

# On the Global Analysis of Generalized Volterra-Lotka Models

A thesis submitted in partial fulfilment of the  
degree of Master of Scientific Studies of  
the University of New England  
February 1992

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*To  
Rizki , Gayuh & Our Parents*

## DECLARATION

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*I CERTIFY that:*

- 1. The substance of this thesis has not already been submitted for any degree and is not currently being submitted for any other degree.*
  - 2. Any help received in preparing this thesis, and all sources used, have been acknowledged in this thesis.*
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*Armidale, 4 February 1992*



*Maximus Gorky Sembiring*

## ACKNOWLEDGEMENTS

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*I AM especially grateful to Dr. C. J. Radford and Prof. E. N. Dancer for assistance in doing this thesis. I also would like to thanks Dr. B. Sims, Prof. S. A. Morris, Assoc. Prof. A. F. Horadam, Dr. G. J. Lewis, Dr. M. J. Canfell, Dr. J. E. Pegg, Mr. D. S. Poskitt, Mr. E. T. Baskoro and Mr. I. M. Tirta for their help during my study at the University of New England. Thanks are also extended to all staffs of the Department of Mathematics, Statistics and Computing Science and the many others without whose help I would never have been completed my study. Lastly, I would like to express my great gratitude to the International Development Program of Australian Universities and Colleges for funding and to the Universitas Terbuka Indonesia for allowing me to continue my study.*

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## ABSTRACT

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*STABILITY PROPERTIES of the generalized Volterra-Lotka models are investigated. The aim is to evaluate the given sufficient conditions and ultimately to improve the results in analysing global stability of the models. The application of the Poincare transformation and Lyapunov function are demonstrated in deriving the sufficient conditions and proving them respectively. At the same time, a set of sufficient conditions is established for a specific model of Volterra-Lotka type as a generalization. Some numerical examples and computer simulations of the models are also given to demonstrate how the theorems work and meet each other. Finally, the global properties of the models are revealed as much in a simple manner as possible.*

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## INTRODUCTION

A MATHEMATICAL model is the representation of a system or process in mathematical form, most commonly as an equation or set of equations.

As an example consider two or more species of animals. For simplicity, namely foxes and rabbits wherein one of which feeds on the other. Given the natural growth rates of the species and the effect of the interaction, what can be said on the growth of the species? This leads to a question of modelling which is known as *predator-prey* systems. Differential equations are ideally suited to describe the change of a given quantity as the time passes.

Even the simplest equations of population biology are nonlinear. Either predator-prey interactions, competing species or mutualism in ecological processes, for instance, consists of ordinary differential equations with quadratic right-hand sides. These models were first introduced by Vito Volterra about 70 years ago. Many investigations have since been conducted into this field of study.

### 1.1 GENERAL BACKGROUND

Recently there has been considerable interest in the generalized Volterra-Lotka models particularly in analysing global stability of systems of either two or more species interactions. Local stability of a critical point in systems of ordinary differential equations obviously does not necessarily imply its global stability. By giving a simple example, Goh (1976) showed that two-species interactions in Volterra-Lotka models may have a locally stable equilibrium without being globally stable. It also then follows that for many-species interactions the generalized Volterra-Lotka model whose nontrivial equilibrium is locally stable may not be globally stable (Goh, 1977). However, there are some specific conditions under which the local stability of the equilibrium of the generalized Volterra-Lotka model implies global stability.

In addition to Goh's work (1976, 1977), there is the work of Hsu (1978) who attempted to enrich the results by the use of the Poincare transformation as a tool for analysing the stability of the models. Hastings (1978) also extended and developed sufficient conditions for global stability of generalized Volterra-Lotka models whose the per capita growth rates are nonlinear. On the other hand, it is very unfortunate that the few global results that have been achieved up until now hold only under very restrictive hypothesis. The limitation, for example, is very weak results that could not be employed to real ecosystems (Krikorian, 1979). Furthermore, the results obtained in Hastings (1978), according to Kuang (1990), especially the last part of the theorem in establishing sufficient conditions for global stability if the per capita growth rates are nonlinear, is not rigorously proven. It is a well known fact that global analysis in higher dimension is far more relevant to ecology than that of local eigenvalue analysis.

The philosophy underpinning this thesis is inspired by those articles (Goh 1976, 1977 and Hsu, 1978). These projects, especially the former, proposed sufficient conditions not only for two-species systems to be globally stable but also for multispecies interactions of the generalized Volterra-Lotka models. This suggested the set of sufficient conditions of the models to be globally stable if it has a feasible equilibrium and at the same time there exists a positive diagonal matrix  $F$  such that  $FE + E^T F < 0$ . Yet, in two species systems, it is still likely to find a constant positive diagonal matrix  $F$  such that  $FE + E^T F$  is negative definite even though  $E + E^T$  is not negative definite. As a result, there is a set of three conditions specifically introduced by Goh (1976) which are sufficient for the systems to be globally stable, *viz.* it has a positive equilibrium in the feasible region, the equilibrium is locally stable, and both species sustain density-dependent mortalities due to intraspecific interactions.

Mathematically, the last part of the condition means that  $\epsilon_{ii} < 0$  ( $i = 1, 2$ ). As a matter of fact, we can still establish global stability of such models, in some cases, even if the condition  $\epsilon_{ii} < 0$  ( $i = 1, 2$ ) is violated; we do this by first subjecting the models to the so-called the Poincare transformation. The objective of this project is therefore to evaluate the given sufficient conditions and specifically to establish the set of sufficient conditions

under the Poincare transformation. It is also of interest to examine a specific Volterra-Lotka model and ultimately to construct its sufficient conditions.

Besides, the discussion, especially in giving a generalization and some numerical examples, is wittingly focussing on system of the two and three-species interactions only. This is so to avoid complicated computations; they are difficult to analyze and can have complicated behavior. In addition, according to Smale (1976), differential equations used in ecosystems to describe competing species do not reveal much if the number of species is more than three. At the same time, some numerical examples and simulations of the models are implemented to the system of two and three-species interactions. To find the eigenvalues of the corresponding matrices at the equilibria of the systems, available computer software, i. e., Matcalc is used. To implement numerical simulations, a simple program is created by using Minitab.

It is of interest that this thesis is ultimately enhancing the results that have been achieved by the preceding projects. These phenomena will therefore eliminate the point of view which says Volterra-Lotka model is too simple to realistically reflect the ecological processes. Finally, global properties of the solutions of the models will be revealed as much in a simple manner as possible on the basis that have just been described.

## 1.2 STABILITY IN ECOSYSTEMS

A general method to study stability in an ecosystems model is by an investigation of the eigenvalues of a matrix at an equilibrium. This method establishes stability only relative to small perturbations of the initial state. Therefore it is described as local stability of such model. In the concrete case, on the other hand, ecological processes are subjected to large perturbations of the initial state and dynamical systems. The most powerful analytical method for examining stability relative to finite perturbations of the initial state of the model is the direct method of Lyapunov. This is usually referred to as global stability. Hence the construction of a certain function, called Lyapunov function, is of course required.

Any point  $(x_0, y_0)$  such that  $F(x_0, y_0) = G(x_0, y_0) = 0$  is described as a *critical point* or *equilibrium point*. That is, if a system is at a stationary point at one instant in time, it will remain at that point at the next instant. The point that is *not* a critical point is termed as a *regular point*. The critical point, furthermore, could either be *stable* or *unstable*. If a system is disturbed slightly from the critical point and it returns to that point, then the critical point is called *stable*; more precisely, it possesses *neighborhood stability*. If, conversely, a system is disturbed slightly from a critical point and it continues to move further away from that point, then the critical point is *unstable* (Figure 1).

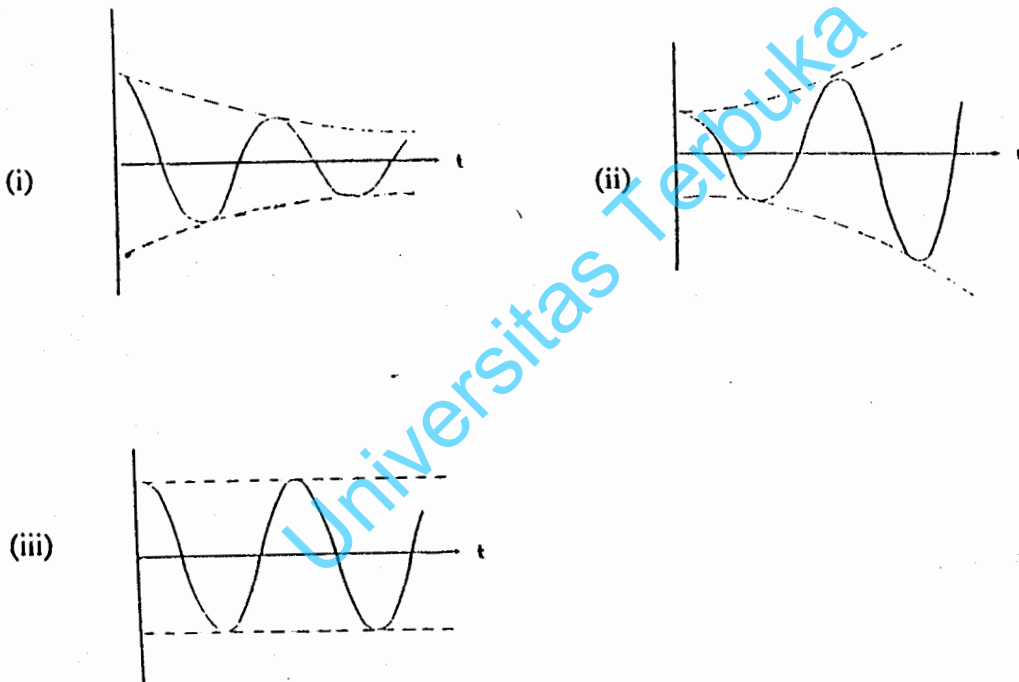


Figure 1: (i) Stable, (ii) Unstable and (iii) Asymptotically stable critical point

The functions  $F(x, y)$  and  $G(x, y)$  can be nonlinear. A solution, that is a curve of the system is described as a *trajectory*. It might be thought further of as the path of a particle moving in the *xy-plane* which is often called the *phase plane*. In the case of two trajectories which are *close* at some time and they remain *close* as  $t \rightarrow \infty$ , such situation is referred to as *asymptotic stability*. The behavior in the neighbourhood of the critical

point is a question of *local* stability and the larger matter of what happens in case the original state is not near critical point is one of *global* stability.

Most critical points are of one of the following types; they are *node*, *saddle point*, *centre* and *spiral point* (Figure. 2, 3, 4 and 5 respectively)

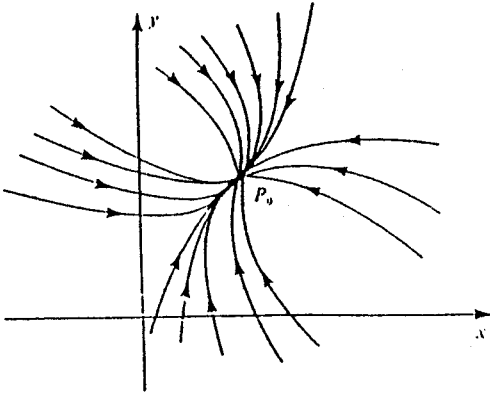


Figure 2: Node at  $P_0$

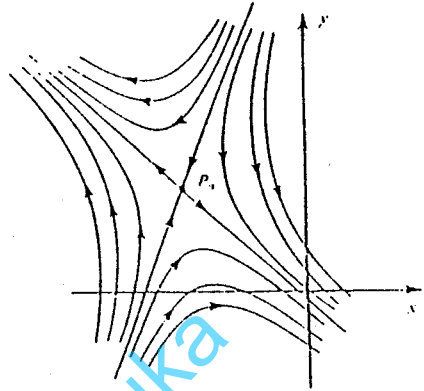


Figure 3: Saddle Point at  $P_0$

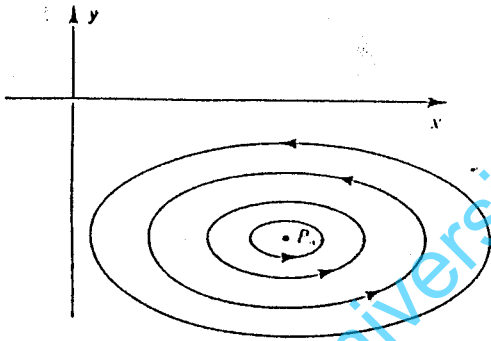


Figure 4: Centre at  $P_0$

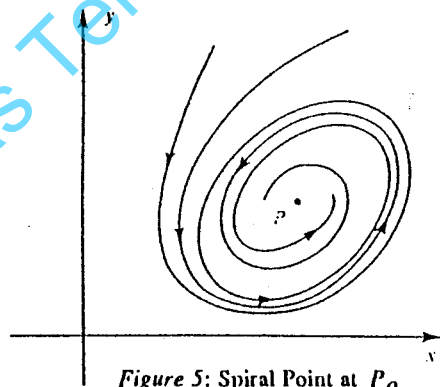


Figure 5: Spiral Point at  $P_0$

### Definition 1.1

Consider system of the form

$$X' = mx + ny$$

$$Y' = px + qy$$

(2)

with  $m, n, p$  and  $q$  are constants such that  $mq - np \neq 0$ . Then, the origin  $(0, 0)$  is the only critical point of the systems. If  $\lambda_1$  and  $\lambda_2$  are the roots of *characteristics* equation of the two by two matrix  $\begin{bmatrix} m & n \\ p & q \end{bmatrix}$ , and the roots are the *eigenvalues* of this matrix yields  $\lambda^2 - (m + q)\lambda + (mq - np) = 0$ , then there are *five possible cases*, viz.

CASE 1. If  $\lambda_1$  and  $\lambda_2$  are real, unequal and of the same sign, the critical point is termed as a node. It is asymptotically stable if  $\lambda_1, \lambda_2 < 0$  and it is unstable if  $\lambda_1, \lambda_2 > 0$ .

CASE 2. If  $\lambda_1$  and  $\lambda_2$  are real and equal, the critical point is called node. If  $\lambda_1 < 0$ , it is asymptotically stable; if  $\lambda_1 > 0$ , it is unstable.

CASE 3. If  $\lambda_1$  and  $\lambda_2$  are real, unequal and of opposite sign, the critical point is referred to as saddle point and it is unstable.

CASE 4. If  $\lambda_1$  and  $\lambda_2$  are in the form of complex conjugates with nonzero real parts, the critical point is described as a spiral point. If  $\lambda_1$  and  $\lambda_2$  have positive real parts, it is unstable. If  $\lambda_1$  and  $\lambda_2$  have negative real parts, it is asymptotically stable.

CASE 5. If  $\lambda_1$  and  $\lambda_2$  are pure imaginary, the critical point is a centre and it is stable.

In connection with the discussion on global stability as proposed by Goh (1976, 1977) and Hsu (1978), the case that is desired is particularly if  $\lambda_1$  and  $\lambda_2$  are having negative real parts (Goh, 1980).

### Definition 1.2

Consider system of the form

$$\begin{aligned} X' &= mx + ny + V(x, y) \\ Y' &= px + qy + W(x, y) \end{aligned} \tag{3}$$

Assume that

- (a)  $mq - np \neq 0$ ,  $V(x, y)$ ,  $W(x, y)$  have continuous first partial derivatives for  $x$  and  $y$

$$(b) \lim_{(x,y) \rightarrow (0,0)} \left\{ \frac{V(x,y)}{\sqrt{x^2 + y^2}} \right\} = \lim_{(x,y) \rightarrow (0,0)} \left\{ \frac{W(x,y)}{\sqrt{x^2 + y^2}} \right\} = 0$$

(c)  $(0, 0)$  is a critical point, i. e.,  $V(0, 0) = 0$  and  $W(0, 0) = 0$ .

Then, let  $\lambda_1$  and  $\lambda_2$  be the roots of  $\lambda^2 - (m + q)\lambda + (mq - np) = 0$ , the auxiliary equation of the associated linear system (2). Then, (2) and (3) both have the same behavior at  $(0, 0)$  in the following cases, viz.

CASE A. The system (3) and (2) have a node at  $(0, 0)$  if  $\lambda_1 = \lambda_2$  and real, except for  $m = q \neq 0$  and  $n = p = 0$ . If the latter occurs,  $(0, 0)$  is a node of the system (3), but may be either a node or spiral point of (2).

CASE B. The system (2) and (3) both have a node at  $(0, 0)$  if  $\lambda_1$  and  $\lambda_2$  are real, unequal and of the same sign.

CASE C. The system (2) and (3) both have a saddle point at  $(0, 0)$  if  $\lambda_1$  and  $\lambda_2$  are real and of opposite sign.

CASE D. The system (2) and (3) both have a spiral point at  $(0, 0)$  if  $\lambda_1$  and  $\lambda_2$  are complex conjugates with nonzero real parts.

#### 1.4 PREDATOR-PREY MODELS

Generally speaking, direct interactions between two or more species can be categorized into *three* classifications, they are:

- (i) *Predation* (+, -): one species (predator) has an inhibiting effect on the growth of the other (prey) and at the same time the prey has an enhancing effect on the predator
- (ii) *Competition* (-, -): each species has an inhibiting effect on the growth of the other
- (iii) *Mutualism* (+, +): each species has an accelerating effect on the growth of the other.

An *inhibiting* effect implies either a decrease in the birth rate or an increase in the death rate. Then let  $X$  be the prey density and  $Y$  the predator's with assumptions:

- (i) the density of a species is represented as a function of a single variable; age and sex differences are negligible

- (ii) there are no random effects in the environment influencing the interaction between  $X$  and  $Y$ ; changes in density are deterministic
- (iii) the effects of interactions within and between species are instantaneous; the delay between the moment a predator kills a prey as well as the moment when the ingested material is converted into part of a new predator are ignored.

