta_3 u_1 + \zeta_2 v_1$ that does not belong to the set of convergent power series: $p(u_1, v_1) = \sum_{i+j=2, i, j \geq 0}^{\infty} a_{ij} u_1^i v_1^j$, we have to continue the regular transformation until we replace $\zeta_3 u_1 + \zeta_2 v_1$ by something in the form of $a_{ij} u_1^i v_1^j$.

Let $u_2 = \zeta_3 u_1 + \zeta_2 v_1$ and $v_2 = v_1$, then

$$\begin{aligned} \dot{u}_2 &= \zeta_3 \dot{u}_1 + \zeta_2 \dot{v}_1 \\ &= \zeta_3 [-\rho u_1^3 - \zeta_4 u_1^2 - u_1 v_1 - (\zeta_3 u_1 + \zeta_2 v_1)] + \zeta_2 (\zeta_1 u_1 v_1 + \zeta v_1) \\ &= \zeta_3 (-\rho u_1^3 - \zeta_4 u_1^2 - u_1 v_1) + \zeta_2 \zeta_1 u_1 v_1 - \zeta_3^2 u_1 - \zeta_3 \zeta_2 v_1 + \zeta_2 \zeta v_1 \\ &= \zeta_3 \left(-\rho \frac{(u_2 - \zeta_2 v_2)^3}{\zeta_3^3} - \zeta_4 \frac{(u_2 - \zeta_2 v_2)^2}{\zeta_3^2} - \frac{u_2 - \zeta_2 v_2}{\zeta_3} v_2 \right) + \zeta_2 \zeta_1 \frac{u_2 - \zeta_2 v_2}{\zeta_3} v_2 \\ &\quad - \zeta_3^2 \frac{u_2 - \zeta_2 v_2}{\zeta_3} - \zeta_3 \zeta_2 v_2 + \zeta_2 \zeta v_2 \\ &= -\rho \frac{(u_2 - \zeta_2 v_2)^3}{\zeta_3^2} - \zeta_4 \frac{(u_2 - \zeta_2 v_2)^2}{\zeta_3} - (u_2 - \zeta_2 v_2) v_2 + \zeta_2 \zeta_1 \frac{u_2 - \zeta_2 v_2}{\zeta_3} v_2 \\ &\quad - \zeta_3 u_2 + \zeta_2 \zeta v_2 \\ &= \frac{(u_2 - \zeta_2 v_2)}{\zeta_3} \left(-\rho \frac{(u_2 - \zeta_2 v_2)^2}{\zeta_3} - \zeta_4 (u_2 - \zeta_2 v_2) - \zeta_3 v_2 + \zeta_2 \zeta_1 v_2 \right) \\ &\quad - \zeta_3 u_2 + \zeta_2 \zeta v_2 \end{aligned}$$

and

$$\dot{v}_2 = \dot{v}_1 = \zeta_1 u_1 v_1 + \zeta v_1 = \zeta_1 \frac{(u_2 - \zeta_2 v_2)}{\zeta_3} v_2 + \zeta v_2.$$

Under the condition of $1 - \frac{\gamma}{\beta - \gamma\rho} = \alpha$, we can derive that

$$\zeta = \beta - \alpha\beta - \gamma - \gamma\rho + \alpha\gamma\rho = 0.$$

That is, the terms above with ζ should be equal to 0. Thus, $\zeta_2\zeta v_2 = 0$. Then, we obtain the following system which is equivalent to (5.2.6):

$$\begin{cases} \dot{u}_2 = \frac{(u_2 - \zeta_2 v_2)}{\zeta_3} \left(-\rho \frac{(u_2 - \zeta_2 v_2)^2}{\zeta_3} - \zeta_4(u_2 - \zeta_2 v_2) - \zeta_3 v_2 + \zeta_2 \zeta_1 v_2 \right) - \zeta_3 u_2, \\ \dot{v}_2 = \zeta_1 \frac{(u_2 - \zeta_2 v_2)^3}{\zeta_3} v_2. \end{cases} \quad (5.2.7)$$

In order to have the system (5.2.7) be in the form of $\dot{u}_1 = p(u_1, v_1)$ and $\dot{v}_1 = \varrho v_1 + q(u_1, v_1)$, we again use the transformation by letting $u_3 = v_2$ and $v_3 = u_2$. Finally, we have the following equivalent system that has required form as indicated in Lemma 2.4.1:

$$\begin{cases} \dot{u}_3 = \frac{(v_3 - \zeta_2 u_3)}{\zeta_3} \left(-\rho \frac{(v_3 - \zeta_2 u_3)^2}{\zeta_3} - \zeta_4(v_3 - \zeta_2 u_3) - \zeta_3 u_3 + \zeta_2 \zeta_1 u_3 \right) - \zeta_3 v_3, \\ \dot{v}_3 = \zeta_1 \frac{(v_3 - \zeta_2 u_3)^3}{\zeta_3} u_3. \end{cases} \quad (5.2.8)$$

Clearly, $\varrho = \zeta_3 \neq 0$ since $1 - \alpha > 0$. Besides, $a_{20} = -\frac{\zeta_4}{\zeta_3} \neq 0$. Therefore, the result of (2) follows by Lemma 2.4.1.

(3) We see the expression of $\text{tr}(A(1, 0))$ from above that if $|A(1, 0)| > 0$, then $\text{tr}(A(1, 0)) = -|A(1, 0)| - 1 < 0$. Next, we need to investigate $[\text{tr}(A(1, 0))]^2 - 4|A(1, 0)|$:

$$\begin{aligned} [\text{tr}(A(1, 0))]^2 - 4|A(1, 0)| &= (-|A(1, 0)| - 1)^2 - 4|A(1, 0)| \\ &= (|A(1, 0)|)^2 + 2|A(1, 0)| + 1 - 4|A(1, 0)| \\ &= (|A(1, 0)| - 1)^2. \end{aligned}$$

Since $(|A(1, 0)| - 1)^2 \geq 0$, it implies $[\text{tr}(A(1, 0))]^2 - 4|A(1, 0)| \geq 0$. Further, under conditions of (3)(i) – (iii), we have $|A(1, 0)| > 0$ by Lemma 5.2.2 (1)(2)(3). Thus, if one of (3)(i) – (iii) holds, the equilibrium point $(1, 0)$ is a stable node for (5.1.3) by Lemma 2.3.1. $\square$

Remark 5.2.2. As we discussed in Remark 5.2.1, when $\rho = 0$, (5.1.3) likewise becomes (4.1.2) whose stability analysis on equilibrium $(1, 0)$ is special case of Theorem 5.2.2. By adding the parameter ρ , (whose biological meaning is handling time for predators), we obtained similar outcomes as Theorem 4.2.1: in both models, the local stability of the boundary equilibrium $(1, 0)$ is one of saddle point, saddle-node or stable node under respective conditions. Moreover, in paper [8, 13], they did not specify the results of stability analysis on boundary equilibria as we did in Theorem 5.2.1 and Theorem 5.2.2.

Next, we will study the local stability of positive interior equilibrium (u^*, v^*) .

