

Mathematical Modelling and it's Applications in Biology, Ecology and Population Study

J17405

September 12, 2016

Abstract

This thesis explores the topic of mathematical modelling involving the simulation of population growth associated with mathematical biology and more specifically ecology.

Chapter 1 studies how populations are modelled by looking at single equation models as well as systems of equation models of continuous and discrete nature. We also consider interacting populations including predator-prey, competition and mutualism and symbiosis relationships.

In Chapters 2 and 3, we review stability properties for both continuous and discrete cases including differential and difference equations respectively. For each case, we examine linear examples involving equilibrium solutions and stability theory, and non-linear examples by implementing eigenvalue, linearisation and Lyapunov methods.

Chapter 4 is a study of the research paper - A Model of a Three Species Ecosystem with Mutualism Between The Predators by K. S. Reddy and N. C. Pattabhiramacharyulu [32]. Here, we study the basic definitions and assumptions of the model, examine different cases for equilibrium solutions, prove global stability of the system and implement numerical examples for the model before reviewing existence and uniqueness and permanence properties.

In Chapter 5, we construct a discrete scheme of the model from Chapter 4. We do this in two ways, by using Euler's method to create one autonomous time-invariant form of the system, and utilising the method of piecewise constant arguments implemented in [6] to establish another autonomous time-invariant form of the system. For both discretisations, we study equilibrium solutions, stability, numerical examples and existence and uniqueness, and permanence properties.

Finally, we conclude the findings of the thesis, summarising what we have discovered, stating new questions that arise from the investigation and examine how this work could be taken further and built upon in future.

Contents

| Chapt | ter 1: Δ | An Introduction to Population Modelling | 5 |
|----------|-----------------------------|--|-----------------|
| 1 | Intro | duction / Background | 5 |
| 2 | Single | e Equation Models | 7 |
| | 2.1 | Continuous / Differential Equation Models | 7 |
| | 2.2 | Discrete / Difference Equation Models | 12 |
| 3 | Systems of Equations Models | | |
| | 3.1 | Continuous / Differential Equation Models | 16 |
| | | 3.1.1 The Elimination Method | 16 |
| | | 3.1.2 The Eigenvalue-Eigenvector Method | 17 |
| | 3.2 | Discrete / Difference Equation Models | 19 |
| | | 3.2.1 Systems of Linear Difference Equations | 19 |
| | | 3.2.2 Systems of Non-linear Difference Equations | 19 |
| | 3.3 | Interacting Populations | 20 |
| | | 3.3.1 Predator-Prey Models | 20 |
| | | 3.3.2 Competition Models | 21 |
| | | 3.3.3 Mutualism / Symbiosis Models | 21 |
| | | 3.3.4 Discrete Growth Models for Interacting Populations | 22 |
| | | 3.3.5 More Complex Population Growth | 24 |
| Chapt | ter 2: (| Continuous Differential Equation Systems | 25 |
| - л Л | Lines | ar Systems of Differential Equations | 25 25 |
| т | 4 1 | Equilibrium Solutions / Critical Points | $\frac{20}{25}$ |
| | 4.2 | Stability Theory | 26 |
| 5 | Non-l | linear Systems of Differential Equations | 29 |
| 0 | 5.1 | Figenvalue Method | 29 |
| | 5.2 | Linearisation Method | 31 |
| | 5.3 | Lyapunov Method | 33 |
| Chapt | ter 3: 1 | Difference Equation Systems | |
| - A | n Intr | roduction to Stability Analysis | 37 |
| 6 | Linea | ar Systems of Difference Equations | 37 |
| | 6.1 | Equilibrium Solutions / Critical Points | 37 |
| | 6.2 | Stability Theory | 38 |
| 7 | Non-l | linear Systems of Difference Equations | 40 |
| | 7.1 | Linearisation Method | 40 |
| | 7.2 | Lyapunov Method | 43 |

| Chapte | er 4: A Model of a Three Species Ecosystem with Mutualism Between | | |
|---------|---|-----------|--|
| The | Predators - K. S. Reddy & N. C. Pattabhiramacharyulu [32] | 45 | |
| 8 | Introduction | 45 | |
| 9 | The Mathematical Model | 45 | |
| 10 | Existence of Equilibrium Points | 46 | |
| 11 | Global Stability | 52 | |
| 12 | Numerical Examples | 54 | |
| 13 | Existence and Uniqueness | 66 | |
| | 13.1 Proving Existence and Uniqueness of The System | 69 | |
| 14 | Permanence and Persistence | 70 | |
| | 14.1 Proving Permanence and Persistence of The System | 70 | |
| Chapte | er 5: Constructing a Discrete System of Difference Equations Model | 73 | |
| 15 | Converting a Continuous System of Differential Equations to a Discrete System | | |
| | of Difference Equations | 73 | |
| | 15.1 Euler's Method \ldots | 73 | |
| | 15.1.1 Application of Euler's Method | 74 | |
| | 15.2 Method of Piecewise Constant Arguments | 75 | |
| | 15.2.1 Application of the Method of Piecewise Constant Arguments | 75 | |
| 16 | Existence of Equilibrium Points | 77 | |
| | 16.1 Discrete Form of System Using Euler's Method | 77 | |
| | 16.2 Discrete Form of System Using Method of Piecewise Constant Arguments | 83 | |
| 17 | Stability | 91 | |
| | 17.1 Discrete Form of System Using Euler's Method | 91 | |
| | 17.1.1 Linearisation Method | 91 | |
| | 17.2 Discrete Form of System Using Method of Piecewise Constant Arguments | 93 | |
| | 17.2.1 Linearisation Method | 93 | |
| 18 | Numerical Examples | 95 | |
| | 18.1 Discrete Form of System Using Euler's Method | 95 | |
| | 18.2 Discrete Form of System Using Method of Piecewise Constant Arguments 1 | 01 | |
| | 18.3 Comparison of Both Methods | 07 | |
| 19 | Existence and Uniqueness of The System | 12 | |
| | 19.1 Proving Existence and Uniqueness of The System | 14 | |
| | 19.1.1 Discrete Form of System Using Euler's Method | 14 | |
| | 19.1.2 Discrete Form of System Using Method of Piecewise Constant | | |
| | Arguments | 14 | |
| 20 | Permanence | | |
| | 20.1 Discrete Form of System Using Euler's Method | 16 | |
| | 20.2 Discrete Form of System Using Method of Piecewise Constant Arguments 1 | 18 | |
| Conclu | sion 1: | 20 | |
| Bibliog | graphy 1 | 21 | |

Chapter 1: An Introduction to Population Modelling

1 Introduction / Background

In this chapter we look at the relationship between Mathematics and Biology, Ecology and the application of Mathematical Modelling in Ecology and how we use and construct continuous differential equations and discrete difference equations whilst modelling populations. We will analyse linear and non-linear types of these equations as well as single equation models and models consisting of systems of equations.

Mathematics and Biology are said to have a synergistic relationship [36]. Biology presents interesting problems that Mathematics models to understand them before Biology can then be used to test these models. Mathematical Biology therefore exploits the natural relationship between Biology and Mathematics. Biology is a complex subject. Whilst mathematical models cannot fully calculate and describe biological processes, they can be useful [35]. In order to develop a model, detailed knowledge of the studied topic is needed. When constructing the model, small initial steps are taken that are built upon to create larger more complex models. As Shonkwiler and Herod [36] suggest, Mathematical models ask new questions of biological processes that can only be tested on real biological systems.

Ecology is the study of the interrelationships between different species and their environment or, in it's simplest terms, the study of population biology [30], [33]. This area of biology involving the study of population change has a long history. Of all aspects of Biology, Ecology has been the most mathematically used and developed. The application of mathematical modelling can be used to simulate predator-prev systems, competition interactions, renewable resource management pest control strategies, the evolution of pesticide resistant strains, multispecies societies, plant-herbivore systems as well as a continually expanding list of additional applications [30]. The use of these applications in turn help to understand dynamic processes involved in biology and allow biologists to make practical predictions. Early studies conducted included small mammals and laboratory controlled organisms which were easily associated with mathematical formulation [33]. In recent years, there has been an increase in the study of realistic, practical and useful applications of mathematical modelling in biology [30]. This research has mainly focused on human populations including and not including age distribution, the study of endangered species, bacterial and viral growth as well as the highly practical applications of single-species models in biomedical sciences. Recent research has also focused on modelling mult-species and spatial population growth despite uncertain predictions involving their behaviour outside the laboratory [33]. This uncertainty is associated with the fact that populations in their natural environment are regulated from within by density-dependent factors or external density-independent factors. As noted by Renshaw [33], theoretical developments in modelling generally use density-dependent factors. This is primarily due to the lack of information available regarding external factors because of their complex and variable nature [10].

Scientists propose that mathematical models represent real population systems [36]. But, in most cases, real population systems are too complex for this proposal and are prone to a range of changes in their many influencing factors. Despite these changes, a "wrong model" can be adapted and developed further whilst a "right model" may be too complex or contain too much detail [35]. As Renshaw [33] states, whilst considering the implementation of mathematics in biology, we need to develop models which are strongly influenced by considerations and ideas of mathematical simplicity [28], [39]. The simplest model should be descriptive. Here, the "essence" of the subject is captured whilst the detail is neglected by concentrating on the essential aspects to include in the model [35]. Differential equations can be used to utilise continuous changes in population whilst difference equations are implemented to monitor discrete changes in population. Therefore a good mathematical model should be simple whilst exhibiting the behaviour of a real system to the best of it's ability [4], [13], [15], [20].

2 Single Equation Models

We start by exploring single equation models of a continuous differential equation nature:

2.1 Continuous / Differential Equation Models

Despite single-species models being of relevance to laboratory studies, in real-world situations, a telescoping of effects, where events that take place are not percieved in correct order along a given time period, occurs which influences the dynamics of the population [30]. When studying a culture of bacteria, there is little purpose in taking account of every single bacterium. Instead, the focus should be on the mass, volume and optical density of the culture [46]. This leads us to the implementation of continuous variables.

Let N(t) denote the population of species at time t, then the rate of change in a population can be calculated by:

$$\frac{dN}{dt} = \text{Births} - \text{Deaths} + \text{Migration} \tag{1}$$

Factoring migration can make the model more complex. The simplest model contains no migration whilst births and deaths are proportional to N(t):

Malthus Model (1798) [27]

The earliest application of mathematics and mathematical modelling to population theory was conducted by Thomas Robert Malthus [27]. A British clergyman and economist, Malthus formulated the following model using the law of exponential growth [46]:

$$\frac{dN}{dt} = bN - dN \tag{2}$$

where b and d are positive constants and are proportional to N(t).

Rearranging and integrating (2), we have:

$$\frac{dN}{dt} = N(b-d) \tag{3}$$

$$\int \frac{1}{N} dN = \int (b-d)dt \tag{4}$$

$$\ln N = (b - d)t + C \qquad \text{where C is a constant.}$$
(5)

$$N = e^{(b-d)t+C} \tag{6}$$

$$N = e^{(\sigma - \sigma)^2} e^{\sigma} \tag{7}$$

$$N(t) = Ce^{(b-d)t} \tag{8}$$

At t = 0, we have:

$$N(0) = N_0 = Ce^{(b-d)(0)}$$
(9)

$$N_0 = C \tag{10}$$

Therefore

$$N(t) = N_0 e^{(b-d)t} \tag{11}$$

where $N(0) = N_0$ denotes the initial population.

Here, if:

b<d - The population N(t) grows exponentially.

b>d - The population N(t) dies out, eventually becoming extinct.

Whilst this model is fairly unrealistic, it can be used as a form of estimation, for example, estimating world population [30]. The approximation assumes that populations change continuously and differentiably over time. A linear model for population growth is satisfactory if the studied population is not too large [2]. For a large population, this becomes a much less accurate model considering the influences of individuals competing for limited living space, natural resources and food available. Therefore, an improved population model must implement competition as a contributing factor. This leads us to the Verhulst model or Logistic Growth Model:

Verhulst Model - Logistic Growth Model (1838,1845)[45]

Pierre-Francois Verhulst [45], a Belgian mathematician, proposed a sigmoidal logistic growth function, often encountered in microbial populations, and formulated the following logistic growth model [46]:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \tag{12}$$

where

- r and K are positive constants.
- K is the carrying capacity of the environment (determined by the available sustaining resources).
- $r\left(1-\frac{N}{K}\right)$ denotes the per capita birth rate dependent on N(t) at time t.

Rearranging (12), we have:

$$rdt = \frac{dN}{N(1 - \frac{N}{K})}\tag{13}$$

Using Partial Fractions:

$$\frac{1}{N\left(1-\frac{N}{K}\right)} = \frac{A}{N} + \frac{B}{\left(1-\frac{N}{K}\right)} \tag{14}$$

$$1 = A\left(1 - \frac{N}{K}\right) + BN\tag{15}$$

$$1 = A + N\left(B - \frac{A}{K}\right) \tag{16}$$

$$B - \frac{A}{K} = 0$$
 or $B = \frac{A}{K}$ (17)

Substituting $B = \frac{A}{K}$ in (16) yields:

$$1 = A + N\left(\frac{A}{K} - \frac{A}{K}\right) \tag{18}$$

$$A = 1 \tag{19}$$

Hence, by (17), we get:

$$B = \frac{1}{K} \tag{20}$$

Substituting values for A and B in (14), we have

$$\frac{1}{N\left(1-\frac{N}{K}\right)} = \frac{1}{N} + \frac{\frac{1}{K}}{\left(1-\frac{N}{K}\right)}$$
(21)

Hence, (13) becomes:

$$rdt = \frac{dN}{N\left(1 - \frac{N}{K}\right)}\tag{22}$$

$$=\frac{dN}{N} + \frac{\frac{dN}{K}}{\left(1 - \frac{N}{K}\right)} \tag{23}$$

Integrating both sides of (23), we get:

$$\int r dt = \int \frac{1}{N} dN + \int \frac{\frac{dN}{K}}{1 - \frac{N}{K}}$$
(24)

$$rt + C = \ln N - \ln \left(1 - \frac{N}{K}\right) \tag{25}$$

$$rt + C = \ln\left[\frac{N}{1 - \frac{N}{K}}\right] \tag{26}$$

$$e^{rt+C} = \frac{N}{1 - \frac{N}{K}} \tag{27}$$

$$e^{rt}e^C = \frac{N}{1 - \frac{N}{K}} \tag{28}$$

$$Ce^{rt} = \frac{N}{1 - \frac{N}{K}} \tag{29}$$

At t = 0, we have:

$$C = \frac{N_0}{1 - \frac{N_0}{K}} = \frac{N_0}{1 - \frac{N_0}{K}} \frac{K}{K} = \frac{N_0 K}{K - N_0}$$
(30)

where $N(0) = N_0$.

Therefore

$$\left(1 - \frac{N}{K}\right)Ce^{rt} = N \tag{31}$$

$$Ce^{rt} = N\left[1 + \frac{Ce^{rt}}{K}\right] \tag{32}$$

Solving for N(t), we have:

$$N(t) = \frac{Ce^{rt}}{1 + \frac{Ce^{rt}}{K}}$$
(33)

$$=\frac{\frac{KN_{0}}{K-N_{0}}e^{rt}}{1+\frac{\frac{KN_{0}}{K-N_{0}}e^{rt}}{K}}$$
(34)

Multiplying the numerator and denominator by $(K - N_0)e^{-rt}$ yields:

$$N(t) = \frac{KN_0}{N_0 + (K - N_0)e^{-rt}}$$
(35)

$$N(t) = \frac{N_0 K e^n}{[K + N_0 (e^{rt} - 1)]}$$
(36)

Here

$$N(t) = \frac{N_0 K e^{rt}}{[K + N_0 (e^{rt} - 1)]} \to K \text{ as } t \to \infty$$
(37)

If:

- $N_0 < K$ The population N(t) increases monotonically to K.
- $N_0 > K$ The population N(t) decreases monotonically to K.

This model provides a algebraicly simple and preliminary qualitative idea for further development and realistic forms [30].

Subsequent literature involving populations has focused on human, animal, plant, bacteria, cell and virus population growth. The majority of this research has involved simple, non-linear functions of continuous and discrete nature as well as using solutions of ordinary differential equations (ODEs) [46]. Differential equations have been greatly utilized in these models due to being easier to analyse and understand than discrete and stochastic models as well as being effective forms of capturing growth behaviour.

Noted below are some additional well-known models that have been used in population studies:

Richards Function[34]

Widely used in plant-science, agriculture and forestry [34], [46].

$$N_R(t) = K \{ 1 + Q e^{-\alpha v(t-t_0)} \}^{-\frac{1}{v}}$$
(38)

where

- N_R is the population function of time t.
- $N_0 = N_R(0)$ is the population size at time t = 0.
- *K* is the carrying capacity.
- α , v are positive parameters.

•
$$Q = \left(\frac{K}{N_0}\right)^v - 1.$$

Gompertz Growth Law [8]

Often used in actuarial sciences [8], [46].

$$N_G(t) = K e^{-be^{-rt}} \tag{39}$$

where

- *K* is the carrying capacity.
- r is the growth rate.
- *b* is a positive parameter.

Example - Monod's Nightmare [20], [31]

Jaques Monod (1910-1976) was a recipient of the Nobel Prize for Medicine for his work on gene regulation in 1965. He also conducted several innovative experimental studies on kinetics and stoichiometry of microbial growth [31]. His model, commonly known as "Monod's Nightmare" simulates the growth of *Escherichia coli* or E. coli, a bacterium used extensively in microbiological studies [20]. The bacterium consists of rod shaped cells that are $0.75\mu m$ wide and $2\mu m$ long. In ideal conditions, the population of these cells would double in just over 20 minutes. Here, the model consists of one continuous differential equation:

The Model

Consider a per capita growth rate that decreases linearly, the population size is denoted by:

$$\frac{1}{N}\frac{dN}{dt} = r\left(1 - \frac{N}{k}\right) \tag{40}$$

where:

- The decrease in per capita growth rate is a simple form of density- regulation.
- The per capita growth rate $\rightarrow 0$ at the carrying capacity k.

Defects / Problems with the Model

- 1. The constant per capita birth and death rates generate limitless growth, which is patently unrealistic.
- 2. This is a deterministic model, hence, chance is ignored as well as stochastic effects. These stochastic effects are very important to small population sizes.
- 3. Lags are ignored. Here, the growth rate does not depend on the past. The population responds instantaneously to changes in current population size.
- 4. Temporal and spatial variability is ignored.

2.2 Discrete / Difference Equation Models

When studying different organisms, it becomes apparent that in many species, births take place in regular and well-defined "breeding seasons" [20].

Plants have a range of flowering patterns that greatly differ from species to species. Herbs are monocarpic, they flower once then die after setting seed, roots included [20]. Bamboo are types of grasses that grow vegetatively for 20 years before flowering and consequently dying. Other plant species have flowering times ranging from 1 to 60 years such as trees, which flower repeatedly over a number of decades [29]. Insects are divided into three categories: univoltine, bivoltine and multivoltine [20]. Univoltine species only have one generation a year, bivoltine have two generations a year and multivoltine have multiple generations in one year. Mayflies or Dayflies are well-known for their semel parity (monocarpy in plants) or being univoltine. Most species of insects are univoltine but tend to be bivoltine or multivoltine if they come from warmer climates [43]. There are 22,000 different species of fish with varying migration patterns. Less than one percent of these are semelparous - die after spawning. They can live up to 10-15 years in freshwater lakes before the majority migrate to the sea, spawn and die [7]. All birds are iteroparous. In other words, they have multiple reproductive cycles over the course of a lifetime [20]. They also have short breeding seasons and various migration patterns. Mammals have the widest range of birth patterns, including univoltine, bivoltine and multivoltine [20].

Differential equations such as ordinary, delay, partial and stochastic equations imply a continuous overlap of generations when studying populations [30]. Many species have no overlap between successive generations therefore population growth is said to be discrete. Various changes in "breeding seasons" and birth patterns contradict the assumption, when using differential equations, that births occur continuously. Therefore we must apply a discrete approach using difference equations.

The mathematics of difference equations is a topic that has been studied in depth and applied in a range of diverse fields. These include cancer growth, aging, cell proliferation and genetics. But their largest use, by far, has been in Ecology [30]. Difference equations describe the evolution of certain phenomena over the course of time [5]. Therefore, they can be used to model populations and the generations found within them.

Density-Independent Growth

Let:

- N_t be the size of the population in year / generation t.
- R_0 be the net productive rate where each individual leaves R_0 offspring before dying.

Then, we have the following linear first-order difference equation with constant coefficients [20]:

$$N_{t+1} = R_0 N_t \tag{41}$$

Since the offspring leave the same number of offspring with each generation:

$$N_{1} = R_{0}N_{0}$$

$$N_{2} = R_{0}N_{1} = R_{0}(R_{0}N_{0}) = R_{0}^{2}N_{0}$$

$$\vdots$$

$$N_{t} = R_{0}^{t}N_{0}$$
(42)

The solution of (41) will display geometric growth or decay.

If:

- *R*₀ > 1 Each individual leaves more than one descendent.
 ⇒ Population grows exponentially.
- $0 < R_0 < 1$ Each individual leaves only one descendent (on average). \Rightarrow Population decays geometrically.

Density-Dependent Growth

Density-dependent growth occurs if the number of offspring per adult varies with density and is associated with non-linear difference equations [20]. Here, we have two cases:

1. Assuming that the per capita number of offspring is inversely proportional to a linearly increasing function of the number of adults, we have:

$$\frac{N_{t+1}}{N_t} = \frac{R_0}{1 + \left[\frac{(R_0 - 1)}{K}\right]N_t} \tag{43}$$

which results in the following difference equation also known as the Beverton-Holt Stock-Recruitment Curve [1]:

$$N_{t+1} = \frac{R_0 N_t}{1 + \left[\frac{(R_0 - 1)}{K}\right] N_t} \tag{44}$$

which is a monotonically increasing hyperbolic mapping [20].

2. The second type of density-dependent growth has a similar form to the logistic differential equation but does not resemble the same solution. It is also a direct approximation of the logistic differential equation.

Here, we have:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \tag{45}$$

Approximating the LHS derivative of (45) with a finite-difference quotient yields:

$$\frac{\Delta N}{\Delta t} = rN\left(1 - \frac{N}{K}\right) \tag{46}$$

For the organism in question, time step Δt is one generation, hence, let $\Delta t = 1$. Therefore:

$$N_{t+1} - N_t = rN_t \left(1 - \frac{N_t}{K}\right) \tag{47}$$

which yields the following logistic difference equation:

$$N_{t+1} = (1+r)N_t - \frac{r}{K}N_t^2$$
(48)

Example 1 - Fibonacci Sequence [30]

In the 18th century, Leonardo of Pisa, more well know as Fibonacci, conducted a modelling exercise involving a hypothetical growing rabbit population in the arithmetic book of 1202 [30]. Here, the model starts at the beginning of the breeding season with a pair of immature rabbits, male and female. After one reproductive season, the first pair produce 2 pairs of male and female immature rabbits after which the first pair of rabbits, or parents, stop reproducing. The offspring then replicate this process. Here, the question is, how to determine the number of pairs of rabbits at each reproductive period?

Let

- N_t be the number of pairs, male and female, of rabbits.
- Hence, at the tth reproductive stage, we have:

$$N_{t+1} = N_t + N_{t-1}$$
 for $t = 2, 3, \dots$ (49)

• If $N_0 = 1$, we have the following Fibonacci sequence:

$$1, 1, 2, 3, 5, 8, 13, \dots$$
 (50)

where each term in the sequence is the sum of the previous two.

Example 2 - Cell Division[4]

Edelstein-Keshet [4] notes the following model involving cell division. A population of cells divide synchronously where each member produces a daughter cell.

Let

• M_1, M_2, \ldots, M_n be the number of cells in each generation. Therefore, successive generations are denoted by:

$$M_{n+1} = aM_n \tag{51}$$

where M_0 is the initial cell population.