In the absence of predators, it is expected that no inhibition in the growth of the prey.

A simple growth relation for  $X$  could be

$$X' = aX \quad (4)$$

where  $t$  is time and  $a$  is positive integer rate constant.

$$X = X_0 e^{at} \quad (5)$$

is the solution of ordinary differential equation (4); where  $X_0$  is the initial population density. According to (4),  $X$  will incline in time exponentially. Such growth behavior, however, is reasonable for a limited time only; gradually an enhancing population will exhaust its resources. Therefore,  $X$  will either settle down to some steady value, fluctuate between various level or decline.

Without prey, the predators  $Y$  are expected to decline in the absence of prey. Their decline can be represented in terms of the exponentially decaying solution

$$Y_0 e^{-bt}$$

of the differential equation

$$Y' = -bY \quad (6)$$

where  $b$  is constant integer. Similar to (5), the exponentially decreasing population of predators  $Y$  is only reasonable for a limited period of time, as  $Y$  becomes extinct in a finite rather than an infinite amount of time if lack of prey  $X$ .

Assuming, as Volterra-Lotka did, that in the absence of predation  $X$  follows a logistic growth curve and that the rate at which prey is killed is proportional to the product of the densities of predator and prey, then we are led to the following model

$$\begin{aligned} X' &= mX - nX^2 - pXY \\ Y' &= -qY + rXY \end{aligned} \tag{7}$$

where  $m, n, p, q$ , and  $r$  are all positive constants. The assumptions in (7) are valid under the following conditions: (Jones & Sleeman, 1983)

- (i) one or both species move at random
- (ii) when they meet, there is a constant probability that the predator will kill the prey
- (iii) the time taken by the predator to consume the prey is negligible.

Suppose, for instance, a constant number  $X^*$  of the prey can find some cover or refuge which makes them safe from the predator, system (7) is modified to the form

$$\begin{aligned} X' &= mX - nX^2 - pY(X - X^*) \\ Y' &= -qY + rY(X - X^*) \end{aligned} \tag{8}$$

## Chapter Two

## THE MODELS AND ANALYSIS

## 2.1 THE MODELS

The model to be considered here is the generalized Volterra-Lotka models for many-species interactions in which the species might be competitors, predators and prey, or otherwise related (Goh, 1977), that is

$$X_i'(t) = X_i(t) \left\{ \phi_i + \sum_{j=1}^n \varepsilon_{ij} X_j(t) \right\} \quad (9)$$

$X_i' = \frac{dX_i}{dt}$  denotes differentiation with respect to time  $t$  for  $i = 1, 2, \dots, n$  and  $\phi_i$  are positive constants. The growth coefficients are given by

$$\phi_i + \sum_{j=1}^n \varepsilon_{ij} X_j \quad (10)$$

A nontrivial equilibrium at  $(X_1^*, X_2^*, \dots, X_n^*)$  is a solution of

$$\phi_i + \sum_{j=1}^n \varepsilon_{ij} X_j = 0 \quad (10a)$$

for  $i = 1, \dots, n$  and matrix  $E = \varepsilon_{ij}$  is nonsingular. By definition, this equilibrium is feasible if  $X_i^* > 0$  for  $i = 1, \dots, n$ .

Volterra-Lotka models form the simplest class of nonlinear population models. A highly nonlinear population may always be approached by this model in the neighbourhood of the equilibrium. Therefore the analysis of a model of a community may provide more information on its stability properties of that community rather than the eigenvalues analysis of a more nonlinear model of the system.

## 2.2 THE LYAPUNOV FUNCTIONS

A general way of establishing global stability in system of differential equations is that of applying a Lyapunov function. All the same, in nonlinear system, it is not easy to find the appropriate one. The Lyapunov function itself, however, should have the following conditions (Goh, 1977), viz.

- (i) it should have a unique global minimum at the equilibrium
- (ii) its time derivative should be negative.

Goh (1976) proposed the Lyapunov function for model (9)

$$\psi = \sum_{i=1}^n f_i \{ X_i - X_i^* - X_i^* \ln (X_i/X_i^*) \} \quad (11)$$

with  $F = \text{diag} (f_1, f_2, \dots, f_n)$ . We need to show that (11) satisfies condition (i) and (ii) above, that is by letting

$$H(x) = x - x^* - x^* \ln (x/x^*)$$

where  $x^* > 0$ .

Then, it is clear that  $H(x)$  is defined for  $x > 0$ .

$$H'(x) = 1 - (x^*/x)$$

If  $0 < x < x^*$ , then  $H'(x) < 0$

If  $x > x^*$ , then  $H'(x) > 0$

Therefore  $H(x)$  has a global minimum at  $x^*$ , for  $x > 0$ . Condition (i) holds.

The time derivative of the  $\psi$  function in (11) computed along the solutions of (9), where  $\phi_i + \sum_{j=1}^n \epsilon_{ij} X_j = 0$ , as follows

$$\psi' = \sum_{i=1}^n f_i (X_i - X_i^*) (X_i^*/X_i)$$

$$\psi' = \frac{1}{2} [(X - X^*)^T (F E + E^T F) (X - X^*)] < 0$$

for all  $(X \neq X^*)$ , since  $(F E + E^T F) < 0$ , i. e.,  $(F E + E^T F)$  is negative definite. Condition (ii) holds.

Note: the complete description of this result is discussed in the part of Theorem 2.2.

### 2.3 LOCAL STABILITY

The usual method of studying two-species interactions of the generalized Volterra-Lotka models is by graphical analysis. Instead, the graphical analysis of the two-competing-species specifically suggests that local stability of the model implies its global stability. However, for model with three or more competing species, this result is not necessarily true. Moreover, for model whose having a single prey and a single predator system, it is likely to have a positive critical point which is just locally stable.

Consider model (9) for two-species systems, that is

$$X_i' = X_i \left\{ \phi_i + \sum_{j=1}^2 \epsilon_{ij} X_j \right\} \quad (12)$$

with  $i = 1, 2$ . Model (12), furthermore, can be written in the following form

$$\begin{aligned} X_1' &= X_1 (\phi_1 + \varepsilon_{11} X_1 + \varepsilon_{12} X_2) \\ X_2' &= X_2 (\phi_2 + \varepsilon_{21} X_1 + \varepsilon_{22} X_2) \end{aligned} \quad (13)$$

where  $\phi_i$  and  $\varepsilon_{ij}$  are positive constants. There are four possible nontrivial critical points of (13), denoted by  $(X_1^*, X_2^*)$ , given by

$$\begin{aligned} \text{(i)} \quad C_1 &= (0, 0), \quad \text{(ii)} \quad C_2 = (0, -\phi_2/\varepsilon_{22}), \quad \text{(iii)} \quad C_3 = (-\phi_1/\varepsilon_{11}, 0), \text{ and} \\ \text{(iv)} \quad C_4 &= \left( \frac{\phi_2 \varepsilon_{12} - \phi_1 \varepsilon_{22}}{\delta}, \frac{\phi_1 \varepsilon_{21} - \phi_2 \varepsilon_{11}}{\delta} \right) \end{aligned} \quad (14)$$

where  $\delta = (\varepsilon_{11} \varepsilon_{22} - \varepsilon_{12} \varepsilon_{21})$ . For feasible equilibrium we require

$$\phi_1 < \frac{\phi_2 \varepsilon_{12}}{\varepsilon_{22}}, \quad \phi_2 < \frac{\phi_1 \varepsilon_{21}}{\varepsilon_{11}} \text{ for } \delta > 0$$

and

$$\phi_1 > \frac{\phi_2 \varepsilon_{12}}{\varepsilon_{22}}, \quad \phi_2 > \frac{\phi_1 \varepsilon_{21}}{\varepsilon_{11}} \text{ for } \delta < 0$$

The diagonal elements of  $\varepsilon_{ij}$  give intraspecific interactions. If the equilibrium level of the first species  $X_1^*$  is low, it is possible that  $\varepsilon_{11} > 0$ . Whereas, if  $X_1^*$  is large, it is likely that  $\varepsilon_{11} < 0$ . This is to say that density-dependent mortalities due to intraspecific interactions occurred. Similar remarks apply to the relationship between  $X_2^*$  and  $\varepsilon_{22}$ .

System (13) is locally stable if it satisfies the following sufficient conditions, viz.

$$X_1^* \varepsilon_{11} + X_2^* \varepsilon_{22} < 0 \quad (15)$$

and

$$(X_1^* X_2^*) (\varepsilon_{11} \varepsilon_{22} - \varepsilon_{12} \varepsilon_{21}) > 0 \quad (16)$$

As neutral or asymptotic stability is irrelevant in theoretical ecology, therefore (15) and (16) are necessary and sufficient conditions for  $(X_1^*, X_2^*)$  to be locally stable which is known as Routh-Hurwitz stability criterion (see Goh, 1980).

In a two species competition,  $\epsilon_{12}, \epsilon_{21} < 0$ . In two species mutualism,  $\epsilon_{12}, \epsilon_{21} > 0$ .

It implies that for both cases,  $\epsilon_{12} \epsilon_{21} > 0$ . In order for (15) and (16) to be satisfied at  $X_1^*, X_2^* > 0$ , then  $\epsilon_{11}, \epsilon_{22}$  need to be negative. In a model of an interaction between a single prey and a single predator, it is not necessary for  $\epsilon_{11}$  and  $\epsilon_{22}$  to be both negative.

Correspondingly, in many species interactions, the nontrivial equilibrium given by  $(X_1^*, X_2^*, \dots, X_n^*)$  of model (9) is the solution of (10a). This model may have up to a maximum of  $2^n$  equilibrium (Goh, 1980; p. 187). By definition,  $X^*$  is a feasible (or positive) equilibrium if  $X_i^* > 0$  ( $i = 0, \dots, n$ ). Applying (10a) to (9), gives

$$X_i' = X_i \sum_{j=1}^n \epsilon_{ij} (X_j - X_j^*) \quad (17)$$

Provided that  $\epsilon_{ij} = F_i'(X_j)$  at  $X^*$  and  $X^*$  is the equilibrium of (9), then (17) is a local approximation of (9). The equilibrium  $X^*$  is locally stable if all the real parts of the eigenvalues of  $(X_i^* \epsilon_{ij})$  are negative. However, stability properties of the matrix  $(X_i^* \epsilon_{ij})$  can be different from those of the matrix  $E = (\epsilon_{ij})$ .

## 2.4 GLOBAL STABILITY ANALYSIS

There are two theorems introduced in this section as a tool for analysing global stability of the models. The first one is the theorem of many-species interactions. This theorem, proved by Goh (1977), implies that a Volterra-Lotka model has a globally stable feasible equilibrium provided there exists a positive diagonal matrix  $F$  such that  $FE + E^T F$  is negative definite [ $E$  is the matrix of interactions,  $E = (\epsilon_{ij})$ ]. The second one is the elaboration of sufficient conditions of the two-species systems (Goh, 1976).

**Theorem 2.1** (Goh, 1977)

Model (9) is globally stable if

- (i) it has a feasible equilibrium, i. e.,  $X_i^* > 0$ , for  $i = 1, \dots, n$
- (ii) there exists a constant positive diagonal matrix  $F$  such that  $FE + E^TF$  is negative definite

**Proof** (Following Goh, 1977)

In the universe of all possible  $n \times n$  matrices, the set of singular matrices is of measure zero. Hence for model which are not structurally unstable we can assume  $E$  to be nonsingular. This means that  $X_i^*$  ( $i = 1, \dots, n$ ) is a unique solution of

$$\phi_i + \sum_{j=1}^n \epsilon_{ij} X_j = 0 \quad (18)$$

It is obvious that for a viable biological system  $X_i^* > 0$ , for  $i = 1, \dots, n$ . Condition (ii) of the theorem means  $FE + E^TF < 0$  where  $F = \text{diag}(f_1, \dots, f_n)$ ,  $f_i > 0$  with  $i = 1, \dots, n$ . The appropriate Lyapunov function for the model is (11). Its time derivative computed along the solution of (9), with the help of (18), is

$$\begin{aligned} \psi' &= \sum_{i=1}^n f_i (X_i - X_i^*) (X_i' / X_i) \\ &= \sum_{i=1}^n f_i (X_i - X_i^*) \{X_i (\phi_i + \sum_{j=1}^n \epsilon_{ij} X_j) / X_i\} \\ &= \sum_{i=1}^n f_i (X_i - X_i^*) (\phi_i + \sum_{j=1}^n \epsilon_{ij} X_j) \end{aligned}$$

$$= \sum_{i=1}^n f_i (X_i - X_i^*) \sum_{j=1}^n \varepsilon_{ij} (X_j - X_j^*)$$

$$\psi' = \frac{1}{2} \{(X - X^*)^T (F E + E^T F) (X - X^*)\}$$

$(F E + E^T F) < 0$  for all  $(X \neq X^*)$ . Therefore,  $\psi' < 0$ . This means that the model is globally stable. This completes the proof.

Note: this result will be used in the next theorem.

In general cases, it is difficult to construct a constant positive diagonal matrix  $F$  such that  $F E + E^T F$  is negative semidefinite for  $n > 2$ . At the same time, when  $n = 2$ , it is still possible to find a constant positive diagonal matrix  $F$  such that  $F E + E^T F < 0$  even though matrix  $E + E^T$  is not negative definite. Goh (1976) established a set of sufficient conditions for a Volterra-Lotka model of the two-species systems, to be globally stable.

### Theorem 2.2 (Goh, 1976)

Model (13) is globally stable if

- (i) it has a feasible equilibrium
- (ii) the equilibrium is local asymptotically stable
- (iii) both species sustain density-dependent mortalities due to intraspecific interaction.

### Proof

Mathematically, condition (i) of the theorem means there exists  $X_1^* > 0$  and  $X_2^* > 0$ ; condition (ii) implies that  $\varepsilon_{11} \varepsilon_{22} - \varepsilon_{12} \varepsilon_{21} > 0$ ; condition (iii) implies  $\varepsilon_{11} < 0$  and  $\varepsilon_{22} < 0$ . By a graphical analysis of a given Volterra-Lotka model of the two-species systems, for the system to persist, its nontrivial equilibrium must be positive. As  $X_i^* > 0$ ,  $\varepsilon_{ii} < 0$

( $i = 1, 2$ ) and  $(\det \varepsilon_{ij}) > 0$  ( $i, j = 1, 2$ ), then (15) and (16) satisfied. Therefore the model is locally stable. It is clear, from (13), that

$$\begin{aligned}\phi_1 &= -\varepsilon_{11} X_1^* - \varepsilon_{12} X_2^* \\ \phi_2 &= -\varepsilon_{21} X_1^* - \varepsilon_{22} X_2^*\end{aligned}\tag{19}$$

Substituting (19) to (13), gives

$$\begin{aligned}X_1' &= X_1 (-\varepsilon_{11} X_1^* - \varepsilon_{12} X_2^* + \varepsilon_{11} X_1 + \varepsilon_{12} X_2) \\ X_2' &= X_2 (-\varepsilon_{21} X_1^* - \varepsilon_{22} X_2^* + \varepsilon_{21} X_1 + \varepsilon_{22} X_2)\end{aligned}\tag{20}$$

Equations (20) can be rewritten as follows

$$\begin{aligned}X_1' &= X_1 \{(X_1 - X_1^*) \varepsilon_{11} + (X_2 - X_2^*) \varepsilon_{12}\} \\ X_2' &= X_2 \{(X_1 - X_1^*) \varepsilon_{21} + (X_2 - X_2^*) \varepsilon_{22}\}\end{aligned}\tag{21}$$

A suitable Lyapunov function for this model, following from (11), is

$$\psi(x) = f_1 \{X_1 - X_1^* - X_1^* \ln (X_1/X_1^*)\} + f_2 \{X_2 - X_2^* - X_2^* \ln (X_2/X_2^*)\}\tag{22}$$

where  $f_1$  and  $f_2$  are positive constants. Along the solutions of (21), (22) becomes

$$\psi' = f_1 (X_1 - X_1^*) (X_1'/X_1) + f_2 (X_2 - X_2^*) (X_2'/X_2)$$

$$\begin{aligned}
 = & f_1 (X_1 - X_1^*)^2 \varepsilon_{11} + f_1 (X_1 - X_1^*) (X_2 - X_2^*) \varepsilon_{12} + \\
 & f_2 (X_2 - X_2^*) (X_1 - X_1^*) \varepsilon_{21} + f_2 (X_2 - X_2^*)^2 \varepsilon_{22}
 \end{aligned} \quad (23)$$

For convenience, let  $W_1 = (X_1 - X_1^*)$  and  $W_2 = (X_2 - X_2^*)$ . Then (23) can be written as

$$\psi' = (W_1)^2 f_1 \varepsilon_{11} + (W_1) (W_2) f_1 \varepsilon_{12} + (W_1) (W_2) f_2 \varepsilon_{21} + (W_2)^2 f_2 \varepsilon_{22} \quad (24)$$

Equation (24), however, can be expressed either as

$$\psi' = [W_1 \ W_2] \begin{bmatrix} f_1 & 0 \\ 0 & f_2 \end{bmatrix} \begin{bmatrix} \varepsilon_{11} & \varepsilon_{12} \\ \varepsilon_{21} & \varepsilon_{22} \end{bmatrix} \begin{bmatrix} W_1 \\ W_2 \end{bmatrix} \quad (25)$$

or

$$\psi' = [W_1 \ W_2] \begin{bmatrix} \varepsilon_{11} & \varepsilon_{21} \\ \varepsilon_{12} & \varepsilon_{22} \end{bmatrix} \begin{bmatrix} f_1 & 0 \\ 0 & f_2 \end{bmatrix} \begin{bmatrix} W_1 \\ W_2 \end{bmatrix} \quad (26)$$

From (25) and (26) we have

$$\begin{aligned}
 \psi' = & \frac{1}{2} \left\{ [W_1 \ W_2] \begin{bmatrix} f_1 & 0 \\ 0 & f_2 \end{bmatrix} \begin{bmatrix} \varepsilon_{11} & \varepsilon_{12} \\ \varepsilon_{21} & \varepsilon_{22} \end{bmatrix} \begin{bmatrix} W_1 \\ W_2 \end{bmatrix} + \right. \\
 & \left. [W_1 \ W_2] \begin{bmatrix} \varepsilon_{11} & \varepsilon_{21} \\ \varepsilon_{12} & \varepsilon_{22} \end{bmatrix} \begin{bmatrix} f_1 & 0 \\ 0 & f_2 \end{bmatrix} \begin{bmatrix} W_1 \\ W_2 \end{bmatrix} \right\}
 \end{aligned} \quad (27)$$

And so

$$\psi' = \frac{1}{2} \{ (W)^T (F E + E^T F) (W) \} \quad (28)$$

where  $W = \begin{bmatrix} W_1 \\ W_2 \end{bmatrix}$ ,  $E = \begin{bmatrix} \varepsilon_{11} & \varepsilon_{12} \\ \varepsilon_{21} & \varepsilon_{22} \end{bmatrix}$ ,  $F = \begin{bmatrix} f_1 & 0 \\ 0 & f_2 \end{bmatrix}$ .  $(W)^T$  and  $E^T$  are the matrix

transpose of  $W$  and  $E$  respectively.