Lemma 5.2.3. *Substituting u^* and v^* of (5.1.10) into (5.2.2), we obtain the following new jacobian matrix at interior equilibrium (u^*, v^*) :*

$$A(u^*, v^*) = \begin{pmatrix} 1 - 2u^* - \frac{v^*(\beta - \gamma\rho)^2}{\beta^2} & -\frac{\gamma}{\beta} \\ \frac{v^*(\beta - \gamma\rho)^2}{\beta} & 0 \end{pmatrix}. \quad (5.2.9)$$

Proof. By (5.1.10), we have known the expressions of u^* and v^* in terms of parameters α , β , γ and ρ . Further, using those expressions to simplify each element of (5.2.2):

$$\begin{aligned} 1 - 2u^* - \frac{v^*}{[1 + \rho(u^* - \alpha)]^2} &= 1 - 2u^* - v^* \left(\frac{\gamma}{(u^* - \alpha)\beta} \right) \left(\frac{\gamma}{(u^* - \alpha)\beta} \right) \\ &= 1 - 2u^* - v^* \left[\frac{\gamma}{\left(\frac{\gamma}{\beta - \gamma\rho} \right)\beta} \right] \left[\frac{\gamma}{\left(\frac{\gamma}{\beta - \gamma\rho} \right)\beta} \right] \\ &= 1 - 2u^* - \frac{v^*(\beta - \gamma\rho)^2}{\beta^2}, \end{aligned}$$

$$-\frac{u^* - \alpha}{1 + \rho(u^* - \alpha)} = -(u^* - \alpha) \frac{\gamma}{(u^* - \alpha)\beta} = -\frac{\gamma}{\beta},$$

$$\frac{\beta v^*}{[1 + \rho(u^* - \alpha)]^2} = \beta \left(\frac{v^*(\beta - \gamma\rho)^2}{\beta^2} \right) = \frac{v^*(\beta - \gamma\rho)^2}{\beta},$$

$$\frac{\beta(u^* - \alpha)}{1 + \rho(u^* - \alpha)} - \gamma = \beta(u^* - \alpha) \frac{\gamma}{(u^* - \alpha)\beta} - \gamma = \beta \left(\frac{\gamma}{\beta} \right) - \gamma = 0.$$

Thus, $A(u^*, v^*)$ is obtained by replacing each element of (5.2.2) with $1 - 2u^* - \frac{v^*(\beta - \gamma\rho)^2}{\beta^2}$, $-\frac{\gamma}{\beta}$, $\frac{v^*(\beta - \gamma\rho)^2}{\beta}$ and 0 respectively.

□

Notation: Let $\alpha_0 = \frac{1}{2} - \frac{\gamma}{\beta - \gamma\rho}$, $\alpha_1 = 1 - \frac{\gamma}{\beta - \gamma\rho}$,

$$\alpha_2 = \frac{\gamma^2\rho}{(\beta - \gamma\rho)^2} + \frac{1}{2}, \quad \alpha_3 = 1 + \frac{4\gamma^4\rho^2}{(\beta - \gamma\rho)^4} + \frac{4\gamma^2(\gamma\rho + \beta)}{(\beta - \gamma\rho)^3}$$

and

$$\phi(\alpha) = \gamma^2((2\alpha - 1)(\beta - \gamma\rho)\rho + \gamma\rho + \beta) + \alpha(1 - \alpha)(\beta - \gamma\rho)^3.$$

Lemma 5.2.4. Assume that $0 < \gamma < \beta$ and $\frac{\beta}{\gamma} \geq 3 + 2\sqrt{2}$, then the following assertions hold:

(i) If

$$\frac{\frac{\beta}{\gamma} - 1 + \sqrt{(\frac{\beta}{\gamma} - 1)^2 - \frac{4\beta}{\gamma}}}{2} \leq \rho < \frac{\beta}{\gamma} - 1$$

or

$$0 < \rho \leq \frac{\frac{\beta}{\gamma} - 1 - \sqrt{(\frac{\beta}{\gamma} - 1)^2 - \frac{4\beta}{\gamma}}}{2} < \frac{\beta}{\gamma} - 1,$$

then $\alpha_2 \leq \frac{\sqrt{\alpha_3}}{2}$;

(ii) If

$$\frac{\frac{\beta}{\gamma} - 1 - \sqrt{(\frac{\beta}{\gamma} - 1)^2 - \frac{4\beta}{\gamma}}}{2} < \rho < \frac{\frac{\beta}{\gamma} - 1 + \sqrt{(\frac{\beta}{\gamma} - 1)^2 - \frac{4\beta}{\gamma}}}{2} < \frac{\beta}{\gamma} - 1,$$

then $\alpha_2 > \frac{\sqrt{\alpha_3}}{2}$.

Proof. First of all, we compare α_2 with $\frac{\sqrt{\alpha_3}}{2}$ by checking the result of $\alpha_2 - \frac{\sqrt{\alpha_3}}{2}$. If we obtain $\alpha_2 - \frac{\sqrt{\alpha_3}}{2} \leq 0$ under the corresponding conditions, then Lemma 5.2.4(i) holds.

$$\begin{aligned} \alpha_2 - \frac{\sqrt{\alpha_3}}{2} &= \frac{\gamma^2 \rho}{(\beta - \gamma \rho)^2} + \frac{1}{2} - \frac{\sqrt{\alpha_3}}{2} \\ &= \frac{2\gamma^2 \rho + (\beta - \gamma \rho)^2 - (\beta - \gamma \rho)^2 \sqrt{\alpha_3}}{2(\beta - \gamma \rho)^2} \\ &= \frac{[2\gamma^2 \rho + (\beta - \gamma \rho)^2]^2 - (\beta - \gamma \rho)^4 \alpha_3}{2(\beta - \gamma \rho)^2 [2\gamma^2 \rho + (\beta - \gamma \rho)^2 + (\beta - \gamma \rho)^2 \sqrt{\alpha_3}]} \\ &= \frac{[2\gamma^2 \rho + (\beta - \gamma \rho)^2]^2 - [(\beta - \gamma \rho)^4 + 4\gamma^4 \rho^2 + 4\gamma^2(\gamma \rho + \beta)(\beta - \gamma \rho)]}{2(\beta - \gamma \rho)^2 [2\gamma^2 \rho + (\beta - \gamma \rho)^2 + (\beta - \gamma \rho)^2 \sqrt{\alpha_3}]} \\ &= \frac{4\gamma^2 \rho(\beta - \gamma \rho)^2 - 4\gamma^2(\gamma \rho + \beta)(\beta - \gamma \rho)}{2(\beta - \gamma \rho)^2 [2\gamma^2 \rho + (\beta - \gamma \rho)^2 + (\beta - \gamma \rho)^2 \sqrt{\alpha_3}]} \\ &= \frac{4\gamma^2(\beta - \gamma)[\rho(\beta - \gamma \rho) - (\gamma \rho + \beta)]}{2(\beta - \gamma \rho)^2 [2\gamma^2 \rho + (\beta - \gamma \rho)^2 + (\beta - \gamma \rho)^2 \sqrt{\alpha_3}]} \\ &= \frac{-4\gamma^2(\beta - \gamma)(\rho^2 \gamma - \rho \beta + \gamma \rho + \beta)}{2(\beta - \gamma \rho)^2 [2\gamma^2 \rho + (\beta - \gamma \rho)^2 + (\beta - \gamma \rho)^2 \sqrt{\alpha_3}]} \end{aligned}$$