• By applying (51) recursively, we get:

$$M_{n+1} = a(aM_{n-1}) = a[a(aM_{n-2})] = ... = a^{n+1}M_0$$
(52)

• Therefore, the n^{th} generation is given by:

$$M_n = a^n M_0 \tag{53}$$

Here, a determines the growth of the population. If:

- 1. |a| > 1 M_n increases over successive generations.
- 2. |a| < 1 M_n decreases over successive generations.
- 3. $a = 1 M_n$ is constant.

Example 3 - An Insect Population[4]

As previously mentioned, insects have more than one stage in their life cycle, from progeny to maturity. The complete cycle can last from weeks to months to years. A single generation represents a basic unit of time. But, to model several stages of a life cycle, several equations must be used to construct a model, which we will look at in Chapter 3.

Poplar Gall Aphid

An aphid is a small insect that commonly takes the form of a fly. They are capable of very quick reproduction and can cause large amounts of damage to plants and crops [20]. An adult female aphid produces galls, a type of growth, on leaves of poplars, a tall and fast-growing tree. The progeny of a single aphid are contained in one gall with only a fraction of these surviving and maturing to adulthood [49].

Here, let:

- a_n be the number of adult female aphids in the nth generation.
- p_n be the number of progeny in the nth generation.
- *m* be the fractional mortality of young aphids.
- f be the number of progeny per female aphid.
- r be the ratio of female aphids to total adult aphids.

Each female produces f progeny, thus:

$$p_{n+1} = fa_n \tag{54}$$

denotes the number of progeny in the $(n + 1)^{st}$ generation. This is equal to the number of females in the previous generation, a_n , multiplied by the number of offspring per female, f.

Here, the fraction (1 - m) survives to a dulthood, yielding a final proportion of r females. Hence:

$$a_{n+1} = r(1-m)p_{n+1} \tag{55}$$

(54) and (55) can be combined into the following linear first-order difference equation that describes the aphid population:

$$a_{n+1} = fr(1-m)a_n (56)$$

Noting that f, r and m are constants, we have:

$$a_n = [fr(1-m)]^n a_0 \tag{57}$$

where a_0 is the initial number of adult females.

3 Systems of Equations Models

Mathematical models as equations or sets of equations are processes that describe phenomena that occur in science, economics and engineering [23]. Here we examine their application in biology, more importantly ecology. A model aims to provide a qualitative prediction as well as make sense of the natural world. But, in most cases, scientific exactness must be sacrificed for mathematical tractability. The complexity of a model derives from the large numbers of parameters and variables considered [23]. A one population model would indicate that a size of a population converges to a constant value whilst a population of two species may show different behaviour in the form of periodical cycles [17]. These cycles are often observed in nature and therefore justify the use of systems of equations. Systems of equations allow us to start on the side of simplicity before building upon the complexity of the model as needed [23]. Systems of equations are of continuous type, consisting of systems of differential equations, and discrete type, with the application of difference equation systems. These can then be included in models of interacting species including predator-prey, competition and mutualism or symbiosis relationships [20], [30].

3.1 Continuous / Differential Equation Models

3.1.1 The Elimination Method

Consider the following system of two first-order equations [4]:

$$\frac{dx}{dt} = a_{11}x + a_{12}y \tag{58}$$

$$\frac{dy}{dt} = a_{21}x + a_{22}y \tag{59}$$

The system of equations (58) and (59) can be reduced to a single second-order equation in x(t) using the following procedure of elimination:

1. First, we differentiate equation (58) with respect to t:

$$\frac{d^2x}{dt^2} = a_{11}\frac{dx}{dt} + a_{12}\frac{dy}{dt}$$
(60)

2. Substituting (59) in (60), we get:

$$\frac{d^2x}{dt^2} = a_{11}\frac{dx}{dt} + a_{12}\left(a_{21}x + a_{22}y\right)
= a_{11}\frac{dx}{dt} + a_{12}a_{21}x + a_{12}a_{22}y$$
(61)

3. Rearranging (58), we have:

$$y = \frac{1}{a_{12}} \frac{dx}{dt} - \frac{a_{11}}{a_{12}} x \tag{62}$$

4. Substituting (62) in (61) yields:

$$\frac{d^2x}{dt^2} = a_{11}\frac{dx}{dt} + a_{12}a_{21}x + a_{12}a_{22}\left(\frac{1}{a_{12}}\frac{dx}{dt} - \frac{a_{11}}{a_{12}}x\right)$$
(63)

$$\frac{d^2x}{dt^2} = a_{11}\frac{dx}{dt} + a_{12}a_{21}x + a_{22}\frac{dx}{dt} - a_{11}a_{22}x \tag{64}$$

$$\frac{d^2x}{dt^2} = (a_{11} + a_{22})\frac{dx}{dt} + (a_{12}a_{21} - a_{11}a_{22})x$$
(65)

$$\frac{d^2x}{dt^2} - (a_{11} + a_{22})\frac{dx}{dt} + (a_{11}a_{22} - a_{12}a_{21})x = 0$$
(66)

(67)

(70)

5. Therefore

$$\frac{d^2x}{dt^2} - \beta \frac{dx}{dt} + \gamma x = 0 \tag{68}$$

where $\beta = a_{11} + a_{22}$ and $\gamma = a_{11}a_{22} - a_{12}a_{21}$.

The general solution of (68) has the form:

$$x(t) = c_1 e^{\lambda_1 t} + c_2 e^{\lambda_2 t} \tag{69}$$

where $\lambda_1, \lambda_2 = \frac{\beta \pm \sqrt{\beta^2 - 4\gamma}}{2}$.

Let $\delta = \beta^2 - 4\gamma$. When $\delta < 0$, equation (69) produces complex eigenvalues.

3.1.2 The Eigenvalue-Eigenvector Method

Consider the following system of first order differential equations in vector notation [4]:

where
$$x = \begin{pmatrix} x \\ y \end{pmatrix}$$
 and $A = \begin{pmatrix} a_{11} & \cdots & a_{1n} \\ \vdots & \ddots & \vdots \\ a_{n1} & \cdots & a_{nn} \end{pmatrix}$ for $n = 2, 3, \dots$

Finding the eigenvalues and corresponding eigenvectors of A yields the following general solution:

$$x(t) = c_1 v_1 e^{\lambda_1 t} + \ldots + c_n v_n e^{\lambda_n t} \quad \text{for } n = 2, 3, \ldots \quad \lambda_1 \neq \lambda_2 \tag{71}$$

where v_1, \ldots, v_n are eigenvectors of A and $\lambda_1, \ldots, \lambda_n$ are eigenvalues of A.

For different eigenvalues of A we have the following special cases:

• $\lambda_1 = \lambda_2$ - Repeated Eigenvalues

 \Rightarrow Here only one eigenvector is produced. Therefore the form of the general solution must be amended to allow for two distinct linearly independent eigenvectors.

• $\lambda_1, \lambda_2 = r \pm ci$ - Complex Eigenvalues

 \Rightarrow Here eigenvectors v_1, v_2 have the form $a \pm bi$ which produce the general solution:

$$x(t)c_1(a+bi)e^{(r+ci)t} + c_2(a-bi)e^{(r-ci)t}$$
(72)

ectors of A and

Example 1: A System of Two Ordinary Differential Equations with Exponential Solutions [35]

Here, we have the following linear system of 2 ODEs:

$$\frac{dx}{dt} = -3x - y \tag{73}$$

$$\frac{dy}{dt} = x \tag{74}$$

Solution

1. First, we differentiate both sides of (73) with respect to t:

$$\frac{d^2x}{dt^2} = -3\frac{dx}{dt} - \frac{dy}{dt} \tag{75}$$

2. Substituting (74) in (75), we get:

$$\frac{d^2x}{dt^2} = -3\frac{dx}{dt} - x\tag{76}$$

3. Rearranging (76), we have the following second-order ODE:

$$\frac{d^2x}{dt^2} + 3\frac{dx}{dt} + x = 0$$
(77)

4. Using (77), we can write the characteristic equation:

$$m^2 + 3m + 1 = 0 \tag{78}$$

which produces the following two real roots:

$$m_1 = -\frac{3}{2} + \frac{\sqrt{5}}{2} \approx -0.38 \qquad m_2 = -\frac{3}{2} - \frac{\sqrt{5}}{2} \approx -2.62$$
 (79)

3.2 Discrete / Difference Equation Models

Consider the following Autonomous or Time-Invariant system of k linear equations [5]:

$$x_{1}(n+1) = a_{11}x_{1}(n) + a_{12}x_{2}(n) + \dots + a_{1k}x_{k}(n)$$

$$x_{2}(n+1) = a_{21}x_{1}(n) + a_{22}x_{2}(n) + \dots + a_{2k}x_{k}(n)$$

$$\vdots$$

$$x_{k}(n+1) = a_{k1}x_{1}(n) + a_{k2}x_{2}(n) + \dots + a_{kk}x_{k}(n)$$
(80)

and Non-autonomous or Time-Variant system of k linear equations [5]:

$$x_{1}(n+1) = a_{11}(n)x_{1}(n) + a_{12}(n)x_{2}(n) + \ldots + a_{1k}(n)x_{k}(n)$$

$$x_{2}(n+1) = a_{21}(n)x_{1}(n) + a_{22}(n)x_{2}(n) + \ldots + a_{2k}(n)x_{k}(n)$$

$$\vdots$$

$$x_{k}(n+1) = a_{k1}(n)x_{1}(n) + a_{k2}(n)x_{2}(n) + \ldots + a_{kk}(n)x_{k}(n)$$
(81)

Systems (80) and (81) can be written in the following matrix form respectively:

Autonomous Time-Invariant:

$$x(n+1) = Ax(n) \tag{82}$$

Non-autonomous Time-Variant:

$$x(n+1) = A(n)x(n) \tag{83}$$

where

- $x(n) = (x_1(n), x_2(n), \dots, x_k(n))^T \in \mathbb{R}^k$.
- A, A(n) are $k \times k$ real non-singular matrices.

3.2.1 Systems of Linear Difference Equations

A system of linear first-order difference equations has the general form [4]:

$$\begin{aligned} x_{n+1} &= a_{11}x_n + a_{12}y_n \\ y_{n+1} &= a_{21}x_n + a_{22}y_n \end{aligned} \tag{84}$$

3.2.2 Systems of Non-linear Difference Equations

A system of non-linear first-order difference equations has the general form [4]:

$$x_{n+1} = f(x_n, y_n)
 y_{n+1} = g(x_n, y_n)
 (85)$$

3.3 Interacting Populations

Different species within a population or biosystem interact with each other on a regular basis. This affects the population dynamics for each species [30]. There are three types of interaction in populations:

- 1. Predator-Prey
- 2. Competition
- 3. Mutualism / Symbiosis

This section examines each type as well as relevant mathematical models.

3.3.1 Predator-Prey Models

Predator-Prey models occur when the growth rate of one population is decreased whilst the other population is increased [30].

The Lotka-Volterra Model [25], [26], [47]

The Lotka-Volterra Model is a simple model that implements the predation of one species by another, for example, being able to explain the oscillatory levels of fish catches in the Adriatic sea [30]. Here, we have the following model:

Definitions

- N(t) The prey population at time t.
- P(t) The predator population at time t.

Assumptions

- 1. The prey population grows unboundedly in a Malthusian way in the absence of a predator, denoted by aN.
- 2. The effect of predation reduces the prey per capita growth rate which is proportional to the population of predator and prey, denoted by -bNP.
- 3. The predator death rate exhibits exponential decay in the absence of prey, denoted by -dP.
- 4. The prey's contribution to the predator's growth rate is proportional to the available prey and size of the predator population, denoted by -cNP.

The Model

• The population of predator and prey is given by:

$$\frac{dN}{dt} = N(a - bP) \tag{86}$$

$$\frac{dP}{dt} = P(cN - d) \tag{87}$$

where a, b, c and d are positive constants and N(t) and P(t) are proportional to time t.

• Despite the model's structural instability it can be of considerable value. It presents relevant questions and a base for further development by it's application to real-world oscillatory problems.

Example - Canadian Lynx and Snowshoe Hare [30]

The Canadian Lynx and Snowshoe Hare were interacting species in the fur catch records of the Hudson Bay Company, Canada from 1845 to the 1930s. Applying the Lotka-Volterra Model to this situation produced questionable data whilst assuming that the numbers recorded reflected a fixed proportion of the total population. This inconsistent data suggested that the hare population were eating the lynx, which was highly doubtful. This was a result of complications with unaccounted factors such as culling of the hare and diseases that occurred in both populations.

Therefore, when constructing a model, it is not adequate to simply produce a system which only exhibits oscillations. Here, proper explanation of the studied phenomenon is needed which can stand up to ecological and biological scrutiny.

In conclusion, the Lotka-Volterra Model, in general, is unrealistic due to the fact that it suggests that a simple predator-prey interaction can result in periodic behaviour of populations.

3.3.2 Competition Models

Competition between two or more species occurs when the growth rate of each population is decreased [30]. Here, two or more species compete for the same limited food source which inhibits each other's population growth. This competition can also result in territory that contains food and other valuable resources. A simple competition model consists of two species competing for the same limited resources which results in one of the species eventually becoming extinct.

We consider the following basic two-species Lotka-Volterra competition model with each species, denoted by N_1 and N_2 respectively, demonstrating logistic growth in the absence of the other [30]. Here, the inclusion of logistic growth makes the model more realistic.

Let

- r_1, r_2 be the linear birth rates.
- K_1, K_2 be the carrying capacities.
- b_{12} , b_{21} measure the competitive effect of N_2 on N_1 and N_1 on N_2 , which are generally not equal.

Hence

$$\frac{dN_1}{dt} = r_1 N_1 \left[1 - \frac{N_1}{K_1} - b_{12} \frac{N_2}{K_1} \right]$$
(88)

$$\frac{dN_2}{dt} = r_2 N_2 \left[1 - \frac{N_2}{K_2} - b_{21} \frac{N_1}{K_2} \right]$$
(89)

3.3.3 Mutualism / Symbiosis Models

A mutualistic or symbiotic relationship takes place when the growth rate of each population is increased [30]. Mutualism or Symbiosis plays a crucial role in promoting and maintaining the

advantage of interaction between two or more species. It's importance in ecology is comparable to that of Predator-Prey and Competition systems but is not as widely studied. This is somewhat associated with the fact that it often produces incorrect or inconsistent results.

Considering the simplest form of a mutualism model, equivalent to a Lotka-Volterra system, we have [30]:

$$\frac{dN_1}{dt} = r_1 N_1 + a_1 N_1 N_2 \tag{90}$$

$$\frac{dN_2}{dt} = r_2 N_2 + a_2 N_2 N_1 \tag{91}$$

where r_1 , r_2 , a_1 and a_2 are positive constants.

Here, since $\frac{dN_1}{dt} > 0$ and $\frac{dN_2}{dt} > 0$, N_1 and N_2 grow unboundedly.

3.3.4 Discrete Growth Models for Interacting Populations

The above systems and models for interacting species all assume a continuous form by using differential equations. When considering interacting species, models can also be constructed using a discrete form using difference equations. If we consider two interacting species with non-overlapping generations, each species affects each other's population dynamics. Along with unpredictable environmental factors, this produces complex solutions to single equation models which are greatly increased when modelling systems of equations. When studying predator-prey systems, species such as insects have a substantial body of experimental data. Insects life cycles are modelled by two-species discrete models [30].

Here, we present a discrete form of the predator-prey model. Consider the interaction for prey, N, and predator, P, to be governed by the following discrete time t system of coupled equations [30]:

$$N_{t+1} = rN_t f(N_t, P_t) \tag{92}$$

$$P_{t+1} = N_t g(N_t, P_t) \tag{93}$$

where:

- r > 0 is the net linear increase rate of the prey.
- f and g relate to the predator influence reproductive efficiency of prey and searching efficiency of the predator respectively.

Example: Host-Parasitoid Systems [4]

Discrete difference equations apply most readily to groups such as insects [5]. This is due to the natural division of time in discrete generations of the species. A host-parasitoid system has been the topic of considerable study and has seen a great increase of research conducted in the area in recent years. Both species, the host and the parasite, have multiple life-cycle stages. The parasite generally develops from egg to larvae to pupae to mature, fully grown adult. Then the adult female parasite searches for a host to oviposit her eggs, also known as implanting the eggs. In some cases, these eggs are attached to the outer surface of the host during their larval or pupal stage. From here, the eggs are injected into the host's flesh. Then, the larval parasitoids develop and mature at the expense of the host, consuming and eventually killing the host before pupating. Here, Elaydi [5] presents the following discrete difference equation model for the host-parasite relationship:

Assumptions

- 1. Hosts that have been parasitized give rise to the next generation of parasites.
- 2. Hosts that have not been parasitized give rise to their own progeny or offspring.
- 3. The percentage of hosts that have been parasitized depend on the rate of interaction between the two species as well as the densities and population sizes of both host and parasite.

Definitions

- N_t Density of host species in generation t.
- P_t Density of parasitoid in generation t.
- $f f(N_t, P_t)$ Fraction of hosts not parasitized.
- λ Reproductive Rate of Host.
- c The average number of viable eggs laid by parasitoid on a single host.

The 3 assumptions also lead to the following definitions:

- N_{t+1} The number of hosts in previous generation $(N_t) \times$ Fraction of hosts not parasitized $(f) \times$ Reproductive Rate of Host (λ) .
- P_{t+1} The number of hosts parasitized in previous generation $(P_t) \times$ The average number of viable eggs laid by parasitoid on a single host (c).

The Model

• Where 1 - f denotes the fraction of hosts parasitized, we have the following model for a parasitoid-host interaction:

$$N_{t+1} = \lambda N_t f(N_t, P_t) P_{t+1} = c N_t [1 - f(N_t, P_t)]$$
(94)

This model outlines a general framework and provides a good base for further development.

3.3.5 More Complex Population Growth

Population growth generally follows certain laws which are collected over time. Although this is true, there is no guarantee that data that is collected from populations that adhere to these laws can be accurately modelled [46].

An example of this is the calculation of the maximal size of a human population. If the growth function of the population is known, then the maximal size is easily determined. Human populations are unpredictable. They require agent-based modelling techniques using computer simulations. This is due to heuristic rules that occur in human populations that guide their decisions and interactions with other members. Although these models can become highly complex and commonly produce incorrect results as well as being very difficult to mathematically analyse, they can be very powerful and useful as a form of approximation [46].

An unsolved problem in population dynamics is the formulation and analysis of models for metapopulations. Metapopulations consist of hundreds or thousands of different species of microbes. These microbes compete for space and nutrients and rely upon each other in order to survive. Typical population studies ignore spatial considerations which are very important. These present problems in modelling due to their complex and ever changing nature. An example of this is the following study of the spread of an introduced pest [46]:

Example: Spread of an Introduced Pest - Red and Black Fire Ant [22], [46]

The Black Fire Ant or *Solenopsis richteri* was introduced in the US in 1918, reaching the port of Mobile, Alabama. In the 1930s, it was joined by the more aggressive Red Fire Ant or *Solenopsis invicta*. In the absence of any significant predators, the two species spread very quickly which was fitting of the red ant's Latin name meaning "undefeated". In 1953, the US Department of Agriculture announced that both species had invaded 102 counties in 10 states. In 1996, 300,000 acres of land throughout the south were infected. An organized modelling approach to this situation would provide biological strategies in order to control the pest as well as decrease the species population.

Chapter 2: Continuous Differential Equation Systems - An Introduction to Stability Analysis

4 Linear Systems of Differential Equations

Consider functions $x_1(t), x_2(t), \ldots, x_n(t)$ of time t that satisfy the following system of n linear differential equations [2], [42]:

$$\frac{dx_1}{dt} = a_{11}x_1 + a_{12}x_2 + \ldots + a_{1n}x_n$$

$$\frac{dx_2}{dt} = a_{21}x_1 + a_{22}x_2 + \ldots + a_{2n}x_n$$

$$\vdots$$

$$\frac{dx_n}{dt} = a_{n1}x_1 + a_{n2}x_2 + \ldots + a_{nn}x_n$$
(95)

where $a_{11}, a_{12}, \ldots, a_{nn}$ are constants.

4.1 Equilibrium Solutions / Critical Points

An equilibrium solution is a solution to (95) where $v(t) = \begin{pmatrix} x_1(t) \\ x_2(t) \\ \vdots \\ x_n(t) \end{pmatrix}$ is a constant vector and

 $x_1, x_2, \ldots, x_n = x_1^0, x_2^0, \ldots, x_n^0$ are independent of t.

Let $\phi(t)$ be the equilibrium solution obtained by

$$\frac{d}{dt}v = 0\tag{96}$$

and

$$a_{11}x_1^0 + a_{12}x_2^0 + \dots + a_{1n}x_n^0 = 0$$

$$a_{21}x_1^0 + a_{22}x_2^0 + \dots + a_{2n}x_n^0 = 0$$

$$\vdots$$

$$a_{n1}x_1^0 + a_{n2}x_2^0 + \dots + a_{nn}x_n^0 = 0$$
(97)

where the system (97) consists of line equations that go through the origin in the xy-plane. Here, if the equilibrium solutions exist, they are points where the two lines intersect in the xy-plane [2], [42].

4.2 Stability Theory

Considering the system (95) in matrix form, we have:

$$x' = Ax \tag{98}$$

where

$$x' = \begin{pmatrix} x'_1 \\ x'_2 \\ \vdots \\ x'_n \end{pmatrix} \qquad A = \begin{pmatrix} a_{11} & a_{12} & \cdots & a_{1n} \\ a_{21} & a_{22} & \cdots & a_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ a_{n1} & a_{n2} & \cdots & a_{nn} \end{pmatrix} \qquad x = \begin{pmatrix} x_1 \\ x_2 \\ \vdots \\ x_n \end{pmatrix}$$
(99)

Here, we have the following theorems:

Theorem 1 (Stability of a System of Differential Equations [2]). Consider the following system of differential equations in matrix form:

$$x' = Ax \tag{100}$$

- If all eigenvalues of A have negative real part \Rightarrow Every equilibrium solution $x = \phi(t)$ is stable.
- If at least one eigenvalue of A has positive real part \Rightarrow Every equilibrium solution $x = \phi(t)$ is unstable.
- Let the eigenvalues of A have real part ≤ 0 , then:
 - If A has k_j linearly independent eigenvectors for each eigenvalue $\lambda_j = i\sigma_j$ \Rightarrow Equilibrium solution $x = \phi(t)$ is stable.
 - Otherwise \Rightarrow Equilibrium solution $x = \phi(t)$ is unstable.

Theorem 2 (Asymptotic Stability of a System of Differential Equations [2]). An equilibrium solution $x = \phi(t)$ is said to be asymptotically stable if:

- 1. The equilibrium solution $x = \phi(t)$ is stable.
- 2. Every equilibrium solution $\rightarrow \phi(t)$ as $t \rightarrow \infty$.

Example 1 - An Asymptotically Stable System [2]

Determine whether each solution x(t) of the following system of differential equations:

$$\frac{dx_1}{dt} = -x_1
\frac{dx_2}{dt} = -2x_1 - x_2 + 2x_3
\frac{dx_3}{dt} = -3x_1 - 2x_2 - x_3$$
(101)

is stable, asymptotically stable or unstable.

Solution

1. First, we write system (101) in matrix form $\dot{x} = Ax$:

$$\dot{x} = \begin{pmatrix} -1 & 0 & 0 \\ -2 & -1 & 2 \\ -3 & -2 & -1 \end{pmatrix} x \tag{102}$$

where $\dot{x} = \begin{pmatrix} x'_1 \\ x'_2 \\ x'_3 \end{pmatrix}$ and $x = \begin{pmatrix} x_1 \\ x_2 \\ x_3 \end{pmatrix}$.