We will apply the sufficient conditions for global stability that there exists a feasible equilibrium,  $X_1^*, X_2^* > 0$ , and positive diagonal matrix  $F$  exists so that  $FE + E^TF < 0$ .

$$\begin{aligned} FE + E^TF &= \begin{bmatrix} f_1 & 0 \\ 0 & f_2 \end{bmatrix} \begin{bmatrix} \epsilon_{11} & \epsilon_{12} \\ \epsilon_{21} & \epsilon_{22} \end{bmatrix} + \begin{bmatrix} \epsilon_{11} & \epsilon_{21} \\ \epsilon_{12} & \epsilon_{22} \end{bmatrix} \begin{bmatrix} f_1 & 0 \\ 0 & f_2 \end{bmatrix} \\ &= \begin{bmatrix} f_1 \epsilon_{11} & f_1 \epsilon_{12} \\ f_2 \epsilon_{21} & f_2 \epsilon_{22} \end{bmatrix} + \begin{bmatrix} f_1 \epsilon_{11} & f_2 \epsilon_{21} \\ f_1 \epsilon_{12} & f_2 \epsilon_{22} \end{bmatrix} \\ &= \begin{bmatrix} 2 f_1 \epsilon_{11} & f_1 \epsilon_{12} + f_2 \epsilon_{21} \\ f_2 \epsilon_{21} + f_1 \epsilon_{12} & 2 f_2 \epsilon_{22} \end{bmatrix} \end{aligned}$$

$$\begin{aligned} \det (FE + E^TF) &= (2 f_1 \epsilon_{11}) (2 f_2 \epsilon_{22}) - (f_2 \epsilon_{21} + f_1 \epsilon_{12}) (f_1 \epsilon_{12} + f_2 \epsilon_{21}) \\ &= 4 f_1 f_2 \epsilon_{11} \epsilon_{22} - \{f_1 f_2 \epsilon_{12} \epsilon_{21} + (f_2 \epsilon_{21})^2 + (f_1 \epsilon_{12})^2 + f_1 f_2 \epsilon_{12} \epsilon_{21}\} \\ &= 4 f_1 f_2 \epsilon_{11} \epsilon_{22} - \{(f_1 \epsilon_{12})^2 + 2 f_1 f_2 \epsilon_{12} \epsilon_{21} + (f_2 \epsilon_{21})^2\} \\ &= 4 f_1 f_2 \epsilon_{11} \epsilon_{22} - (f_1 \epsilon_{12} + f_2 \epsilon_{21})^2 \end{aligned} \tag{29}$$

$$\text{Therefore, } \begin{bmatrix} f_1 & 0 \\ 0 & f_2 \end{bmatrix} \begin{bmatrix} \epsilon_{11} & \epsilon_{12} \\ \epsilon_{21} & \epsilon_{22} \end{bmatrix} + \begin{bmatrix} \epsilon_{11} & \epsilon_{21} \\ \epsilon_{12} & \epsilon_{22} \end{bmatrix} \begin{bmatrix} f_1 & 0 \\ 0 & f_2 \end{bmatrix} < 0 \text{ if}$$

$$f_1 \epsilon_{11} < 0, \quad f_2 \epsilon_{22} < 0 \tag{30}$$

and

$$4 f_1 f_2 \epsilon_{11} \epsilon_{22} - (f_1 \epsilon_{12} + f_2 \epsilon_{21})^2 > 0 \tag{31}$$

It is clear that condition (iii) of the theorem implies  $\epsilon_{ii} < 0$ , and  $f_i > 0$  ( $i = 1, 2$ ).

Therefore, (30) holds. There are three possible cases for (31), they are:

$$(I) \ \varepsilon_{12} \ \varepsilon_{21} = 0, \quad (II) \ \varepsilon_{12} \ \varepsilon_{21} > 0, \quad (III) \ \varepsilon_{12} \ \varepsilon_{21} < 0$$

In case (I), either  $\varepsilon_{12} = 0$ ,  $\varepsilon_{21} = 0$  or  $\varepsilon_{12} = 0 = \varepsilon_{21}$ . If  $\varepsilon_{12} = 0$ , then (31) becomes

$$4 f_1 f_2 \ \varepsilon_{11} \ \varepsilon_{22} - (f_2 \ \varepsilon_{21})^2 > 0$$

or

$$f_2 \{4 f_1 \ \varepsilon_{11} \ \varepsilon_{22} - f_2 \ (\varepsilon_{21})^2\} > 0 \quad (32)$$

It is possible to choose  $f_1$  and  $f_2$  be positive numbers such that (32) holds. Next suppose that  $\varepsilon_{21} = 0$ . Then (31) becomes

$$4 f_1 f_2 \ \varepsilon_{11} \ \varepsilon_{22} - (f_1 \ \varepsilon_{12})^2 > 0$$

or

$$f_1 \{4 f_2 \ \varepsilon_{11} \ \varepsilon_{22} - f_1 \ (\varepsilon_{12})^2\} > 0 \quad (33)$$

Again we can choose  $f_1$  and  $f_2$  be positive so that (33) holds. If  $\varepsilon_{12} = 0$  and  $\varepsilon_{21} = 0$ , then obviously

$$4 f_1 f_2 \ \varepsilon_{11} \ \varepsilon_{22} > 0$$

As  $\varepsilon_{11} \ \varepsilon_{22} > 0$  we can choose  $f_1$  and  $f_2$  to be any positive numbers.

In case (II),  $\varepsilon_{12} \ \varepsilon_{21} > 0$ . This implies that either  $\varepsilon_{12}, \varepsilon_{21} < 0$  or  $\varepsilon_{12}, \varepsilon_{21} > 0$ .

Equation (31) can be written as

$$4 f_1 f_2 \ \varepsilon_{11} \ \varepsilon_{22} - \{(f_1 \ \varepsilon_{12})^2 + 2 f_1 f_2 \ \varepsilon_{12} \ \varepsilon_{21} + (f_2 \ \varepsilon_{21})^2\} > 0$$

$$4 f_1 f_2 \ \varepsilon_{11} \ \varepsilon_{22} - (f_1 \ \varepsilon_{12})^2 - 2 f_1 f_2 \ \varepsilon_{12} \ \varepsilon_{21} - (f_2 \ \varepsilon_{21})^2 > 0$$

$$4 f_1 f_2 \ \varepsilon_{11} \ \varepsilon_{22} - 4 f_1 f_2 \ \varepsilon_{12} \ \varepsilon_{21} - (f_1 \ \varepsilon_{12})^2 + 2 f_1 f_2 \ \varepsilon_{12} \ \varepsilon_{21} - (f_2 \ \varepsilon_{21})^2 > 0$$

$$4 f_1 f_2 (\epsilon_{11} \epsilon_{22} - \epsilon_{12} \epsilon_{21}) - (f_1 \epsilon_{12} - f_2 \epsilon_{21})^2 > 0 \quad (34)$$

As  $\epsilon_{12}$  and  $\epsilon_{21} > 0$  have the same sign we can always choose positive numbers for  $f_1$  and  $f_2$  such that

$$f_1 \epsilon_{12} = f_2 \epsilon_{21}$$

By assumption, the equilibrium is locally stable; i. e.,  $(\epsilon_{11} \epsilon_{22} - \epsilon_{12} \epsilon_{21}) > 0$ . Therefore (34) holds.

In case (III),  $\epsilon_{12} \epsilon_{21} < 0$ . This implies  $\epsilon_{12}$  and  $\epsilon_{21}$  are nonzero and having opposite signs. So, we can choose  $f_1$  and  $f_2$  to be positive numbers so that

$$f_1 \epsilon_{12} + f_2 \epsilon_{21} = 0$$

Now  $\epsilon_{11}, \epsilon_{22} < 0$  and  $f_1, f_2 > 0$ , hence (31) is satisfied. Thus, in all three cases,  $F$  can be chosen so that  $F E + E^T F < 0$ . Therefore,  $\psi' < 0$ . This completes the proof.

### Chapter Three

## STATEMENT OF RESULTS

### 3.1 THE POINCARÉ TRANSFORMATION

It is clear that Theorem 2.2 can only be applied to the generalized Volterra-Lotka models on condition that both species sustain density-dependent mortalities due to intraspecific interaction, i. e.,  $\epsilon_{ii} < 0$  for  $i = 1, 2$ . All the same, it is still likely to find global stability of such models despite the conditions being violated. This can be obtained by first subjecting the models to the Poincaré transformation. The goal here is to attempt this method in analysing the likelihood of globally stable of a local stability at infinity.

This procedure should enhance the result in Goh (1976), i.e., Theorem 2.2 especially in investigating the global stability of the more general models of Volterra-Lotka type. The global stability theorems, particularly of the two-species systems, are examined and some improvements are given in section 3.2 and 3.3.

To begin with, reconsider model (9). Introduce new variables (Hsu, 1978), for each  $i, 1 \leq i \leq n$  and  $j = 1, \dots, n$ ,

$$\begin{aligned} r_j &= \frac{X_j}{X_i} \quad (j \neq i), & r_j &= \frac{1}{X_i} \quad (j = i) \\ \text{or} & & & \\ X_j &= \frac{r_j}{r_i} \quad (j \neq i), & X_i &= \frac{1}{r_j} \quad (j = i) \end{aligned} \quad (35)$$

From (35),

$$X_j' = -r_j' / (r_i)^2, \quad \text{for } j = i \quad (36)$$

Under (35), called the Poincaré transformation, model (9) becomes

$$X_i' = X_i \left\{ \phi_i + \sum_{k=1}^n \varepsilon_{ik} X_k \right\}$$

$$j = 1, \dots, n$$

$$X_j' = X_j \left\{ \phi_j + \sum_{k=1}^n \varepsilon_{jk} X_k \right\}$$

For  $j = i$ ,

$$X_j' = \frac{1}{r_j} \left\{ \phi_j + \sum_{k=1}^{i-1} \varepsilon_{jk} X_k + \sum_{k=i+1}^n \varepsilon_{jk} X_k + \varepsilon_{ii} (1/r_i) \right\}$$

$$X_j' = \frac{1}{r_j} \left\{ \phi_j + \sum_{k=1}^{i-1} \varepsilon_{jk} (r_k/r_i) + \sum_{k=i+1}^n \varepsilon_{jk} (r_k/r_i) + \varepsilon_{ii} (1/r_i) \right\} \quad (37)$$

By (36), then (37) becomes

$$-r_j'/(r_i)^2 = 1/(r_i r_i) \left\{ r_i \phi_j + \sum_{k=1}^{i-1} \varepsilon_{jk} r_k + \sum_{k=i+1}^n \varepsilon_{jk} r_k + \varepsilon_{ii} \right\}$$

$$r_j' = - \left\{ (r_i \phi_j + \varepsilon_{ii}) + \sum_{k=1}^{i-1} \varepsilon_{jk} r_k + \sum_{k=i+1}^n \varepsilon_{jk} r_k \right\} \quad \text{for } j = i \quad (38)$$

For  $j \neq i$ ,  $r_j = \frac{X_j}{X_i}$ , then  $r_j' = \frac{X_j' X_i - X_j X_i'}{(X_i)^2}$

$$r_j' = \frac{X_i X_j}{(X_i)^2} \left\{ (\phi_j + \sum_{k=1}^n \varepsilon_{jk} X_k) - (\phi_i + \sum_{k=1}^n \varepsilon_{ik} X_k) \right\}$$

$$= \frac{X_j}{X_i} \left\{ (\phi_j - \phi_i) + \left( \sum_{k=1}^{i-1} \varepsilon_{jk} (r_k/r_i) + \sum_{k=i+1}^n \varepsilon_{jk} (r_k/r_i) + \varepsilon_{ji} (1/r_i) \right) \right.$$

$$\left. - \left( \sum_{k=1}^{i-1} \varepsilon_{ik} (r_k/r_i) + \sum_{k=i+1}^n \varepsilon_{ik} (r_k/r_i) + \varepsilon_{ii} (1/r_i) \right) \right\}$$

$$r_j' = \frac{X_j}{X_i} \frac{1}{r_i} \left\{ (r_i(\phi_j - \phi_i) + \sum_{k=1}^{i-1} \varepsilon_{jk} r_k + \sum_{k=i+1}^n \varepsilon_{jk} r_k + \varepsilon_{ji} - \sum_{k=1}^{i-1} \varepsilon_{ik} r_k - \sum_{k=i+1}^n \varepsilon_{ik} r_k - \varepsilon_{ii}) \right\}$$

$X_j = \frac{r_j}{r_i}$ ,  $X_i = \frac{1}{r_i}$ , then

$$r_j' = \frac{r_j}{r_i} \left\{ r_i(\phi_j - \phi_i) + \sum_{k=1}^{i-1} (\varepsilon_{jk} r_k - \varepsilon_{ik} r_k) + \sum_{k=i+1}^n (\varepsilon_{jk} r_k - \varepsilon_{ik} r_k) + (\varepsilon_{ji} - \varepsilon_{ii}) \right\}$$

$$r_j' = \frac{r_j}{r_i} \left\{ r_i(\phi_j - \phi_i) + (\varepsilon_{ji} - \varepsilon_{ii}) + \sum_{k=1}^{i-1} (\varepsilon_{jk} - \varepsilon_{ik}) r_k + \sum_{k=i+1}^n (\varepsilon_{jk} - \varepsilon_{ik}) r_k \right\} \quad (39)$$

### 3.2 RESULT 1

As mentioned early, it is clear that Theorem 2.2 can only be utilized to a Volterra-Lotka model on condition that  $\varepsilon_{11} < 0$  and  $\varepsilon_{22} < 0$ . All the same, it is still likely to find globally stable equilibrium eventhough conditions  $\varepsilon_{11} < 0$  and  $\varepsilon_{22} < 0$  are violated. We will establish sufficient conditions of such models by subjecting the model first to the Poincare transformation as introduced in section 3.1. Indeed, this will enable us to investigate more general models. In other words, the capability of Theorem 2.2 is improved particularly in investigating the two-species systems.