Let $\xi(\rho) = \rho^2 \gamma - \rho \beta + \gamma \rho + \beta$. Then, by factoring $\xi(\rho)$ with respect to ρ , we have:

$$\begin{aligned} \xi(\rho) &= \gamma(\rho^2 - \rho(\frac{\beta}{\gamma} - 1) + \frac{\beta}{\gamma}) \\ &= \gamma\left(\rho - \frac{\frac{\beta}{\gamma} - 1 + \sqrt{(\frac{\beta}{\gamma} - 1)^2 - \frac{4\beta}{\gamma}}}{2}\right)\left(\rho - \frac{\frac{\beta}{\gamma} - 1 - \sqrt{(\frac{\beta}{\gamma} - 1)^2 - \frac{4\beta}{\gamma}}}{2}\right). \end{aligned}$$

In order to let $\sqrt{(\frac{\beta}{\gamma} - 1)^2 - \frac{4\beta}{\gamma}}$ be well defined in real numbers, we must have $(\frac{\beta}{\gamma} - 1)^2 - \frac{4\beta}{\gamma} \geq 0$. That is,

$$(\frac{\beta}{\gamma} - 1)^2 - \frac{4\beta}{\gamma} = \frac{\beta^2}{\gamma^2} - \frac{6\beta}{\gamma} + 1 = [\frac{\beta}{\gamma} - (3 + 2\sqrt{2})][\frac{\beta}{\gamma} - (3 - 2\sqrt{2})] \geq 0.$$

Since $\beta > \gamma$, then $\frac{\beta}{\gamma} > 1 \Rightarrow \frac{\beta}{\gamma} - (3 - 2\sqrt{2}) > 0$. On the other hand, there must be $\frac{\beta}{\gamma} - (3 + 2\sqrt{2}) \geq 0$. Thus, $\frac{\beta}{\gamma} \geq 3 + 2\sqrt{2}$ such that $\sqrt{(\frac{\beta}{\gamma} - 1)^2 - \frac{4\beta}{\gamma}}$ be well defined in real numbers.

Besides, it is easy to verify that $\frac{\beta}{\gamma} - 1 > \sqrt{(\frac{\beta}{\gamma} - 1)^2 - \frac{4\beta}{\gamma}}$, which implies

$$\begin{aligned} 2(\frac{\beta}{\gamma} - 1) &> \frac{\beta}{\gamma} - 1 + \sqrt{(\frac{\beta}{\gamma} - 1)^2 - \frac{4\beta}{\gamma}} \\ \Rightarrow \frac{\beta}{\gamma} - 1 &> \frac{\frac{\beta}{\gamma} - 1 + \sqrt{(\frac{\beta}{\gamma} - 1)^2 - \frac{4\beta}{\gamma}}}{2}. \end{aligned}$$

For (i), if

$$\begin{aligned} \frac{\frac{\beta}{\gamma} - 1 + \sqrt{(\frac{\beta}{\gamma} - 1)^2 - \frac{4\beta}{\gamma}}}{2} &\leq \rho < \frac{\beta}{\gamma} - 1 \text{ or} \\ 0 < \rho &\leq \frac{\frac{\beta}{\gamma} - 1 - \sqrt{(\frac{\beta}{\gamma} - 1)^2 - \frac{4\beta}{\gamma}}}{2}, \end{aligned}$$

then $\alpha_2 \leq \frac{\sqrt{\alpha_3}}{2}$.

For (ii), if

$$\frac{\frac{\beta}{\gamma} - 1 - \sqrt{(\frac{\beta}{\gamma} - 1)^2 - \frac{4\beta}{\gamma}}}{2} < \rho < \frac{\frac{\beta}{\gamma} - 1 + \sqrt{(\frac{\beta}{\gamma} - 1)^2 - \frac{4\beta}{\gamma}}}{2},$$

then $\alpha_2 > \frac{\sqrt{\alpha_3}}{2}$.

□

Theorem 5.2.3. (1) If Lemma 5.2.4(i) holds and $0 \leq \alpha < \alpha_1 < \alpha_2 + \frac{\sqrt{\alpha_3}}{2}$, then (u^*, v^*) is asymptotically stable.

(2) Assume that Lemma 5.2.4(ii) holds. Then,

(i) (u^*, v^*) is unstable if $0 \leq \alpha < \alpha_2 - \frac{\sqrt{\alpha_3}}{2}$;

(ii) (u^*, v^*) is stable if $\alpha_2 - \frac{\sqrt{\alpha_3}}{2} \leq \alpha < 1 - \frac{\gamma}{\beta - \gamma\rho}$.

u^* and v^* satisfy $u^* > \alpha$ and $v^* > 0$ under either conditions of (1) or (2).

Proof. By (5.2.9), we have $\text{tr}(A(u^*, v^*))$ as following:

$$\begin{aligned}
\text{tr}(A(u^*, v^*)) &= 1 - 2u^* - \frac{v^*(\beta - \gamma\rho)^2}{\beta^2} \\
&= 1 - 2\left(\alpha + \frac{\gamma}{\beta - \rho\gamma}\right) - \left[\frac{\beta}{\gamma}\left(\alpha + \frac{\gamma}{\beta - \rho\gamma} - \left(\alpha + \frac{\gamma}{\beta - \rho\gamma}\right)^2\right)\frac{(\beta - \rho\gamma\rho)^2}{\beta^2}\right] \\
&= 1 - 2\left(\alpha + \frac{\gamma}{\beta - \rho\gamma}\right) - \left[\left(\alpha + \frac{\gamma}{\beta - \rho\gamma} - \left(\alpha + \frac{\gamma}{\beta - \rho\gamma}\right)^2\right)\frac{(\beta - \gamma\rho)^2}{\beta\gamma}\right] \\
&= \frac{(\beta - \gamma\rho)^2}{\beta\gamma} \left[\frac{\beta\gamma}{(\beta - \gamma\rho)^2} - 2\frac{\beta\gamma}{(\beta - \gamma\rho)^2}\left(\alpha + \frac{\gamma}{\beta - \rho\gamma}\right) \right. \\
&\quad \left. - \left(\alpha + \frac{\gamma}{\beta - \rho\gamma}\right)\left(1 - \alpha - \frac{\gamma}{\beta - \rho\gamma}\right)\right] \\
&= \frac{(\beta - \gamma\rho)^2}{\beta\gamma} \left[\frac{\beta\gamma - 2\alpha\beta\gamma}{(\beta - \gamma\rho)^2} - 2\frac{\beta\gamma^2}{(\beta - \gamma\rho)^3} - \alpha(1 - \alpha) + \frac{\alpha\gamma}{\beta - \gamma\rho} \right. \\
&\quad \left. - (1 - \alpha)\left(\frac{\gamma}{\beta - \gamma\rho}\right) + \frac{\gamma^2}{(\beta - \gamma\rho)^2}\right] \\
&= \frac{(\beta - \gamma\rho)^2}{\beta\gamma} \left[\frac{(\beta\gamma - 2\alpha\beta\gamma)(\beta - \gamma\rho) - 2\beta\gamma^2 + (2\alpha\gamma - \gamma)(\beta - \gamma\rho)^2 + \gamma^2(\beta - \gamma\rho)}{(\beta - \gamma\rho)^3} \right. \\
&\quad \left. - \alpha(1 - \alpha)\right] \\
&= \frac{(\beta - \gamma\rho)^2}{\beta\gamma} \left[\frac{\gamma(2\alpha - 1)(\beta - \gamma\rho)(\beta - \gamma\rho - \beta) + \gamma(\gamma\beta - \gamma^2\rho - 2\beta\gamma)}{(\beta - \gamma\rho)^3} - \alpha(1 - \alpha)\right] \\
&= \frac{(\beta - \gamma\rho)^2}{\beta\gamma} \left[\frac{-\gamma^2((2\alpha - 1)(\beta - \gamma\rho)\rho + \gamma\rho + \beta)}{(\beta - \gamma\rho)^3} - \alpha(1 - \alpha)\right] \\
&= \frac{1}{\beta\gamma(\beta - \gamma\rho)} [-\phi(\alpha)].
\end{aligned}$$