2. Next, we calculate the eigenvalues of A. Here, we have the following characteristic polynomial:

$$p(\lambda) = |A - \lambda I| = \begin{vmatrix} -1 - \lambda & 0 & 0\\ -2 & -1 - \lambda & 2\\ -3 & -2 & -1 - \lambda \end{vmatrix}$$
(103)

$$= (-1 - \lambda) \begin{vmatrix} -1 - \lambda & 2\\ -2 & -1 - \lambda \end{vmatrix}$$
(104)

$$= -(1+\lambda)^3 - 4(1+\lambda)$$
(105)

$$= -(1+\lambda)(\lambda^2 + 2\lambda + 5) \tag{106}$$

Here, our first eigenvalue is $\lambda_1 = -1$. In order to find λ_2 and λ_3 , we must use the quadratic formula to solve $\lambda^2 + 2\lambda + 5$:

$$\lambda = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a} \tag{107}$$

where a = 1, b = 2 and c = 5, we get:

$$\lambda = \frac{-2 \pm \sqrt{2^2 - 4(1)(5)}}{2(1)} \tag{108}$$

$$=\frac{-2\pm\sqrt{4-20}}{2}$$
(109)

$$=\frac{-2\pm\sqrt{-16}}{2}$$
(110)

$$=\frac{-2\pm4i}{2}\tag{111}$$

$$= -1 \pm 2i \tag{112}$$

Therefore

$$\lambda_1 = -1$$
 $\lambda_2 = -1 + 2i$ $\lambda_3 = -1 - 2i$ (113)

- 3. Since all 3 eigenvalues of A have negative real part. \Rightarrow Every equilibrium solution of (101) is Stable.
- 4. Since every equilibrium solution of (101) is stable and $\rightarrow x(t)$ as $t \rightarrow \infty$. \Rightarrow Every equilibrium solution of (101) is Asymptotically Stable.

Example 2 - An Unstable System [2]

Determine whether each solution x(t) of the following system of differential equations:

$$\frac{dx_1}{dt} = x_1 + 5x_2$$

$$\frac{dx_2}{dt} = 5x_1 + x_2$$
(114)

is stable, asymptotically stable or unstable.

Solution

1. First, we write system (114) in matrix form $\dot{x} = Ax$:

$$\dot{x} = \begin{pmatrix} 1 & 5\\ 5 & 1 \end{pmatrix} x \tag{115}$$

where $\dot{x} = \begin{pmatrix} x'_1 \\ x'_2 \end{pmatrix}$ and $x = \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}$.

2. Next, we calculate the eigenvalues of A. Here, we have the following characteristic polynomial:

$$p(\lambda) = |A - \lambda I| = \begin{vmatrix} 1 - \lambda & 5\\ 5 & 1 - \lambda \end{vmatrix}$$
(116)

$$= (1 - \lambda)^2 - 25 \tag{117}$$

$$=\lambda^2 - 2\lambda - 24 \tag{118}$$

$$= (\lambda - 6)(\lambda + 4) \tag{119}$$

Therefore

$$\lambda_1 = 6 \qquad \lambda_2 = -4 \tag{120}$$

- 3. Since one eigenvalue of A has positive real part.
 - \Rightarrow Every equilibrium solution of system (114) is Unstable.

5 Non-linear Systems of Differential Equations

For the non-linear case of differential equation systems, we present the following mathematical techniques for calculating stability:

5.1 Eigenvalue Method

For a nonlinear system of differential equations, we use the same process as the linear case but separate the nonlinear terms from the matrix A. Considering a nonlinear system in matrix form, we have [2]:

$$x' = Ax + g(x) \tag{121}$$

where

$$x' = \begin{pmatrix} x'_1 \\ x'_2 \\ \vdots \\ x'_n \end{pmatrix} \qquad A = \begin{pmatrix} a_{11} & a_{12} & \cdots & a_{1n} \\ a_{21} & a_{22} & \cdots & a_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ a_{n1} & a_{n2} & \cdots & a_{nn} \end{pmatrix} \qquad x = \begin{pmatrix} x_1 \\ x_2 \\ \vdots \\ x_n \end{pmatrix} \qquad \text{and} \qquad g(x) = \begin{pmatrix} g_1(x) \\ g_2(x) \\ \vdots \\ g_n(x) \end{pmatrix}$$

where the non-linear terms are included in g(x).

Here, we present the following example:

Example - An Asymptotically Stable System: Non-linear Case [2]

Determine whether each solution x(t) of the following non-linear system of differential equations:

$$\frac{dx_1}{dt} = -2x_1 + x_2 + 3x_3 + 9x_2^3
\frac{dx_2}{dt} = -6x_2 - 5x_3 + 7x_3^5
\frac{dx_3}{dt} = -x_3 + x_1^2 + x_2^2$$
(122)

is stable, asymptotically stable or unstable.

Solution

1. First, we write system (122) in matrix form:

$$\dot{x} = Ax + g(x) \tag{123}$$

Hence

$$\dot{x} = \begin{pmatrix} -2 & 1 & 3\\ 0 & -6 & -5\\ 0 & 0 & -1 \end{pmatrix} x + \begin{pmatrix} 9x_2^3\\ 7x_3^5\\ x_1^2 + x_2^2 \end{pmatrix}$$
(124)

where
$$\dot{x} = \begin{pmatrix} x'_1 \\ x'_2 \\ x'_3 \end{pmatrix}$$
 and $x = \begin{pmatrix} x_1 \\ x_2 \\ x_3 \end{pmatrix}$.

2. Next, we calculate the eigenvalues of A. Here, we have the following characteristic polynomial:

$$p(\lambda) = |A - \lambda I| = \begin{vmatrix} -2 - \lambda & 1 & 3\\ 0 & -6 - \lambda & -5\\ 0 & 0 & -1 - \lambda \end{vmatrix}$$
(125)

$$= (-2 - \lambda) \begin{vmatrix} -6 - \lambda & -5 \\ 0 & -1 - \lambda \end{vmatrix}$$
(126)

$$= (-2 - \lambda)(\lambda^2 + 7\lambda + 6) \tag{127}$$

$$= (-2 - \lambda)(\lambda + 1)(\lambda + 6) \tag{128}$$

Therefore

$$\lambda_1 = -2 \qquad \lambda_2 = -1 \qquad \lambda_3 = -6 \tag{129}$$

- 3. Since all 3 eigenvalues of A have negative real part. \Rightarrow Every equilibrium solution of (122) is Stable.
- 4. Since every equilibrium solution of (122) is stable and $\rightarrow x(t)$ as $t \rightarrow \infty$. \Rightarrow Every equilibrium solution of (122) is Asymptotically Stable.

5.2 Linearisation Method

Consider the following system of non-linear differential equations [2], [42]:

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

$$\frac{dy}{dt} = g(x, y)$$
(130)

Since (130) is a non-linear system, it must be linearised using the following method:

1. First, we calculate the equilibrium points, (x_0, y_0) of (130).

2. Next we let
$$W = \begin{pmatrix} x \\ y \end{pmatrix}$$
, hence:

$$\frac{dW}{dt} = J_{(x_0,y_0)}W$$
(131)

where J is the Jacobian matrix of system (130).

3. Calculating the Jacobian matrix of (130), we have:

Jacobian
$$= J_{(x_0,y_0)} = \begin{pmatrix} \frac{\partial f(x_0,y_0)}{\partial x} & \frac{\partial f(x_0,y_0)}{\partial y} \\ \frac{\partial g(x_0,y_0)}{\partial x} & \frac{\partial g(x_0,y_0)}{\partial y} \end{pmatrix}$$
 (132)

4. Then we find the eigenvalues λ_1 and λ_2 of J.

If:

- $\lambda_1 < 0$ and $\lambda_2 < 0$
 - $\Rightarrow (x_0, y_0)$ is a Stable equilibrium solution.
- $\lambda_1 < 0$ and $\lambda_2 > 0$ or $\lambda_1 > 0$ and $\lambda_2 < 0$ $\Rightarrow (x_0, y_0)$ is an Unstable equilibrium solution.
- $\lambda_1 > 0$ and $\lambda_2 > 0$ $\Rightarrow (x_0, y_0)$ is an Unstable equilibrium solution.

Example - Linearisation Method [2]

Consider the following non-linear system of differential equations:

$$\frac{dx}{dt} = f(x, y) = 3x - y^2$$

$$\frac{dy}{dt} = g(x, y) = \sin y - x$$
(133)

Since (133) is a non-linear system, it must be linearised using the following method:

1. Here, (133) has two equilibrium points. One of these equilibrium points is (0,0).

2. Next, we let
$$W = \begin{pmatrix} x \\ y \end{pmatrix}$$
 hence:

$$\frac{dW}{dt} = J_{(0,0)}W$$
(134)

where J is the Jacobian matrix of system (133).

3. Calculating the Jacobian matrix of (133), we have the following partial derivatives of system (133):

$$\frac{\partial f}{\partial x} = 3 \qquad \Rightarrow \qquad \frac{\partial f(0,0)}{\partial x} = 3 \tag{135}$$

$$\frac{\partial f}{\partial y} = -2y \qquad \Rightarrow \qquad \frac{\partial f(0,0)}{\partial y} = 0 \tag{136}$$

$$\frac{\partial g}{\partial x} = -1 \qquad \Rightarrow \qquad \frac{\partial g(0,0)}{\partial x} = -1$$
 (137)

$$\frac{\partial g}{\partial y} = \cos y \qquad \Rightarrow \qquad \frac{\partial g(0,0)}{\partial y} = 1$$
 (138)

Hence:

Jacobian
$$= J_{(0,0)} = \begin{pmatrix} \frac{\partial f(0,0)}{\partial x} & \frac{\partial f(0,0)}{\partial y} \\ \frac{\partial g(0,0)}{\partial x} & \frac{\partial g(0,0)}{\partial y} \end{pmatrix} = \begin{pmatrix} 3 & 0 \\ -1 & 1 \end{pmatrix}$$
 (139)

4. Finding the eigenvalues of J, we have

$$|J_{(0,0)} - \lambda I| = \begin{vmatrix} 3 & 0 \\ -1 & 1 \end{vmatrix}$$
(140)

$$= (3 - \lambda)(1 - \lambda) \tag{141}$$

Therefore:

$$\lambda_1 = 3 \qquad \lambda_2 = 1 \tag{142}$$

5. Since $\lambda_1 > 0$ and $\lambda_2 > 0$ $\Rightarrow (0,0)$ is an Unstable equilibrium point of system (133).

5.3 Lyapunov Method

In his famous memoir of 1892, A.M. Liapunov, sometimes spelt Lyapunov, a Russian mathematician suggested a new method of investigating the qualitative nature of solutions without the calculation of the solutions themselves. This method became known as Liapunov / Lyapunov's Direct Method, one of the major tools in stability theory [5].

Here, we have the following definitions and theorems:

Definition 1 (Positive / Negative - Definite / Semi-definite [2]). Let V(x, y) be a continuous Lyapunov function on the domain $D \subset \mathbb{R}^2$, where D is the origin (0,0). Assuming that V(0,0) = 0:

- 1. If V(x,y) > 0 for any $(x,y) \in D$ {(0,0)} then V is called positive definite on D.
- 2. If $V(x,y) \ge 0$ for any $(x,y) \in D$ {(0,0)} then V is called positive semi-definite on D.
- 3. If V(x,y) < 0 for any $(x,y) \in D$ {(0,0)} then V is called negative definite on D.
- 4. If $V(x,y) \leq 0$ for any $(x,y) \in D$ {(0,0)} then V is called negative semi-definite on D.

Definition 2 (Derivative of a Lyapunov Function [2]). The derivative of a Lyapunov function V(x, y) is denoted by:

$$\dot{V}(x,y) = \frac{\partial V}{\partial x}\frac{dx}{dt} + \frac{\partial V}{\partial y}\frac{dy}{dt}$$
(143)

where $\frac{dx}{dt} = f(x, y)$ and $\frac{dy}{dt} = g(x, y)$.

Theorem 3 (Lyapunov's Stability Theorem [2]). Let V(x, y) be a positive definite Lyapunov function on the domain D containing the origin (0,0). Assume that (0,0) is an isolated equilibrium point for the following system:

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

$$\frac{dy}{dt} = g(x, y)$$
(144)

Then:

- If $\dot{V}(x,y) < 0$ for any $(x,y) \in D$ {(0,0)}, then (0,0) is an Asymptotically Stable equilibrium point for the system (144).
- If $\dot{V}(x,y) \leq 0$ for any $(x,y) \in D$ {(0,0)}, then (0,0) is a Stable equilibrium point for the system (144).

Theorem 4 (Lyapunov's Instability Theorem [2]). Let V(x, y) be a defined and continuous Lyapunov function on the domain D containing the origin (0,0). Assume that (0,0) is an isolated equilibrium point for the following system:

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

$$\frac{dy}{dt} = g(x, y)$$
(145)

If:

- 1. $\dot{V}(x,y) > 0$ for any $(x,y) \in D \{(0,0)\}.$
- 2. In every disk or circle $Br(0,0) = \{(x,y) \in \mathbb{R}^2 : \sqrt{x^2 + y^2} < r\}$ centred at the origin (0,0), there is at least one point $(a,b) \in Br$ such that V(a,b) > 0.
- \Rightarrow (0,0) is an Unstable equilibrium point of (145).

Example 1: A Positive Definite Lyapunov Function [2]

Consider the Lyapunov function V(x, y) with domain D where V(0, 0) = 0 [2]:

$$V(x,y) = \frac{x^2}{2} + \frac{y^2}{2} - \frac{x^4}{4} \qquad D = \{(x,y) : |x| < 1, |y| < 1\}$$
(146)

determine whether V(x, y) is positive / negative definite / semi-definite.

Solution

- 1. Here, $|x| < 1 \implies \frac{x^2}{2} > \frac{x^4}{4}$.
- 2. Therefore V(x, y) > 0 on domain D.
 - $\Rightarrow V(x,y)$ is Positive Definite on domain D.

Example 2: Lyapunov's Direct Method [2]

Use Lyapunov's direct method to determine the stability of the origin (0,0) for the system:

$$\frac{dx}{dt} = -2y^3$$

$$\frac{dy}{dt} = x - 3y^3$$
(147)

Solution

1. First we find the equilibrium points of system (147). Here, we have:

$$-2y^3 = 0 (148)$$

$$x - 3y^3 = 0 (149)$$

Hence, from (148), we get:

$$y = 0 \tag{150}$$

Substituting (150) in (149) yields:

$$x = 0 \tag{151}$$

Therefore, (0,0) is the only equilibrium point of the system (147).

- 2. Here, (147) is not an almost linear system. Therefore we cannot apply the linearisation method to characterise the stability of the equilibrium point (0, 0).
- 3. Let us consider a candidate Lyapunov function:

$$V(x,y) = ax^{2} + by^{4} \qquad a,b > 0$$
(152)

Hence:

- (a) V(x,y) > 0 for any $(x,y) \in \mathbb{R}^2 \{(0,0)\}.$
- (b) Calculating $\dot{V}(x, y)$:

$$\dot{V}(x,y) = \frac{\partial V}{\partial x}\frac{dx}{dt} + \frac{\partial v}{\partial y}\frac{dy}{dt}$$
(153)

$$= 2ax(-2y^3) + 4by^3(x - 3y^3)$$
(154)

$$=4(b-a)xy^3 - 12by^6 (155)$$

Let b = a, then

$$\dot{V}(x,y) = -12by^6$$
 (156)

$$< 0$$
 (157)

for any $(x, y) \in \mathbb{R}^2 \{(0, 0)\}, b > 0.$

 \Rightarrow By Lyapunov's Stability Theorem, (0,0) is an Asymptotically Stable equilibrium point of the system (147).

Example 3: Lyapunov's Direct Method [2]

Use Lyapunov's direct method to determine the stability of the origin (0,0) for the system:

$$\frac{dx}{dt} = -y^3$$

$$\frac{dy}{dt} = -x^3$$
(158)

Solution

1. First we find the equilibrium points of system (158). Here, we have:

$$-y^3 = 0 (159)$$

$$-x^3 = 0$$
 (160)

Hence, from (159), we have

$$y = 0 \tag{161}$$

and from (160), we have:

$$x = 0 \tag{162}$$

Therefore, (0,0) is the only equilibrium point of the system (158).

- 2. Here, (158) is not an almost linear system. Therefore we cannot apply the linearisation method to characterise the stability of the equilibrium point (0, 0).
- 3. Let us consider a candidate Lyapunov function:

$$V(x,y) = -xy \tag{163}$$

where V(x, y) is continuous on \mathbb{R}^2 .

Hence:

(a) Calculating $\dot{V}(x, y)$:

$$\dot{V}(x,y) = \frac{\partial V}{\partial x}\frac{dx}{dt} + \frac{\partial V}{\partial y}\frac{dy}{dt}$$
(164)

$$= (-y)(-y^3) + (-x)(-x^3)$$
(165)

$$= y^4 + x^4 \tag{166}$$

$$< 0$$
 (167)

for any $(x, y) \in \mathbb{R}^2 \{(0, 0)\}.$

(b) For any
$$(x, y) \in \mathbb{R}^2 \{(0, 0)\}$$
 with $x < 0, y > 0$ or $x > 0, y < 0$ we have:

$$V(x,y) > 0 \tag{168}$$

 \Rightarrow By Lyapunov's Instability Theorem, (0,0) is an Unstable equilibrium point of the system (158).
Chapter 3: Difference Equation Systems - An Introduction to Stability Analysis

6 Linear Systems of Difference Equations

When studying the stability of systems, we are interested in the qualitative behaviour of their solutions without their calculation [5]. Most problems in practice occur in nonlinear cases which are mostly unsolvable. The investigation of difference equations is of vital importance in science, engineering as well as applied mathematics. In order to examine the stability of discrete systems, differential equation methods and techniques must be adapted to difference equations [5].

Consider the following Autonomous or Time-Invariant system of k linear equations [5]:

$$x_{1}(n+1) = a_{11}x_{1}(n) + a_{12}x_{2}(n) + \ldots + a_{1k}x_{k}(n)$$

$$x_{2}(n+1) = a_{21}x_{1}(n) + a_{22}x_{2}(n) + \ldots + a_{2k}x_{k}(n)$$

$$\vdots$$

$$x_{k}(n+1) = a_{k1}x_{1}(n) + a_{k2}x_{2}(n) + \ldots + a_{kk}x_{k}(n)$$
(169)

and Non-autonomous or Time-Variant system of k linear equations [5]:

$$x_{1}(n+1) = a_{11}(n)x_{1}(n) + a_{12}(n)x_{2}(n) + \dots + a_{1k}(n)x_{k}(n)$$

$$x_{2}(n+1) = a_{21}(n)x_{1}(n) + a_{22}(n)x_{2}(n) + \dots + a_{2k}(n)x_{k}(n)$$

$$\vdots$$

$$x_{k}(n+1) = a_{k1}(n)x_{1}(n) + a_{k2}(n)x_{2}(n) + \dots + a_{kk}(n)x_{k}(n)$$
(170)

6.1 Equilibrium Solutions / Critical Points

Consider system (169) in the following vector difference equation form [5]:

$$x(n+1) = f(n, x(n))$$
(171)

where $x(n_0) = x_0, x(n) \in \mathbb{R}^k, f : \mathbb{Z}^+ \times \mathbb{R}^k \to \mathbb{R}^k.$

Assuming that f(n, x) is continuous in x, a point x^* in \mathbb{R}^k is called an equilibrium point of (169) if $f(n, x^*) = x^*$ for all $n \ge n_0$.

6.2 Stability Theory

The Autonomous, Time-Invariant system (169) in matrix form can be written as [5]:

$$x(n+1) = Ax(n) \tag{172}$$

where

$$x(n) = (x_1(n), x_2(n), \dots, x_k(n))^T, \qquad x(n+1) = (x_1(n+1), x_2(n+1), \dots, x_k(n+1))^T$$

and

$$A = \begin{pmatrix} a_{11} & a_{12} & \cdots & a_{1n} \\ a_{21} & a_{22} & \cdots & a_{2n} \\ \vdots & \vdots & \ddots & \vdots \\ a_{n1} & a_{n2} & \cdots & a_{nn} \end{pmatrix}$$
(173)

and the Non-autonomous, Time-Variant system (170) in matrix form can be written as [5]:

$$x(n+1) = A(n)x(n)$$
(174)

where

$$x(n) = (x_1(n), x_2(n), \dots, x_k(n))^T, \qquad x(n+1) = (x_1(n+1), x_2(n+1), \dots, x_k(n+1))^T$$

and

$$A(n) = \begin{pmatrix} a_{11}(n) & a_{12}(n) & \cdots & a_{1n}(n) \\ a_{21}(n) & a_{22}(n) & \cdots & a_{2n}(n) \\ \vdots & \vdots & \ddots & \vdots \\ a_{n1}(n) & a_{n2}(n) & \cdots & a_{nn}(n) \end{pmatrix}$$
(175)

When considering the stability of systems (172) and (174), we use the following Theorem:

Theorem 5 (Stability of a System of Difference Equations [5]). Consider the matrix A:

- If the characteristic polynomial of A, $\rho(A) \leq 1$ and the eigenvalues of A are semi-simple. \Rightarrow Every equilibrium solution $x = \phi(t)$ is stable.
- If the characteristic polynomial of A, ρ(A) < 1
 ⇒ Every equilibrium solution x = φ(t) is Asymptotically Stable.

Example - Unstable System of Difference Equations [5]

Determine whether each equilibrium solution of the following system of difference equations:

$$x_1(n+1) = -x_1(n) + x_2(n)$$

$$x_2(n+1) = 2x_2(n)$$
(176)

is stable, asymptotically stable or unstable.

Solution

1. First, we write system (176) in the following matrix form:

$$x(n+1) = Ax(n) \tag{177}$$

$$\begin{bmatrix} x_1(n+1) \\ x_2(n+1) \end{bmatrix} = \begin{bmatrix} -1 & 1 \\ 0 & 2 \end{bmatrix} = \begin{bmatrix} x_1(n) \\ x_2(n) \end{bmatrix}$$
(178)

2. Next , we calculate the following characteristic polynomial $\rho(A)$:

$$\rho(A) = |A - \lambda I| = \begin{vmatrix} -1 - \lambda & 1\\ 0 & 2 - \lambda \end{vmatrix}$$
(179)

$$= (-1 - \lambda)(2 - \lambda) - 0$$
 (180)

$$=\lambda^2 - \lambda - 2 \tag{181}$$

3. Since $\rho(A) \nleq 1$

 \Rightarrow Every equilibrium solution of system (176) is Unstable.

7 Non-linear Systems of Difference Equations

7.1 Linearisation Method

The linearization method is the oldest method in stability theory and is frequently used by scientists and engineers in the design of control systems and feedback devices [5]. The method was originated by the mathematicians Liapunov / Lyapunov and Perron in order to study the stability theory of differential equations. Although their use of the method was for continuous systems, it can also be used for discrete forms of difference equation systems.

Consider the following Non-autonomous system of difference equations:

$$y(n+1) = A(n)y(n) + g(n, y(n))$$
(182)

where

- A(n) is a $k \times k$ non-singular matrix $\forall n \in \mathbb{Z}^+$.
- $g: \mathbb{Z}^+ \times G \to \mathbb{R}^k, G \subset \mathbb{R}^k$ is a continuous function.

(174) can be written in the vector form:

$$y(n+1) = f(n, y(n))$$
 (183)

Applying the linearisation method, we calculate the Jacobian matrix of (174):

Jacobian
$$= \frac{\partial f(n,y)}{\partial y}\Big|_{y=0} = \frac{\partial f(n,0)}{\partial y} = \begin{pmatrix} \frac{\partial f_1(n,0)}{\partial y_1} & \frac{\partial f_1(n,0)}{\partial y_2} & \dots & \frac{\partial f_1(n,0)}{\partial y_k} \\ \frac{\partial f_2(n,0)}{\partial y_1} & \frac{\partial f_2(n,0)}{\partial y_2} & \dots & \frac{\partial f_2(n,0)}{\partial y_k} \\ \vdots & \vdots & \ddots & \vdots \\ \frac{\partial f_k(n,0)}{\partial y_1} & \frac{\partial f_k(n,0)}{\partial y_2} & \dots & \frac{\partial f_k(n,0)}{\partial y_k} \end{pmatrix}$$
(184)

which produces a linear solution for system (182).