Reconsider model (13), that is

$$X_1' = X_1 (\phi_1 + \varepsilon_{11} X_1 + \varepsilon_{12} X_2) \quad (40a)$$

$$X_2' = X_2 (\phi_2 + \varepsilon_{21} X_1 + \varepsilon_{22} X_2) \quad (40b)$$

Introducing the new variables, following from (35) and with the help of (38) and (39), as follows

$$X_1 = \frac{1}{r_1}, \text{ then } X'_1 = -\frac{\dot{r}_1}{r_1^2}$$

and

$$X_2 = \frac{r_2}{r_1}, \text{ then } X'_2 = \frac{\dot{r}_2 r_1 - r_2 \dot{r}_1}{r_1^2} \quad (41)$$

Under (41), (40a) becomes

$$\begin{aligned} -\frac{\dot{r}_1}{r_1^2} &= \frac{1}{r_1} (\phi_1 + \epsilon_{11} \frac{1}{r_1} + \epsilon_{12} \frac{r_2}{r_1}) \\ \dot{r}_1 &= -r_1^2 \frac{1}{r_1} (\phi_1 r_1 + \epsilon_{11} + \epsilon_{12} r_2) \frac{1}{r_1} \\ \dot{r}_1 &= r_1 (-\epsilon_{11} - \phi_1 r_1 - \epsilon_{12} r_2)/r_1 \end{aligned} \quad (42a)$$

Equation (40b), under (41), becomes

$$\begin{aligned} \frac{\dot{r}_2 r_1 - r_2 \dot{r}_1}{r_1^2} &= \frac{r_2}{r_1} (\phi_2 + \epsilon_{21} \frac{1}{r_1} + \epsilon_{22} \frac{r_2}{r_1}) \\ \dot{r}_2 r_1 &= r_1 r_2 (\phi_2 r_1 + \epsilon_{21} + \epsilon_{22} r_2) \frac{1}{r_1} + r_2 \dot{r}_1 \\ \dot{r}_2 &= r_2 \frac{1}{r_1} (\epsilon_{21} + \phi_2 r_1 + \epsilon_{22} r_2) + r_2 \{r_1 (-\epsilon_{11} - \phi_1 r_1 - \epsilon_{12} r_2) \frac{1}{r_1}\} \\ \dot{r}_2 &= r_2 \{(\epsilon_{21} - \epsilon_{11}) + (\phi_2 - \phi_1) r_1 + (\epsilon_{22} - \epsilon_{12}) r_2\}/r_1 \end{aligned} \quad (42b)$$

From (42a),

$$(-\varepsilon_{11} - \phi_1 r_1^* - \varepsilon_{12} r_2^*)/r_1 = 0$$

$$-\varepsilon_{11} = \phi_1 r_1^* + \varepsilon_{12} r_2^* \quad (43a)$$

From (42b),

$$\{(\varepsilon_{21} - \varepsilon_{11}) + (\phi_2 - \phi_1) r_1^* + (\varepsilon_{22} - \varepsilon_{12}) r_2^*\}/r_1 = 0$$

$$\varepsilon_{21} - \varepsilon_{11} = -(\phi_2 - \phi_1) r_1^* - (\varepsilon_{22} - \varepsilon_{12}) r_2^*$$

$$\varepsilon_{21} = -(\phi_2 - \phi_1) r_1^* - (\varepsilon_{22} - \varepsilon_{12}) r_2^* + \varepsilon_{11}$$

$$= -(\phi_2 - \phi_1) r_1^* - (\varepsilon_{22} - \varepsilon_{12}) r_2^* - \phi_1 r_1^* - \varepsilon_{12} r_2^*$$

$$= -\phi_2 r_1^* + \phi_1 r_1^* - \varepsilon_{22} r_2^* + \varepsilon_{12} r_2^* - \phi_1 r_1^* - \varepsilon_{12} r_2^*$$

$$\varepsilon_{21} = -\phi_2 r_1^* - \varepsilon_{22} r_2^* \quad (43b)$$

Substituting (43a) and (43b) to (42a) and (42b) respectively, yields

$$r_1' = r_1 (\phi_1 r_1^* + \varepsilon_{12} r_2^* - \phi_1 r_1 - \varepsilon_{12} r_2)/r_1 \quad (44a)$$

$$r_2' = r_2 \{-\phi_2 r_1^* - \varepsilon_{22} r_2^* + \phi_1 r_1^* + \varepsilon_{12} r_2^* + (\phi_2 - \phi_1) r_1 + (\varepsilon_{22} - \varepsilon_{12}) r_2\}/r_1$$

$$= r_2 \{(-\phi_2 + \phi_1) r_1^* + (-\varepsilon_{22} + \varepsilon_{12}) r_2^* + (\phi_2 - \phi_1) r_1 + (\varepsilon_{22} - \varepsilon_{12}) r_2\}/r_1$$

$$= r_2 \{-(\phi_2 - \phi_1) r_1^* - (\varepsilon_{22} - \varepsilon_{12}) r_2^* + (\phi_2 - \phi_1) r_1 + (\varepsilon_{22} - \varepsilon_{12}) r_2\}/r_1$$

$$\dot{r}_2 = r_2 \{(\phi_2 - \phi_1)(r_1 - r_1^*) + (\varepsilon_{22} - \varepsilon_{12})(r_2 - r_2^*)\}/r_1 \quad (44b)$$

Equation (44a) and (44b) can be rewritten as follows

$$\begin{aligned} \dot{r}_1 &= r_1 \{-\phi_1(r_1 - r_1^*) - \varepsilon_{12}(r_2 - r_2^*)\}/r_1 \\ \dot{r}_2 &= r_2 \{(\phi_2 - \phi_1)(r_1 - r_1^*) + (\varepsilon_{22} - \varepsilon_{12})(r_2 - r_2^*)\}/r_1 \end{aligned} \quad (45)$$

This means that the equilibrium is mapped into the positive equilibrium

$$(r_1^*, r_2^*) = (1/X_1^*, X_2^*/X_1^*)$$

Rewrite equation (42a) and (42b),

$$\begin{aligned} \dot{r}_1 &= r_1 (-\varepsilon_{11} - \phi_1 r_1 - \varepsilon_{12} r_2)/r_1 \\ \dot{r}_2 &= r_2 \{(\varepsilon_{21} - \varepsilon_{11}) + (\phi_2 - \phi_1)r_1 + (\varepsilon_{22} - \varepsilon_{12})r_2\}/r_1 \end{aligned} \quad (46)$$

We are now in a position to prove the following theorem.

### Theorem 3.1

Model (40) is globally stable if:

- (i) there exists a feasible equilibrium, and
- (ii)  $\phi_1 > 0$ ,  $\varepsilon_{12} > \varepsilon_{22}$  and  $\varepsilon_{12} \phi_2 > \varepsilon_{22} \phi_1$

### Proof

A Lyapunov function for the model, following from (11), is

$$\psi = f_1 \{r_1 - r_1^* - r_1^* \ln(r_1/r_1^*)\} + f_2 \{r_2 - r_2^* - r_2^* \ln(r_2/r_2^*)\} \quad (47)$$

The time derivative of (47) is

$$\psi' = f_1 (r_1 - r_1^*) (\dot{r}_1/r_1) + f_2 (r_2 - r_2^*) (\dot{r}_2/r_2) \quad (48)$$

where  $\dot{r}_1$  and  $\dot{r}_2$  as in (45). Therefore,

$$\begin{aligned} \psi' = & f_1 (r_1 - r_1^*) r_1 \{-\phi_1 (r_1 - r_1^*) - \varepsilon_{12} (r_2 - r_2^*)\}/r_1 (1/r_1) + \\ & f_2 (r_2 - r_2^*) [r_2 \{(\phi_2 - \phi_1) (r_1 - r_1^*) + (\varepsilon_{22} - \varepsilon_{12}) (r_2 - r_2^*)\}/r_1 (1/r_2)] \end{aligned}$$

$$\begin{aligned} \psi' = & f_1 (r_1 - r_1^*) \{-\phi_1 (r_1 - r_1^*) - \varepsilon_{12} (r_2 - r_2^*)\}/r_1 + \\ & f_2 (r_2 - r_2^*) \{(\phi_2 - \phi_1) (r_1 - r_1^*) + (\varepsilon_{22} - \varepsilon_{12}) (r_2 - r_2^*)\}/r_1 \end{aligned}$$

$(\varepsilon_{22} - \varepsilon_{12}) = -(\varepsilon_{12} - \varepsilon_{22})$ , then

$$\begin{aligned} \psi' = & (1/r_1) \{-f_1 \phi_1 (r_1 - r_1^*)^2 - f_1 \varepsilon_{12} (r_1 - r_1^*) (r_2 - r_2^*) + \\ & f_2 (\phi_2 - \phi_1) (r_1 - r_1^*) (r_2 - r_2^*) - f_2 (\varepsilon_{12} - \varepsilon_{22}) (r_2 - r_2^*)^2\} \end{aligned} \quad (49)$$

For convenience, let  $(r_1 - r_1^*) = m$  and  $(r_2 - r_2^*) = n$ .

Then (49) can be written as

$$\begin{aligned} \psi' = & (1/r_1) \{-f_1 \phi_1 m^2 - f_1 \varepsilon_{12} m n + \\ & f_2 (\phi_2 - \phi_1) m n - f_2 (\varepsilon_{12} - \varepsilon_{22}) n^2\} \end{aligned} \quad (50)$$

Put  $A = \frac{m}{n}$ , or  $m = A n$ . Then (50) becomes

$$\begin{aligned} \psi' = & (1/r_1) \{-f_1 \phi_1 A^2 n^2 - f_1 \varepsilon_{12} A n^2 + \\ & f_2 (\phi_2 - \phi_1) A n^2 - f_2 (\varepsilon_{12} - \varepsilon_{22}) n^2\} \end{aligned}$$

$$\begin{aligned}
&= \frac{n^2}{r_1} \{-f_1 \phi_1 A^2 - f_1 \epsilon_{12} A + f_2 (\phi_2 - \phi_1) A - f_2 (\epsilon_{12} - \epsilon_{22})\} \\
&= \frac{n^2}{r_1} [-f_1 \phi_1 A^2 + \{f_2 (\phi_2 - \phi_1) - f_1 \epsilon_{12}\} A - f_2 (\epsilon_{12} - \epsilon_{22})] < 0
\end{aligned}$$

$\frac{n^2}{r_1} > 0$ ; so we require

$$G(A) = [-f_1 \phi_1 A^2 + \{f_2 (\phi_2 - \phi_1) - f_1 \epsilon_{12}\} A - f_2 (\epsilon_{12} - \epsilon_{22})] < 0$$

Now, as  $f_1 \phi_1 > 0$ ,  $G(A) < 0$  implies that the quadratic  $G(A) = 0$  can have no real roots for  $A$ , that is

$$\{f_2 (\phi_2 - \phi_1) - f_1 \epsilon_{12}\}^2 - 4 [-f_1 \phi_1 \{-f_2 (\epsilon_{12} - \epsilon_{22})\}] < 0$$

$$\{f_2^2 (\phi_2 - \phi_1)^2 + f_1^2 (\epsilon_{12})^2 - 2 f_1 f_2 \epsilon_{12} (\phi_2 - \phi_1) - 4 f_1 f_2 \phi_1 (\epsilon_{12} - \epsilon_{22})\} < 0$$

$$[f_2^2 (\phi_2 - \phi_1)^2 + f_1^2 (\epsilon_{12})^2 - 2 f_1 f_2 \{\epsilon_{12} (\phi_2 - \phi_1) + 2 \phi_1 (\epsilon_{12} - \epsilon_{22})\}] < 0 \quad (51)$$

We are required to show under what condition (51) is satisfied. Next, we let

$$C = \frac{f_2}{f_1} \quad \text{or} \quad f_2 = f_1 C$$

then (51) becomes

$$[f_1^2 C^2 (\phi_2 - \phi_1)^2 + f_1^2 (\epsilon_{12})^2 - 2 f_1^2 C \{\epsilon_{12} (\phi_2 - \phi_1) + 2 \phi_1 (\epsilon_{12} - \epsilon_{22})\}] < 0$$

$$[f_1^2 \{C^2 (\phi_2 - \phi_1)^2 + (\epsilon_{12})^2 - 2 C (\epsilon_{12} \phi_2 - \epsilon_{12} \phi_1 + 2 \epsilon_{12} \phi_1 - 2 \epsilon_{22} \phi_1)\}] < 0$$

$$[f_1^2 \{C^2 (\phi_2 - \phi_1)^2 + (\epsilon_{12})^2 - 2 C (\epsilon_{12} \phi_2 - \epsilon_{12} \phi_1 - 2 \epsilon_{22} \phi_1)\}] < 0$$

$$f_1^2 [C^2 (\phi_2 - \phi_1)^2 + (\epsilon_{12})^2 - 2 C \{(\epsilon_{12} \phi_2 - \epsilon_{22} \phi_1) + (\epsilon_{12} \phi_1 - \epsilon_{22} \phi_1)\}] < 0$$

$$f_1^2 [C^2 (\phi_2 - \phi_1)^2 + (\epsilon_{12})^2 - 2 C \{(\epsilon_{12} \phi_2 - \epsilon_{22} \phi_1) + \phi_1 (\epsilon_{12} - \epsilon_{22})\}] < 0 \quad (52)$$

We require (generally) real positive roots for  $C$  so that (52) holds. For our convenience, put

$$\alpha_1 = (\phi_2 - \phi_1) \quad ; \quad \alpha_1 \neq 0$$

$$\beta_1 = (\epsilon_{12} \phi_2 - \epsilon_{22} \phi_1) \quad (53)$$

$$\gamma_1 = \phi_1 (\epsilon_{12} - \epsilon_{22})$$

Substituting (53) to (52), to obtain solution for  $C$ , yields

$$f_1^2 \{C^2 (\alpha_1)^2 - 2 C (\beta_1 + \gamma_1) + (\epsilon_{12})^2\} = 0$$

$$C = \frac{2 (\beta_1 + \gamma_1) \pm \sqrt{4 (\beta_1 + \gamma_1)^2 - 4 (\alpha_1)^2 (\epsilon_{12})^2}}{2 (\alpha_1)^2}, \quad \alpha_1 \neq 0$$

$$= \frac{(\beta_1 + \gamma_1) \pm \sqrt{(\beta_1 + \gamma_1)^2 - (\alpha_1)^2 (\epsilon_{12})^2}}{(\alpha_1)^2}$$

$$(\beta_1 + \gamma_1) > 0 \text{ and } (\beta_1 + \gamma_1)^2 - (\alpha_1)^2 (\epsilon_{12})^2 > 0.$$

Now,

$$(\beta_1 + \gamma_1)^2 - (\alpha_1)^2 (\epsilon_{12})^2 > 0$$

i.e.,

$$(\beta_1 + \gamma_1 - \alpha_1 \epsilon_{12}) (\beta_1 + \gamma_1 + \alpha_1 \epsilon_{12}) > 0 \quad (54)$$

Substituting (53) to (54) to obtain

$$\{\epsilon_{12} \phi_2 - \epsilon_{22} \phi_1 + \phi_1 (\epsilon_{12} - \epsilon_{22}) - \epsilon_{12} (\phi_2 - \phi_1)\} \{\epsilon_{12} \phi_2 - \epsilon_{22} \phi_1 + \phi_1 (\epsilon_{12} - \epsilon_{22}) + \epsilon_{12} (\phi_2 - \phi_1)\} > 0$$

$$(\epsilon_{12} \phi_2 - \epsilon_{22} \phi_1 + \epsilon_{12} \phi_1 - \epsilon_{22} \phi_1 - \epsilon_{12} \phi_2 + \epsilon_{12} \phi_1) (\epsilon_{12} \phi_2 - \epsilon_{22} \phi_1 + \epsilon_{12} \phi_1 - \epsilon_{22} \phi_1 + \epsilon_{12} \phi_2 - \epsilon_{12} \phi_1) > 0$$

$$(2 \epsilon_{12} \phi_1 - 2 \epsilon_{22} \phi_1) (2 \epsilon_{12} \phi_2 - 2 \epsilon_{22} \phi_1) > 0$$

$$\{2 \phi_1 (\epsilon_{12} - \epsilon_{22})\} \{2 (\epsilon_{12} \phi_2 - \epsilon_{22} \phi_1)\} > 0$$

$$\{4 \phi_1 (\epsilon_{12} - \epsilon_{22}) (\epsilon_{12} \phi_2 - \epsilon_{22} \phi_1)\} > 0 \quad (55)$$

By assumption,

$$\phi_1 > 0, \epsilon_{12} > \epsilon_{22} \text{ and } \epsilon_{12} \phi_2 > \epsilon_{22} \phi_1$$

Therefore (55) is satisfied. This result implies that (48) is negative definite. Hence (40) is globally stable. This completes the proof.

### 3.3 RESULT II

As in Section 3.2, it is of interest to construct another sufficient condition for global stability model (40) where the Poincare transformation, following from (35) and with the help of (38) and (39), as follows

$$X_1 = \frac{r_1}{r_2}, \text{ then } X_1' = \frac{\dot{r}_1 r_2 - r_1 \dot{r}_2}{r_2^2}$$

and

$$X_2 = \frac{1}{r_2}, \text{ then } X_2' = -\frac{\dot{r}_2}{r_2^2}$$

(56)

Under (56), model (40b) becomes

$$-\frac{\dot{r}_2}{r_2^2} = \frac{1}{r_2^2} (\phi_2 + \varepsilon_{21} \frac{r_1}{r_2} + \varepsilon_{22} \frac{1}{r_2})$$

$$-\dot{r}_2 = r_2 (\phi_2 r_2 + \varepsilon_{21} r_1 + \varepsilon_{22}) \frac{1}{r_2}$$

$$\dot{r}_2 = r_2 (-\varepsilon_{22} - \varepsilon_{21} r_1 - \phi_2 r_2) / r_2$$

(57a)

Model (40a), under (56), becomes

$$\frac{\dot{r}_1 r_2 - r_1 \dot{r}_2}{r_2^2} = \frac{r_1}{r_2} (\phi_1 + \varepsilon_{11} \frac{r_1}{r_2} + \varepsilon_{12} \frac{1}{r_2})$$

$$\dot{r}_1 r_2 = r_2 r_1 (\phi_1 r_2 + \varepsilon_{11} r_1 + \varepsilon_{12}) \frac{1}{r_2} + r_1 \dot{r}_2$$

$$= r_2 r_1 (\phi_1 r_2 + \varepsilon_{11} r_1 + \varepsilon_{12})/r_2 + r_1 \{r_2 (-\varepsilon_{22} - \varepsilon_{21} r_1 - \phi_2 r_2)\}/r_2$$

$$\dot{r}_1 = r_1 \{(\varepsilon_{12} - \varepsilon_{22}) + (\varepsilon_{11} - \varepsilon_{21}) r_1 + (\phi_1 - \phi_2) r_2\}/r_2 \quad (57b)$$

Therefore,

$$\dot{r}_1 = r_1 \{(\varepsilon_{12} - \varepsilon_{22}) + (\varepsilon_{11} - \varepsilon_{21}) r_1 + (\phi_1 - \phi_2) r_2\}/r_2$$

(58)

$$\dot{r}_2 = r_2 (-\varepsilon_{22} - \varepsilon_{21} r_1 - \phi_2 r_2)/r_2$$

We are now going to prove the following theorem.