By (5.2.9), we have $|A(u^*, v^*)|$ as following:

$$|A(u^*, v^*)| = -\left(-\frac{\gamma}{\beta}\right)\left(\frac{v^*(\beta - \gamma\rho)^2}{\beta}\right) = \frac{v^*(\beta - \gamma\rho)^2\gamma}{\beta^2}.$$

Further, $\phi(\alpha)$ has the following alternate polynomial form with respect to α :

$$\begin{aligned}\phi(\alpha) &= \gamma^2((2\alpha - 1)(\beta - \gamma\rho)\rho + \gamma\rho + \beta) + \alpha(1 - \alpha)(\beta - \gamma\rho)^3 \\ &= -\alpha^2(\beta - \gamma\rho)^3 + \alpha(2\gamma^2(\beta - \gamma\rho)\rho + (\beta - \gamma\rho)^3) - \gamma^2(\beta - \gamma\rho)\rho + \gamma^3\rho + \gamma^2\beta.\end{aligned}$$

From above, the discriminant of $\phi(\alpha) = 0$ with respect to α denoted by Δ_α is:

$$\begin{aligned}\Delta_\alpha &= (2\gamma^2(\beta - \gamma\rho)\rho + (\beta - \gamma\rho)^3)^2 + 4(\beta - \gamma\rho)^3(-\gamma^2(\beta - \gamma\rho)\rho + \gamma^3\rho + \gamma^2\beta) \\ &= (\beta - \gamma\rho)^6 + 4\gamma^4(\beta - \gamma\rho)^2\rho^2 + 4(\beta - \gamma\rho)^3(\gamma^3\rho + \gamma^2\beta) \\ &= (\beta - \gamma\rho)^6 + 4\gamma^4(\beta - \gamma\rho)^2\rho^2 + 4\gamma^2(\beta - \gamma\rho)^3(\gamma\rho + \beta) \\ &= (\beta - \gamma\rho)^6\left(1 + \frac{4\gamma^4\rho^2}{(\beta - \gamma\rho)^4} + \frac{4\gamma^2(\gamma\rho + \beta)}{(\beta - \gamma\rho)^3}\right) \\ &= (\beta - \gamma\rho)^6\alpha_3.\end{aligned}$$

It implies that $\beta - \gamma\rho > 0$ by the condition of $\rho < \frac{\beta}{\gamma} - 1$ from Lemma 5.2.4. Therefore, we always have $\Delta_\alpha > 0$.

Using the roots form of $\phi(\alpha)$ in terms of α to factor $\phi(\alpha)$, we have

$$\begin{aligned}\phi(\alpha) &= (\beta - \gamma\rho)^3\left(\alpha - \frac{(2\gamma^2(\beta - \gamma\rho)\rho + (\beta - \gamma\rho)^3) + \sqrt{\Delta_\alpha}}{2(\beta - \gamma\rho)^3}\right) \\ &\quad \left(\alpha - \frac{(2\gamma^2(\beta - \gamma\rho)\rho + (\beta - \gamma\rho)^3) - \sqrt{\Delta_\alpha}}{2(\beta - \gamma\rho)^3}\right) \\ &= (\beta - \gamma\rho)^3\left[\alpha - \left(\frac{\gamma^2\rho}{(\beta - \gamma\rho)^2} + \frac{1}{2} + \frac{\sqrt{\alpha_3}}{2}\right)\right]\left[\alpha - \left(\frac{\gamma^2\rho}{(\beta - \gamma\rho)^2} + \frac{1}{2} - \frac{\sqrt{\alpha_3}}{2}\right)\right] \\ &= (\beta - \gamma\rho)^3\left[\alpha - \left(\alpha_2 + \frac{\sqrt{\alpha_3}}{2}\right)\right]\left[\alpha - \left(\alpha_2 - \frac{\sqrt{\alpha_3}}{2}\right)\right].\end{aligned}$$

We see from Δ_α that $\alpha_3 > 1$, which implies $\frac{1}{2} + \frac{\sqrt{\alpha_3}}{2} > 1$.

Thus,

$$\begin{aligned}\alpha_2 + \frac{\sqrt{\alpha_3}}{2} - \alpha_1 &= \frac{\gamma^2 \rho}{(\beta - \gamma \rho)^2} + \frac{1}{2} + \frac{\sqrt{\alpha_3}}{2} - \left(1 - \frac{\gamma}{\beta - \gamma \rho}\right) \\ &= \frac{\gamma^2 \rho}{(\beta - \gamma \rho)^2} + \frac{\gamma}{\beta - \gamma \rho} + \left(\frac{1}{2} + \frac{\sqrt{\alpha_3}}{2} - 1\right) > 0\end{aligned}$$

Moreover, since $0 \leq \alpha < \alpha_1$, it implies that $\alpha < \alpha_1 < \alpha_2 + \frac{\sqrt{\alpha_3}}{2}$.

(1) By Lemma 5.2.4 (i), we have $\alpha_2 - \frac{\sqrt{\alpha_3}}{2} \leq 0$ and $\alpha - (\alpha_2 - \frac{\sqrt{\alpha_3}}{2}) > 0$. Also, $\delta(\alpha) > 0$ by Lemma 5.1.2(1)(i). Thus,

$$\phi(\alpha) > 0 \Rightarrow \text{tr}(A(u^*, v^*)) < 0,$$

$$|A(u^*, v^*)| = \frac{v^*(\beta - \gamma \rho)^2 \gamma}{\beta^2} = \frac{\delta(\alpha)(\beta - \gamma \rho)^2}{\beta} > 0,$$

which implies (u^*, v^*) is asymptotically stable.