Similarly, we can use the same technique for the following Autonomous case:

$$y(n+1) = Ay(n) + g(y(n))$$
(185)

in vector form:

$$y(n+1) = f(y(n))$$
 (186)

Theorem 6 (Exponential Stability of a System of Non-linear Difference Equations [5]). *Consider the matrix A:*

If the characteristic polynomial, $\rho(A) < 1$, then \Rightarrow The equilibrium solution of the non-linear system:

$$y(n+1) = Ay(n) + g(n)$$
 (187)

is Exponentially Stable.

Example 1 - Linearisation Method [5]

Investigate the stability of the equilibrium point (0,0) of the planar system:

$$y_1(n+1) = \frac{ay_2(n)}{1+y_1^2(n)}$$

$$y_2(n+1) = \frac{by_1(n)}{1+y_2^2(n)}$$
(188)

Solution

1. Let $f = (f_1, f_2)^T$ where

$$f_1 = \frac{ay_2(n)}{1+y_1^2(n)}$$
 $f_2 = \frac{by_1(n)}{1+y_2^2(n)}$

2. Applying the linearisation method, at the equilibrium point (0,0), we have the following Jacobian matrix:

$$J = \left. \frac{\partial f}{\partial y} \right|_{(0,0)} = \left(\begin{array}{cc} \frac{\partial f_1(0,0)}{\partial y_1} & \frac{\partial f_1(0,0)}{\partial y_2} \\ \frac{\partial f_2(0,0)}{\partial y_1} & \frac{\partial f_2(0,0)}{\partial y_2} \end{array} \right) = \left(\begin{array}{cc} 0 & a \\ b & 0 \end{array} \right)$$
(189)

3. Hence, system (188) can be written in the form:

$$y(n+1) = Ay(n) + g(y(n))$$

$$\begin{pmatrix} y_1(n+1) \\ y_2(n+1) \end{pmatrix} = \begin{pmatrix} 0 & a \\ b & 0 \end{pmatrix} \begin{pmatrix} y_1(n) \\ y_2(n) \end{pmatrix} + \begin{pmatrix} \frac{-ay_2(n)y_1^2(n)}{1+y_1^2(n)} \\ \frac{-by_2^2(n)y_1(n)}{1+y_2^2(n)} \end{pmatrix}$$

- 4. Here, the eigenvalues of A are $\lambda_1 = \sqrt{ab}$, $\lambda_2 = -\sqrt{ab}$.
 - If |ab| < 1. \Rightarrow The equilibrium point (0,0) is Asymptotically Stable.

Since g(y) is continuously differentiable at (0,0), g(y) is 0(y). \Rightarrow The equilibrium point (0,0) is Exponentially Stable.

Example 2 - Linearisation Method: An Asymptotically Stable System [5] Prove that the equilibrium solution (0,0) of the following system of 2 difference equations:

$$\begin{aligned} x_1(n+1) &= x_2(n) - x_2(n) [x_1^2(n) + x_2^2(n)] \\ x_2(n+1) &= x_1(n) - x_1(n) [x_1^2(n) + x_2^2(n)] \end{aligned}$$
(190)

is Asymptotically Stable.

Solution

1. Let $f = (f_1, f_2)^T$ where

$$f_1 = x_2(n) - x_2(n)[x_1^2(n) + x_2^2(n)] \qquad f_2 = x_1(n) - x_1(n)[x_1^2(n) + x_2^2(n)]$$

2. Applying the linearisation method, at the equilibrium point (0,0), we have the following Jacobian matrix:

$$J = \left. \frac{\partial f}{\partial x} \right|_{(0,0)} = \left(\begin{array}{cc} \frac{\partial f_1(0,0)}{\partial x_1} & \frac{\partial f_1(0,0)}{\partial x_2} \\ \frac{\partial f_2(0,0)}{\partial x_1} & \frac{\partial f_2(0,0)}{\partial x_2} \end{array} \right)$$
(191)

Here, we have:

$$\frac{\partial f_1}{\partial x_1} = \frac{\partial}{\partial x_1} (x_2 - x_2(x_1^2 + x_2^2))
= \frac{\partial}{\partial x_1} (x_2 - x_1^2 x_2 - x_2^3)
= -2x_1 x_2$$
(192)

$$\frac{\partial f_1}{\partial x_2} = \frac{\partial}{\partial x_2} (x_2 - x_2(x_1^2 + x_2^2))
= \frac{\partial}{\partial x_2} (x_2 - x_1^2 x_2 - x_2^3)
= 1 - x_1^2 - 3x_2^2$$
(193)

$$\frac{\partial f_2}{\partial x_1} = \frac{\partial}{\partial x_1} (x_1 - x_1 (x_1^2 + x_2^2))
= \frac{\partial}{\partial x_1} (x_1 - x_1^3 - x_1 x_2^2)
= 1 - 3x_1^2 - x_2^2$$
(194)

$$\frac{\partial f_2}{\partial x_2} = \frac{\partial}{\partial x_2} (x_1 - x_1 (x_1^2 + x_2^2))
= \frac{\partial}{\partial x_2} (x_1 - x_1^3 - x_1 x_2^2)
= -2x_1 x_2$$
(195)

3. Hence, the Jacobian matrix of system (190) can be written in the form:

$$J = \frac{\partial f}{\partial x}\Big|_{(0,0)} = \begin{pmatrix} -2(0)(0) & 1 - (0)^2 - 3(0)^2 \\ 1 - 3(0)^2 - (0)^2 & -2(0)(0) \end{pmatrix} = \begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix}$$
(196)

4. Therefore, system (190) can be written in the form:

$$\begin{aligned} x(n+1) &= Ax(n) + g(x(n)) \\ \begin{pmatrix} x_1(n+1) \\ x_2(n+1) \end{pmatrix} &= \begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix} \begin{pmatrix} x_1(n) \\ x_2(n) \end{pmatrix} + \begin{pmatrix} x_2(n) - x_2(n)[x_1^2(n) + x_2^2(n)] \\ x_1(n) - x_1(n)[x_1^2(n) + x_2^2(n)] \end{pmatrix} \end{aligned}$$

5. Finding the eigenvalues of A, we have

$$|A - \lambda I| = \begin{vmatrix} -\lambda & 1\\ 1 & -\lambda \end{vmatrix}$$
(197)

$$=\lambda^2 - 1 \tag{198}$$

Therefore

$$\lambda_1 = 1 \qquad \lambda_2 = -1 \tag{199}$$

 \Rightarrow The equilibrium point (0,0) is Asymptotically Stable.

7.2 Lyapunov Method

Adapting Liapunov / Lyapunov's direct method to difference equations, we consider the following Autonomous difference equation:

$$x(n+1) = f(x(n))$$
(200)

Here, we have the following theorem:

Theorem 7 (Lyapunov's Stability Theorem [5]). Let V be a Lyapunov function for the system (200). If:

- V is positive definite in the neighbourhood H of the equilibrium point x^{*}, then
 ⇒ x^{*} is a Stable equilibrium solution.
- $\Delta V(x) < 0$, whenever $x, f(x) \in H$ and $x \neq x^*$, then $\Rightarrow x^*$ is an Asymptotically Stable equilibrium solution.
- $G = H = \mathbb{R}^k$ and

$$V(x) \to \infty$$
 as $||x|| \to \infty$ (201)

then

 $\Rightarrow x^*$ is a Globally Asymptotically Stable equilibrium solution.

Example - Lyapunov Method: A Globally Asymptotically Stable System [5] Consider the following planar system:

$$x_1(n+1) = \frac{x_2(n)}{1+x_1^2(n)}$$
(202)

$$x_2(n+1) = \frac{x_1(n)}{1+x_2^2(n)} \tag{203}$$

Find the equilibrium solutions and determine their stability using the Lyapunov method.

Solution

1. First, we find the equilibrium points of the system of equations (202)(203). From (202), we have:

$$\frac{x_2}{1+x_1^2} = 0 \qquad \Rightarrow \qquad x_2 = 0 \tag{204}$$

From (203), we have:

$$\frac{x_1}{1+x_2^2} = 0 \qquad \Rightarrow \qquad x_1 = 0 \tag{205}$$

Therefore, the only equilibrium solution of system (202)(203) is (0,0).

2. Considering the stability of the equilibrium solution (0,0). Let $V(x_1, x_2)$ be a Lyapunov function, hence:

$$\dot{V}(x_1, x_2) = \frac{\partial V}{\partial x_1} \left(\frac{x_2}{1 + x_1^2} \right) + \frac{\partial V}{\partial x_2} \left(\frac{x_1}{1 + x_2^2} \right)$$
(206)

$$= 2x_1 \left(\frac{x_2}{1+x_1^2}\right) + 2x_2 \left(\frac{x_1}{1+x_2^2}\right)$$
(207)
$$2x_1x_2 - 2x_1x_2$$
(207)

$$=\frac{2x_1x_2}{1+x_1^2} + \frac{2x_1x_2}{1+x_2^2} \tag{208}$$

$$=2x_1x_2\left(\frac{1}{1+x_1^2}+\frac{1}{1+x_2^2}\right)$$
(209)

3. Here, let $x_1 = x_2$:

$$\dot{V}(x_1, x_2) = \frac{4x_1^2}{x_1 + 1} \tag{210}$$

If:

| $x_1 < 0$ | \Rightarrow | $\dot{V}(x_1, x_2) \le 0$ |
|-----------|---------------|---------------------------|
| $x_1 = 0$ | \Rightarrow | $\dot{V}(x_1, x_2) = 0$ |
| $x_1 > 0$ | \Rightarrow | $\dot{V}(x_1, x_2) > 0$ |

 \Rightarrow By Lyapunov's Stability Theorem, the equilibrium solution (0,0) is Globally Asymptotically Stable.

Chapter 4: A Model of a Three Species Ecosystem with Mutualism Between The Predators - K. S. Reddy & N. C. Pattabhiramacharyulu [32]

8 Introduction

The research paper [32] studies a system of three first order non-linear differential equations in the form of a population model. It proves the asymptotic stability and examines the local and global stability of the system. The model consists of a prey (S_1) and two predators (S_2, S_3) which are in mutualism with each other whilst preying on the same prey (S_1) . For the given system, equilibrium points and stability conditions are stated.

9 The Mathematical Model

The model uses the following definitions:

Definitions

- $N_i(t)$ Population density of species S_i at time t, where i = 1, 2, 3.
- a_i Natural growth rates of species S_i , where i = 1, 2, 3.
- α_{11} The decrease rate of species S_i due to own insufficient resources, where i = 1, 2, 3.
- α_{12} The decrease rate of prey (S_1) due to inhibition by predator (S_2) .
- α_{13} The decrease rate of prey (S_1) due to inhibition by predator (S_3) .
- α_{21} The increase rate of predator (S_2) due to its successful attacks on prey (S_1) .
- α_{23} The increase rate of predator (S_2) due to its successful attacks on predator (S_3) .
- α_{31} The increase rate of predator (S_3) due to its successful attacks on prey (S_1) .
- α_{32} The increase rate of predator (S_3) due to its successful attacks on predator (S_2) .
- $K_i = \frac{a_i}{\alpha_{ii}}$ Carrying capacity of species S_i , where i = 1, 2, 3.

Here, N_1 , N_2 and N_3 are non-negative variables. We also assume that a_i , K_i and α_{ij} are non-negative constants, where i = 1, 2, 3 and j = 1, 2, 3.

Hence, we have the following multi-system model in the form of a system of three first order non-linear ODEs:

$$\frac{dN_1}{dt} = a_1 N_1 - \alpha_{11} N_1^2 - \alpha_{12} N_1 N_2 - \alpha_{13} N_1 N_3$$

$$\frac{dN_2}{dt} = a_2 N_2 - \alpha_{22} N_2^2 + \alpha_{21} N_1 N_2 + \alpha_{23} N_2 N_3$$

$$\frac{dN_3}{dt} = a_3 N_3 - \alpha_{33} N_3^2 + \alpha_{31} N_1 N_3 + \alpha_{32} N_2 N_3$$
(211)

10 Existence of Equilibrium Points

Finding the equilibrium points of the system (211), we have the following cases:

Case 1

$$a_1 N_1 - \alpha_{11} N_1^2 - \alpha_{12} N_1 N_2 - \alpha_{13} N_1 N_3 = 0$$
(212)

$$a_2N_2 - \alpha_{22}N_2^2 + \alpha_{21}N_1N_2 + \alpha_{23}N_2N_3 = 0$$
(213)

$$a_3N_3 - \alpha_{33}N_3^2 + \alpha_{31}N_1N_3 + \alpha_{32}N_2N_3 = 0 \tag{214}$$

By using (213), we get:

$$a_{2}N_{2} - \alpha_{22}N_{2}^{2} + \alpha_{21}N_{1}N_{2} + \alpha_{23}N_{2}N_{3} = 0$$

$$N_{2}(a_{2} - \alpha_{22}N_{2} + \alpha_{21}N_{1} + \alpha_{23}N_{3}) = 0$$

$$N_{2} = 0 \quad \text{or} \quad a_{2} - \alpha_{22}N_{2} + \alpha_{21}N_{1} + \alpha_{23}N_{3} = 0$$
(215)

By using (214), we get:

$$a_{3}N_{3} - \alpha_{33}N_{3}^{2} + \alpha_{31}N_{1}N_{3} + \alpha_{32}N_{2}N_{3} = 0$$

$$N_{3}(a_{3} - \alpha_{33}N_{3} + \alpha_{31}N_{1} + \alpha_{32}N_{2}) = 0$$

$$N_{3} = 0 \quad \text{or} \quad a_{3} - \alpha_{33}N_{3} + \alpha_{31}N_{1} + \alpha_{32}N_{2} = 0$$
(216)

Substituting $N_2 = N_3 = 0$ in (212), we have:

$$a_1 N_1 - \alpha_{11} N_1^2 = 0$$

$$N_1 (a_1 - \alpha_{11} N_1) = 0$$

$$N_1 = 0$$
(217)

Hence we have the following equilibrium point in the absence of all species:

$$(N_1, N_2, N_3) = (0, 0, 0) = E_1(0, 0, 0)$$

Therefore the population is extinct and this state always exists.

Case 2

In the absence of the second predator (S_3) we have $N_3 = 0$, hence (211) becomes

$$\frac{dN_1}{dt} = a_1 N_1 - \alpha_{11} N_1^2 - \alpha_{12} N_1 N_2$$

$$\frac{dN_2}{dt} = a_2 N_2 - \alpha_{22} N_2^2 + \alpha_{21} N_1 N_2$$
(218)

Finding the equilibrium points of (218), we have:

$$a_1 N_1 - \alpha_{11} N_1^2 - \alpha_{12} N_1 N_2 = 0 (219)$$

$$a_2 N_2 - \alpha_{22} N_2^2 + \alpha_{21} N_1 N_2 = 0 \tag{220}$$

By using (219), we get:

$$a_1 N_1 - \alpha_{11} N_1^2 - \alpha_{12} N_1 N_2 = 0$$

$$N_1 (a_1 - \alpha_{11} N_1 - \alpha_{12} N_2) = 0$$

$$N_1 = 0 \quad \text{or} \quad a_1 - \alpha_{11} N_1 - \alpha_{12} N_2 = 0$$
(221)

Assuming a positive solution \overline{N}_1 of N_1 , we have:

$$a_1 - \alpha_{11}N_1 - \alpha_{12}N_2 = 0 \tag{222}$$

$$-\alpha_{11}N_1 = -a_1 + \alpha_1 2N_2 \tag{223}$$

$$\therefore \qquad \bar{N}_1 = N_1 = \frac{a_1 - \alpha_{12}N_2}{\alpha_{11}} \tag{224}$$

Substituting (224) in (220) and assuming a positive solution \bar{N}_2 of N_2 yields:

$$a_2 N_2 - \alpha_{22} N_2^2 + \alpha_{21} N_1 N_2 = 0$$

$$N_2 (a_2 - \alpha_{22} N_2 + \alpha_{21} N_1) = 0$$

$$N_2 = 0 \quad \text{or} \quad a_2 - \alpha_{22} N_2 + \alpha_{21} N_1 = 0$$
(225)

$$\therefore \qquad a_2 - \alpha_{22}N_2 + \alpha_{21}N_1 = 0 \tag{226}$$

$$a_2 - \alpha_{22}N_2 + \alpha_{21}\left(\frac{a_1 - \alpha_{12}N_2}{\alpha_{11}}\right) = 0$$
(227)

$$a_2 - \alpha_{22}N_2 + \frac{a_1\alpha_{21}}{\alpha_{11}} - \frac{\alpha_{12}\alpha_{21}}{\alpha_{11}}N_2 = 0$$
(228)

$$-\alpha_{22}N_2 - \frac{\alpha_{12}\alpha_{21}}{\alpha_{11}}N_2 = -a_2 - \frac{a_1\alpha_{21}}{\alpha_{11}}$$
(229)

$$\left(-\alpha_{22} - \frac{\alpha_{12}\alpha_{21}}{\alpha_{11}}\right)N_2 = \frac{-a_2\alpha_{11} - a_1\alpha_{21}}{\alpha_{11}}$$
(230)

$$\left(\frac{-\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}}{\alpha_{11}}\right)N_2 = \frac{-a_2\alpha_{11} - a_1\alpha_{21}}{\alpha_{11}}$$
(231)

$$\therefore \qquad \bar{N}_2 = N_2 = \frac{a_2\alpha_{11} + a_1\alpha_{21}}{\alpha_{11}\alpha_{22} + \alpha_{12}\alpha_{21}} \tag{232}$$

Substituting (232) in (224) yields:

$$\bar{N}_1 = N_1 = \frac{a_1 - \alpha_{12}N_2}{\alpha_{11}} \tag{233}$$

$$=\frac{a_{1}-\alpha_{12}\left(\frac{a_{2}\alpha_{11}+a_{1}\alpha_{21}}{\alpha_{11}\alpha_{22}+\alpha_{12}\alpha_{21}}\right)}{\alpha_{11}}$$
(234)

$$=\frac{a_1\alpha_{22} - a_2\alpha_{12}}{\alpha_{11}\alpha_{22} + \alpha_{12}\alpha_{21}} \tag{235}$$

Therefore, assuming \bar{N}_1 and \bar{N}_2 are positive solutions of N_1 and N_2 , then

$$\bar{N}_1 = \frac{a_1 \alpha_{22} - a_2 \alpha_{12}}{\alpha_{11} \alpha_{22} + \alpha_{12} \alpha_{21}} \quad \text{and} \quad \bar{N}_2 = \frac{a_2 \alpha_{11} + a_1 \alpha_{21}}{\alpha_{11} \alpha_{22} + \alpha_{12} \alpha_{21}}$$
(236)

where \bar{N}_1 is positive provided that $a_1\alpha_{22} > a_2\alpha_{12}$.

In conclusion, we have the following equilibrium point in the absence of the second predator (S_3) :

$$(N_1, N_2, N_3) = (N_1, N_2, 0) = E_2(\bar{N}_1, \bar{N}_2, 0)$$

Case 3

In the absence of the first predator (S_2) , we have $N_2 = 0$ hence (211) becomes

$$\frac{dN_1}{dt} = a_1 N_1 - \alpha_{11} N_1^2 - \alpha_{13} N_1 N_3$$

$$\frac{dN_3}{dt} = a_3 N_3 - \alpha_{33} N_3^2 + \alpha_{31} N_1 N_3$$
(237)

Finding the equilibrium points of (237), we have:

$$a_1 N_1 - \alpha_{11} N_1^2 - \alpha_{13} N_1 N_3 = 0 (238)$$

$$a_3N_3 - \alpha_{33}N_3^2 + \alpha_{31}N_1N_3 = 0 \tag{239}$$

By using (238), we get

$$a_1 N_1 - \alpha_{11} N_1^2 - \alpha_{13} N_1 N_3 = 0$$

$$N_1 (a_1 - \alpha_{11} N_1 - \alpha_{13} N_3) = 0$$

$$N_1 = 0 \quad \text{or} \quad a_1 - \alpha_{11} N_1 - \alpha_{13} N_3 = 0$$
(240)

Assuming a positive solution N_1^{ϕ} of N_1 , we have:

$$a_1 - \alpha_{11}N_1 - \alpha_{13}N_3 = 0 \tag{241}$$

$$-\alpha_{11}N_1 = -a_1 + \alpha_{13}N_3 \tag{242}$$

$$\therefore \qquad N_1^{\phi} = N_1 = \frac{a_1 - \alpha_{13}N_3}{\alpha_{11}} \tag{243}$$

Substituting (243) in (239) and assuming a positive solution N_3^{ϕ} of N_3 yields:

$$a_{3}N_{3} - \alpha_{33}N_{3}^{2} + \alpha_{31}N_{1}N_{3} = 0$$

$$N_{3}(a_{3} - \alpha_{33}N_{3} + \alpha_{31}N_{1}) = 0$$

$$N_{3} = 0 \quad \text{or} \quad a_{3} - \alpha_{33}N_{3} + \alpha_{31}N_{1} = 0$$
(244)

Chapter 4: A Model of a Three Species Ecosystem with Mutualism Between The Predators - K. S. Reddy & N. C. Pattabhiramacharyulu

$$\therefore \qquad a_3 - \alpha_{33} N_3 + \alpha_{31} N_1 = 0 \tag{245}$$

$$a_3 - \alpha_{33}N_3 + \alpha_{31}\left(\frac{a_1 - \alpha_{13}N_3}{\alpha_{11}}\right) = 0 \tag{246}$$

$$a_3 - \alpha_{33}N_3 + \frac{a_1\alpha_{31}}{\alpha_{11}} - \frac{\alpha_{13}\alpha_{31}}{\alpha_{11}}N_3 = 0$$
(247)

$$-\alpha_{33}N_3 - \frac{\alpha_{13}\alpha_{31}}{\alpha_{11}}N_3 = -a_3 - \frac{a_1\alpha_{31}}{\alpha_{11}}$$
(248)

$$\left(-\alpha_3 3 - \frac{\alpha_{13}\alpha_{31}}{\alpha_{11}}\right) N_3 = -a_3 - \frac{a_1\alpha_{31}}{\alpha_{11}}$$
(249)

$$\left(\frac{-\alpha_{11}\alpha_{33} - \alpha_{13}\alpha_{31}}{\alpha_{11}}\right)N_3 = \frac{-a_3\alpha_{11} - a_1\alpha_{31}}{\alpha_{11}} \tag{250}$$

$$\therefore \qquad N_3^{\phi} = N_3 = \frac{a_3 \alpha_{11} + a_1 \alpha_{31}}{\alpha_{11} \alpha_{33} + \alpha_{13} \alpha_{31}} \tag{251}$$

Substituting (251) in (243) yields:

.

$$N_1^{\phi} = N_1 = \frac{a_1 - \alpha_{13}N_3}{\alpha_{11}} \tag{252}$$

$$=\frac{a_1 - \alpha_{13} \left(\frac{a_3 \alpha_{11} + a_1 \alpha_{31}}{\alpha_{11} \alpha_{33} + \alpha_{13} \alpha_{31}}\right)}{\alpha_{11}} \tag{253}$$

$$=\frac{a_1\alpha_{33}-a_3\alpha_{13}}{\alpha_{11}\alpha_{33}+\alpha_{13}\alpha_{31}}$$
(254)

Therefore, assuming N_1^{ϕ} and N_3^{ϕ} are positive solutions of N_1 and N_3 , then

$$N_{1}^{\phi} = \frac{a_{1}\alpha_{33} - a_{3}\alpha_{13}}{\alpha_{11}\alpha_{33} + \alpha_{13}\alpha_{31}} \quad \text{and} \quad N_{3}^{\phi} = \frac{a_{3}\alpha_{11} + a_{1}\alpha_{31}}{\alpha_{11}\alpha_{33} + \alpha_{13}\alpha_{31}}$$
(255)

where N_1^{ϕ} is positive provided that $a_1 \alpha_{33} > a_3 \alpha_{13}$.