### Theorem 3.2

Model (40) is globally stable if:

- (i) there exists a feasible equilibrium, and
- (ii)  $\phi_2 > 0$ ,  $\varepsilon_{21} > \varepsilon_{11}$  and  $\varepsilon_{21} \phi_1 > \varepsilon_{11} \phi_2$

### Proof

From (58),

$$\{(\varepsilon_{12} - \varepsilon_{22}) + (\varepsilon_{11} - \varepsilon_{21}) r_1^* + (\phi_1 - \phi_2) r_2^*\}/r_2 = 0 \quad (59a)$$

$$(-\varepsilon_{22} - \varepsilon_{21} r_1^* - \phi_2 r_2^*)/r_2 = 0 \quad (59b)$$

From (59b),

$$\varepsilon_{22} = -\varepsilon_{21} r_1^* - \phi_2 r_2^* \quad (60a)$$

From (59a),

$$\begin{aligned}
 \varepsilon_{12} - \varepsilon_{22} &= -(\varepsilon_{11} - \varepsilon_{21}) r_1^* - (\phi_1 - \phi_2) r_2^* \\
 \varepsilon_{12} &= -(\varepsilon_{11} - \varepsilon_{21}) r_1^* - (\phi_1 - \phi_2) r_2^* - \varepsilon_{21} r_1^* - \phi_2 r_2^* \\
 &= -\varepsilon_{11} r_1^* + \varepsilon_{21} r_1^* - \phi_1 r_2^* + \phi_2 r_2^* - \varepsilon_{21} r_1^* - \phi_2 r_2^* \\
 &= -\varepsilon_{11} r_1^* - \phi_1 r_2^*
 \end{aligned} \tag{60b}$$

Substitute (60a) and (60b) to (58), yields

$$\begin{aligned}
 r_1' &= r_1 \{ -\varepsilon_{11} r_1^* - \phi_1 r_2^* + \varepsilon_{21} r_1^* + \phi_2 r_2^* + (\varepsilon_{11} - \varepsilon_{21}) r_1 + (\phi_1 - \phi_2) r_2 \} / r_2 \\
 &= r_1 \{ (\varepsilon_{21} - \varepsilon_{11}) r_1^* + (\phi_2 - \phi_1) r_2^* + (\varepsilon_{11} - \varepsilon_{21}) r_1 + (\phi_1 - \phi_2) r_2 \} / r_2 \\
 &= r_1 \{ (\varepsilon_{11} - \varepsilon_{21}) r_1 + (\phi_1 - \phi_2) r_2 - (\varepsilon_{11} - \varepsilon_{21}) r_1^* - (\phi_1 - \phi_2) r_2^* \} / r_2 \\
 &= r_1 \{ (\varepsilon_{11} - \varepsilon_{21}) (r_1 - r_1^*) + (\phi_1 - \phi_2) (r_2 - r_2^*) \} / r_2
 \end{aligned} \tag{61a}$$

$$\begin{aligned}
 r_2' &= r_2 (\varepsilon_{21} r_1^* + \phi_2 r_2^* - \varepsilon_{21} r_1 - \phi_2 r_2) / r_2 \\
 &= -r_2 (\varepsilon_{21} r_1 + \phi_2 r_2 - \varepsilon_{21} r_1^* - \phi_2 r_2^*) / r_2 \\
 &= -r_2 \{ (r_1 - r_1^*) \varepsilon_{21} + (r_2 - r_2^*) \phi_2 \} / r_2
 \end{aligned} \tag{61b}$$

These, (61a) and (61b), imply the equilibrium are mapped into the positive equilibrium

$$(r_1^*, r_2^*) = (X_1^* / X_2^*, I / X_2^*)$$

If (58) is globally stable, then the original model, i. e., (40) is also globally stable.

Lyapunov function for the model, following from (11), is similar to (47). Its time derivative is as in (48), with  $r_1$  and  $r_2$  as in (61a) and (61b). Therefore,

$$\begin{aligned}\psi' &= f_1 (r_1 - r_1^*) [r_1 \{(\epsilon_{11} - \epsilon_{21}) (r_1 - r_1^*) + (\phi_1 - \phi_2) (r_2 - r_2^*)\} / r_2] / r_1 \\ &\quad + f_2 (r_2 - r_2^*) [-r_2 \{(r_1 - r_1^*) \epsilon_{21} + (r_2 - r_2^*) \phi_2\} / r_2] / r_2 \\ &= (1/r_2) \{-f_1 (\epsilon_{21} - \epsilon_{11}) (r_1 - r_1^*)^2 + f_1 (\phi_1 - \phi_2) (r_1 - r_1^*) (r_2 - r_2^*) \\ &\quad - f_2 \epsilon_{21} (r_1 - r_1^*) (r_2 - r_2^*) - f_2 \phi_2 (r_2 - r_2^*)^2\} \quad (62)\end{aligned}$$

For convenience, let  $(r_1 - r_1^*) = p$  and  $(r_2 - r_2^*) = q$ . Then (62) becomes

$$\begin{aligned}\psi' &= (1/r_2) \{-f_1 (\epsilon_{21} - \epsilon_{11}) p^2 + f_1 (\phi_1 - \phi_2) p q \\ &\quad - f_2 \epsilon_{21} p q - f_2 \phi_2 q^2\} \quad (63)\end{aligned}$$

Then put  $K = \frac{p}{q}$ , or  $p = K q$ . Then (63) becomes

$$\begin{aligned}\psi' &= (1/r_2) \{-f_1 (\epsilon_{21} - \epsilon_{11}) K^2 q^2 + f_1 (\phi_1 - \phi_2) K q^2 \\ &\quad - f_2 \epsilon_{21} K q^2 - f_2 \phi_2 q^2\} \\ &= \frac{q^2}{r_2} \{-f_1 (\epsilon_{21} - \epsilon_{11}) K^2 + f_1 (\phi_1 - \phi_2) K - f_2 \epsilon_{21} K - f_2 \phi_2\} \\ &= \frac{q^2}{r_2} [-f_1 (\epsilon_{21} - \epsilon_{11}) K^2 + \{f_1 (\phi_1 - \phi_2) - f_2 \epsilon_{21}\} K - f_2 \phi_2] < 0\end{aligned}$$

$\frac{q^2}{r_2} > 0$ ; so we require

$$H(K) = [-f_1 (\epsilon_{21} - \epsilon_{11}) K^2 + \{f_1 (\phi_1 - \phi_2) - f_2 \epsilon_{21}\} K - f_2 \phi_2] < 0$$

As with Result I (see p. 30),  $H(K) < 0$  requires that  $H(K) = 0$  has no real roots, that is

$$\begin{aligned} & [f_1 (\phi_1 - \phi_2) - f_2 \epsilon_{21}]^2 - 4 f_1 f_2 \phi_2 (\epsilon_{21} - \epsilon_{11})] < 0 \\ & [f_1^2 (\phi_1 - \phi_2)^2 + f_2^2 (\epsilon_{21})^2 - 2 f_1 f_2 \epsilon_{21} (\phi_1 - \phi_2) - 4 f_1 f_2 \phi_2 (\epsilon_{21} - \epsilon_{11})] < 0 \\ & [f_1^2 (\phi_1 - \phi_2)^2 + f_2^2 (\epsilon_{21})^2 - 2 f_1 f_2 \{\epsilon_{21} (\phi_1 - \phi_2) + 2 \phi_2 (\epsilon_{21} - \epsilon_{11})\}] < 0 \end{aligned} \quad (64)$$

It is required to show when condition (64) holds. Next, let  $L = \frac{f_1}{f_2}$ , or  $f_1 = f_2 L$  to obtain

$$\begin{aligned} & [f_2^2 L^2 (\phi_1 - \phi_2)^2 + f_2^2 (\epsilon_{21})^2 - 2 f_2^2 L \{\epsilon_{21} (\phi_1 - \phi_2) + 2 \phi_2 (\epsilon_{21} - \epsilon_{11})\}] < 0 \\ & [f_2^2 \{L^2 (\phi_1 - \phi_2)^2 + (\epsilon_{21})^2 - 2 L (\epsilon_{21} \phi_1 - \epsilon_{21} \phi_2 + 2 \epsilon_{21} \phi_2 - 2 \epsilon_{11} \phi_2)\}] < 0 \\ & [f_2^2 \{L^2 (\phi_1 - \phi_2)^2 + (\epsilon_{21})^2 - 2 L (\epsilon_{21} \phi_1 + \epsilon_{21} \phi_2 - 2 \epsilon_{11} \phi_2)\}] < 0 \\ & f_2^2 [L^2 (\phi_1 - \phi_2)^2 + (\epsilon_{21})^2 - 2 L \{(\epsilon_{21} \phi_1 - \epsilon_{11} \phi_2) + (\epsilon_{21} \phi_2 - \epsilon_{11} \phi_2)\}] < 0 \\ & f_2^2 [L^2 (\phi_1 - \phi_2)^2 - 2 L \{(\epsilon_{21} \phi_1 - \epsilon_{11} \phi_2) + \phi_2 (\epsilon_{21} - \epsilon_{11})\} + (\epsilon_{21})^2] < 0 \end{aligned} \quad (65)$$

In general, we require real positive roots for  $L$  such that (65) is satisfied. For our convenience, let

$$\begin{aligned} \alpha_2 &= (\phi_1 - \phi_2) \quad ; \quad \alpha_2 \neq 0 \\ \beta_2 &= (\epsilon_{21} \phi_1 - \epsilon_{11} \phi_2) \\ \gamma_2 &= \phi_2 (\epsilon_{21} - \epsilon_{11}) \end{aligned} \quad (66)$$

Substituting (66) to (65), gives

$$f_2^2 \{L^2 (\alpha_2)^2 - 2 L \{(\beta_2 + \gamma_2) + (\epsilon_{21})^2\} = 0$$

$$L = \frac{2 (\beta_2 + \gamma_2) \pm \sqrt{4 (\beta_2 + \gamma_2)^2 - 4 (\alpha_2)^2 (\epsilon_{21})^2}}{2 (\alpha_2)^2}, \quad \alpha_2 \neq 0$$

$$= \frac{(\beta_2 + \gamma_2) \pm \sqrt{(\beta_2 + \gamma_2)^2 - (\alpha_2)^2 (\epsilon_{21})^2}}{(\alpha_2)^2}$$

As the roots are required to be real, we have

$$(\beta_2 + \gamma_2) > 0 \text{ and } (\beta_2 + \gamma_2)^2 - (\alpha_2)^2 (\epsilon_{21})^2 > 0.$$

Now,

$$(\beta_2 + \gamma_2)^2 - (\alpha_2)^2 (\epsilon_{21})^2 > 0$$

i.e.,

$$(\beta_2 + \gamma_2 + \alpha_2 \epsilon_{21}) (\beta_2 + \gamma_2 - \alpha_2 \epsilon_{21}) > 0 \quad (67)$$

Substituting (66) to (67) to obtain

$$[(\epsilon_{21} \phi_1 - \epsilon_{11} \phi_2 + \phi_2 (\epsilon_{21} - \epsilon_{11}) + \epsilon_{21} (\phi_1 - \phi_2)) \{ \epsilon_{21} \phi_1 - \epsilon_{11} \phi_2 + \phi_2 (\epsilon_{21} - \epsilon_{11}) - \epsilon_{21} (\phi_1 - \phi_2) \}] > 0$$

$$\{(\epsilon_{21} \phi_1 - \epsilon_{11} \phi_2 + \epsilon_{21} \phi_2 - \epsilon_{11} \phi_2 + \epsilon_{21} \phi_1 - \epsilon_{21} \phi_2) (\epsilon_{21} \phi_1 - \epsilon_{11} \phi_2 + \epsilon_{21} \phi_2 - \epsilon_{11} \phi_2 - \epsilon_{21} \phi_1 + \epsilon_{21} \phi_2)\} > 0$$

$$[(2 \epsilon_{21} \phi_1 - 2 \epsilon_{11} \phi_2) (2 \epsilon_{21} \phi_2 - 2 \epsilon_{11} \phi_2)] > 0$$

$$[2 \phi_2 (\epsilon_{21} - \epsilon_{11})] [2 (\epsilon_{21} \phi_1 - \epsilon_{11} \phi_2)] > 0$$

$$\{4 \phi_2 (\epsilon_{21} - \epsilon_{11}) (\epsilon_{21} \phi_1 - \epsilon_{11} \phi_2)\} > 0 \quad (68)$$

By assumption

$$\phi_2 > 0, \epsilon_{21} > \epsilon_{11} \text{ and } \epsilon_{21} \phi_1 > \epsilon_{11} \phi_2$$

Therefore (68) is satisfied. This result implies that (40) is globally stable. This completes the proof.

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## Chapter Four

### GENERALIZATIONS AND EXAMPLES

This section is devoted to introducing another use of Lyapunov function in proving a sufficient conditions of more specific model of Volterra-Lotka type. Then some numerical examples and simulations of the models, especially of the two and three-species systems, are also given. All findings and results found in this chapter, as well as the result in the previous chapters, are discussed in further detail in the last part of the thesis.

#### 4.1 GENERALIZATIONS FOR SPECIFIC TWO AND THREE-SPECIES SYSTEMS

In this section, sufficient conditions for global stability of a specific Volterra-Lotka model are established; especially for two and three species systems. The method developed is the same as that in Theorem 2.2.

##### *Example 4.1*

Consider this specific Volterra-Lotka model given by

$$\begin{aligned} X_1' &= X_1 (\phi_1 - \epsilon_{12} X_2) \\ X_2' &= X_2 (-\phi_2 + f \epsilon_{12} X_1 - \epsilon_{22} X_2) \end{aligned} \tag{69}$$

where  $X_1, X_2$  be prey and predator densities respectively. The parameter  $f$  is the conversion efficiency of prey into predator. In addition,  $\phi_1$  and  $\phi_2$  are the per capita birth rates of prey and predator respectively.

### Corollary 4.1

Provided that the parameters  $f, \phi_1, \phi_2, \epsilon_{12}$ , and  $\epsilon_{22}$  are all positive, then model (69) is globally stable.

### Proof

It is obvious, from (69), that

$$\begin{aligned}\phi_1 - \epsilon_{12} X_2^* &= 0 \\ -\phi_2 + f \epsilon_{12} X_1^* - \epsilon_{22} X_2^* &= 0\end{aligned}\tag{70}$$

Then,  $X_2^* = \phi_1/\epsilon_{12}$  and  $f \epsilon_{12} X_1^* = \phi_2 + \epsilon_{22} X_2^*$ . So  $X_1^* = \frac{\phi_2 + \epsilon_{22} \phi_1/\epsilon_{12}}{f \epsilon_{12}}$ . Therefore,

(69) has a unique feasible equilibrium given by

$$(X_1^*, X_2^*) = \left( \frac{\phi_1 \epsilon_{22} + \phi_2 \epsilon_{12}}{f (\epsilon_{12})^2}, \frac{\phi_1}{\epsilon_{12}} \right)$$

Equations (70) can be rewritten as follows

$$\begin{aligned}\phi_1 &= \epsilon_{12} X_2^* \\ -\phi_2 &= -f \epsilon_{12} X_1^* + \epsilon_{22} X_2^*\end{aligned}\tag{71}$$

Substituting (71) to (69), gives

$$X_1' = X_1 (\epsilon_{12} X_2^* - \epsilon_{12} X_2)$$

$$X_2' = X_2 (-f \epsilon_{12} X_1^* + \epsilon_{22} X_2^* + f \epsilon_{12} X_1 - \epsilon_{22} X_2)$$

or

$$X_1' = -\varepsilon_{12} X_1 (X_2 - X_2^*)$$

$$X_2' = X_2 \{f \varepsilon_{12} (X_1 - X_1^*) - \varepsilon_{22} (X_2 - X_2^*)\}$$

(72)

As in (11), let the Lyapunov function for (69) be

$$\psi(x) = f \{X_1 - X_1^* - X_1^* \ln (X_1/X_1^*)\} + \{X_2 - X_2^* - X_2^* \ln (X_2/X_2^*)\}$$

The time derivative of this function computed along solutions of (72) is

$$\begin{aligned} \psi' &= f (X_1 - X_1^*) (X_1'/X_1) + (X_2 - X_2^*) (X_2'/X_2) \\ &= f (X_1 - X_1^*) \{(-\varepsilon_{12} X_1 (X_2 - X_2^*)/X_1)\} + \\ &\quad (X_2 - X_2^*) \{f \varepsilon_{12} X_2 (X_1 - X_1^*) - \varepsilon_{22} (X_2 - X_2^*)\}/X_2 \\ &= -f \varepsilon_{12} (X_1 - X_1^*) (X_2 - X_2^*) + f \varepsilon_{12} (X_1 - X_1^*) (X_2 - X_2^*) \\ &\quad - \varepsilon_{22} (X_2 - X_2^*) (X_2 - X_2^*) \\ &= -\varepsilon_{22} (X_2 - X_2^*)^2 \end{aligned}$$

Therefore,  $\psi' < 0$  for  $X_1, X_2 > 0$  and  $X_2 \neq X_2^*$ .

If  $X_2 = X_2^*$  then  $\psi' = 0$ ; and in fact  $\psi'' = 0$  (for  $X_2 = X_2^*$ ) also. However,  $\psi''' < 0$  (for  $X_2 = X_2^*$ ), so that the required result follows.

Note: similar remarks apply to all Examples in section 4.1.