(2) By the conditions of (2), we have $\alpha_2 - \frac{\sqrt{\alpha_3}}{2} > 0$ by Lemma 5.2.4(ii). In addition,

$$\begin{aligned}\alpha_2 - \frac{\sqrt{\alpha_3}}{2} &= \frac{\gamma^2 \rho}{(\beta - \gamma \rho)^2} + \frac{1}{2} - \frac{\sqrt{\alpha_3}}{2} \\ &= \frac{2\gamma^2 \rho + (\beta - \gamma \rho)^2 - (\beta - \gamma \rho)^2 \sqrt{\alpha_3}}{2(\beta - \gamma \rho)^2} \\ &= \frac{2\gamma^2 \rho + (\beta - \gamma \rho)^2 - \sqrt{(\beta - \gamma \rho)^4 + 4\gamma^4 \rho^2 + 4\gamma^2(\gamma \rho + \beta)(\beta - \gamma \rho)}}{2(\beta - \gamma \rho)^2} \\ &= \frac{2\gamma^2 \rho + (\beta - \gamma \rho)^2 - \sqrt{(\beta - \gamma \rho)^4 + 4\gamma^4 \rho^2 + 4\gamma^2(\beta - \gamma \rho + 2\gamma \rho)(\beta - \gamma \rho)}}{2(\beta - \gamma \rho)^2} \\ &= \frac{2\gamma^2 \rho + (\beta - \gamma \rho)^2 - \sqrt{(\beta - \gamma \rho)^4 + 4\gamma^2[\gamma^2 \rho^2 + (\beta - \gamma \rho)^2 + 2\gamma \rho(\beta - \gamma \rho)]}}{2(\beta - \gamma \rho)^2} \\ &= \frac{2\gamma^2 \rho + (\beta - \gamma \rho)^2 - \sqrt{(\beta - \gamma \rho)^4 + 4\gamma^2[\gamma \rho + (\beta - \gamma \rho)]^2}}{2(\beta - \gamma \rho)^2}\end{aligned}$$

which means

$$\begin{aligned}
\alpha_2 - \frac{\sqrt{\alpha_3}}{2} &= \frac{2\gamma^2\rho + (\beta - \gamma\rho)^2 - \sqrt{(\beta - \gamma\rho)^4 + 4\gamma^2[\gamma\rho + (\beta - \gamma\rho)]^2}}{2(\beta - \gamma\rho)^2} \\
&< \frac{2\gamma^2\rho + (\beta - \gamma\rho)^2 - \sqrt{4\gamma^2[\gamma\rho + (\beta - \gamma\rho)]^2}}{2(\beta - \gamma\rho)^2} \\
&= \frac{2\gamma^2\rho + (\beta - \gamma\rho)^2 - 2\gamma[\gamma\rho + (\beta - \gamma\rho)]}{2(\beta - \gamma\rho)^2} \\
&= \frac{2\gamma^2\rho + (\beta - \gamma\rho)^2 - 2\gamma^2\rho - 2\gamma(\beta - \gamma\rho)}{2(\beta - \gamma\rho)^2} \\
&= \frac{(\beta - \gamma\rho)^2 - 2\gamma(\beta - \gamma\rho)}{2(\beta - \gamma\rho)^2} \\
&= \frac{1}{2} - \frac{\gamma}{\beta - \gamma\rho} \\
&< 1 - \frac{\gamma}{\beta - \gamma\rho}.
\end{aligned}$$

(i) By $0 \leq \alpha < \alpha_2 - \frac{\sqrt{\alpha_3}}{2}$, we have $\alpha - (\alpha_2 - \frac{\sqrt{\alpha_3}}{2}) < 0$ and $\delta(\alpha) > 0$ by Lemma 5.1.2(1)(i). Thus,

$$\begin{aligned}
\phi(\alpha) < 0 &\Rightarrow \text{tr}(A(u^*, v^*)) > 0, \\
|A(u^*, v^*)| &= \frac{v^*(\beta - \gamma\rho)^2\gamma}{\beta^2} = \frac{\delta(\alpha)(\beta - \gamma\rho)^2}{\beta} > 0.
\end{aligned}$$

With above conclusions of $\text{tr}(A(u^*, v^*)) > 0$ and $|A(u^*, v^*)| > 0$, the result of (2)(i) follows.

(ii) By $\alpha_2 - \frac{\sqrt{\alpha_3}}{2} \leq \alpha < 1 - \frac{\gamma}{\beta - \gamma\rho}$, we have $\alpha - (\alpha_2 - \frac{\sqrt{\alpha_3}}{2}) \geq 0$ and likewise $|A(u^*, v^*)| > 0$. Therefore, $\phi(\alpha) \geq 0 \Rightarrow \text{tr}(A(u^*, v^*)) \leq 0$ and we can conclude that (u^*, v^*) is stable by Lemma 2.3.1. $\square$

Remark 5.2.3. The results of Theorem 5.2.3 were also proved by Chen's paper in [8]. However, the author of [8] did not specify under what conditions $u^* > \alpha$. $u^* > \alpha$ has an important biological meaning that the constant prey refuge α should be strictly less than the whole population of prey u , because prey refuge is excluded from its greater group u .

From the proof of the Theorem 5.2.3, we have processed the expressions $|A(u^*, v^*)|$ and $\text{tr}(A(u^*, v^*))$, which are:

$$\text{tr}(A(u^*, v^*)) = \frac{-\phi(\alpha)}{\beta\gamma(\beta - \gamma\rho)}, \quad (5.2.10)$$

$$|A(u^*, v^*)| = \frac{v^*(\beta - \gamma\rho)^2\gamma}{\beta^2} = \frac{\delta(\alpha)(\beta - \gamma\rho)^2}{\beta}. \quad (5.2.11)$$

Let

$$\Omega(\alpha, \rho) := [\text{tr}(A(u^*, v^*))]^2 - 4|A(u^*, v^*)| \quad (5.2.12)$$

and for $0 < \gamma < \beta$, let

$$\omega(\beta, \gamma) = \beta^2 - 8\beta\gamma^2 + 4\gamma^2. \quad (5.2.13)$$

Lemma 5.2.5. (1) If $\frac{4\beta^2}{1+4\beta} \leq \gamma < \beta$, then $\Omega(0, 0) \geq 0$.

(2) If $\beta > 0$ and $\gamma > \max\{0, \frac{(2\beta - 1)}{4}\}$, then $\Omega'_\alpha(0, 0) > 0$.

(3) If $0 < \gamma < \beta$ and $0 \leq \alpha < \alpha_1$, then

$$\Omega''_\alpha(\alpha, 0) = \frac{12\beta^2}{\gamma^2} \left[\left(\alpha - \frac{1}{2}\right)^2 - \frac{\omega(\beta, \gamma)}{12\beta^2} \right]. \quad (5.2.14)$$

Proof. By (5.2.11) and (5.2.10), we have

$$\Omega(\alpha, \rho) = \left(\frac{-\phi(\alpha)}{\beta\gamma(\beta - \gamma\rho)} \right)^2 - 4 \frac{\delta(\alpha)(\beta - \gamma\rho)^2}{\beta}. \quad (5.2.15)$$

(1) Since $\Omega(0, 0) = \frac{\gamma^2}{\beta^2} - 4\beta[\frac{1}{4} - \alpha_0^2]$ and $\alpha_0 = \frac{1}{2} - \frac{\gamma}{\beta - \gamma\rho}$, we have

$$\begin{aligned} \Omega(0, 0) &= \frac{\gamma^2}{\beta^2} - \beta + 4\beta\left(\frac{1}{2} - \frac{\gamma}{\beta}\right)^2 = \frac{\gamma^2}{\beta^2} - 4\gamma + 4\frac{\gamma^2}{\beta^2} \\ &= \frac{\gamma}{\beta^2}(\gamma - 4\beta^2 + 4\beta\gamma) = \frac{\gamma(1 + 4\beta)}{\beta^2} \left(\gamma - \frac{4\beta^2}{1 + 4\beta} \right), \end{aligned}$$

from which we see that the result holds.