In conclusion, we have the following equilibrium point in the absence of the first predator (S_2) :

$$(N_1, N_2, N_3) = (N_1, 0, N_3) = E_3(N_1^{\phi}, 0, N_3^{\phi})$$

Case 4

The interior equilibrium can be calculated, using (211), by the following:

$$a_1 N_1 - \alpha_{11} N_1^2 - \alpha_{12} N_1 N_2 - \alpha_{13} N_1 N_3 = 0$$
(256)

$$a_2N_2 - \alpha_{22}N_2^2 + \alpha_{21}N_1N_2 + \alpha_{23}N_2N_3 = 0$$
(257)

$$a_3N_3 - \alpha_{33}N_3^2 + \alpha_{31}N_1N_3 + \alpha_{32}N_2N_3 = 0 \tag{258}$$

Using (256), we get

$$a_1 N_1 - \alpha_{11} N_1^2 - \alpha_{12} N_1 N_2 - \alpha_{13} N_1 N_3 = 0$$

$$N_1 (a_1 - \alpha_{11} N_1 - \alpha_{12} N_2 - \alpha_{13} N_3) = 0$$

$$N_1 = 0 \quad \text{or} \quad a_1 - \alpha_{11} N_1 - \alpha_{12} N_2 - \alpha_{13} N_3 = 0$$
(259)

Assuming a positive solution N_1^* of N_1 , we have:

$$a_1 - \alpha_{11}N_1 - \alpha_{12}N_2 - \alpha_{13}N_3 = 0 \tag{260}$$

$$-\alpha_{11}N_1 = -a_1 + \alpha_{12}N_2 + \alpha_{13}N_3 \tag{261}$$

$$\therefore \qquad N_1^* = N_1 = \frac{a_1 - \alpha_{12}N_2 - \alpha_{13}N_3}{\alpha_{11}}$$
(262)

Substituting (262) in (257) and assuming a positive solution N_2^* of N_2 yields:

$$a_{2}N_{2} - \alpha_{22}N_{2}^{2} + \alpha_{21}N_{1}N_{2} + \alpha_{23}N_{2}N_{3} = 0$$

$$N_{2}(a_{2} - \alpha_{22}N_{2} + \alpha_{21}N_{1} + \alpha_{23}N_{3}) = 0$$

$$N_{2} = 0 \quad \text{or} \quad a_{2} - \alpha_{22}N_{2} + \alpha_{21}N_{1} + \alpha_{23}N_{3} = 0$$
(263)

$$\therefore \quad a_2 - \alpha_{22}N_2 + \alpha_{21}N_1 + \alpha_{23}N_3 = 0 \tag{264}$$

$$a_2 - \alpha_{22}N_2 + \alpha_{21} \left(\frac{a_1 - \alpha_{12}N_2 - \alpha_{13}N_3}{\alpha_{11}} \right) + \alpha_{23}N_3 = 0$$
(265)

$$a_2 - \alpha_{22}N_2 + \frac{a_1\alpha_{21}}{\alpha_{11}} - \frac{\alpha_{12}\alpha_{21}}{\alpha_{11}}N_2 - \frac{\alpha_{13}\alpha_{21}}{\alpha_{11}}N_3 + \alpha_{23}N_3 = 0$$
(266)

$$-\alpha_{22}N_2 - \frac{\alpha_{12}\alpha_{21}}{\alpha_{11}}N_2 = -a_2 - \frac{a_1\alpha_{21}}{\alpha_{11}} + \frac{\alpha_{13}\alpha_{21}}{\alpha_{11}}N_3 + \alpha_{23}N_3$$
(267)

$$\left(-\alpha_{22} - \frac{\alpha_{12}\alpha_{21}}{\alpha_{11}}\right)N_2 = \frac{-a_2\alpha_{11} - a_1\alpha_{21}}{\alpha_{11}} + \left(\alpha_{23} + \frac{\alpha_{13}\alpha_{21}}{\alpha_{11}}\right)N_3$$
(268)

$$\left(\frac{-\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}}{\alpha_{11}}\right)N_2 = -\frac{a_2\alpha_{11} - a_1\alpha_{21}}{\alpha_{11}} + \left(\frac{\alpha_{11}\alpha_{23} + \alpha_{13}\alpha_{21}}{\alpha_{11}}\right)N_3$$
(269)

$$\therefore \qquad N_2^* = N_2 = \frac{a_2 \alpha_{11} a_1 \alpha_{21}}{\alpha_{11} \alpha_{22} + \alpha_{12} \alpha_{21}} + \left(\frac{\alpha_{11} \alpha_{23} + \alpha_{13} \alpha_{21}}{-\alpha_{22} \alpha_{11} - \alpha_{12} \alpha_{21}}\right) N_3 \tag{270}$$

Substituting (270) and (262) in (258) and assuming a positive solution N_3^* of N_3 yields:

$$a_{3}N_{3} - \alpha_{33}N_{3}^{2} + \alpha_{31}N_{1}N_{3} + \alpha_{32}N_{2}N_{3} = 0$$

$$N_{3}(a_{3} - \alpha_{33}N_{3} + \alpha_{31}N_{1} + \alpha_{32}N_{2}) = 0$$

$$N_{3} = 0 \quad \text{or} \quad a_{3} - \alpha_{33}N_{3} + \alpha_{31}N_{1} + \alpha_{32}N_{2} = 0$$
(271)

$$a_{3} - \alpha_{33}N_{3} + \alpha_{31}\left(\frac{a_{1} - \alpha_{12}N_{2} - \alpha_{13}N_{3}}{a_{11}}\right) + \alpha_{32}\left(\frac{a_{2}\alpha_{11}a_{1}\alpha_{21}}{\alpha_{11}\alpha_{22} + \alpha_{12}\alpha_{21}} + \left(\frac{\alpha_{11}\alpha_{23} + \alpha_{13}\alpha_{21}}{-\alpha_{22}\alpha_{11} - \alpha_{12}\alpha_{21}}\right)N_{3}\right) = 0 \quad (272)$$

$$a_{3} - \alpha_{33}N_{3} + \alpha_{31} \left(\frac{a_{1} - \alpha_{12} \left(\frac{a_{2}\alpha_{11}a_{1}\alpha_{21}}{\alpha_{11}\alpha_{22} + \alpha_{12}\alpha_{21}} + \left(\frac{\alpha_{11}\alpha_{23} + \alpha_{13}\alpha_{21}}{-\alpha_{22}\alpha_{11} - \alpha_{12}\alpha_{21}} \right) N_{3} \right) - \alpha_{13}N_{3}}{\alpha_{11}} \right) + \alpha_{32} \left(\frac{a_{2}\alpha_{11}a_{1}\alpha_{21}}{\alpha_{11}\alpha_{22} + \alpha_{12}\alpha_{21}} + \left(\frac{\alpha_{11}\alpha_{23} + \alpha_{13}\alpha_{21}}{-\alpha_{22}\alpha_{11} - \alpha_{12}\alpha_{21}} \right) N_{3} \right) = 0 \quad (273)$$

$$\therefore N_3^* = N_3 = \frac{a_1(\alpha_{21}\alpha_{32} + \alpha_{22}\alpha_{31}) + a_2(\alpha_{11}\alpha_{32} - \alpha_{12}\alpha_{31}) + \alpha_3(\alpha_{11}\alpha_{22} + \alpha_{12}\alpha_{21})}{\alpha_{11}(\alpha_{22}\alpha_{33} - \alpha_{23}\alpha_{32}) + \alpha_{12}(\alpha_{21}\alpha_{33} + \alpha_{31}\alpha_{23}) + \alpha_{13}(\alpha_{31}\alpha_{32} + \alpha_{31}\alpha_{22})}$$
(274)

Substituting (274) in (270) yields:

$$N_{2}^{*} = N_{2} = \frac{a_{1}(\alpha_{21}\alpha_{33} + \alpha_{31}\alpha_{23}) + a_{2}(\alpha_{11}\alpha_{33} + \alpha_{13}\alpha_{31}) + a_{3}(\alpha_{11}\alpha_{23} - \alpha_{13}\alpha_{21})}{\alpha_{11}(\alpha_{22}\alpha_{33} - \alpha_{23}\alpha_{32}) + \alpha_{12}(\alpha_{21}\alpha_{33} + \alpha_{31}\alpha_{23}) + \alpha_{13}(\alpha_{31}\alpha_{32} + \alpha_{31}\alpha_{22})}$$
(275)

Substituting (274) and (275) in (262) yields:

$$N_{1}^{*} = N_{1} = \frac{a_{1}(\alpha_{22}\alpha_{33} - \alpha_{23}\alpha_{32}) - a_{2}(\alpha_{12}\alpha_{33} + \alpha_{13}\alpha_{32}) - a_{3}(\alpha_{12}\alpha_{23} + \alpha_{13}\alpha_{22})}{\alpha_{11}(\alpha_{22}\alpha_{33} - \alpha_{23}\alpha_{32}) + \alpha_{12}(\alpha_{21}\alpha_{33} + \alpha_{31}\alpha_{23}) + \alpha_{13}(\alpha_{31}\alpha_{32} + \alpha_{31}\alpha_{22})}$$
(276)

Therefore

$$N_1^* = \frac{\rho_1}{D} \qquad N_2^* = \frac{\rho_2}{D} \qquad N_3^* = \frac{\rho_3}{D}$$
 (277)

where

$$\rho_1 = a_1(\alpha_{22}\alpha_{33} - \alpha_{23}\alpha_{32}) - a_2(\alpha_{12}\alpha_{33} + \alpha_{13}\alpha_{32}) - a_3(\alpha_{12}\alpha_{23} + \alpha_{13}\alpha_{22})$$
(278)

$$\rho_2 = a_1(\alpha_{21}\alpha_{33} + \alpha_{31}\alpha_{23}) + a_2(\alpha_{11}\alpha_{33} + \alpha_{13}\alpha_{31}) + a_3(\alpha_{11}\alpha_{23} - \alpha_{13}\alpha_{21})$$
(279)

$$\rho_3 = a_1(\alpha_{21}\alpha_{33} + \alpha_{31}\alpha_{23}) + a_2(\alpha_{11}\alpha_{33} + \alpha_{13}\alpha_{31}) + a_3(\alpha_{11}\alpha_{23} - \alpha_{13}\alpha_{21})$$
(280)

$$D = \alpha_{11}(\alpha_{22}\alpha_{33} - \alpha_{23}\alpha_{32}) + \alpha_{12}(\alpha_{21}\alpha_{33} + \alpha_{31}\alpha_{23}) + \alpha_{13}(\alpha_{31}\alpha_{32} + \alpha_{31}\alpha_{22})$$
(281)

provided that the following expressions hold:

$$\begin{aligned} [a_2(\alpha_{12}\alpha_{33} + \alpha_{13}\alpha_{32}) + a_3(\alpha_{12}\alpha_{23} + \alpha_{13}\alpha_{22})] < a_1(\alpha_{22}\alpha_{33} - \alpha_{23}\alpha_{32}) \\ & \alpha_{11}\alpha_{23} > \alpha_{13}\alpha_{21} \\ & \alpha_{11}\alpha_{32} > \alpha_{12}\alpha_{31} \\ & \alpha_{22}\alpha_{33} > \alpha_{23}\alpha_{32} \end{aligned}$$

In conclusion, we have the following equilibrium point for the interior equilibrium:

$$(N_1, N_2, N_3) = E_4(N_1^*, N_2^*, N_3^*)$$

11 Global Stability

Theorem 8. The equilibrium point $E_4(N_1^*, N_2^*, N_3^*)$ is globally asymptotically stable. Proof. Considering the following Lyapunov function:

$$V(N_1, N_2, N_3) = N_1 - N_1^* - N_1^* \ln\left[\frac{N_1}{N_1^*}\right] + d_1^* \left\{ N_2 - N_2^* - N_2^* \ln\left[\frac{N_2}{N_2^*}\right] \right\} + d_2^* \left\{ N_3 - N_3^* - N_3^* \ln\left[\frac{N_3}{N_3^*}\right] \right\}$$
(282)

Differentiating V with respect to t yields:

$$\frac{dV}{dt}(N_1, N_2, N_3) = \left(\frac{N_1 - N_1^*}{N_1}\right) \frac{dN_1}{dt} + d_1^* \left(\frac{N_2 - N_2^*}{N_2}\right) \frac{dN_2}{dt} + d_2^* \left(\frac{N_3 - N_3^*}{N_3}\right) \frac{dN_3}{dt}$$
(283)

$$= \left(\frac{N_1 - N_1^*}{N_1}\right) (a_1 N_1 - \alpha_{11} N_1^2 - \alpha_{12} N_1 N_2 - \alpha_{13} N_1 N_3) + d_1^* \left[\left(\frac{N_2 - N_2^*}{N_2}\right) (a_2 N_2 - \alpha_{22} N_2^2 + \alpha_{21} N_1 N_2 + \alpha_{23} N_2 N_3) \right] + d_2^* \left[\left(\frac{N_3 - N_3^*}{N_3}\right) (a_3 N_3 - \alpha_{33} N_3^2 + \alpha_{31} N_1 N_3 + \alpha_{32} N_2 N_3) \right]$$
(284)

$$= -\alpha_{11}(N_1 - N_1^*)^2 - \alpha_{12}(N_1 - N_1^*)(N_2 - N_2^*) - \alpha_{13}(N_1 - N_1^*)(N_3 - N_3^*) + d_1^* \left[\alpha_{21}(N_1 - N_1^*)(N_2 - N_2^*) - \alpha_{22}(N_2 - N_2^*)^2 + \alpha_{23}(N_2 - N_2^*)(N_3 - N_3^*) \right] + d_2^* \left[\alpha_{31}(N_1 - N_1^*)(N_3 - N_3^*) + \alpha_{32}(N_2 - N_2^*)(N_3 - N_3^*) - \alpha_{33}(N_3 - N_3^*)^2 \right]$$
(285)

$$< -\alpha_{11}(N_{1} - N_{1}^{*})^{2} - (\alpha_{12} - \alpha_{21}d_{1}^{*})\left[\frac{(N_{1} - N_{1}^{*})^{2}}{2} + \frac{(N_{2} - N_{2}^{*})^{2}}{2}\right] - (\alpha_{13} - \alpha_{31}d_{2}^{*})\left[\frac{(N_{1} - N_{1}^{*})^{2}}{2} + \frac{(N_{3} - N_{3}^{*})^{2}}{2}\right] - d_{1}^{*}\alpha_{22}(N_{2} - N_{2}^{*})^{2} + (d_{1}^{*}\alpha_{23} + \alpha_{32}d_{2}^{*})\left[\frac{(N_{2} - N_{2}^{*})^{2}}{2} + \frac{(N_{3} - N_{3}^{*})^{2}}{2}\right] - d_{2}^{*}\alpha_{33}(N_{3} - N_{3}^{*})^{2}$$

$$(286)$$

Choosing $d_1^* = \frac{a_{12}}{a_{21}}$ and $d_2^* = \frac{a_{13}}{a_{31}}$, then

$$= -\alpha_{11}(N_1 - N_1^*)^2 - (\alpha_{12} - \alpha_{21}\frac{a_{12}}{a_{21}}) \left[\frac{(N_1 - N_1^*)^2}{2} + \frac{(N_2 - N_2^*)^2}{2}\right] - (\alpha_{13} - \alpha_{31}\frac{a_{13}}{a_{31}}) \left[\frac{(N_1 - N_1^*)^2}{2} + \frac{(N_3 - N_3^*)^2}{2}\right] - \frac{a_{12}}{a_{21}}\alpha_{22}(N_2 - N_2^*)^2 + (\frac{a_{12}}{a_{21}}\alpha_{23} + \alpha_{32}\frac{a_{13}}{a_{31}}) \left[\frac{(N_2 - N_2^*)^2}{2} + \frac{(N_3 - N_3^*)^2}{2}\right] - \frac{a_{13}}{a_{31}}\alpha_{33}(N_3 - N_3^*)^2$$
(287)

$$= -\alpha_{11}(N_1 - N_1^*)^2 - (\alpha_{12} - \alpha_{12}) \left[\frac{(N_1 - N_1^*)^2}{2} + \frac{(N_2 - N_2^*)^2}{2} \right] - (\alpha_{13} - \alpha_{13}) \left[\frac{(N_1 - N_1^*)^2}{2} + \frac{(N_3 - N_3^*)^2}{2} \right] - \frac{\alpha_{12}}{\alpha_{21}} \alpha_{22} (N_2 - N_2^*)^2 + (\frac{\alpha_{12}}{\alpha_{21}} \alpha_{23} + \alpha_{32} \frac{\alpha_{13}}{\alpha_{31}}) \left[\frac{(N_2 - N_2^*)^2}{2} + \frac{(N_3 - N_3^*)^2}{2} \right] - \frac{\alpha_{13}}{\alpha_{31}} \alpha_{33} (N_3 - N_3^*)^2$$
(288)

Chapter 4: A Model of a Three Species Ecosystem with Mutualism Between The Predators - K. S. Reddy & N. C. Pattabhiramacharyulu

$$= -\alpha_{11}(N_1 - N_1^*)^2 - \frac{\alpha_{12}}{\alpha_{21}}\alpha_{22}(N_2 - N_2^*)^2 + \frac{1}{2}\frac{\alpha_{12}}{\alpha_{21}}\alpha_{23}(N_2 - N_2^*)^2 + \frac{1}{2}\frac{\alpha_{12}}{\alpha_{21}}\alpha_{23}(N_3 - N_3^*)^2 + \frac{1}{2}\alpha_{32}\frac{\alpha_{13}}{\alpha_{31}}(N_2 - N_2^*)^2 + \frac{1}{2}a_{32}\frac{\alpha_{13}}{\alpha_{31}}(N_3 - N_3^*)^2 - \frac{\alpha_{13}}{\alpha_{31}}\alpha_{33}(N_3 - N_3^*)^2$$
(289)

$$= -\alpha_{11}(N_1 - N_1^*)^2 + \left(-\frac{\alpha_{12}}{\alpha_{21}}\alpha_{22} + \frac{1}{2}\frac{\alpha_{12}}{\alpha_{21}}\alpha_{23} + \frac{1}{2}\alpha_{32}\frac{\alpha_{13}}{\alpha_{31}}\right)(N_2 - N_2^*)^2 + \left(-\frac{\alpha_{13}}{\alpha_{31}}\alpha_{33} + \frac{1}{2}\frac{\alpha_{12}}{\alpha_{21}}\alpha_{23} + \frac{1}{2}\alpha_{32}\frac{\alpha_{13}}{\alpha_{31}}\right)(N_3 - N_3^*)^2$$
(290)

$$= -\alpha_{11}(N_1 - N_1^*)^2 + \left(-\frac{\alpha_{12}}{\alpha_{21}}\alpha_{22} + \frac{1}{2}\left(\frac{\alpha_{12}}{\alpha_{21}}\alpha_{23} + \alpha_{32}\frac{\alpha_{13}}{\alpha_{31}}\right)\right)(N_2 - N_2^*)^2 + \left(-\frac{\alpha_{13}}{\alpha_{31}}\alpha_{33} + \frac{1}{2}\left(\frac{\alpha_{12}}{\alpha_{21}}\alpha_{23} + \frac{1}{2}\alpha_{32}\frac{\alpha_{13}}{\alpha_{31}}\right)\right)(N_3 - N_3^*)^2$$
(291)

$$\therefore \qquad \frac{dV}{dt} < -\alpha_{11}(N_1 - N_1^*)^2 - \left(\frac{\alpha_{12}}{\alpha_{21}}\alpha_{22} - \frac{1}{2}\left(\frac{\alpha_{12}}{\alpha_{21}}\alpha_{23} + \alpha_{32}\frac{\alpha_{13}}{\alpha_{31}}\right)\right)(N_2 - N_2^*)^2 - \left(\frac{\alpha_{13}}{\alpha_{31}}\alpha_{33} - \frac{1}{2}\left(\frac{\alpha_{12}}{\alpha_{21}}\alpha_{23} + \frac{1}{2}\alpha_{32}\frac{\alpha_{13}}{\alpha_{31}}\right)\right)(N_3 - N_3^*)^2 < 0$$

$$(292)$$

provided that the following inequalities hold:

$$\frac{\alpha_{12}}{\alpha_{21}}\alpha_{22} > \frac{1}{2} \left(\frac{\alpha_{12}}{\alpha_{21}}\alpha_{23} + \alpha_{32} \frac{a_{13}}{a_{31}} \right)$$
$$\frac{\alpha_{13}}{\alpha_{31}}\alpha_{33} > \frac{1}{2} \left(\frac{\alpha_{12}}{\alpha_{21}}\alpha_{23} + \alpha_{32} \frac{\alpha_{13}}{\alpha_{31}} \right)$$

 $\therefore E_4(N_1^*, N_2^*, N_3^*)$ is globally asymptotically stable.

12 Numerical Examples

Example 1

Here, let

 $\begin{array}{rrrr} a_1 = 8 & a_2 = 1 & a_3 = 1.5 \\ \alpha_{11} = 0.05 & \alpha_{21} = 0.7 & \alpha_{31} = 0.15 \\ \alpha_{12} = 0.6 & \alpha_{22} = 0.17 & \alpha_{32} = 0.18 \\ \alpha_{13} = 0.7 & \alpha_{23} = 0.13 & \alpha_{33} = 0.4 \end{array}$

with initial values:

 $N_1 = 10$ $N_2 = 10$ $N_3 = 10$

for the Time t interval 0 < t < 20.

Hence, we have the following MATLAB function:

```
% dN1/dt = a1N1-a11N1^2-a12N1N2-a13N1N3
% dN2/dt = a2N2-a22N2^2+a21N1N2+a23N2N3
% dN3/dt = a3N3-a33N3^2+a31N1N3+a32N2N3
function dNdt = odefcn(t,N)
% Numerical Example 1
a1 = 8;
a11 = 0.05;
a12 = 0.6;
a13 = 0.7;
a2 = 1;
a21 = 0.7;
a22 = 0.17;
a23 = 0.13;
a3 = 1.5;
a31 = 0.15;
a32 = 0.18;
a33 = 0.4;
dNdt = zeros(3,1);
dNdt(1) = a1*N(1)-a11*(N(1).^2)-a12*N(1)*N(2)-a13*N(1)*N(3);
dNdt(2) = a2*N(2)-a22*(N(2).^2)+a21*N(1)*N(2)+a23*N(2)*N(3);
dNdt(3) = a3*N(3)-a33*(N(3).^2)+a31*N(1)*N(3)+a32*N(2)*N(3);
```

and MATLAB script for solving the system with ODE solver ode45 as well as plotting the results on a 2D and 3D plane:

% dN1/dt = a1N1-a11N1^2-a12N1N2-a13N1N3 % dN2/dt = a2N2-a22N2^2+a21N1N2+a23N2N3 % dN3/dt = a3N3-a33N3^2+a31N1N3+a32N2N3

```
% Solving system of equations (Using ODE45)
%Example 1
[t,N] = ode45('odefcn', [0, 20], [10 10 10]);
%2D Plot
plot(t,N(:,1),'-o',t,N(:,2),'-.',t,N(:,3),'--')
title('Example 1')
xlabel('Time'), ylabel('Population')
%3D Plot
plot3(N(:,1),N(:,2),N(:,3))
title('Example 1')
xlabel('Prey Population'),
ylabel('Predator 1 Population'), zlabel('Predator 2 Population')
```

which yields the following 2D and 3D plots:

Chapter 4: A Model of a Three Species Ecosystem with Mutualism Between The Predators - K. S. Reddy & N. C. Pattabhiramacharyulu



Figure 1: Example 1 2D Plot



Figure 2: Example 1 3D Plot

Example 2

Here, let

 $a_{1} = 3 \qquad a_{2} = 1 \qquad a_{3} = 1$ $\alpha_{11} = 0.01 \qquad \alpha_{21} = 0.1 \qquad \alpha_{31} = 0.1$ $\alpha_{12} = 0.1 \qquad \alpha_{22} = 0.2 \qquad \alpha_{32} = 0.1$ $\alpha_{13} = 0.1 \qquad \alpha_{23} = 0.1 \qquad \alpha_{33} = 0.3$

with initial values:

 $N_1 = 50$ $N_2 = 75$ $N_3 = 60$

for the Time t interval 0 < t < 20.