### Example 4.2

Consider the following model given by

$$\begin{aligned}
 X_1' &= X_1 (\phi_1 - \epsilon_{11} X_1 - \epsilon_{12} X_2) \\
 X_2' &= X_2 (-\phi_2 + f \epsilon_{12} X_1)
 \end{aligned}
 \tag{73}$$

The nontrivial equilibrium of (73) is given by

$$(X_1^*, X_2^*) = \left( \frac{\phi_2}{f \epsilon_{12}}, \frac{\phi_1 f \epsilon_{12} - \phi_2 \epsilon_{11}}{f (\epsilon_{12})^2} \right)$$

This equilibrium, however, is positive if and only if

$$\phi_2 < \frac{\phi_1 f \epsilon_{12}}{\epsilon_{11}}$$

Then from (73),

$$\begin{aligned}
 \phi_1 &= \epsilon_{11} X_1^* + \epsilon_{12} X_2^* \\
 \phi_2 &= f \epsilon_{12} X_1^*
 \end{aligned}
 \tag{74}$$

Substituting (74) to (73), gives

$$X_1' = X_1 (\epsilon_{11} X_1^* + \epsilon_{12} X_2^* - \epsilon_{11} X_1 - \epsilon_{12} X_2)$$

$$X_2' = X_2 (-f \epsilon_{12} X_1^* + f \epsilon_{12} X_1)$$

or

$$X_1' = -X_1 \{ \epsilon_{11} (X_1 - X_1^*) + \epsilon_{12} (X_2 - X_2^*) \}$$

$$X_2' = X_2 \{ f (X_1 - X_1^*) \epsilon_{12} \}$$

(75)

For this model the Lyapunov function (11) is

$$\psi(x) = f \{X_1 - X_1^* - X_1^* \ln (X_1/X_1^*)\} + \{X_2 - X_2^* - X_2^* \ln (X_2/X_2^*)\}$$

The time derivative of this function computed along the solutions of (75), is as follows

$$\begin{aligned} \psi' &= f (X_1 - X_1^*) (X_1'/X_1) + (X_2 - X_2^*) (X_2'/X_2) \\ &= f (X_1 - X_1^*) [-\{\epsilon_{11} (X_1 - X_1^*) + \epsilon_{12} (X_2 - X_2^*)\}] + \\ &\quad (X_2 - X_2^*) \{f \epsilon_{12} (X_1 - X_1^*)\} \\ &= -f \epsilon_{11} (X_1 - X_1^*)^2 - f \epsilon_{12} (X_1 - X_1^*) (X_2 - X_2^*) \\ &\quad + f \epsilon_{12} (X_1 - X_1^*) (X_2 - X_2^*) \\ &= -f \epsilon_{11} (X_1 - X_1^*)^2 \end{aligned}$$

Therefore,  $\psi' < 0$  for  $X_1 = X_1^*$ .

If  $X_1 = X_1^*$  then, as in Example 4.1, we have  $\psi'' = 0$  (for  $X_1 = X_1^*$ ) and  $\psi''' < 0$  (for  $X_1 = X_1^*$ ); and the result follows, i. e., (73) is also globally stable.

### Example 4.3

Then, consider the following model in which the predator has an alternative prey that provides it with an excessive and continuous supply of energy per predator. Model (69) becomes

$$\begin{aligned} X_1' &= X_1 (\phi_1 - \epsilon_{12} X_2) \\ X_2' &= X_2 (\phi_2 + f \epsilon_{12} X_1 - \epsilon_{22} X_2) \end{aligned} \tag{76}$$

This model will also be examined, under Corollary 4.1, to investigate whether or not the model is globally stable. From (76), the nontrivial equilibrium is given by

$$\begin{aligned}\phi_1 - \epsilon_{12} X_2^* &= 0 \\ \phi_2 + f \epsilon_{12} X_1^* - \epsilon_{22} X_2^* &= 0\end{aligned}\tag{77}$$

$X_2^* = \phi_1/\epsilon_{12}$  and  $f \epsilon_{12} X_1^* = -\phi_2 + \epsilon_{22} X_2^*$ . Then  $X_1^* = \frac{-\phi_2 + \epsilon_{22} \phi_1/\epsilon_{12}}{f \epsilon_{12}}$ . Therefore,

$$(X_1^*, X_2^*) = \left( \frac{\phi_1 \epsilon_{22} - \phi_2 \epsilon_{12}}{f (\epsilon_{12})^2}, \frac{\phi_1}{\epsilon_{12}} \right)$$

This equilibrium, however, is feasible if and only if

$$\phi_2 < \frac{\phi_1 \epsilon_{22}}{\epsilon_{12}}$$

Equations (77) can be rewritten as follows

$$\begin{aligned}\phi_1 &= \epsilon_{12} X_2^* \\ \phi_2 &= -f \epsilon_{12} X_1^* + \epsilon_{22} X_2^*\end{aligned}\tag{78}$$

Substituting (78) to (76), gives

$$\begin{aligned}X_1' &= X_1 (\epsilon_{12} X_2^* - \epsilon_{12} X_2) \\ X_2' &= X_2 (-f \epsilon_{12} X_1^* + \epsilon_{22} X_2^* + f \epsilon_{12} X_1 - \epsilon_{22} X_2)\end{aligned}$$

or

$$\begin{aligned} X_1' &= -\varepsilon_{12} X_1 (X_2 - X_2^*) \\ X_2' &= X_2 \{f \varepsilon_{12} (X_1 - X_1^*) - \varepsilon_{22} (X_2 - X_2^*)\} \end{aligned} \quad (79)$$

System (79) is in fact the same as that of (72). It can be concluded, therefore, that (76) is also globally stable if all the parameters are positive.

#### Example 4.4

Consider a model where the species at the lowest trophic level is self-regulating. The three species food chain model is given by

$$\begin{aligned} X_1' &= X_1 (\phi_1 - \varepsilon_{11} X_1 - \varepsilon_{12} X_2) \\ X_2' &= X_2 (-\phi_2 + f_1 \varepsilon_{12} X_1 - \varepsilon_{23} X_3) \\ X_3' &= X_3 (-\phi_3 + f_2 \varepsilon_{23} X_2) \end{aligned} \quad (80)$$

#### Corollary 4.2

Model (80) is globally stable if it has a feasible equilibrium and also the parameters  $f_i > 0$  ( $i = 1, 2$ ),  $\phi_i > 0$  ( $i = 1, 2, 3$ ) and  $\varepsilon_{11}, \varepsilon_{12}, \varepsilon_{23} > 0$ .

#### Proof

From (80) the nontrivial equilibrium is given by

$$\phi_1 - \epsilon_{11} X_1^* - \epsilon_{12} X_2^* = 0$$

$$-\phi_2 + f_1 \epsilon_{12} X_1^* - \epsilon_{23} X_3^* = 0 \quad (81)$$

$$-\phi_3 + f_2 \epsilon_{23} X_2^* = 0$$

i.e., 
$$X_1^* = \frac{f_2 \phi_1 \epsilon_{23} - \phi_3 \epsilon_{12}}{f_2 \epsilon_{11} \epsilon_{23}}, \quad X_2^* = \frac{\phi_3}{f_2 \epsilon_{23}} \quad \text{and}$$

$$X_3^* = \frac{f_1 \epsilon_{12} (f_2 \phi_1 \epsilon_{23} - \phi_3 \epsilon_{12}) - f_2 \phi_1 \epsilon_{11} \epsilon_{23}}{f_2 \epsilon_{11} (\epsilon_{23})^2}$$

Equations (81) are the same as

$$\phi_1 = \epsilon_{11} X_1^* + \epsilon_{12} X_2^*$$

$$-\phi_2 = -f_1 \epsilon_{12} X_1^* + \epsilon_{23} X_3^* \quad (82)$$

$$\phi_3 = f_2 \epsilon_{23} X_2^*$$

Substituting (82) to (80), yields

$$X_1' = X_1 (\epsilon_{11} X_1^* + \epsilon_{12} X_2^* - \epsilon_{11} X_1 - \epsilon_{12} X_2)$$

$$X_2' = X_2 (-f_1 \epsilon_{12} X_1^* + \epsilon_{23} X_3^* + f_1 \epsilon_{12} X_1 - \epsilon_{23} X_3)$$

$$X_3' = X_3 (-f_2 \epsilon_{23} X_2^* + f_2 \epsilon_{23} X_2)$$

or

$$\begin{aligned} X_1' &= -X_1 \{ \epsilon_{11} (X_1 - X_1^*) + \epsilon_{12} (X_2 - X_2^*) \} \\ X_2' &= X_2 \{ (f_1 \epsilon_{12} (X_1 - X_1^*) - \epsilon_{23} (X_3 - X_3^*)) \} \\ X_3' &= X_3 \{ f_2 \epsilon_{23} (X_2 - X_2^*) \} \end{aligned} \quad (83)$$

Our Lyapunov function for this model, as in (11), is

$$\begin{aligned} \psi &= f_1 \{ X_1 - X_1^* - X_1^* \ln (X_1/X_1^*) \} + f_2 \{ X_2 - X_2^* - X_2^* \ln (X_2/X_2^*) \} \\ &\quad + \{ X_3 - X_3^* - X_3^* \ln (X_3/X_3^*) \} \end{aligned}$$

The time derivative of this function computed along the solutions of (83) is

$$\begin{aligned} \psi' &= f_1 (X_1 - X_1^*) (X_1'/X_1) + f_2 (X_2 - X_2^*) (X_2'/X_2) + (X_3 - X_3^*) (X_3'/X_3) \\ &= f_1 (X_1 - X_1^*) \{ -\epsilon_{11} (X_1 - X_1^*) - \epsilon_{12} (X_2 - X_2^*) \} + \\ &\quad f_2 (X_2 - X_2^*) \{ (f_1 \epsilon_{12} (X_1 - X_1^*) - \epsilon_{23} (X_3 - X_3^*)) \} + \\ &\quad (X_3 - X_3^*) \{ f_2 \epsilon_{23} (X_2 - X_2^*) \} \\ &= -f_1 \epsilon_{11} (X_1 - X_1^*) (X_1 - X_1^*) - f_1 \epsilon_{12} (X_1 - X_1^*) (X_2 - X_2^*) + \\ &\quad f_1 f_2 \epsilon_{12} (X_1 - X_1^*) (X_2 - X_2^*) - f_2 \epsilon_{23} (X_2 - X_2^*) (X_3 - X_3^*) + \\ &\quad f_2 \epsilon_{23} (X_2 - X_2^*) (X_3 - X_3^*) \end{aligned}$$

Let  $f_1 = 1 = f_2$ , then  $\psi' = -\epsilon_{11} (X_1 - X_1^*)^2 < 0$  for all  $X_1, X_2, X_3 > 0$  and  $X_1 \neq X_1^*$ .

If  $X_1 = X_1^*$  then as in Example 4.2 we have  $\psi'' = 0$  (for  $X_1 = X_1^*$ ) and  $\psi''' < 0$  (for  $X_1 = X_1^*$ ). By Corollary 4.2, (80) is globally stable.

### Example 4.5

Consider the three-species model of food chain given by

$$\begin{aligned} X_1' &= X_1 (\phi_1 - \epsilon_{12} X_2) \\ X_2' &= X_2 (-\phi_2 + f_1 \epsilon_{12} X_1 - \epsilon_{23} X_3) \\ X_3' &= X_3 (-\phi_3 + f_2 \epsilon_{23} X_2 - \epsilon_{33} X_3) \end{aligned} \quad (84)$$

### Corollary 4.3

Model (84) is globally stable if it has a feasible equilibrium and at the same time all the parameters  $f_i$  ( $i = 1, 2$ ),  $\phi_i$  ( $i = 1, 2, 3$ ) and  $\epsilon_{12}, \epsilon_{23}, \epsilon_{33}$  are positive.

### Proof

From (84) the nontrivial equilibrium is given by

$$\begin{aligned} \phi_1 - \epsilon_{12} X_2^* &= 0 \\ -\phi_2 + f_1 \epsilon_{12} X_1^* - \epsilon_{23} X_3^* &= 0 \\ -\phi_3 + f_2 \epsilon_{23} X_2^* - \epsilon_{33} X_3^* &= 0 \end{aligned} \quad (85)$$

Therefore,

$$(X_1^*, X_2^*, X_3^*) = \left( \frac{f_2 \phi_1 (\epsilon_{23})^2 + \epsilon_{12} (\phi_2 \epsilon_{33} - \phi_3 \epsilon_{23})}{f_1 (\epsilon_{12})^2 \epsilon_{33}}, \frac{\phi_1}{\epsilon_{12}}, \frac{f_2 \phi_1 \epsilon_{23} - \phi_3 \epsilon_{12}}{\epsilon_{12} \epsilon_{33}} \right)$$

Equations (85) can be rewritten as

$$\begin{aligned} \phi_1 &= \epsilon_{12} X_2^* \\ -\phi_2 &= -f_1 \epsilon_{12} X_1^* + \epsilon_{23} X_3^* \\ -\phi_3 &= -f_2 \epsilon_{23} X_2^* + \epsilon_{33} X_3^* \end{aligned} \quad (86)$$

Substituting (86) to (84), yields

$$\begin{aligned} X_1' &= X_1 (\epsilon_{12} X_2^* - \epsilon_{12} X_2) \\ X_2' &= X_2 (-f_1 \epsilon_{12} X_1^* + \epsilon_{23} X_3^* + f_1 \epsilon_{12} X_1 - \epsilon_{23} X_3) \\ X_3' &= X_3 (-f_2 \epsilon_{23} X_2^* + \epsilon_{33} X_3^* + f_2 \epsilon_{23} X_2 - \epsilon_{33} X_3) \end{aligned}$$

or

$$\begin{aligned} X_1' &= -X_1 \{\epsilon_{12} (X_2 - X_2^*)\} \\ X_2' &= X_2 \{f_1 \epsilon_{12} (X_1 - X_1^*) - \epsilon_{23} (X_3 - X_3^*)\} \\ X_3' &= X_3 \{f_2 \epsilon_{23} (X_2 - X_2^*) - \epsilon_{33} (X_3 - X_3^*)\} \end{aligned} \quad (87)$$

Let the Lyapunov function of this model, following (11), is

$$\begin{aligned}\psi &= f_1 \{X_1 - X_1^* - X_1^* \ln (X_1/X_1^*)\} + f_2 \{X_2 - X_2^* - X_2^* \ln (X_2/X_2^*)\} \\ &\quad + \{X_3 - X_3^* - X_3^* \ln (X_3/X_3^*)\}\end{aligned}$$

The time derivative of this function computed along the solutions of (87) is

$$\begin{aligned}\psi' &= f_1 (X_1 - X_1^*) (X_1'/X_1) + f_2 (X_2 - X_2^*) (X_2'/X_2) + (X_3 - X_3^*) (X_3'/X_3) \\ &= f_1 (X_1 - X_1^*) \{-\varepsilon_{12} (X_2 - X_2^*)\} + f_2 (X_2 - X_2^*) \{f_1 \varepsilon_{12} (X_1 - X_1^*) - \\ &\quad \varepsilon_{23} (X_3 - X_3^*)\} + (X_3 - X_3^*) \{f_2 \varepsilon_{23} (X_2 - X_2^*) - \varepsilon_{33} (X_3 - X_3^*)\} \\ &= -f_1 \varepsilon_{12} (X_1 - X_1^*) (X_2 - X_2^*) + f_1 f_2 \varepsilon_{12} (X_2 - X_2^*) (X_1 - X_1^*) \\ &\quad - f_2 \varepsilon_{23} (X_2 - X_2^*) (X_3 - X_3^*) + f_2 \varepsilon_{23} (X_2 - X_2^*) (X_3 - X_3^*) \\ &\quad - \varepsilon_{33} (X_3 - X_3^*) (X_3 - X_3^*)\end{aligned}$$

If we choose  $f_1 = f_2 = 1$  our formula for  $\psi'$  becomes

$$\psi' = -\varepsilon_{33} (X_3 - X_3^*)^2 < 0$$

for all  $X_1, X_2, X_3 > 0$  and  $X_3 \neq X_3^*$ .

If  $X_3 = X_3^*$  then as in Example 4.4 we have  $\psi'' = 0$  (for  $X_3 = X_3^*$ ) and  $\psi''' < 0$  (for  $X_3 = X_3^*$ ). Hence, by Corollary 4.3, (84) is also globally stable.

## 4.2 NUMERICAL EXAMPLES

There are five different numerical examples introduced in this section. The first four are system of the two-species interactions and the other is a three-species systems. The theorems introduced in the previous chapter are utilized to investigate all these numerical examples. A simple program, moreover, is created to implement numerical simulations of the models. It is acknowledge, however, that the results from computer simulations applied only as tentative, not as final results. The program for computer simulations can be seen in the Appendices.

### Example 4.6

Consider the two-species systems of numerical example below given by

$$\begin{aligned} \dot{X}_1 &= X_1 (1 - X_1 + 0.5 X_2) \\ \dot{X}_2 &= X_2 (2.5 + 0.25 X_1 - 1.5 X_2) \end{aligned} \quad (88)$$

In (88),  $\phi_1 = 1$ ,  $\phi_2 = 2.5$ ,  $\epsilon_{11} = -1$ ,  $\epsilon_{12} = 0.5$ ,  $\epsilon_{21} = 0.25$ ,  $\epsilon_{22} = -1.5$ . According to (14), the feasible equilibrium of (88) is given by

$$\begin{aligned} (X_1^*, X_2^*) &= \left( \frac{(2.5)(0.5) - (1)(-1.5)}{(-1)(-1.5) - (0.5)(0.25)}, \frac{(1)(0.25) - (2.5)(-1)}{(-1)(-1.5) - (0.5)(0.25)} \right) \\ &= \left( \frac{1.25 + 1.5}{1.5 - 0.125}, \frac{0.25 + 2.5}{1.5 - 0.125} \right) \\ &= \left( \frac{2.75}{1.375}, \frac{2.75}{1.375} \right) \\ &= (2, 2) \end{aligned}$$

Local stability of the equilibrium of the model depends on the eigenvalues of the matrix

$$\begin{aligned}
 (X_i^* \ \varepsilon_{ij})_{i,j=1,2} &= \begin{bmatrix} X_1^* & \varepsilon_{11} & X_1^* & \varepsilon_{12} \\ X_2^* & \varepsilon_{21} & X_2^* & \varepsilon_{22} \end{bmatrix} \\
 &= \begin{bmatrix} 2 & (-1) & 2 & (0.5) \\ 2 & (0.25) & 2 & (-1.5) \end{bmatrix} \\
 &= \begin{bmatrix} 2 & 1 \\ 0.5 & -3 \end{bmatrix}
 \end{aligned}$$

The eigenvalues of this matrix are given by  $\det \begin{bmatrix} (-2-\lambda) & 1 \\ 0.5 & (-3-\lambda) \end{bmatrix} = 0$

i. e.,

$$(-2-\lambda)(-3-\lambda) - 0.5 = 0$$

$$\lambda^2 + 5\lambda + 5.5 = 0$$

So the eigenvalues are

$$\begin{aligned}
 &\frac{-5 \pm \sqrt{25 - 22}}{2} \\
 &= \frac{-5 \pm \sqrt{3}}{2}
 \end{aligned}$$

According to Definition 1.1, the nature of this critical point is a node. As the eigenvalues are negative, it is locally stable. Besides,  $X_i^* > 0$ ,  $\varepsilon_{ii} < 0$  and  $\det(\varepsilon_{ij}) > 0$  for  $i, j = 1, 2$ .