(2) By (5.2.15) with $\rho = 0$ and (5.1.9), we have for $\alpha \geq 0$,

$$\Omega(\alpha, 0) = \frac{\beta^2}{\gamma^2} \rho_1^2 - 4\beta \rho_0 = \frac{\beta^2}{\gamma^2} \left[\frac{\gamma^2}{\beta^2} - \alpha(\alpha - 1) \right]^2 - 4\beta \left[\frac{1}{4} - (\alpha - \alpha_0)^2 \right] \quad (5.2.16)$$

and

$$\Omega'_\alpha(\alpha, 0) = \frac{2\beta^2}{\gamma^2} \left[\frac{\gamma^2}{\beta^2} - \alpha(\alpha - 1) \right] (1 - 2\alpha) + 8\beta(\alpha - \alpha_0). \quad (5.2.17)$$

It follows that

$$\begin{aligned} \Omega'_\alpha(0, 0) &= \frac{2\beta^2}{\gamma^2} \left(\frac{\gamma^2}{\beta^2} - 0 \right) (1 - 2\alpha) + 8\beta(0 - \alpha_0) \\ &= 2 - 8\beta\alpha_0 = 2 - 8\beta(1/2 - \gamma/\beta) \\ &= 8 \left(\gamma - \frac{2\beta - 1}{4} \right) > 0. \end{aligned}$$

(3) By (4.2.13), we have for $\alpha \geq 0$,

$$\begin{aligned} \Omega''(\alpha, 0) &= \frac{2\beta^2}{\gamma^2} (2\alpha - 1)^2 - \frac{4}{\gamma^2} [\gamma^2 - \beta^2 \alpha(\alpha - 1)] + 8\beta \\ &= \frac{12\beta^2}{\gamma^2} \left[\left(\alpha - \frac{1}{2} \right)^2 - \frac{\beta^2 - 8\beta\gamma^2 + 4\gamma^2}{12\beta^2} \right] = \frac{12\beta^2}{\gamma^2} \left[\left(\alpha - \frac{1}{2} \right)^2 - \frac{\omega(\beta, \gamma)}{12\beta^2} \right]. \end{aligned}$$

The result (3) holds. □

Lemma 5.2.6. (1) If either $0 < \beta \leq 5/8$ and $0 < \gamma < \beta$ or $\beta > \frac{5}{8}$ and $0 < \gamma < \frac{\beta}{2\sqrt{2\beta-1}}$, then $\omega(\beta, \gamma) > 0$.

(2) If $\beta > \frac{5}{8}$ and $\frac{\beta}{2\sqrt{2\beta-1}} \leq \gamma < \beta$, then $\omega(\beta, \gamma) \leq 0$.

Proof. (1) If $0 < \gamma < \beta \leq 1/2$, then by (5.2.13), $\omega(\beta, \gamma) = \beta^2 + 4\gamma^2(1 - 2\beta) > 0$. If $\beta > 1/2$, then

$$\omega(\beta, \gamma) = 4(2\beta - 1) \left(\frac{\beta}{2\sqrt{2\beta-1}} + \gamma \right) \left(\frac{\beta}{2\sqrt{2\beta-1}} - \gamma \right). \quad (5.2.18)$$

It is easy to verify that if $1/2 < \beta \leq 5/8$, then $\beta \leq \frac{\beta}{2\sqrt{2\beta-1}}$. If $1/2 < \beta \leq 5/8$ and $0 < \gamma < \beta$ or $\beta > \frac{5}{8}$ and $0 < \gamma < \frac{\beta}{2\sqrt{2\beta-1}}$, then by (5.2.18), $\omega(\beta, \gamma) > 0$.

(2) Since $\beta > \frac{5}{8}$ and $\frac{\beta}{2\sqrt{2\beta-1}} \leq \gamma < \beta$, by (5.2.18) we have $\omega(\beta, \gamma) \leq 0$. $\square$

Lemma 5.2.7. (i) If $0 < \gamma < \beta$, $0 \leq \rho < \frac{\beta}{\gamma} - 1$, $\max\{0, \alpha_0\} \leq \alpha < \alpha_1$,

then $\phi(\alpha) > \delta(\alpha)$.

(ii) $2\gamma < \beta$, $0 \leq \rho < \frac{\beta}{\gamma} - 1$, $0 \leq \alpha < \alpha_0$, then $\phi(\alpha) < \delta(\alpha)$.

Proof.

$$\begin{aligned}
\phi(\alpha) - \delta(\alpha) &= \frac{\gamma^2((2\alpha - 1)(\beta - \gamma\rho)\rho + \gamma\rho + \beta)}{(\beta - \gamma\rho)^3} + \alpha(1 - \alpha) - (\alpha + \frac{\gamma}{\beta - \gamma\rho} - (\alpha + \frac{\gamma}{\beta - \gamma\rho})^2) \\
&= \frac{\gamma^2((2\alpha - 1)(\beta - \gamma\rho)\rho + \gamma\rho + \beta)}{(\beta - \gamma\rho)^3} - \frac{\gamma}{\beta - \gamma\rho} + \frac{2\alpha\gamma}{\beta - \gamma\rho} + (\frac{\gamma}{\beta - \gamma\rho})^2 \\
&= \frac{\gamma^2}{(\beta - \gamma\rho)^3}[(2\alpha - 1)(\beta - \gamma\rho)\rho + \gamma\rho + \beta + \beta - \gamma\rho] + \frac{\gamma(2\alpha - 1)}{\beta - \gamma\rho} \\
&= \frac{\gamma^2}{(\beta - \gamma\rho)^3}[(2\alpha - 1)(\beta - \gamma\rho)\rho + 2\beta] + \frac{\gamma(2\alpha - 1)}{\beta - \gamma\rho} \\
&= \frac{\gamma}{(\beta - \gamma\rho)^3}[\gamma((2\alpha - 1)(\beta - \gamma\rho)\rho + 2\beta) + (2\alpha - 1)(\beta - \gamma\rho)^2] \\
&= \frac{\gamma}{(\beta - \gamma\rho)^3}[(2\alpha - 1)(\beta - \gamma\rho)(\gamma\rho + \beta - \gamma\rho) + 2\gamma\beta] \\
&= \frac{\gamma}{(\beta - \gamma\rho)^3}[(2\alpha - 1)(\beta - \gamma\rho)\beta + 2\gamma\beta] \\
&= \frac{\beta\gamma}{(\beta - \gamma\rho)^3}[(2\alpha - 1)(\beta - \gamma\rho) + 2\gamma]
\end{aligned}$$

(i) Since $\alpha > \alpha_0$, we have

$$\begin{aligned}
\alpha > 1/2 - \frac{\gamma}{\beta - \gamma\rho} &\Leftrightarrow 2\alpha > 1 - \frac{2\gamma}{\beta - \gamma\rho} \\
&\Leftrightarrow 2\alpha - 1 > \frac{-2\gamma}{\beta - \gamma\rho} \\
&\Leftrightarrow (2\alpha - 1)(\beta - \gamma\rho) > -2\gamma \\
&\Leftrightarrow (2\alpha - 1)(\beta - \gamma\rho) + 2\gamma > 0
\end{aligned}$$

In addition, $0 \leq \rho < \frac{\beta}{\gamma} - 1$ gives that $\beta - \rho\gamma > \gamma > 0$, thus

$$\frac{\beta\gamma}{(\beta - \gamma\rho)^3}[(2\alpha - 1)(\beta - \gamma\rho) + 2\gamma] > 0$$

which means $\phi(\alpha) > \delta(\alpha)$.