Hence, we have the following MATLAB function:

```
% dN1/dt = a1N1-a11N1^2-a12N1N2-a13N1N3
% dN2/dt = a2N2-a22N2^2+a21N1N2+a23N2N3
% dN3/dt = a3N3-a33N3^2+a31N1N3+a32N2N3
function dNdt = odefcn2(t,N)
% Numerical Example 2
a1 = 3;
a11 = 0.01;
a12 = 0.1;
a13 = 0.1;
a2 = 1;
a21 = 0.1;
a22 = 0.2;
a23 = 0.1;
a3 = 1;
a31 = 0.1;
a32 = 0.1;
a33 = 0.3;
dNdt = zeros(3,1);
dNdt(1) = a1*N(1)-a11*(N(1).^2)-a12*N(1)*N(2)-a13*N(1)*N(3);
dNdt(2) = a2*N(2)-a22*(N(2).^2)+a21*N(1)*N(2)+a23*N(2)*N(3);
dNdt(3) = a3*N(3)-a33*(N(3).^{2})+a31*N(1)*N(3)+a32*N(2)*N(3);
and MATLAB script for solving the system with ODE solver ode45 as well as plotting the
results on a 2D and 3D plane:
```

```
% dN1/dt = a1N1-a11N1^2-a12N1N2-a13N1N3
% dN2/dt = a2N2-a22N2^2+a21N1N2+a23N2N3
% dN3/dt = a3N3-a33N3^2+a31N1N3+a32N2N3
% Solving system of equations (Using ODE45)
```

Chapter 4: A Model of a Three Species Ecosystem with Mutualism Between The Predators - K. S. Reddy & N. C. Pattabhiramacharyulu

```
%Example 2
[t,N] = ode45('odefcn2', [0, 20], [50 75 60]);
%2D Plot
plot(t,N(:,1),'-o',t,N(:,2),'-.',t,N(:,3),'--')
title('Example 2')
xlabel('Time'), ylabel('Population')
%3D Plot
plot3(N(:,1),N(:,2),N(:,3))
title('Example 2')
xlabel('Prey Population'),
ylabel('Predator 1 Population'), zlabel('Predator 2 Population')
```

which yields the following 2D and 3D plots:

Chapter 4: A Model of a Three Species Ecosystem with Mutualism Between The Predators -K. S. Reddy & N. C. Pattabhiramacharyulu



Figure 3: Example 2 2D Plot



Figure 4: Example 2 3D Plot

Here, comparing the above MATLAB plots and the figures included in [32], there seems to be an error between the values for Examples 1 and 2 and the corresponding plots of [32]. Rather than the given values for Example 1 and Example 2, the figures (1) and (2) of the research paper [32] correspond to Example 2 with initial values $N_1 = 50$, $N_2 = 75$, $N_3 = 60$ whilst figures (3) and (4) correspond to Example 2 with initial values $N_1 = N_2 = N_3 = 10$. Therefore, the values in Example 1 of the paper [32] are not correct. Implementing these corrections, we have the following MATLAB code and plots which correspond to the figures included in the research paper [32]:

Example 1 (with corrections)

Here, let

 $\begin{array}{rrrr} a_1 = 3 & a_2 = 1 & a_3 = 1 \\ \alpha_{11} = 0.01 & \alpha_{21} = 0.1 & \alpha_{31} = 0.1 \\ \alpha_{12} = 0.1 & \alpha_{22} = 0.2 & \alpha_{32} = 0.1 \\ \alpha_{13} = 0.1 & \alpha_{23} = 0.1 & \alpha_{33} = 0.3 \end{array}$

with initial values:

 $N_1 = 50$ $N_2 = 75$ $N_3 = 60$

for the Time t interval 0 < t < 20.

Hence, we have the following MATLAB function:

```
% dN1/dt = a1N1-a11N1^2-a12N1N2-a13N1N3
% dN2/dt = a2N2-a22N2^2+a21N1N2+a23N2N3
% dN3/dt = a3N3-a33N3^2+a31N1N3+a32N2N3
function dNdt = odefcn2(t,N)
% Numerical Example 1
a1 = 3;
a11 = 0.01;
a12 = 0.1;
a13 = 0.1;
a2 = 1;
a21 = 0.1;
a22 = 0.2;
a23 = 0.1;
a3 = 1;
a31 = 0.1;
a32 = 0.1;
a33 = 0.3;
dNdt = zeros(3,1);
dNdt(1) = a1*N(1)-a11*(N(1).^2)-a12*N(1)*N(2)-a13*N(1)*N(3);
dNdt(2) = a2*N(2)-a22*(N(2).^2)+a21*N(1)*N(2)+a23*N(2)*N(3);
```

Chapter 4: A Model of a Three Species Ecosystem with Mutualism Between The Predators - K. S. Reddy & N. C. Pattabhiramacharyulu

dNdt(3) = a3*N(3)-a33*(N(3).^2)+a31*N(1)*N(3)+a32*N(2)*N(3);

and MATLAB script for solving the system with ODE solver ode45 as well as plotting the results on a 2D and 3D plane:

```
% dN1/dt = a1N1-a11N1^2-a12N1N2-a13N1N3
% dN2/dt = a2N2-a22N2^2+a21N1N2+a23N2N3
% dN3/dt = a3N3-a33N3^2+a31N1N3+a32N2N3
% Solving system of equations (Using ODE45)
%Example 1
[t,N] = ode45('odefcn2', [0, 20], [50 75 60]);
%2D Plot
plot(t,N(:,1),'-o',t,N(:,2),'-.',t,N(:,3),'--')
title('Example 1')
xlabel('Time'), ylabel('Population')
%3D Plot
plot3(N(:,1),N(:,2),N(:,3))
title('Example 1')
xlabel('Prey Population'),
ylabel('Predator 1 Population'), zlabel('Predator 2 Population')
```

which yields the following 2D and 3D plots, which correspond to figures (1) and (2) of the research paper [32]:

Chapter 4: A Model of a Three Species Ecosystem with Mutualism Between The Predators - K. S. Reddy & N. C. Pattabhiramacharyulu



Figure 5: Example 1 (with corrections) 2D Plot



Figure 6: Example 1 (with corrections) 3D Plot

Example 2 (with corrections)

Here, let

 $a_{1} = 3 \qquad a_{2} = 1 \qquad a_{3} = 1$ $\alpha_{11} = 0.01 \qquad \alpha_{21} = 0.1 \qquad \alpha_{31} = 0.1$ $\alpha_{12} = 0.1 \qquad \alpha_{22} = 0.2 \qquad \alpha_{32} = 0.1$ $\alpha_{13} = 0.1 \qquad \alpha_{23} = 0.1 \qquad \alpha_{33} = 0.3$

with initial values:

 $N_1 = 10$ $N_2 = 10$ $N_3 = 10$

for the Time t interval 0 < t < 20.

Hence, we have the following MATLAB function:

```
% dN1/dt = a1N1-a11N1^2-a12N1N2-a13N1N3
% dN2/dt = a2N2-a22N2^2+a21N1N2+a23N2N3
% dN3/dt = a3N3-a33N3^2+a31N1N3+a32N2N3
function dNdt = odefcn2(t,N)
% Numerical Example 2
a1 = 3;
a11 = 0.01;
a12 = 0.1;
a13 = 0.1;
a2 = 1;
a21 = 0.1;
a22 = 0.2;
a23 = 0.1;
a3 = 1;
a31 = 0.1;
a32 = 0.1;
a33 = 0.3;
dNdt = zeros(3,1);
dNdt(1) = a1*N(1)-a11*(N(1).^2)-a12*N(1)*N(2)-a13*N(1)*N(3);
dNdt(2) = a2*N(2)-a22*(N(2).^2)+a21*N(1)*N(2)+a23*N(2)*N(3);
dNdt(3) = a3*N(3)-a33*(N(3).^{2})+a31*N(1)*N(3)+a32*N(2)*N(3);
and MATLAB script for solving the system with ODE solver ode45 as well as plotting the
results on a 2D and 3D plane:
```

```
% dN1/dt = a1N1-a11N1^2-a12N1N2-a13N1N3
% dN2/dt = a2N2-a22N2^2+a21N1N2+a23N2N3
% dN3/dt = a3N3-a33N3^2+a31N1N3+a32N2N3
% Solving system of equations (Using ODE45)
```

```
%Example 2
[t,N] = ode45('odefcn2', [0, 20], [50 75 60]);
%2D Plot
plot(t,N(:,1),'-o',t,N(:,2),'-.',t,N(:,3),'--')
title('Example 2')
xlabel('Time'), ylabel('Population')
%3D Plot
plot3(N(:,1),N(:,2),N(:,3))
title('Example 2')
xlabel('Prey Population'),
ylabel('Predator 1 Population'), zlabel('Predator 2 Population')
```

which yields the following 2D and 3D plots, which correspond to figures (3) and (4) of the research paper [32]:

Chapter 4: A Model of a Three Species Ecosystem with Mutualism Between The Predators - K. S. Reddy & N. C. Pattabhiramacharyulu



Figure 7: Example 2 (with corrections) 2D Plot



Figure 8: Example 2 (with corrections) 3D Plot

13 Existence and Uniqueness

In order to study the existence and uniqueness of the system (211), we use the following theorem:

Theorem 9 (Existence and Uniqueness [2]). Let each of the functions $f_1(x_1, \ldots, x_n), \ldots, f_n(x_1, \ldots, x_n)$ have continuous partial derivatives with respect to x_1, \ldots, x_n . Then, the initial-value problem

$$\dot{x} = f(x) \qquad x(t_0) = x^0$$
(293)

has one, and only one solution x = x(t), for every x^0 in \mathbb{R}^n .

Proof. First, we will show that x(t) satisfies the following integral equation

$$x(t) = x_0 + \int_{t_0}^t f(s, x(s))ds$$
(294)

and x(t) is continuous.

The Picard iterates $x_n(t)$ are defined recursively by:

$$x_{n+1}(t) = x_0 + \int_{t_0}^t f(s, x_n(s))ds$$
(295)

Taking limits of both sides of (295) yields:

$$x(t) = x_0 + \lim_{n \to \infty} \int_{t_0}^t f(s, x_n(s)) ds$$
(296)

Showing that the right-hand side of (296) equals:

$$x_0 + \int_{t_0}^t f(s, x(s)) ds$$
 (297)

we must show that:

$$\left|\int_{t_0}^t f(s, x(s))ds - \int_{t_0}^t f(s, x_n(s))ds\right| \to 0 \quad \text{as} \quad n \to \infty$$
(298)

Hence

$$\left| \int_{t_0}^t f(s, x(s)) ds - \int_{t_0}^t f(s, x_n(s)) ds \right| \le \int_{t_0}^t |f(s, x(s)) - f(s, x_n(s))| ds$$
(299)

$$\leq L \int_{t_0}^t |x(s) - x_n(s)| ds$$
 (300)

where $L = \max_{(t,x) \in \mathbb{R}} \left| \frac{\partial f(t,x)}{\partial x} \right|$.

We observe that:

$$x(s) - x_n(s) = \sum_{j=n+1}^{\infty} \left[x_j(s) - x_{j-1}(s) \right]$$
(301)

since

$$x(s) = x_0 + \sum_{j=1}^{\infty} \left[x_j(s) - x_{j-1}(s) \right]$$
(302)

and

$$x_n(s) = x_0 + \sum_{j=1}^n \left[x_j(s) - x_{j-1}(s) \right]$$
(303)

Consequently:

$$\left| \int_{t_0}^t f(s, x(s)) ds - \int_{t_0}^t f(s, x_n(s)) ds \right| \le L \int_{t_0}^t |x(s) - x_n(s)| ds \tag{304}$$

$$\leq L \int_{t_0}^t \left(\sum_{j=n+1}^\infty |x_j(s) - x_{j-1}(s)| \right) ds$$
 (305)

$$\leq M \sum_{j=n+1}^{\infty} \int_{t_0}^{t} L^{j-1} \frac{(s-t_0)^j}{j!} ds$$
(306)

$$\leq M\alpha \sum_{j=n+1}^{\infty} \int_{t_0}^t \frac{(\alpha L)^j}{j!} ds \to 0 \qquad \text{as} \qquad n \to \infty \quad (307)$$

Therefore

$$\lim_{n \to +\infty} \int_{t_0}^t f(s, x_n(s)) ds = \int_{t_0}^t f(s, x(s)) ds$$
(308)

and we have shown that x(t) satisfies:

$$x(t) = x_0 + \int_{t_0}^t f(s, x(s))ds$$
(309)

In order to show that x(t) is continuous, we have, for any $\varepsilon > 0$ and $\delta(\varepsilon) > 0$: $|h| < \delta$, then

$$|x(t+h) - x(t)| < \varepsilon \tag{310}$$

observe that, by choosing a large integer N:

$$x(t+h) - x(t) = [x(t+h) - x_N(t+h)] + [x_N(t+h) - x_N(t)] + [x_N(t) - x(t)]$$
(311)

We choose N, such that:

$$\frac{M}{L}\sum_{j=N+1}^{\infty} \frac{(\alpha L)^j}{j!} < \frac{\varepsilon}{3}$$
(312)

Therefore

$$|x(t+h) - x_N(t+h)| < \frac{\varepsilon}{3} \qquad \text{and} \qquad |x_N(t) - x(t)| < \frac{\varepsilon}{3}$$
(313)

But, choosing $\delta > 0$, we get:

$$|x_N(t+h) - x_N(t)| < \frac{\varepsilon}{3} \qquad \text{for } |h| < \delta \tag{314}$$

since x_N is continuous by it's definition, for any $\varepsilon > 0$ there exists a $\delta(\varepsilon) > 0$.

Consequently:

$$|x(t+h) - x(t)| \le |x(t+h) - x_N(t+h)| + |x_N(t+h) - x_N(t)| + |x_N(t) - x(t)|$$
(315)

$$<\frac{\varepsilon}{3}+\frac{\varepsilon}{3}+\frac{\varepsilon}{3}\tag{316}$$

$$=\varepsilon$$
 (317)

for $|h| < \delta$.

Therefore, x = x(t) is a continuous solution of the initial-value problem (293).

Now we prove the uniqueness of x = x(t). We have already proved the existence of at least one solution x = x(t) of (293). Suppose that y(t) is a second solution. Then:

$$x(t) = x_0 + \int_{t_0}^t f(s, x(s))ds$$
 and $y(t) = x_0 + \int_{t_0}^t f(s, y(s))ds$ (318)

Subtracting each equation of (318), we have:

$$|x(t) - y(t)| = \max\{|x_1(t) - y_1(t)|, \dots, |x_n(t) - y_n(t)|\}$$

$$= \max\{\left|\int_{t_0}^t [f(s, x_1(s)) - f(s, y_1(s))]ds\right|, \dots, \left|\int_{t_0}^t [f(s, x_n(s)) - f(s, y_n(s))]ds\right|\}$$
(319)
(320)

$$\leq \max\{\int_{t_0}^t |f(s, x_1(s)) - f(s, y_1(s))| ds, \dots, \int_{t_0}^t |f(s, x_n(s)) - f(s, y_n(s))| ds\}$$
(321)

$$\leq L\left(\int_{t_0}^t |x_1(s) - y_1(s)| ds, \dots, \int_{t_0}^t |x_n(s) - y_n(s)| ds\right)$$
(322)

where $L = \max_{(t,x) \in \mathbb{R}} \left| \frac{\partial f(t,x)}{\partial x} \right|$.

Using the following Lemma:

Lemma 10 ([2]). Let w(t) be a non-negative function, with

$$w(t) \le L \int_{t_0}^t w(s) ds \tag{323}$$

Then, w(t) is identically zero.

Hence

$$|x(t) - y(t)| \le L \int_{t_0}^t |x(s) - y(s)| ds$$
(324)

$$|w(t)| = L \int_{t_0}^t \tilde{w}(t) ds \tag{325}$$

where $\tilde{w}(s) = |w(s)|$.

Therefore:

$$\tilde{w}(t) \le L \int_{t_0}^t \tilde{w}(s) ds \tag{326}$$

Define:

$$U(t) = \int_{t_0}^t \tilde{w}(s)ds \tag{327}$$

and

$$\frac{dU}{dt} = \tilde{w}(t) \qquad \Rightarrow \qquad \frac{dU}{dt} \le LU \tag{328}$$

Hence

$$\therefore e^{-L(t-t_0)}U(t) \le U(0) = 0 \qquad \Rightarrow \qquad U(t) = 0 \tag{329}$$

$$0 \le \tilde{w}(t) \le L \int_0^{t_0} \tilde{w}(s) ds = LU(t) = 0$$
 (330)

$$\tilde{w}(t) = 0 \qquad \Rightarrow \qquad x(t) = y(t)$$
(331)

Therefore, x = x(t) is a unique solution of the initial-value problem (293).

In conclusion, x = x(t) is a unique and continuous solution of the initial-value problem (293).

13.1 Proving Existence and Uniqueness of The System

Considering the following system:

$$\frac{dN_1}{dt} = a_1 N_1 - \alpha_{11} N_1^2 - \alpha_{12} N_1 N_2 - \alpha_{13} N_1 N_3$$

$$\frac{dN_2}{dt} = a_2 N_2 - \alpha_{22} N_2^2 + \alpha_{21} N_1 N_2 + \alpha_{23} N_2 N_3$$

$$\frac{dN_3}{dt} = a_3 N_3 - \alpha_{33} N_3^2 + \alpha_{31} N_1 N_3 + \alpha_{32} N_2 N_3$$
(332)

in the form:

$$\dot{x} = f(x) \tag{333}$$

$$= f(t,x) = \begin{pmatrix} f_1(t,x) \\ f_2(t,x) \\ f_3(t,x) \end{pmatrix} = \begin{pmatrix} a_1N_1 - \alpha_{11}N_1^2 - \alpha_{12}N_1N_2 - \alpha_{13}N_1N_3 \\ a_2N_2 - \alpha_{22}N_2^2 + \alpha_{21}N_1N_2 + \alpha_{23}N_2N_3 \\ a_3N_3 - \alpha_{33}N_3^2 + \alpha_{31}N_1N_3 + \alpha_{32}N_2N_3 \end{pmatrix}$$
(334)

Calculating the partial derivatives of \dot{x} , we have:

$$\frac{\partial}{\partial N}\dot{x} = \frac{\partial f(x)}{\partial N} \tag{335}$$

$$= \frac{\partial f(t,x)}{\partial N} = \begin{pmatrix} \frac{\partial f_1(t,x)}{\partial N_1} \\ \frac{\partial f_2(t,x)}{\partial N_2} \\ \frac{\partial f_3(t,x)}{\partial N_3} \end{pmatrix} = \begin{pmatrix} a_1 - 2\alpha_{11}N_1 - \alpha_{12}N_2 - \alpha_{13}N_3 \\ a_2 - 2\alpha_{22}N_2 + \alpha_{21}N_1 + \alpha_{23}N_3 \\ a_3 - 2\alpha_{33}N_3^2 + \alpha_{31}N_1 + \alpha_{32}N_2 \end{pmatrix}$$
(336)

Here, we can see that:

$$\frac{\partial f}{\partial N} \to$$
 Continuous in \mathbb{R}^n (337)

Therefore, by Theorem 9 [2], there exists a unique continuous solution to the system of differential equations (332).

14 Permanence and Persistence

When studying systems involved in the modelling of population growth, we begin analysis of the system by studying local stability or steady states, global stability and existence and stability of periodic solutions [21]. Although these concepts are of interest and importance in population study, from a mathematical and biological perspective, the more basic and important topic would be the longevity of the population. The long-term survival of interacting species in a population or ecosystem can be a very important concept of population dynamical systems [52]. This long-term survival is referred to as the permanance of a system of populations [21]. Permanence occurs when all trajectories starting in the interior are ultimately bounded away from the predetermined boundary that is independent of initial values [19]. Here, sufficiently small fluctuations in population cannot lead to the extinction of any species. Here, we have the following definitions:

Definition 3 (Persistence [52]). In general, a population or species x(t) is said to be persistent if:

$$\liminf_{t \to \infty} x(t) > 0. \tag{338}$$

Definition 4 (Uniform Persistence [11]). In general, a population or species x(t) is said to be uniformly persistent if:

$$\liminf_{t \to \infty} x(t) \ge \eta. \tag{339}$$

where $\eta > 0$.

Definition 5 (Permanence [21]). In general, a population or species x(t) is said to be permanent if there exists two positive constants m and M where m < M, such that, for large values of t (dependent on x_0), we have:

$$m \le x(t) \le M. \tag{340}$$

Considering these definitions, then [52]:

- If all involved populations are persistent.
 ⇒ The system is Persistent.
- If all populations eventually have densities which are larger than some positive constant.
 ⇒ The system is Uniformly Persistent.
- If
 - 1. A system is Uniformly Persistent.
 - 2. All involved populations are bounded.

 \Rightarrow The system is Permanent.

14.1 Proving Permanence and Persistence of The System

Considering the following non-linear continuous system of differential equations:

$$\frac{dN_1}{dt} = a_1 N_1 - \alpha_{11} N_1^2 - \alpha_{12} N_1 N_2 - \alpha_{13} N_1 N_3 \tag{341}$$

$$\frac{dN_2}{dt} = a_2 N_2 - \alpha_{22} N_2^2 + \alpha_{21} N_1 N_2 + \alpha_{23} N_2 N_3 \tag{342}$$

$$\frac{dN_3}{dt} = a_3 N_3 - \alpha_{33} N_3^2 + \alpha_{31} N_1 N_3 + \alpha_{32} N_2 N_3 \tag{343}$$

Here, we prove that the system is persistent. Hence, we prove that:

$$\liminf_{t \to \infty} \frac{dN_1(t)}{dt} > 0 \tag{344}$$

$$\liminf_{t \to \infty} \frac{dN_2(t)}{dt} > 0 \tag{345}$$

$$\liminf_{t \to \infty} \frac{dN_3(t)}{dt} > 0 \tag{346}$$

Here, we assume that the parameters $N_i > 0$ and the constants $a_i, \alpha_{ij} > 0$ for i = 1, 2, 3 and j = 1, 2, 3.

1. Considering equation (341):

$$\frac{dN_1}{dt} = a_1 N_1 - \alpha_{11} N_1^2 - \alpha_{12} N_1 N_2 - \alpha_{13} N_1 N_3 \tag{347}$$

If:

$$a_1 N_1 > \alpha_{11} N_1^2 + \alpha_{12} N_1 N_2 + \alpha_{13} N_1 N_3 \tag{348}$$

then:

$$\liminf_{t \to \infty} \frac{dN_1(t)}{dt} > 0 \tag{349}$$

and equation (341)/(347) is said to be persistent.

2. Considering equation (342):

$$\frac{dN_2}{dt} = a_2 N_2 - \alpha_{22} N_2^2 + \alpha_{21} N_1 N_2 + \alpha_{23} N_2 N_3 \tag{350}$$

If:

$$\alpha_{22}N_2^2 < a_2N_2 + \alpha_{21}N_1N_2 + \alpha_{23}N_2N_3 \tag{351}$$

then:

$$\liminf_{t \to \infty} \frac{dN_2(t)}{dt} > 0 \tag{352}$$

and equation (342)/(350) is said to be persistent.

3. Considering equation (343):

$$\frac{dN_3}{dt} = a_3N_3 - \alpha_{33}N_3^2 + \alpha_{31}N_1N_3 + \alpha_{32}N_2N_3 \tag{353}$$

If:

$$\alpha_{33}N_3^2 < a_3N_3 + \alpha_{31}N_1N_3 + \alpha_{32}N_2N_3 \tag{354}$$

then:

$$\liminf_{t \to \infty} \frac{dN_3(t)}{dt} > 0 \tag{355}$$

and equation (343)/(353) is said to be Persistent.