So, by (15) and (16), system (88) is locally stable.

The phase portrait of this model, obtained from computer simulation, shows that (89) is globally stable (see *Figure 6a*). In addition, clearly the conditions (i), (ii) and (iii) of Theorem 2.2 are satisfied by this model. Therefore, (88) is globally stable. The situation between the species  $X_1$  and  $X_2$  is shown in *Figure 6b* (Note: the program on how to create this simulation is attached in the Appendix B).

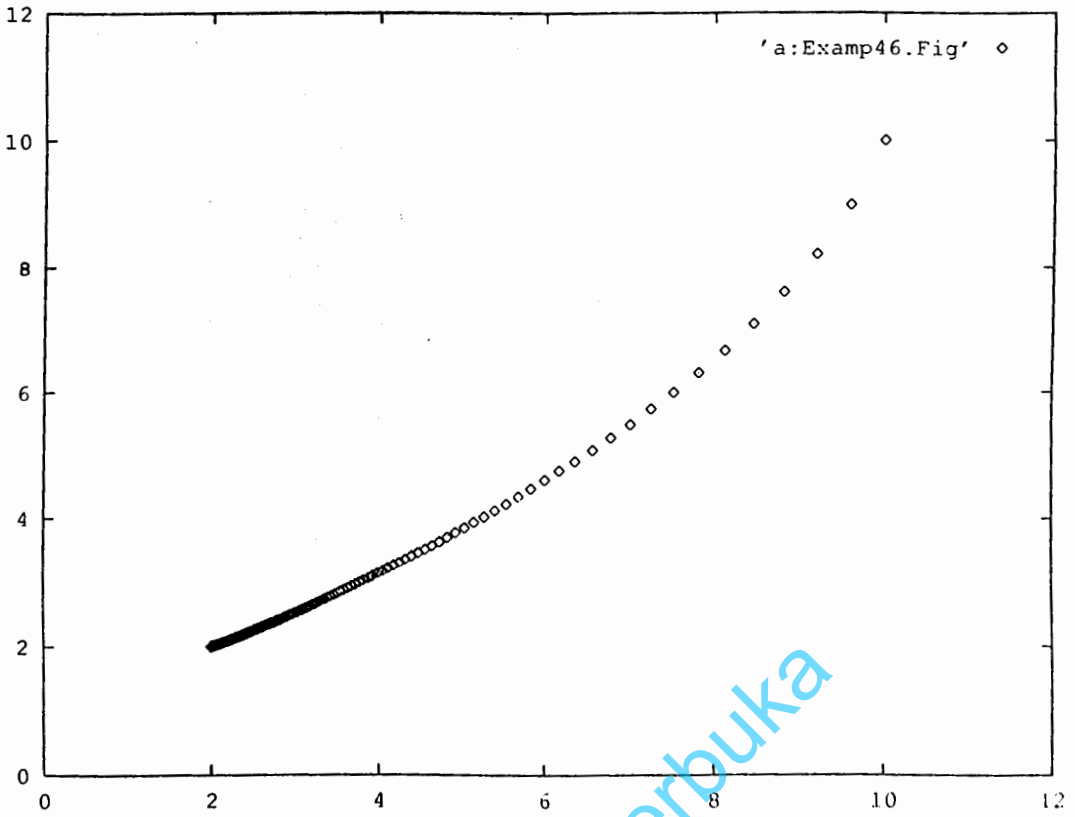


Figure 6a: Phase portrait of Example 4.6

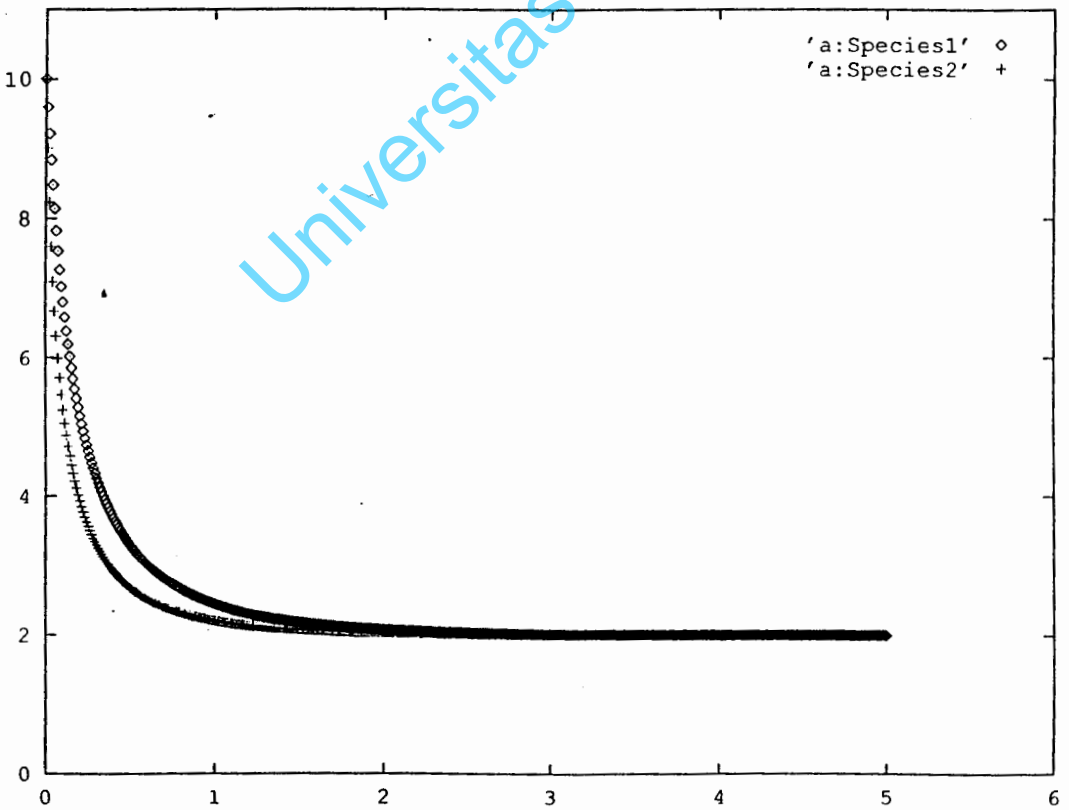


Figure 6b: Numerical Solution of Mutualism Model

**Example 4.7**

Similar to Example 4.6, let the following numerical example given by

$$\begin{aligned} \dot{X}_1 &= X_1 (1.5 - X_1 - 0.5 X_2) \\ \dot{X}_2 &= X_2 (2 - 0.75 X_1 - X_2) \end{aligned} \quad (89)$$

Under (14), model (89) has feasible equilibrium given by

$$(X_1^*, X_2^*) = (0.8, 1.4)$$

Local stability of the model depends on the eigenvalues of matrix

$$(\epsilon_{ij}^*)_{i,j=1,2} = \begin{bmatrix} -0.8 & -0.4 \\ -1.05 & -1.4 \end{bmatrix}$$

for  $i = 1, 2$ .

The eigenvalues are

$$\frac{-2.2 \pm \sqrt{2.04}}{2}$$

As the real part of the eigenvalues are negative, it implies that the equilibrium is locally stable. Computer simulation of this model shows that (89) is in fact globally stable (see Figure 7a).

In (89), moreover,  $X_i^* > 0$ ,  $\epsilon_{ii} < 0$  and  $\det(\epsilon_{ij}^*) > 0$  for  $i = 1, 2$ . Hence this model is in fact globally stable in the positive orthant. For the interaction between species  $X_1$  and  $X_2$  see Figure 7b (Note: the computer program to obtain this simulation attached in the Appendix C).

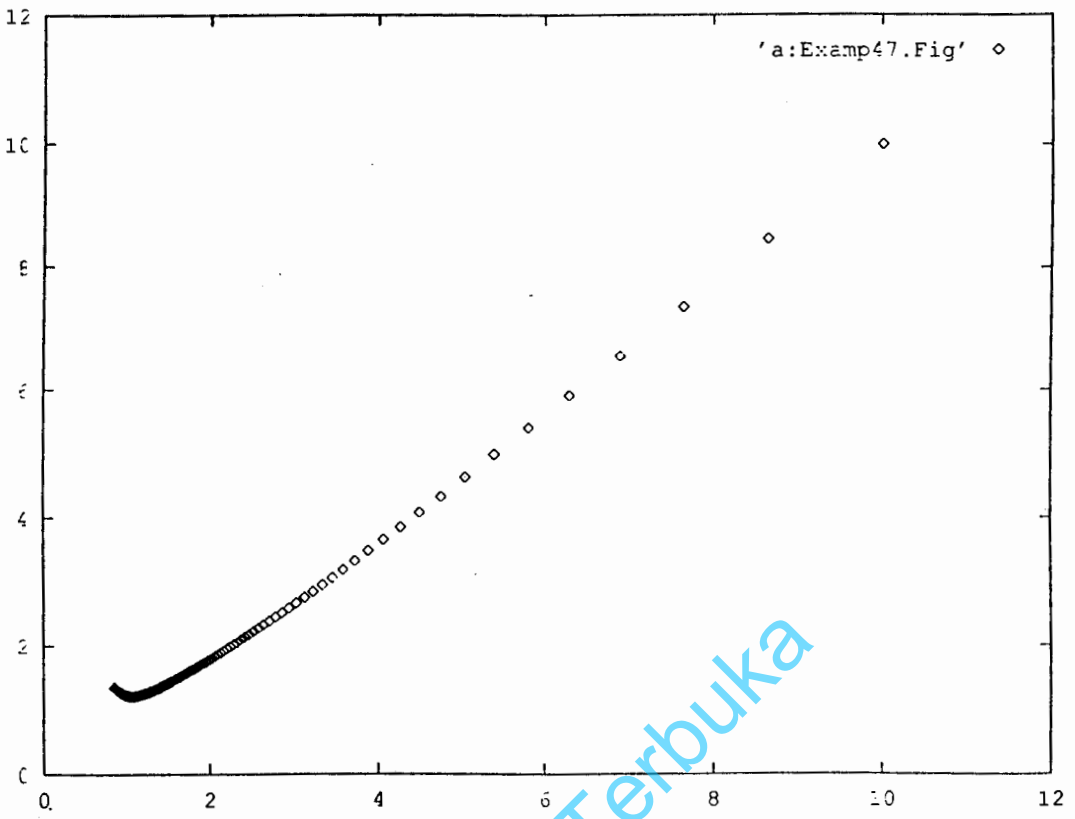


Figure 7a: Phase portrait of Example 4.7

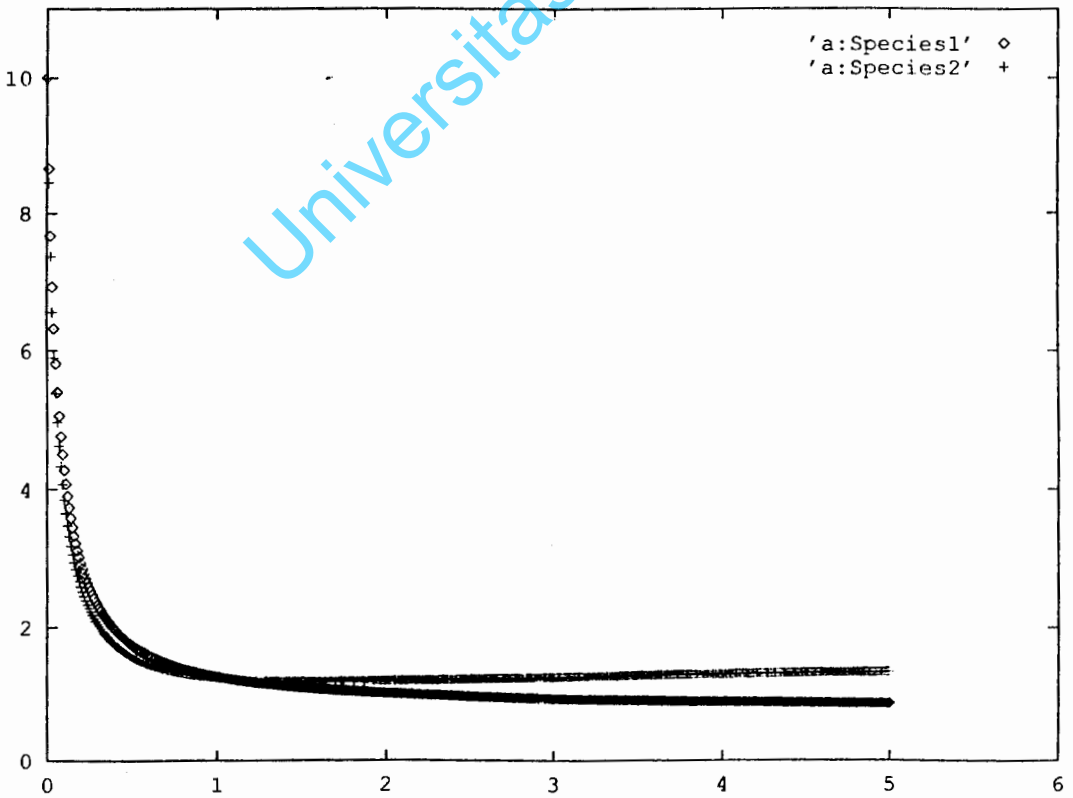


Figure 7b: Numerical Solution of Competition Model

### Examples 4.8

Consider the system below given by

$$\begin{aligned} X_1' &= X_1 (1 + 4 X_1 - 20 X_2) \\ X_2' &= X_2 (-2 + 8 X_1 - 24 X_2) \end{aligned} \quad (90)$$

Feasible equilibrium of (90), under (14), is in fact given by  $(X_1^*, X_2^*) = (1, 0.25)$ .

Moreover,

$$\phi_1 = 1, \phi_2 = -2, \epsilon_{11} = 4, \epsilon_{12} = -20, \epsilon_{21} = 8, \epsilon_{22} = -24$$

Obviously that

$$\phi_1 > 0, \epsilon_{12} > \epsilon_{22} \text{ and } \phi_2 \epsilon_{12} > \phi_1 \epsilon_{22}$$

So, by Theorem 3.1, (90) is globally stable.

### Example 4.9

Next consider the following numerical example given by

$$\begin{aligned} X_1' &= X_1 (-2.5 - X_1 + 1.5 X_2) \\ X_2' &= X_2 (1 - 0.5 X_1 + 0.5 X_2) \end{aligned} \quad (91)$$

where  $X_1$  and  $X_2$  are density of prey and predator respectively. Clearly that this model, under (14), has feasible equilibrium at  $(X_1^*, X_2^*) = (11, 9)$ . Computer simulation of this example shows that it is globally stable, that is