Similarly for (ii), if $\alpha < \alpha_0$, then

$$\frac{\beta\gamma}{(\beta - \gamma\rho)^3}[(2\alpha - 1)(\beta - \gamma\rho) + 2\gamma] < 0$$

which means $\phi(\alpha) < \delta(\alpha)$. □

Theorem 5.2.4. *If $\beta > \frac{5}{8}$, $\max\{\frac{4\beta^2}{1+4\beta}, \frac{\beta}{2\sqrt{2\beta-1}}\} \leq \gamma < \beta$ and $\max\{0, \alpha_0\} \leq \alpha < \alpha_1$, then there exists $\rho_1^* \in (0, \frac{\beta}{\gamma} - 1)$ such that (u^*, v^*) is a stable node of (5.1.3) for $\rho \in [0, \rho_1^*]$.*

Proof. Since $\beta > \frac{5}{8}$, $\max\{\frac{4\beta^2}{1+4\beta}, \frac{\beta}{2\sqrt{2\beta-1}}\} \leq \gamma < \beta$, by Lemma 5.2.6 (2), we have $\omega(\beta, \gamma) \leq 0$. Since $\max\{0, \alpha_0\} \leq \alpha < \alpha_1$, by Lemma 5.2.5 (3), $\Omega''_\alpha(\alpha, 0) \geq 0$. By Lemma 5.2.5 (2),

$$\Omega'_\alpha(\alpha, 0) \geq \Omega'_\alpha(0, 0) > 0 \quad \text{for } \alpha \in [\max\{0, \alpha_0\}, \alpha_1].$$

This, together with Lemma 5.2.5 (1), implies

$$\Omega(\alpha, 0) > \Omega(0, 0) \geq 0 \quad \text{for } \alpha \in [\max\{0, \alpha_0\}, \alpha_1]. \quad (5.2.19)$$

By the continuity of u^* , v^* and $\Omega_\alpha(\alpha, \rho)$ at ρ and (5.2.19), for $\beta > \frac{5}{8}$,

$$\max\{\frac{4\beta^2}{1+4\beta}, \frac{\beta}{2\sqrt{2\beta-1}}\} \leq \gamma < \beta \quad \text{and} \quad \max\{0, \alpha_0\} \leq \alpha < \alpha_1,$$

there exists $\rho_1^* \in (0, \frac{\beta}{\gamma} - 1)$ such that

$$\Omega(\alpha, \rho) > 0 \quad \text{for } \rho \in [0, \rho_1^*].$$

By (5.2.11) and (5.2.10), $|A(u^*, v^*)| > 0$ and $\text{tr}(A(u^*, v^*)) < 0$. The result follows from Lemma 2.3.1 (3). $\square$

Remark 5.2.4. Theorem 5.2.4 is new to the paper [13, 8]. Both authors did not discuss the cases under what suitable conditions the positive interior equilibrium (u^*, v^*) is a stable node. By taking limit and continuity of ρ , we concluded that under conditions of Theorem 5.2.4, (u^*, v^*) is a stable node. Through the whole chapter, we used a new method by applying transformation theory and modified (5.1.2) into the equivalent model (5.1.3) and then discussed the equilibrium points and phase portraits. By using this new method, we also verified the results of [13, 8] in Theorem 5.1.2 and 5.2.3.

In addition, Lemma 5.2.7 is useful for future studies when we introduce an harvesting (a new parameter η) into our model (5.1.3). We are currently still studying the stability of this new model with η and have made a initial conclusion that $\text{tr}(A(u^*, v^*))$ (with η) is closely related to $\phi(\alpha) - \delta(\alpha)$.

Chapter 6

Graphs and Simulations

6.1 Simulation for Lotka-Volterra Equilibria

We have studied the classical Lotka-Volterra predator-prey model in Section 3.1 by using transformation. Remember that the original model is:

$$\begin{cases} \dot{x} = rx - cxy, \\ \dot{y} = exy - dy, \end{cases} \quad (6.1.1)$$

where $x(t)$ and $y(t)$ ($\dot{x} = \frac{dx(t)}{dt}$, $\dot{y} = \frac{dy(t)}{dt}$) denote the density of prey and predator populations at time t , respectively; parameter r is the natural growth rate of the prey, while c is the per capita rate of predation of the predator (fraction of the prey population eaten per predator), e is a conversion rate of eaten prey into new predator abundance, d is the per capita death rate of the predator.

Let $\bar{t} = rt$, $u(\bar{t}) = \frac{ex(t)}{d}$, and $v(\bar{t}) = \frac{cy(t)}{r}$, then by applying the transformation

to (6.1.1), we obtain the following equivalent system¹:

$$\begin{cases} \dot{u} = u - uv, \\ \dot{v} = \alpha(uv - v), \end{cases} \quad (6.1.2)$$

where $\alpha = \frac{d}{r}$ and has the same biological meaning as d . Apparently, $\alpha > 0$ since d and r must be positive.

Theorem 3.1.2 indicates that the system (6.1.2) has two positive equilibria $(0, 0)$ and $(1, 1)$ with the latter one positive interior. Further, the origin $(0, 0)$ is a saddle while the other equilibrium point $(1, 1)$ is a centre. Based on the system (6.1.2), we simulate the solution behavior around two equilibrium points. By setting $\alpha = 1$, Figure 6.1a illustrates the simulation result of interior positive equilibrium $(1, 1)$.

Clearly, the simulated solutions to the system (6.1.2) are circling around the interior positive equilibrium $(1, 1)$. Figure 6.1b shows the evidence that boundary equilibrium $(0, 0)$ is a saddle whereas $(1, 1)$ is a centre. It is feasible that both equilibrium points $((0, 0)$ and $(1, 1))$ can exist in one system.

(a) Lotka-Volterra Interior Equilibrium

(b) Lotka-Volterra Positive Equilibria

Figure 6.1: Equilibria for Lotka-Volterra

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¹For detailed transformation process, please refer to the Page 15 in Section 3.1

6.2 Simulation For Type I Functional Response

We have introduced the concepts of Functional Responses in Section 3.4 and studied Lotka-Volterra model with type I functional response including the factors of capacity and constant prey refuge. Consider again the following model proposed by Ma in his paper[29]:

$$\begin{cases} \dot{x} = rx(1 - \frac{x}{k}) - c(x - p)y, \\ \dot{y} = -dy + e(x - p)y. \end{cases} \quad (6.2.1)$$

Compared with the model (6.1.1) mentioned in Section 6.1, we have two more parameters in the above system: k and p , which represent capacity and constant prey refuge respectively. $x(t)$ and $y(t)$ denotes the density of prey and predator populations at time t as well. r, c, e, d are all positive constants with identical biological meanings as explained in Section 6.1.