Therefore, if:

1.

$$\liminf_{t \to \infty} \frac{dN_1(t)}{dt} > 0 \tag{356}$$

$$\liminf_{t \to \infty} \frac{dN_2(t)}{dt} > 0 \tag{357}$$

$$\liminf_{t \to \infty} \frac{dN_3(t)}{dt} > 0 \tag{358}$$

2. Conditions (348), (351) and (354) are true.

 \Rightarrow The system of equations (211) is Persistent.
Chapter 5: Constructing a Discrete System of Difference Equations Model

15 Converting a Continuous System of Differential Equations to a Discrete System of Difference Equations

In this chapter we create a discrete analogue of the continuous system of differential equations studied in Chapter 4. Here, we aim to convert the system of differential equations to a system of difference equations. We construct a discrete form by using the following two methods:

- 1. Euler's Method
- 2. Method of Piecewise Constant Arguments

These methods produce two Autonomous Time-Invariant systems:

15.1 Euler's Method

Euler's method is regarded as the most elementary approximation technique for finding solutions to initial-value problems [3]. Although the method is only occasionally used in practice, it's simplicity can help in the construction of more advanced techniques without the complex use of algebra involved in other methods. One of these uses is converting a system of differential equations to a system of difference equations. Here we have the following definition:

Definition 6 (Euler's Method [3], [40]). We define the following initial-value problem:

$$\frac{dy}{dt} = f(t, y) \qquad a \le t \le b \qquad y(a) = \alpha \tag{359}$$

The aim of Euler's method is to find approximations for (359). Continuous approximations to the solution y(t) are not obtained. Alternatively, approximations for y values are generated at various values referred to as mesh points in the interval [a, b]. Consecutive approximations are then calculated by interpolation.

Assuming that the mesh points are equally distributed throughout the interval [a, b] and choosing a positive integer \mathbb{N} , we have the following mesh points:

$$t_i = a + ih$$
 for $i = 0, 1, 2, \dots, N$ (360)

with step size:

$$h = t_{i+1} - t_i = \frac{(b-a)}{N} \tag{361}$$

By Taylor's theorem, assuming that y(t) is a unique solution of the initial-value problem (359) and has two continuous derivatives in the interval [a, b] for i = 0, 1, 2, ..., N - 1, we get:

$$y(t_{i+1}) = y(t_i) + (t_{i+1} - t_i)y'(t_i) + \frac{(t_{i+1} - t_i)^2}{2}y''(\xi_i)$$
(362)

for some number $\xi_i \in (t_i, t_{i+1})$.

Let $h = t_{i+1} - t_i$, then:

$$y(t_{i+1}) = y(t_i) + hy'(t_i) + \frac{h^2}{2}y''(\xi_i)$$
(363)

Since y(t) satisfies the initial-value problem (359), we get:

$$y(t_{i+1}) = y(t_i) + hf(t_i, y(t_i)) + \frac{h^2}{2}y''(\xi_i)$$
(364)

Noting that $w_i \approx y(t_i)$ for each i = 1, 2, ..., N, we have the following Euler Method:

$$w_0 = \alpha$$

 $w_{i+1} = w_i + hf(t_i, w_i)$ for $i = 0, 1, \dots, N-1$
(365)

15.1.1 Application of Euler's Method

Here, we have the following continuous system of non-linear differential equations:

$$\frac{dN_1}{dt} = N_1'(t) = a_1 N_1 - \alpha_{11} N_1^2 - \alpha_{12} N_1 N_2 - \alpha_{13} N_1 N_3
\frac{dN_2}{dt} = N_2'(t) = a_2 N_2 - \alpha_{22} N_2^2 + \alpha_{21} N_1 N_2 + \alpha_{23} N_2 N_3
\frac{dN_3}{dt} = N_3'(t) = a_3 N_3 - \alpha_{33} N_3^2 + \alpha_{31} N_1 N_3 + \alpha_{32} N_2 N_3$$
(366)

with the initial conditions:

$$N_{1}(t^{0}) = N_{1}^{0}$$

$$N_{2}(t^{0}) = N_{2}^{0}$$

$$N_{3}(t^{0}) = N_{3}^{0}$$
(367)

Applying Euler's method, we have the following notation [3], [40]:

$$N^{k+1} = N^k + hf(t^k, N^k)$$
(368)

$$N^{k+1} = \begin{pmatrix} N_1^k \\ N_2^k \\ N_3^k \end{pmatrix} + h \begin{pmatrix} a_1 N_1^k - \alpha_{11} N_1^{k^2} - \alpha_{12} N_1^k N_2^k - \alpha_{13} N_1^k N_3^k \\ a_2 N_2^k - \alpha_{22} N_2^{k^2} + \alpha_{21} N_1^k N_2^k + \alpha_{23} N_2^k N_3^k \\ a_3 N_3^k - \alpha_{33} N_3^{k^2} + \alpha_{31} N_1^k N_3^k + \alpha_{32} N_2^k N_3^k \end{pmatrix}$$
(369)

for a uniform partition $t_0 < t_1 < \ldots < t_K$ where $t_k = t_0 + kh$ and step size $h = \frac{t_K - t_0}{K}$.

Therefore, we have the following autonomous time-invariant discrete scheme of system (366):

$$N(k+1) = N(k) + h \begin{pmatrix} a_1 N_1(k) - \alpha_{11} N_1^2(k) - \alpha_{12} N_1(k) N_2(k) - \alpha_{13} N_1(k) N_3(k) \\ a_2 N_2(k) - \alpha_{22} N_2^2(k) + \alpha_{21} N_1(k) N_2(k) + \alpha_{23} N_2(k) N_3(k) \\ a_3 N_3(k) - \alpha_{33} N_3^2(k) + \alpha_{31} N_1(k) N_3(k) + \alpha_{32} N_2(k) N_3(k) \end{pmatrix}$$
(370)

where
$$N(k+1) = \begin{pmatrix} N_1(k+1) \\ N_2(k+1) \\ N_3(k+1) \end{pmatrix}$$
, $N(k) = \begin{pmatrix} N_1(k) \\ N_2(k) \\ N_3(k) \end{pmatrix}$ and $k = 0, 1, 2, \dots$

15.2 Method of Piecewise Constant Arguments

Along with the help of differential equations with piecewise constant arguments, we can find a discrete analogue of continuous time radio-dependent systems [6], [50]. Here, there is no unique way of determining discrete-time versions of dynamical systems corresponding to continuous time formulations. One method of deriving difference equations which model the dynamics of populations with non-overlapping generations is by using appropriate modifications of models with overlapping generations. This approach utilises the use of differential equations with piecewise constant arguments [6].

15.2.1 Application of the Method of Piecewise Constant Arguments

Consider the following continuous system of non-linear differential equations:

$$\frac{dN_1}{dt} = N_1'(t) = a_1 N_1 - \alpha_{11} N_1^2 - \alpha_{12} N_1 N_2 - \alpha_{13} N_1 N_3$$

$$\frac{dN_2}{dt} = N_2'(t) = a_2 N_2 - \alpha_{22} N_2^2 + \alpha_{21} N_1 N_2 + \alpha_{23} N_2 N_3$$

$$\frac{dN_3}{dt} = N_3'(t) = a_3 N_3 - \alpha_{33} N_3^2 + \alpha_{31} N_1 N_3 + \alpha_{32} N_2 N_3$$
(371)

Let us assume that the average growth rates of system (371) change at regular intervals of time. By incorporating this aspect, we obtain the following modified system [6]:

$$\frac{1}{N_{1}(t)} \frac{dN_{1}(t)}{dt} = a_{1}([t])N_{1}([t]) - \alpha_{11}([t])N_{1}^{2}([t]) - \alpha_{12}([t])N_{1}([t])N_{2}([t]) - \alpha_{13}([t])N_{1}([t])N_{3}([t])
\frac{1}{N_{2}(t)} \frac{dN_{2}(t)}{dt} = a_{2}([t])N_{2}([t]) - \alpha_{22}([t])N_{2}^{2}([t]) + \alpha_{21}([t])N_{1}([t])N_{2}([t]) + \alpha_{23}([t])N_{2}([t])N_{3}([t])
\frac{1}{N_{3}(t)} \frac{dN_{3}(t)}{dt} = a_{3}([t])N_{3}([t]) - \alpha_{33}([t])N_{3}^{2}([t]) + \alpha_{31}([t])N_{1}([t])N_{3}([t]) + \alpha_{32}([t])N_{2}([t])N_{3}([t])
(372)$$

for $t \neq 0, 1, 2, \ldots$, where [t] denotes the integer part of $t, t \in (0, +\infty)$.

Equations of type (372) are known as differential equations with piecewise constant arguments. These equations occupy a position midway between differential and difference equations. A solution of (372) is denoted by the function $N = (N_1, N_2, N_3)^T$ defined for $t \in [0, +\infty)$ and has the following properties:

- 1. N is continuous on the interval $[0, \infty)$.
- 2. The derivatives $\frac{dN_1(t)}{dt}$, $\frac{dN_2(t)}{dt}$ and $\frac{dN_3(t)}{dt}$ exist at each point $t \in [0, +\infty)$ with the possible exception of the points $t \in \{0, 1, 2, \ldots\}$, where left-sided derivatives exist.
- 3. The equations of system (372) are satisfied on each interval [k, k+1) where k = 0, 1, 2, ...

On any interval of the form [k, k+1) for k = 0, 1, 2, ..., we can integrate (372) and obtain the following system:

$$N_{1}(t) = N_{1}(k)e^{[a_{1}(k)N_{1}(k) - \alpha_{11}(k)N_{1}^{2}(k) - \alpha_{12}(k)N_{1}(k)N_{2}(k) - \alpha_{13}(k)N_{1}(k)N_{3}(k)](t-k)}$$

$$N_{2}(t) = N_{2}(k)e^{[a_{2}(k)N_{2}(k) - \alpha_{22}(k)N_{2}^{2}(k) + \alpha_{21}(k)N_{1}(k)N_{2}(k) + \alpha_{23}(k)N_{2}(k)N_{3}(k)](t-k)}$$

$$N_{3}(t) = N_{3}(k)e^{[a_{3}(k)N_{3}(k) - \alpha_{33}(k)N_{3}^{2}(k) + \alpha_{31}(k)N_{1}(k)N_{3}(k) + \alpha_{32}(k)N_{2}(k)N_{3}(k)](t-k)}$$
(373)

for $k \leq t \leq k+1$, where $k = 0, 1, 2, \dots$

By letting $t \to k + 1$, we get the following autonomous time-invariant discrete time analogue of the system (371):

$$N_{1}(k+1) = N_{1}(k)e^{a_{1}(k)N_{1}(k) - \alpha_{11}(k)N_{1}^{2}(k) - \alpha_{12}(k)N_{1}(k)N_{2}(k) - \alpha_{13}(k)N_{1}(k)N_{3}(k)}$$

$$N_{2}(k+1) = N_{2}(k)e^{a_{2}(k)N_{2}(k) - \alpha_{22}(k)N_{2}^{2}(k) + \alpha_{21}(k)N_{1}(k)N_{2}(k) + \alpha_{23}(k)N_{2}(k)N_{3}(k)}$$

$$N_{3}(k+1) = N_{3}(k)e^{a_{3}(k)N_{3}(k) - \alpha_{33}(k)N_{3}^{2}(k) + \alpha_{31}(k)N_{1}(k)N_{3}(k) + \alpha_{32}(k)N_{2}(k)N_{3}(k)}$$
(374)

for $k = 0, 1, 2, \dots$

16 Existence of Equilibrium Points

Here we find the equilibrium solutions of each discrete system of difference equations (370) and (374).

16.1 Discrete Form of System Using Euler's Method

Consider the following discrete non-linear autonomous time-invariant system of difference equations:

$$N(k+1) = N(k) + h \begin{pmatrix} a_1 N_1(k) - \alpha_{11} N_1^2(k) - \alpha_{12} N_1(k) N_2(k) - \alpha_{13} N_1(k) N_3(k) \\ a_2 N_2(k) - \alpha_{22} N_2^2(k) + \alpha_{21} N_1(k) N_2(k) + \alpha_{23} N_2(k) N_3(k) \\ a_3 N_3(k) - \alpha_{33} N_3^2(k) + \alpha_{31} N_1(k) N_3(k) + \alpha_{32} N_2(k) N_3(k) \end{pmatrix}$$
(375)
where $N(k) = \begin{pmatrix} N_1(k) \\ N_2(k) \\ N_3(k) \end{pmatrix}$.

Finding the equilibrium points of (375), we have the following cases:

Case 1

$$N_1(k) + h[a_1N_1(k) - \alpha_{11}N_1^2(k) - \alpha_{12}N_1(k)N_2(k) - \alpha_{13}N_1(k)N_3(k)] = 0$$
(376)

$$N_2(k) + h[a_2N_2(k) - \alpha_{22}N_2^2(k) + \alpha_{21}N_1(k)N_2(k) + \alpha_{23}N_2(k)N_3(k)] = 0$$
(377)

$$N_3(k) + h[a_3N_3(k) - \alpha_{33}N_3^2(k) + \alpha_{31}N_1(k)N_3(k) + \alpha_{32}N_2(k)N_3(k)] = 0$$
(378)

By using (377), we get:

$$N_{2}(k) + h[a_{2}N_{2}(k) - \alpha_{22}N_{2}^{2}(k) + \alpha_{21}N_{1}(k)N_{2}(k) + \alpha_{23}N_{2}(k)N_{3}(k)] = 0$$

$$N_{2}(k) + hN_{2}(k)[a_{2} - \alpha_{22}N_{2}(k) + \alpha_{21}N_{1}(k) + \alpha_{23}N_{3}(k)] = 0$$

$$(1+h)N_{2}(k)[a_{2} - \alpha_{22}N_{2}(k) + \alpha_{21}N_{1}(k) + \alpha_{23}N_{3}(k)] = 0$$
(379)

Therefore

 $(1+h)N_2(k) = 0 \Rightarrow N_2(k) = 0$ or $a_2 - \alpha_{22}N_2(k) + \alpha_{21}N_1(k) + \alpha_{23}N_3(k) = 0$ (380) By using (378), we get:

$$N_{3}(k) + h[a_{3}N_{3}(k) - \alpha_{33}N_{3}^{2}(k) + \alpha_{31}N_{1}(k)N_{3}(k) + \alpha_{32}N_{2}(k)N_{3}(k)] = 0$$

$$N_{3}(k) + hN_{3}(k)[a_{3} - \alpha_{33}N_{3}(k) + \alpha_{31}N_{1}(k) + \alpha_{32}N_{2}(k)] = 0$$

$$(1+h)N_{3}(k)[a_{3} - \alpha_{33}N_{3}(k) + \alpha_{31}N_{1}(k) + \alpha_{32}N_{2}(k)] = 0$$
(381)

Therefore

 $(1+h)N_3(k) = 0 \Rightarrow N_3(k) = 0$ or $a_3 - \alpha_{33}N_3(k) + \alpha_{31}N_1(k) + \alpha_{32}N_2(k) = 0$ (382) Substituting $N_2(k) = N_3(k) = 0$ in (376), we have:

$$a_1 N_1(k) - \alpha_{11} N_1^2(k) = 0$$

$$N_1(k)(a_1 - \alpha_{11} N_1(k)) = 0$$

$$N_1(k) = 0 \quad \text{or} \quad a_1 - \alpha_{11} N_1(k) = 0$$
(383)

Hence we have the following equilibrium point in the absence of all species:

 $(N_1(k), N_2(k), N_3(k)) = (0, 0, 0) = E_1(0, 0, 0)$

Therefore the population is extinct and this state always exists.

Case 2

In the absence of the second predator (S_3) we have $N_3(k) = 0$, hence system (375) becomes:

$$N_1(k+1) = N_1(k) + h[a_1N_1(k) - \alpha_{11}N_1^2(k) - \alpha_{12}N_1(k)N_2(k)]$$

$$N_2(k+1) = N_2(k) + h[a_2N_2(k) - \alpha_{22}N_2^2(k) + \alpha_{21}N_1(k)N_2(k)]$$
(384)

Finding the equilibrium points of (384), we have:

$$N_1(k) + h[a_1N_1(k) - \alpha_{11}N_1^2(k) - \alpha_{12}N_1(k)N_2(k)] = 0$$
(385)

$$N_2(k) + h[a_2N_2(k) - \alpha_{22}N_2^2(k) + \alpha_{21}N_1(k)N_2(k)] = 0$$
(386)

By using (385), we get:

(1 +

$$N_{1}(k) + h[a_{1}N_{1}(k) - \alpha_{11}N_{1}^{2}(k) - \alpha_{12}N_{1}(k)N_{2}(k)] = 0$$

$$N_{1}(k) + hN_{1}(k)[a_{1} - \alpha_{11}N_{1}(k) - \alpha_{12}N_{2}(k)] = 0$$

$$(1+h)N_{1}(k)[a_{1} - \alpha_{11}N_{1}(k) - \alpha_{12}N_{2}(k)] = 0$$
(387)

Therefore

$$(1+h)N_1(k) = 0 \Rightarrow N_1(k) = 0$$
 or $a_1 - \alpha_{11}N_1(k) - \alpha_{12}N_2(k) = 0$ (388)

Assuming a positive solution $\bar{N}_1(k)$ of $N_1(k)$, we have:

· .

$$a_1 - \alpha_{11} N_1(k) - \alpha_{12} N_2(k) = 0 \tag{389}$$

$$-\alpha_{11}N_1(k) = -a_1 + \alpha_{12}N_2(k) \tag{390}$$

$$\bar{N}_1(k) = N_1(k) = \frac{a_1 - \alpha_{12}N_2(k)}{\alpha_{11}}$$
(391)

Substituting (391) in (386) and assuming a positive solution $\bar{N}_2(k)$ of $N_2(k)$ yields:

$$N_{2}(k) + h[a_{2}N_{2}(k) - \alpha_{22}N_{2}^{2}(k) + \alpha_{21}N_{1}(k)N_{2}(k)] = 0$$

$$N_{2}(k) + hN_{2}(k)[a_{2} - \alpha_{22}N_{2}(k) + \alpha_{21}N_{1}(k)] = 0$$

$$(1+h)N_{2}(k)[a_{2} - \alpha_{22}N_{2}(k) + \alpha_{21}N_{1}(k)] = 0$$

$$h)N_{2}(k) = 0 \Rightarrow N_{2}(k) = 0 \quad \text{or} \quad a_{2} - \alpha_{22}N_{2}(k) + \alpha_{21}N_{1}(k) = 0$$

$$(392)$$

$$\therefore \quad a_2 - \alpha_{22} N_2(k) + \alpha_{21} N_1(k) = 0 \tag{393}$$

$$a_2 - \alpha_{22}N_2(k) + \alpha_{21}\left(\frac{a_1 - \alpha_{12}N_2(k)}{\alpha_{11}}\right) = 0$$
(394)

$$a_2 - \alpha_{22}N_2(k) + \frac{a_1\alpha_{21}}{\alpha_{11}} - \frac{\alpha_{12}\alpha_{21}}{\alpha_{11}}N_2(k) = 0$$
(395)

$$-\alpha_{22}N_2(k) - \frac{\alpha_{12}\alpha_{21}}{\alpha_{11}}N_2(k) = -a_2 - \frac{a_1\alpha_{21}}{\alpha_{11}}$$
(396)

$$\left(-\alpha_{22} - \frac{\alpha_{12}\alpha_{21}}{\alpha_{11}}\right)N_2(k) = \frac{-a_2\alpha_{11} - a_1\alpha_{21}}{\alpha_{11}}$$
(397)

$$\left(\frac{-\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}}{\alpha_{11}}\right)N_2(k) = \frac{-a_2\alpha_{11} - a_1\alpha_{21}}{\alpha_{11}}$$
(398)

$$\therefore \qquad \bar{N}_2(k) = N_2(k) = \frac{a_2\alpha_{11} + a_1\alpha_{21}}{\alpha_{11}\alpha_{22} + \alpha_{12}\alpha_{21}} \tag{399}$$

Substituting (399) in (391) yields:

$$\bar{N}_1(k) = N_1(k) = \frac{a_1 - \alpha_{12}N_2(k)}{\alpha_{11}}$$
(400)

$$=\frac{a_1 - \alpha_{12} \left(\frac{a_2 \alpha_{11} + a_1 \alpha_{21}}{\alpha_{11} \alpha_{22} + \alpha_{12} \alpha_{21}}\right)}{\alpha_{11}} \tag{401}$$

$$=\frac{a_1\alpha_{22} - a_2\alpha_{12}}{\alpha_{11}\alpha_{22} + \alpha_{12}\alpha_{21}} \tag{402}$$

Therefore, assuming $\bar{N}_1(k)$ and $\bar{N}_2(k)$ are positive solutions of $N_1(k)$ and $N_2(k)$, then

$$\bar{N}_1(k) = \frac{a_1 \alpha_{22} - a_2 \alpha_{12}}{\alpha_{11} \alpha_{22} + \alpha_{12} \alpha_{21}} \quad \text{and} \quad \bar{N}_2(k) = \frac{a_2 \alpha_{11} + a_1 \alpha_{21}}{\alpha_{11} \alpha_{22} + \alpha_{12} \alpha_{21}} \tag{403}$$

where $\bar{N}_1(k)$ is positive provided that $a_1\alpha_{22} > a_2\alpha_{12}$.