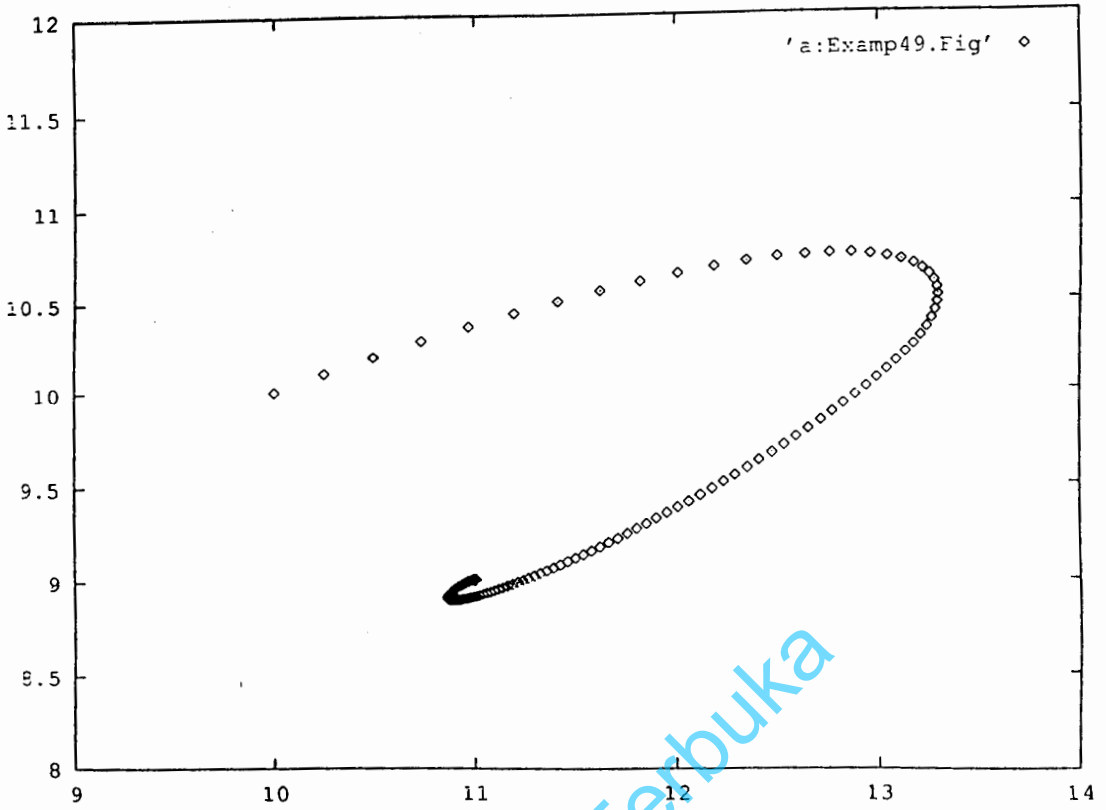


Figure 8a: Phase portrait of Example 4.9

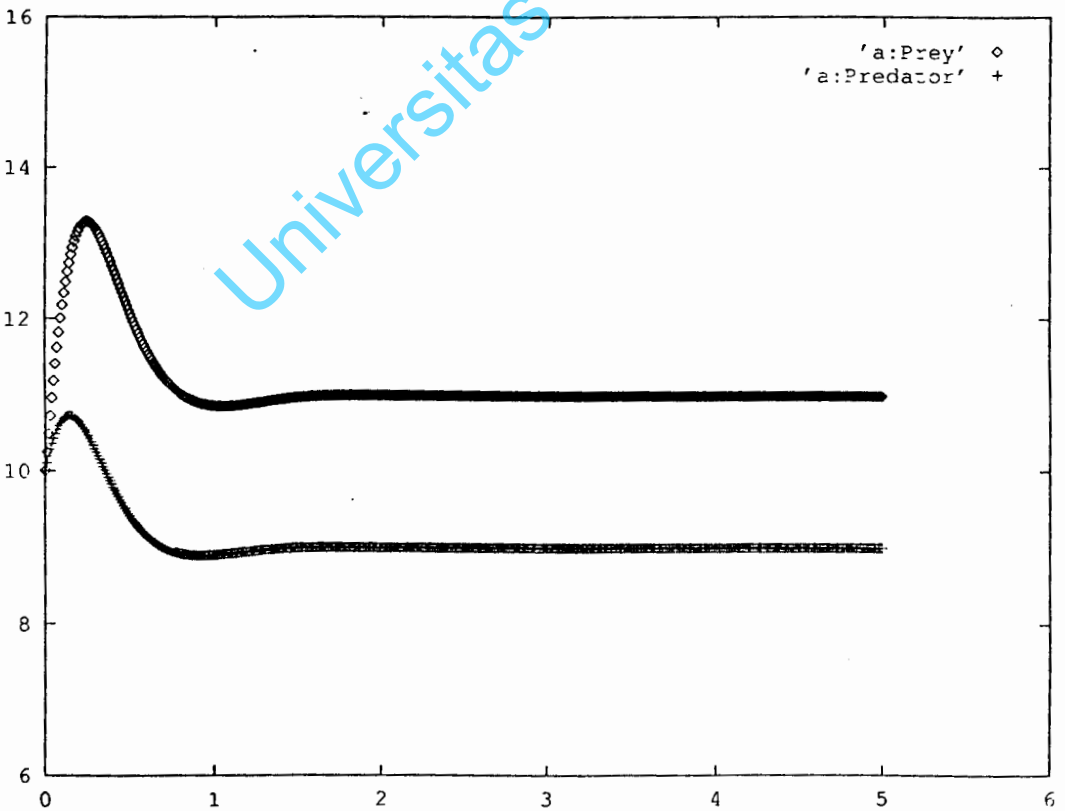


Figure 8b: Numerical Solution of Predator-Prey Model

Here, moreover,

$$\phi_1 = -2.5, \phi_2 = 1, \varepsilon_{11} = -1, \varepsilon_{12} = 1.5, \varepsilon_{21} = -0.5, \varepsilon_{22} = 0.5$$

In other words,

$$\phi_2 > 0, \varepsilon_{21} > \varepsilon_{11} \text{ and } \phi_1 \varepsilon_{21} > \phi_2 \varepsilon_{11}$$

Clearly that the model satisfies the conditions in Theorem 3.2. Therefore (91) is also globally stable. The situation between the prey and predator is shown in *Figure 8b*. The procedure on how to find them is enclosed in the Appendix D.

#### **Example 4.10**

In this example, we are going to use Theorem 2.1, i. e., to examine global stability of many-species systems. Consider the example of the three-species systems given by

$$\begin{aligned} X_1' &= X_1 (5 - 4 X_1 - 2 X_2 + 2 X_3) \\ X_2' &= X_2 (9 - 2 X_1 - 6 X_2 - 2 X_3) \\ X_3' &= X_3 (-2 + 2 X_1 + 2 X_2 - 4 X_3) \end{aligned} \quad (92)$$

The nontrivial equilibrium of (92) is given by

$$-4 X_1 - 2 X_2 + 2 X_3 = -5 \quad (1^*)$$

$$-2 X_1 - 6 X_2 - 2 X_3 = -9 \quad (2^*)$$

$$2 X_1 + 2 X_2 - 4 X_3 = 2 \quad (3^*)$$

Add (2\*) and (3\*) and subtract (1\*) and  $2 \times (2^*)$  respectively to obtain

$$4 X_2 + 6 X_3 = 7 \quad \text{and} \quad 10 X_2 + 6 X_3 = 13 \quad (4^*)$$

From (4\*) gives  $X_2^* = 1$ . Substitute this value to (3\*) yields  $X_3^* = 0.5$ . Use these two values to obtain  $X_1^* = 1$ . Therefore (92) has feasible equilibrium at

$$(X_1^*, X_2^*, X_3^*) = (1, 1, 0.5)$$

The matrix interactions of the model at the equilibrium is

$$E = (X_i^* \ \varepsilon_{ij}) \ (i, j = 1, 2, 3) = \begin{bmatrix} X_1^* & \varepsilon_{11} & X_1^* & \varepsilon_{12} & X_1^* & \varepsilon_{13} \\ X_2^* & \varepsilon_{21} & X_2^* & \varepsilon_{22} & X_2^* & \varepsilon_{23} \\ X_3^* & \varepsilon_{31} & X_3^* & \varepsilon_{32} & X_3^* & \varepsilon_{33} \end{bmatrix}$$

$$= \begin{bmatrix} (1) \ (-4) & (1) \ (-2) & (1) \ (2) \\ (1) \ (-2) & (1) \ (-6) & (1) \ (-2) \\ (0.5) \ (2) & (0.5) \ (2) & (0.5) \ (-4) \end{bmatrix} = \begin{bmatrix} -4 & -2 & 2 \\ -2 & -6 & -2 \\ 1 & 1 & -2 \end{bmatrix}$$

The result from computer shows that the eigenvalues of this matrix are approximately

$$-7.051, -1.466, -3.483$$

Since all the real parts of the eigenvalues are negative, then the model is locally stable.

Here we have

$$E + E^T = \begin{bmatrix} -4 & -2 & 2 \\ -2 & -6 & -2 \\ 1 & 1 & -2 \end{bmatrix} + \begin{bmatrix} -4 & -2 & 1 \\ -2 & -6 & 1 \\ 2 & -2 & -2 \end{bmatrix}$$

$$= \begin{bmatrix} -8 & -4 & 3 \\ -4 & -12 & -1 \\ 3 & -1 & -4 \end{bmatrix}$$

$\text{Det } (E + E^T) = -360 + 180 = -180$ . Hence  $(E + E^T)$  is negative definite.

Then, we let  $F = \text{diag } (1, 1, 1)$ . This means that  $(E + E^T) = (F E + F E^T)$ .

Therefore,  $(F E + F E^T) < 0$ . And this fact implies that the model satisfies the conditions in Theorem 2.1. Hence (93) is globally stable in the feasible region.

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## Chapter Five

# DISCUSSIONS AND CONCLUSION

### 5.1 GENERAL DISCUSSIONS

There are several regards that need to be noted and discussed based on the methods and results developed previously.

Undoubtedly the Lyapunov method, called Lyapunov function in this thesis, is a very powerful method to investigate global stability of the generalized Volterra-Lotka models. And, moreover, this procedure can also be utilized to examine global properties of a specific model of Volterra-Lotka type as demonstrated in section 4.1.

It is clear now that local stability of an equilibrium in system of differential equations does not necessarily imply its global stability. This can be shown by considering the following numerical examples, given by Goh (1976), as follows

$$\begin{aligned} X_1' &= X_1 (-2 + X_1 + X_2) \\ X_2' &= X_2 (5 - 3X_1 - 2X_2) \end{aligned} \tag{93}$$

It has feasible equilibrium at

$$(X_1^*, X_2^*) = (1, 1)$$

and under (15) and (16) the model is in fact locally stable. However, according to computer simulation, this model is only locally stable. In addition, it is clear that in (93)

$$\phi_1 = -2, \quad \phi_2 = 5, \quad \varepsilon_{11} = 1, \quad \varepsilon_{12} = 1, \quad \varepsilon_{21} = -3, \quad \varepsilon_{22} = -2$$

As  $\epsilon_{11} > 0$ , Theorem 2.2 can not be applied. Moreover, as  $\epsilon_{21} < \epsilon_{11}$ , Theorem 3.2 can not be also applied. So we can prove only local stability for this model.

At glance, it seems that Example 4.8 and Example 4.9 do not have global stability as  $\epsilon_{11} > 0$  and  $\epsilon_{22} > 0$  respectively. Under Theorem 3.1, however, Example 4.8 is globally stable; and Example 4.9 is in fact globally stable under Theorem 3.2. These facts mean that the result in Goh (1976) is indeed improved. And this is obtained by subjecting the model first to the Poincare transformation. As a result, we have got another 'tool', which is more capable than that of Theorem 2.2, to analyze global stability more general models of Volterra-Lotka type.

In the proof of Theorem 2.2, i. e., in case (I) of (38),  $\epsilon_{12} \epsilon_{21} = 0$ . This implies that either  $\epsilon_{12} = 0$ ,  $\epsilon_{21} = 0$  or  $\epsilon_{12} = 0 = \epsilon_{21}$ . In case (II),  $\epsilon_{12} \epsilon_{21} > 0$  and this means that either  $\epsilon_{12}, \epsilon_{21} < 0$  or  $\epsilon_{12}, \epsilon_{21} > 0$ . In case (III)  $\epsilon_{12} \epsilon_{21} < 0$ , that is nonzero value for both  $\epsilon_{12}$  and  $\epsilon_{21}$  as well as having opposite sign. Biologically, in case (I), if  $\epsilon_{12} = 0$  then it is referred to as amensalism; if  $\epsilon_{21} = 0$  it is described as commensalism; It is said to be neutralism if both  $\epsilon_{12}$  and  $\epsilon_{21}$  equal to zero. In case (II), it is said to be competition and mutualism if  $\epsilon_{12}, \epsilon_{21} < 0$  and  $\epsilon_{12}, \epsilon_{21} > 0$  respectively. Noting that Example 4.6 is a model of mutualism and Example 4.7 is a competing species model. When  $\epsilon_{12} \epsilon_{21} < 0$  it is commonly known as a predator-prey interactions. The examples of this type are shown in Example 4.8 and Example 4.9. The phase portrait of the equilibrium and the situation between the species are also shown in *Figure 6*, *Figure 7* and *Figure 8*.

In a Volterra-Lotka model of predator-prey systems, it is likely to have global stability of such model although only one of the species sustains density-dependent mortalities due to intraspecific interactions. In a two-species of Volterra-Lotka model of mutualism, as shown in the proof of Theorem 2.2, local stability implies global stability. This result is still valid in a model of mutualism between any finite number of species (Goh, 1979). In a two-species Volterra-Lotka models of competition, local stability implies global stability in the feasible region. Nevertheless, this result is not necessarily true for model of more than three-species systems.

## 5.2 CONCLUDING REMARKS

It has been shown that local stability of the generalized Volterra-Lotka models does not necessarily imply its global stability. By applying the Poincare transformation, the set of sufficient conditions of the models in which both species do not sustain density-dependent due to intraspecific interaction are established. These results have been proven with the help of Lyapunov functions. Undoubtedly these results improve earlier work, particularly the result in Goh (1976). However, it is worth noting that the results found in this thesis still could not solve every form of Volterra-Lotka models, e. g., model (93).

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## APPENDICES

### APPENDIX A

Following is a procedure of creating a program, in Minitab, to implement numerical simulations of the generalized Volterra-Lotka models. The generalized Volterra-Lotka models of the two-species systems is taking form

$$X_1' = X_1 (\phi_1 + \varepsilon_{11} X_1 + \varepsilon_{12} X_2)$$

$$X_2' = X_2 (\phi_2 + \varepsilon_{21} X_1 + \varepsilon_{22} X_2)$$

(\*)

Use

$$X_i'(t) \approx \frac{X_i(t+h) - X_i(t)}{h}$$

where  $h$  is relatively very small.

Measure time in units of  $h$  and put  $t = nh$  for  $n = 0, 1, 2, \dots$ . Then write

$$X_i(nh) = X_i^n$$

So

$$X_i'(t) \approx \frac{X_i^{n+1} - X_i^n}{h}$$

The appropriate version of (\*) is

$$\frac{X_i^{n+1} - X_i^n}{h} \approx X_i^n \left\{ \phi_i + \sum_{j=1}^2 \varepsilon_{ij} X_j^n \right\}$$

i.e.,

$$X_i^{n+1} \approx X_i^n + h X_i^n \left\{ \phi_i + \sum_{j=1}^2 \varepsilon_{ij} X_j^n \right\}$$

If  $X_i^n$  is known, then  $X_i^{n+1}$  can be (approximately) calculated.

To use these informations in the Minitab, we make the following identifications:

$$k1 = n+1,$$

$$k2 = h,$$

$$k3 = \phi_1,$$

$$k4 = \varepsilon_{11},$$

$$k5 = \varepsilon_{12},$$

$$k6 = \phi_1,$$

$$k7 = \varepsilon_{21},$$

$$k8 = \varepsilon_{22},$$

$$t = c1 \text{ (i. e., coloumn of time values),}$$

$$X_1^n = c2(k1),$$

$$X_2^n = c3(k1).$$

A 'loop' is written which will calculate the  $X_i^n$ .

By specifying the values of

$$c1(1), c2(1), c3(1), k1, k2, k3, k4, k5, k6, k7 \text{ and } k8,$$

we can get the result using 'execute' command, i. e., executing the loop as many times as needed.

## APPENDIX B

The program to obtain computer simulation of Example 4.6 is:

Minitab

MTB> store 'filename'

STORE> noecho

STORE> let c1(k1+1)=c1(k1)+k2

STORE> let c2(k1+1)=c2(k1)+k2\*(k3+k4\*c2(k1)+k5\*c3(k1))\*c2(k1)

STORE> let c3(k1+1)=c3(k1)+k2\*(k6+k7\*c2(k1)+k8\*c3(k1))\*c3(k1)

STORE> let k1=k1+1

STORE> end

MTB> let c1(1)=0

MTB> let c2(1)=10 (Note: This is the initial value of  $X_1$ )

MTB> let c3(1)=10 (Note: This is the initial value of  $X_2$ )

MTB> let k1=1

MTB> let k2=0.01 (Note: This is a time step size)

MTB> let k3=1

MTB> let k4=-1

MTB> let k5=0.5

MTB> let k6=2.5

MTB> let k7=0.25

MTB> let k8=-1.5

MTB> execute 'filename'500

MTB> xlabel c2 'Species1'

MTB> ylabel c3 'Species2'

MTB> gplot c3 c2

MTB> write 'Species1' c1 c2

MTB> write 'Species2' c1 c3

MTB> stop

## APPENDIX C

The program to obtain computer simulation of Example 4.7 is:

Minitab

MTB> store 'filename'

STORE> noecho

STORE> let c1(k1+1)=c1(k1)+k2

STORE> let c2(k1+1)=c2(k1)+k2\*(k3+k4\*c2(k1)+k5\*c3(k1))\*c2(k1)

STORE> let c3(k1+1)=c3(k1)+k2\*(k6+k7\*c2(k1)+k8\*c3(k1))\*c3(k1)

STORE> let k1=k1+1

STORE> end

MTB> let c1(1)=0

MTB> let c2(1)=10

MTB> let c3(1)=10

MTB> let k1=1

MTB> let k2=0.01

MTB> let k3=1.5

MTB> let k4=-1

MTB> let k5=-0.5

MTB> let k6=2

MTB> let k7=-0.75

MTB> let k8=-1

MTB> execute 'filename'500

MTB> xlabel c2 'Species1'

MTB> ylabel c3 'Species2'

MTB> gplot c3 c2

MTB> write 'Species1' c1 c2

MTB> write 'Species2' c1 c3

MTB> stop

## APPENDIX D

The program to obtain computer simulation of Example 4.9 is:

Minitab

MTB> store 'filename'

STORE> noecho

STORE> let c1(k1+1)=c1(k1)+k2

STORE> let c2(k1+1)=c2(k1)+k2\*(k3+k4\*c2(k1)+k5\*c3(k1))\*c2(k1)

STORE> let c3(k1+1)=c3(k1)+k2\*(k6+k7\*c2(k1)+k8\*c3(k1))\*c3(k1)

STORE> let k1=k1+1

STORE> end

MTB> let c1(1)=0

MTB> let c2(1)=10

MTB> let c3(1)=10

MTB> let k1=1

MTB> let k2=0.01

MTB> let k3=-2.5

MTB> let k4=-1

MTB> let k5=1.5

MTB> let k6=1

MTB> let k7=-0.5

MTB> let k8=0.5

MTB> execute 'filename'500

MTB> xlabel c2 'Prey'

MTB> ylabel c3 'Predator'

MTB> gplot c3 c2

MTB> write 'Prey' c1 c2

MTB> write 'Predator' c1 c3

MTB> stop