We developed another method to study the system (6.2.1) by using transformation: According to Theorem 4.1.1, by letting $\bar{t} = rt$, $u(\bar{t}) = \frac{x(t)}{k}$, $v(\bar{t}) = \frac{cy(t)}{r}$, we obtained the following equivalent system:

$$\begin{cases} \dot{u} = u(1 - u) - (u - \alpha)v := f(u, v), \\ \dot{v} = \beta(u - \alpha)v - \gamma v := g(u, v). \end{cases} \quad (6.2.2)$$

In Theorem 4.2.3, we proved that if $\beta > \frac{5}{8}$, $\max\{\frac{4\beta^2}{1 + 4\beta}, \frac{\beta}{2\sqrt{2\beta - 1}}\} \leq \gamma < \beta$ and $\max\{0, \alpha_0\} \leq \alpha < \alpha_1$, then (u^*, v^*) is a stable node of (6.2.2), where $\alpha_0 = \frac{1}{2} - \frac{\gamma}{\beta}$, $\alpha_1 = \frac{1}{2} + \alpha_0$. Now, we simulate the solution behavior around equilibrium points by setting α, β, γ under above conditions, and see if the interior positive equilibrium of (6.2.2) is a stable node. First, we set $\alpha = 0.5$, $\beta = 5$, $\gamma = 2$. Then by Theorem 4.1.2,

$$u^* = \frac{\gamma + \alpha\beta}{\beta} \quad \text{and} \quad v^* = \frac{(\gamma + \alpha\beta)(\beta - \gamma - \alpha\beta)}{\beta\gamma}.$$

We do the calculation $u^* = \frac{2 + 0.5 * 5}{5} = 0.9$ and $v^* = u^*(1 - u^*)\frac{\beta}{\gamma} = 0.9 * 0.1 * 2.5 = 0.225$. After simulation, Figure 6.2 shows that solutions expand toward the interior equilibrium point $(0.9, 0.225)$, and the type of solution behavior is proved to be a stable node.

Figure 6.2: Positive Interior of (6.2.2)

Next, we test another simulation by setting $\alpha = \frac{1}{3}$, $\beta = 2$ and $\gamma = 1$. Then, the positive interior equilibrium is $(0.833, 0.2778)$. Figure 6.3 illustrates that $(0.833, 0.2778)$ is a stable node. Theorem 4.1.2(ii) and Theorem 4.2.1(1)(2) are verified by 6.3b if $\alpha = \frac{1}{3}$, $\beta = 2$ and $\gamma = 1$. $(0, 0)$ and $(1, 0)$ show as saddle points and exist together with $(0.833, 2.778)$ in Figure 6.3b.

(a) ii. Positive Interior of (6.2.2)

(b) Positive Equilibria of (6.2.2)

Figure 6.3: Simulation For (6.2.2)

6.3 Simulation For Type II Functional Response

In Chapter 5, we have discussed the predator-prey model with type II functional response. Several papers such as [13, 8] studied the following system that is modified from (6.2.1):

$$\begin{cases} \dot{x} = rx(1 - \frac{x}{k}) - \frac{c(x-p)y}{1+m(x-p)}, \\ \dot{y} = \frac{e(x-p)y}{1+m(x-p)} - dy. \end{cases} \quad (6.3.1)$$

Parameters of r , k , c , p , e and d have same biological meanings we explained in Section 6.2. The only difference between (6.2.1) and (6.3.1) is the term that indicates the total number of prey killed by predators. In type I functional response, this term is expressed as $c(x-p)y$ while in type II functional response, it becomes $\frac{c(x-p)y}{1+m(x-p)}$. m is combination of attack rate a and handling time T' .²

Unlike the traditional method used in [13, 8], we developed a method by applying transformation. According to the Theorem 5.1.1, we let

$$\bar{t} = rt, \quad u(\bar{t}) = x(t)/k \quad \text{and} \quad v(\bar{t}) = cy(t)/r,$$

then (6.3.1) can be changed into the following equivalent system:

$$\begin{cases} \dot{u} = u(1-u) - \frac{(u-\alpha)v}{1+\rho(u-\alpha)} := f(u,v), \\ \dot{v} = \frac{\beta(u-\alpha)v}{1+\rho(u-\alpha)} - \gamma v := g(u,v) \end{cases} \quad (6.3.2)$$

where respectively, $\alpha = \frac{p}{k}$, $\beta = \frac{ek}{r}$, $\gamma = \frac{d}{r}$, and $\rho = mk$ have same biological meanings as p , e , d and m .

In the following, we will simulate the phase portraits of system (6.3.2) by setting specific values for $\alpha, \beta, \gamma, \rho$.

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²See Section 3.4 and Remark 3.4.1 for more details about how the time used on hunting T and handling time T' are related to type II functional response.

By Theorem 5.1.2, we need to satisfy $0 < \gamma < \beta$, $0 \leq \rho < \frac{\beta}{\gamma} - 1$, and $0 \leq \alpha < 1 - \frac{\gamma}{\beta - \gamma\rho}$, such that there are three equilibria for (5.1.3): $(0, 0)$, $(1, 0)$ and (u^*, v^*) satisfying $u^* > \alpha$ and $v^* > 0$, where (u^*, v^*) as the positive interior equilibrium with

$$u^* = \alpha + \frac{\gamma}{\beta - \gamma\rho} \quad \text{and} \quad v^* = \frac{\beta}{\gamma}u(1 - u).$$

For first example, we set $\alpha = \frac{1}{5}$, $\beta = 5$, $\rho = 1$ and $\gamma = 2$. We only tests the solution behavior around the positive interior equilibrium by using this simulation. Then, $u^* = \frac{1}{5} + \frac{2}{5-2} = \frac{13}{15} = 0.8667$ and $v^* = \frac{5}{2} * \frac{13}{15}(1 - \frac{13}{15}) = \frac{13}{45} = 0.2889$. If $\alpha = \frac{1}{5}$, $\beta = 5$, $\rho = 1$ and $\gamma = 2$, then they satisfy the conditions of Theorem 5.2.4: $\beta \geq 1$, $\frac{\beta}{2\sqrt{2\beta-1}} \leq \gamma \leq \frac{\beta}{2}$, $0 \leq \rho < \frac{\beta}{\gamma} - 1$ and $0 \leq \alpha < \alpha_0$. And the conclusion of Theorem 5.2.4 is that (u^*, v^*) is a stable node of (6.3.2) for $\rho \in [0, \rho_1^*]$ ³. The result of simulation shows in the Figure 6.4 below and we see that around the equilibrium point the phase portrait is a stable node.

Figure 6.4: Positive Interior of (6.3.2)

Now, we continue to another example of simulation. By setting $\alpha = \frac{1}{5}$, $\beta = 3.2$, $\rho = 0.5$ and $\gamma = 1.4$, we have $(u^*, v^*) = (0.76, 0.4169)$. $\alpha = \frac{1}{5}$, $\beta = 3.2$, $\rho = 0.5$ and $\gamma = 1.4$ satisfy the conditions of Theorem 5.2.1 (1)(ii) and Theorem

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³ $\rho_1^* \in (0, \frac{\beta}{\gamma} - 1)$

5.2.2(1) as well as Theorem 5.2.4. This time we simulate the solution behavior around all three positive equilibria in one plane. Figure 6.5a shows the stability of $(u^*, v^*) = (0.76, 0.4169)$. Indeed, $(0.76, 0.4169)$ is a stable node for the system (6.3.2). In addition, the boundary equilibria $(0, 0)$ and $(1, 0)$ are both saddle points. Thus, the results of Theorem 5.2.1 (1)(ii), Theorem 5.2.2(1) and Theorem 5.2.4 are verified by Figure 6.5.

Figure 6.5: Simulation For (6.3.2)

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