In conclusion, we have the following equilibrium point in the absence of the second predator (S_3) :

$$(N_1(k), N_2(k), N_3(k)) = (N_1(k), N_2(k), 0) = E_2(\bar{N}_1(k), \bar{N}_2(k), 0)$$

Case 3

In the absence of the first predator (S_2) , we have $N_2(k) = 0$, hence system (375) becomes:

$$N_{1}(k+1) = N_{1}(k) + h[a_{1}N_{1}(k) - \alpha_{11}N_{1}^{2}(k) - \alpha_{13}N_{1}(k)N_{3}(k)]$$

$$N_{3}(k+1) = N_{3}(k) + h[a_{3}N_{3}(k) - \alpha_{33}N_{3}^{2}(k) + \alpha_{31}N_{1}(k)N_{3}(k)]$$
(404)

Finding the equilibrium points of (404), we have:

$$N_1(k) + h[a_1N_1(k) - \alpha_{11}N_1^2(k) - \alpha_{13}N_1(k)N_3(k)] = 0$$
(405)

$$N_3(k) + h[a_3N_3(k) - \alpha_{33}N_3^2(k) + \alpha_{31}N_1(k)N_3(k)] = 0$$
(406)

By using (405), we get

$$N_{1}(k) + h[a_{1}N_{1}(k) - \alpha_{11}N_{1}^{2}(k) - \alpha_{13}N_{1}(k)N_{3}(k)] = 0$$

$$N_{1}(k) + hN_{1}(k)[a_{1} - \alpha_{11}N_{1}(k) - \alpha_{13}N_{3}(k)] = 0$$

$$(1 + h)N_{1}(k)[a_{1} - \alpha_{11}N_{1}(k) - \alpha_{13}N_{3}(k)] = 0$$

$$(1 + h)N_{1}(k) = 0 \quad \text{or} \quad a_{1} - \alpha_{11}N_{1}(k) - \alpha_{13}N_{3}(k) = 0$$

$$(407)$$

Assuming a positive solution $N_1^{\phi}(k)$ of $N_1(k)$, we have:

•

$$a_1 - \alpha_{11}N_1(k) - \alpha_{13}N_3(k) = 0 \tag{408}$$

$$-\alpha_{11}N_1(k) = -a_1 + \alpha_{13}N_3(k) \tag{409}$$

:
$$N_1^{\phi}(k) = N_1(k) = \frac{a_1 - \alpha_{13}N_3(k)}{\alpha_{11}}$$
 (410)

Substituting (410) in (406) and assuming a positive solution $N_3^{\phi}(k)$ of $N_3(k)$ yields:

$$N_{3}(k) + h[a_{3}N_{3}(k) - \alpha_{33}N_{3}^{2}(k) + \alpha_{31}N_{1}(k)N_{3}(k)] = 0$$

$$N_{3}(k) + hN_{3}(k)[a_{3} - \alpha_{33}N_{3}(k) + \alpha_{31}N_{1}(k)] = 0$$

$$(1 + h)N_{3}(k)[a_{3} - \alpha_{33}N_{3}(k) + \alpha_{31}N_{1}(k)] = 0$$

$$(1 + h)N_{3}(k) = 0 \quad \text{or} \quad a_{3} - \alpha_{33}N_{3}(k) + \alpha_{31}N_{1}(k) = 0$$

$$(411)$$

$$\therefore \quad a_3 - \alpha_{33} N_3(k) + \alpha_{31} N_1(k) = 0 \tag{412}$$

$$a_3 - \alpha_{33}N_3(k) + \alpha_{31}\left(\frac{a_1 - \alpha_{13}N_3(k)}{\alpha_{11}}\right) = 0$$
(413)

$$a_3 - \alpha_{33}N_3(k) + \frac{a_1\alpha_{31}}{\alpha_{11}} - \frac{\alpha_{13}\alpha_{31}}{\alpha_{11}}N_3(k) = 0$$
(414)

$$-\alpha_{33}N_3(k) - \frac{\alpha_{13}\alpha_{31}}{\alpha_{11}}N_3(k) = -a_3 - \frac{a_1\alpha_{31}}{\alpha_{11}}$$
(415)

$$\left(-\alpha_{33} - \frac{\alpha_{13}\alpha_{31}}{\alpha_{11}}\right)N_3(k) = -a_3 - \frac{a_1\alpha_{31}}{\alpha_{11}}$$
(416)

$$\left(\frac{-\alpha_{11}\alpha_{33} - \alpha_{13}\alpha_{31}}{\alpha_{11}}\right)N_3(k) = \frac{-a_3\alpha_{11} - a_1\alpha_{31}}{\alpha_{11}}$$
(417)

$$\therefore \qquad N_3^{\phi}(k) = N_3(k) = \frac{a_3\alpha_{11} + a_1\alpha_{31}}{\alpha_{11}\alpha_{33} + \alpha_{13}\alpha_{31}}$$
(418)

Substituting (418) in (410) yields:

$$N_1^{\phi}(k) = N_1(k) = \frac{a_1 - \alpha_{13}N_3(k)}{\alpha_{11}}$$
(419)

$$=\frac{a_{1}-\alpha_{13}\left(\frac{a_{3}\alpha_{11}+a_{1}\alpha_{31}}{\alpha_{11}\alpha_{33}+\alpha_{13}\alpha_{31}}\right)}{\alpha_{11}}$$
(420)

$$=\frac{a_1\alpha_{33}-a_3\alpha_{13}}{\alpha_{11}\alpha_{33}+\alpha_{13}\alpha_{31}} \tag{421}$$

Therefore, assuming $N_1^{\phi}(k)$ and $N_3^{\phi}(k)$ are positive solutions of $N_1(k)$ and $N_3(k)$, then

$$N_1^{\phi}(k) = \frac{a_1 \alpha_{33} - a_3 \alpha_{13}}{\alpha_{11} \alpha_{33} + \alpha_{13} \alpha_{31}} \quad \text{and} \quad N_3^{\phi}(k) = \frac{a_3 \alpha_{11} + a_1 \alpha_{31}}{\alpha_{11} \alpha_{33} + \alpha_{13} \alpha_{31}}$$
(422)

where $N_1^{\phi}(k)$ is positive provided that $a_1\alpha_{33} > a_3\alpha_{13}$.

In conclusion, we have the following equilibrium point in the absence of the first predator (S_2) :

$$(N_1(k), N_2(k), N_3(k)) = (N_1(k), 0, N_3(k)) = E_3(N_1^{\phi}(k), 0, N_3^{\phi}(k))$$

Case 4

The interior equilibrium can be calculated, using system (375), by the following:

$$N_1(k) + h[a_1N_1(k) - \alpha_{11}N_1^2(k) - \alpha_{12}N_1(k)N_2(k) - \alpha_{13}N_1(k)N_3(k)] = 0$$
(423)

$$N_2(k) + h[a_2N_2(k) - \alpha_{22}N_2^2(k) + \alpha_{21}N_1(k)N_2(k) + \alpha_{23}N_2(k)N_3(k)] = 0$$
(424)

$$N_3(k) + h[a_3N_3(k) - \alpha_{33}N_3^2(k) + \alpha_{31}N_1(k)N_3(k) + \alpha_{32}N_2(k)N_3(k)] = 0$$
(425)

By using (423), we get:

$$N_{1}(k) + h[a_{1}N_{1}(k) - \alpha_{11}N_{1}^{2}(k) - \alpha_{12}N_{1}(k)N_{2}(k) - \alpha_{13}N_{1}(k)N_{3}(k)] = 0$$

$$N_{1}(k) + hN_{1}(k)[a_{1} - \alpha_{11}N_{1}(k) - \alpha_{12}N_{2}(k) - \alpha_{13}N_{3}(k)] = 0$$

$$(1+h)N_{1}(k)[a_{1} - \alpha_{11}N_{1}(k) - \alpha_{12}N_{2}(k) - \alpha_{13}N_{3}(k)] = 0$$

$$(426)$$

Therefore

$$(1+h)N_1(k) = 0 \Rightarrow N_1(k) = 0$$
 or $a_1 - \alpha_{11}N_1(k) - \alpha_{12}N_2(k) - \alpha_{13}N_3(k) = 0$ (427)

Assuming a positive solution N_1^* of N_1 , we have:

(1

...

$$a_1 - \alpha_{11}N_1(k) - \alpha_{12}N_2(k) - \alpha_{13}N_3(k) = 0$$
(428)

$$-\alpha_{11}N_1(k) = -a_1 + \alpha_{12}N_2(k) + \alpha_{13}N_3(k)$$
(429)

$$\bar{N}_1(k) = N_1(k) = \frac{a_1 - \alpha_{12}N_2(k) - \alpha_{13}N_3(k)}{\alpha_{11}}$$
(430)

Substituting (430) in (424) and assuming a positive solution N_2^* of N_2 yields:

· .

$$N_{2}(k) + h[a_{2}N_{2}(k) - \alpha_{22}N_{2}^{2}(k) + \alpha_{21}N_{1}(k)N_{2}(k) + \alpha_{23}N_{2}(k)N_{3}(k)] = 0$$

$$N_{2}(k) + hN_{2}(k)[a_{2} - \alpha_{22}N_{2}(k) + \alpha_{21}N_{1}(k) + \alpha_{23}N_{3}(k)] = 0$$

$$(1+h)N_{2}(k)[a_{2} - \alpha_{22}N_{2}(k) + \alpha_{21}N_{1}(k) + \alpha_{23}N_{3}(k)] = 0$$

$$(1+h)N_{2}(k) = 0 \Rightarrow N_{2}(k) = 0 \quad \text{or} \quad a_{2} - \alpha_{22}N_{2}(k) + \alpha_{21}N_{1}(k) + \alpha_{23}N_{3}(k) = 0$$

$$(431)$$

$$a_2 - \alpha_{22}N_2(k) + \alpha_{21}N_1(k) + \alpha_{23}N_3(k) = 0$$
(432)

$$a_2 - \alpha_{22}N_2(k) + \alpha_{21}\left(\frac{a_1 - \alpha_{12}N_2(k) - \alpha_{13}N_3(k)}{\alpha_{11}}\right) + \alpha_{23}N_3(k) = 0$$
(433)

$$a_2 - \alpha_{22}N_2(k) + \frac{a_1\alpha_{21}}{\alpha_{11}} - \frac{\alpha_{12}\alpha_{21}}{\alpha_{11}}N_2(k) - \frac{\alpha_{13}\alpha_{21}}{\alpha_{11}}N_3(k) + \alpha_{23}N_3(k) = 0$$
(434)

$$-\alpha_{22}N_2(k) - \frac{\alpha_{12}\alpha_{21}}{\alpha_{11}}N_2(k) = -a_2 - \frac{a_1\alpha_{21}}{\alpha_{11}} + \frac{\alpha_{13}\alpha_{21}}{\alpha_{11}}N_3(k) + \alpha_{23}N_3(k)$$
(435)

$$\left(-\alpha_{22} - \frac{\alpha_{12}\alpha_{21}}{\alpha_{11}}\right)N_2(k) = \frac{-a_2\alpha_{11} - a_1\alpha_{21}}{\alpha_{11}} + \left(\alpha_{23} + \frac{\alpha_{13}\alpha_{21}}{\alpha_{11}}\right)N_3(k)$$
(436)

$$\left(\frac{-\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}}{\alpha_{11}}\right)N_2(k) = -\frac{a_2\alpha_{11} - a_1\alpha_{21}}{\alpha_{11}} + \left(\frac{\alpha_{11}\alpha_{23} + \alpha_{13}\alpha_{21}}{\alpha_{11}}\right)N_3(k)$$
(437)

$$\therefore \qquad N_2^*(k) = N_2(k) = \frac{a_2\alpha_{11}a_1\alpha_{21}}{\alpha_{11}\alpha_{22} + \alpha_{12}\alpha_{21}} + \left(\frac{\alpha_{11}\alpha_{23} + \alpha_{13}\alpha_{21}}{-\alpha_{22}\alpha_{11} - \alpha_{12}\alpha_{21}}\right)N_3(k) \tag{438}$$

Substituting (438) and (430) in (425) and assuming a positive solution $N_3^*(k)$ of $N_3(k)$ yields:

$$N_{3}(k) + h[a_{3}N_{3}(k) - \alpha_{33}N_{3}^{2}(k) + \alpha_{31}N_{1}(k)N_{3}(k) + \alpha_{32}N_{2}(k)N_{3}(k)] = 0$$

$$N_{3}(k) + hN_{3}(k)[a_{3} - \alpha_{33}N_{3}(k) + \alpha_{31}N_{1}(k) + \alpha_{32}N_{2}(k)] = 0$$

$$(1 + h)N_{3}(k)[a_{3} - \alpha_{33}N_{3}(k) + \alpha_{31}N_{1}(k) + \alpha_{32}N_{2}(k)] = 0$$

$$+ h)N_{3}(k) = 0 \Rightarrow N_{3}(k) = 0 \quad \text{or} \quad a_{3} - \alpha_{33}N_{3}(k) + \alpha_{31}N_{1}(k) + \alpha_{32}N_{2}(k) = 0$$
(439)

$$a_{3} - \alpha_{33}N_{3}(k) + \alpha_{31}\left(\frac{a_{1} - \alpha_{12}N_{2}(k) - \alpha_{13}N_{3}(k)}{a_{11}}\right) + \alpha_{32}\left(\frac{a_{2}\alpha_{11}a_{1}\alpha_{21}}{\alpha_{11}\alpha_{22} + \alpha_{12}\alpha_{21}} + \left(\frac{\alpha_{11}\alpha_{23} + \alpha_{13}\alpha_{21}}{-\alpha_{22}\alpha_{11} - \alpha_{12}\alpha_{21}}\right)N_{3}(k)\right) = 0 \quad (440)$$

$$a_{3} - \alpha_{33}N_{3}(k) + \alpha_{31} \left(\frac{a_{1} - \alpha_{12} \left(\frac{a_{2}\alpha_{11}a_{1}\alpha_{21}}{\alpha_{11}\alpha_{22} + \alpha_{12}\alpha_{21}} + \left(\frac{\alpha_{11}\alpha_{23} + \alpha_{13}\alpha_{21}}{-\alpha_{22}\alpha_{11} - \alpha_{12}\alpha_{21}} \right) N_{3}(k) \right) - \alpha_{13}N_{3}(k)}{\alpha_{11}} \right) + \alpha_{32} \left(\frac{a_{2}\alpha_{11}a_{1}\alpha_{21}}{\alpha_{11}\alpha_{22} + \alpha_{12}\alpha_{21}} + \left(\frac{\alpha_{11}\alpha_{23} + \alpha_{13}\alpha_{21}}{-\alpha_{22}\alpha_{11} - \alpha_{12}\alpha_{21}} \right) N_{3}(k) \right) = 0 \quad (441)$$

$$\therefore N_3^*(k) = N_3(k) = \frac{a_1(\alpha_{21}\alpha_{32} + \alpha_{22}\alpha_{31}) + a_2(\alpha_{11}\alpha_{32} - \alpha_{12}\alpha_{31}) + \alpha_3(\alpha_{11}\alpha_{22} + \alpha_{12}\alpha_{21})}{\alpha_{11}(\alpha_{22}\alpha_{33} - \alpha_{23}\alpha_{32}) + \alpha_{12}(\alpha_{21}\alpha_{33} + \alpha_{31}\alpha_{23}) + \alpha_{13}(\alpha_{31}\alpha_{32} + \alpha_{31}\alpha_{22})}$$
(442)

Substituting (442) in (438) yields:

$$N_{2}^{*}(k) = N_{2}(k) = \frac{a_{1}(\alpha_{21}\alpha_{33} + \alpha_{31}\alpha_{23}) + a_{2}(\alpha_{11}\alpha_{33} + \alpha_{13}\alpha_{31}) + a_{3}(\alpha_{11}\alpha_{23} - \alpha_{13}\alpha_{21})}{\alpha_{11}(\alpha_{22}\alpha_{33} - \alpha_{23}\alpha_{32}) + \alpha_{12}(\alpha_{21}\alpha_{33} + \alpha_{31}\alpha_{23}) + \alpha_{13}(\alpha_{31}\alpha_{32} + \alpha_{31}\alpha_{22})}$$
(443)

Substituting (442) and (443) in (430) yields:

$$N_{1}^{*}(k) = N_{1}(k) = \frac{a_{1}(\alpha_{22}\alpha_{33} - \alpha_{23}\alpha_{32}) - a_{2}(\alpha_{12}\alpha_{33} + \alpha_{13}\alpha_{32}) - a_{3}(\alpha_{12}\alpha_{23} + \alpha_{13}\alpha_{22})}{\alpha_{11}(\alpha_{22}\alpha_{33} - \alpha_{23}\alpha_{32}) + \alpha_{12}(\alpha_{21}\alpha_{33} + \alpha_{31}\alpha_{23}) + \alpha_{13}(\alpha_{31}\alpha_{32} + \alpha_{31}\alpha_{22})}$$
(444)

Therefore

$$N_1^*(k) = \frac{\rho_1}{D} \qquad N_2^*(k) = \frac{\rho_2}{D} \qquad N_3^*(k) = \frac{\rho_3}{D}$$
 (445)

where

$$\rho_1 = a_1(\alpha_{22}\alpha_{33} - \alpha_{23}\alpha_{32}) - a_2(\alpha_{12}\alpha_{33} + \alpha_{13}\alpha_{32}) - a_3(\alpha_{12}\alpha_{23} + \alpha_{13}\alpha_{22})$$
(446)

$$\rho_2 = a_1(\alpha_{21}\alpha_{33} + \alpha_{31}\alpha_{23}) + a_2(\alpha_{11}\alpha_{33} + \alpha_{13}\alpha_{31}) + a_3(\alpha_{11}\alpha_{23} - \alpha_{13}\alpha_{21}) \tag{447}$$

$$\rho_3 = a_1(\alpha_{21}\alpha_{33} + \alpha_{31}\alpha_{23}) + a_2(\alpha_{11}\alpha_{33} + \alpha_{13}\alpha_{31}) + a_3(\alpha_{11}\alpha_{23} - \alpha_{13}\alpha_{21})$$
(448)

$$D = \alpha_{11}(\alpha_{22}\alpha_{33} - \alpha_{23}\alpha_{32}) + \alpha_{12}(\alpha_{21}\alpha_{33} + \alpha_{31}\alpha_{23}) + \alpha_{13}(\alpha_{31}\alpha_{32} + \alpha_{31}\alpha_{22})$$
(449)

provided that the following expressions hold:

$$[a_{2}(\alpha_{12}\alpha_{33} + \alpha_{13}\alpha_{32}) + a_{3}(\alpha_{12}\alpha_{23} + \alpha_{13}\alpha_{22})] < a_{1}(\alpha_{22}\alpha_{33} - \alpha_{23}\alpha_{32})$$
$$\alpha_{11}\alpha_{23} > \alpha_{13}\alpha_{21}$$
$$\alpha_{11}\alpha_{32} > \alpha_{12}\alpha_{31}$$
$$\alpha_{22}\alpha_{33} > \alpha_{23}\alpha_{32}$$

In conclusion, we have the following equilibrium point for the interior equilibrium:

$$(N_1(k), N_2(k), N_3(k)) = E_4(N_1^*(k), N_2^*(k), N_3^*(k))$$

16.2 Discrete Form of System Using Method of Piecewise Constant Arguments

Consider the following discrete non-linear autonomous time-invariant system of difference equations: $N_{-}(l_{-}+1) = N_{-}(l_{-}) - a_{1}(k)N_{1}(k) - a_{11}(k)N_{2}^{2}(k) - a_{12}(k)N_{1}(k)N_{2}(k) - a_{13}(k)N_{1}(k)N_{3}(k)$

$$N_{1}(k+1) = N_{1}(k)e^{a_{1}(k)N_{1}(k)-a_{11}(k)N_{1}(k)-a_{12}(k)N_{1}(k)N_{2}(k)-a_{13}(k)N_{1}(k)N_{3}(k)}$$

$$N_{2}(k+1) = N_{2}(k)e^{a_{2}(k)N_{2}(k)-\alpha_{22}(k)N_{2}^{2}(k)+\alpha_{21}(k)N_{1}(k)N_{2}(k)+\alpha_{23}(k)N_{2}(k)N_{3}(k)}$$

$$N_{3}(k+1) = N_{3}(k)e^{a_{3}(k)N_{3}(k)-\alpha_{33}(k)N_{3}^{2}(k)+\alpha_{31}(k)N_{1}(k)N_{3}(k)+\alpha_{32}(k)N_{2}(k)N_{3}(k)}$$
(450)

Finding the equilibrium points of (450), we have the following cases:

Case 1

$$N_1(k)e^{a_1(k)N_1(k)-\alpha_{11}(k)N_1^2(k)-\alpha_{12}(k)N_1(k)N_2(k)-\alpha_{13}(k)N_1(k)N_3(k)} = 0$$
(451)

$$N_2(k)e^{a_2(k)N_2(k) - \alpha_{22}(k)N_2^2(k) + \alpha_{21}(k)N_1(k)N_2(k) + \alpha_{23}(k)N_2(k)N_3(k)} = 0$$
(452)

$$N_3(k)e^{a_3(k)N_3(k)-\alpha_{33}(k)N_3^2(k)+\alpha_{31}(k)N_1(k)N_3(k)+\alpha_{32}(k)N_2(k)N_3(k)} = 0$$
(453)

By using (452), we get:

$$N_2(k)e^{a_2(k)N_2(k)-\alpha_{22}(k)N_2^2(k)+\alpha_{21}(k)N_1(k)N_2(k)+\alpha_{23}(k)N_2(k)N_3(k)} = 0$$
(454)

Therefore

$$N_2(k) = 0 \qquad \text{or} \qquad e^{a_2(k)N_2(k) - \alpha_{22}(k)N_2^2(k) + \alpha_{21}(k)N_1(k)N_2(k) + \alpha_{23}(k)N_2(k)N_3(k)} = 0 \tag{455}$$

By using (453), we get:

$$N_3(k)e^{a_3(k)N_3(k)-\alpha_{33}(k)N_3^2(k)+\alpha_{31}(k)N_1(k)N_3(k)+\alpha_{32}(k)N_2(k)N_3(k)} = 0$$
(456)

Therefore

$$N_3(k) = 0 \qquad \text{or} \qquad e^{a_3(k)N_3(k) - \alpha_{33}(k)N_3^2(k) + \alpha_{31}(k)N_1(k)N_3(k) + \alpha_{32}(k)N_2(k)N_3(k)} = 0 \tag{457}$$

Substituting $N_2(k) = N_3(k) = 0$ in (451), we have:

$$N_1(k)e^{a_1(k)N_1(k)-\alpha_{11}(k)N_1^2(k)} = 0$$

$$N_1(k) = 0 \quad \text{or} \quad e^{a_1(k)N_1(k)-\alpha_{11}(k)N_1^2(k)} = 0$$
(458)

Hence we have the following equilibrium point in the absence of all species:

$$(N_1(k), N_2(k), N_3(k)) = (0, 0, 0) = E_1(0, 0, 0)$$

Therefore the population is extinct and this state always exists.

Case 2

In the absence of the second predator (S_3) we have $N_3(k) = 0$, hence system (450) becomes:

$$N_{1}(k+1) = N_{1}(k)e^{a_{1}(k)N_{1}(k) - \alpha_{11}(k)N_{1}^{2}(k) - \alpha_{12}(k)N_{1}(k)N_{2}(k)}$$

$$N_{2}(k+1) = N_{2}(k)e^{a_{2}(k)N_{2}(k) - \alpha_{22}(k)N_{2}^{2}(k) + \alpha_{21}(k)N_{1}(k)N_{2}(k)}$$
(459)

Finding the equilibrium points of (459), we have:

$$N_1(k)e^{a_1(k)N_1(k) - \alpha_{11}(k)N_1^2(k) - \alpha_{12}(k)N_1(k)N_2(k)} = 0$$
(460)

$$N_2(k)e^{a_2(k)N_2(k) - \alpha_{22}(k)N_2^2(k) + \alpha_{21}(k)N_1(k)N_2(k)} = 0$$
(461)

By using (460), we get:

$$N_1(k)e^{a_1(k)N_1(k) - \alpha_{11}(k)N_1^2(k) - \alpha_{12}(k)N_1(k)N_2(k)} = 0$$
(462)

Therefore

$$N_1(k) = 0$$
 or $e^{a_1(k)N_1(k) - \alpha_{11}(k)N_1^2(k) - \alpha_{12}(k)N_1(k)N_2(k)} = 0$ (463)

Assuming a positive solution $\bar{N}_1(k)$ of $N_1(k)$, we have:

$$e^{a_1(k)N_1(k) - \alpha_{11}(k)N_1^2(k) - \alpha_{12}(k)N_1(k)N_2(k)} = 0$$
(464)

$$a_1(k)N_1(k) - \alpha_{11}(k)N_1^2(k) - \alpha_{12}(k)N_1(k)N_2(k) = 0$$
(465)

$$N_1(k)[a_1(k) - \alpha_{11}(k)N_1(k) - \alpha_{12}N_2(k)] = 0$$
(466)

$$a_1(k) - \alpha_{11}(k)N_1(k) - \alpha_{12}N_2(k) = 0$$
(467)

$$-\alpha_{11}(k)N_1(k) = -a_1(k) + \alpha_{12}N_2(k)$$
(468)

$$\therefore \qquad \bar{N}_1(k) = N_1(k) = \frac{a_1(k) - \alpha_{12}(k)N_2(k)}{\alpha_{11}(k)} \tag{469}$$

Substituting (469) in (462) and assuming a positive solution $\bar{N}_2(k)$ of $N_2(k)$ yields:

$$N_2(k)e^{a_2(k)N_2(k) - \alpha_{22}(k)N_2^2(k) + \alpha_{21}(k)N_1(k)N_2(k)} = 0$$
(470)

Therefore

$$N_{2}(k) = 0 \qquad \text{or} \qquad e^{a_{2}(k)N_{2}(k) - \alpha_{22}(k)N_{2}^{2}(k) + \alpha_{21}(k)N_{1}(k)N_{2}(k)} = 0 \qquad (471)$$
$$e^{a_{2}(k)N_{2}(k) - \alpha_{22}(k)N_{2}^{2}(k) + \alpha_{21}(k)N_{1}(k)N_{2}(k)} = 0$$

$$a_{2}(k)N_{2}(k) - \alpha_{22}(k)N_{2}^{2}(k) + \alpha_{21}(k)N_{1}(k)N_{2}(k) = 0$$

$$N_{2}(k)[a_{2}(k) - \alpha_{22}(k)N_{2}(k) + \alpha_{21}(k)N_{1}(k)] = 0$$
(472)

$$a_2(k) - \alpha_{22}(k)N_2(k) + \alpha_{21}(k)N_1(k) = 0$$

$$\therefore \quad a_2(k) - \alpha_{22}(k)N_2(k) + \alpha_{21}(k)N_1(k) = 0 \tag{473}$$

$$a_2(k) - \alpha_{22}(k)N_2(k) + \alpha_{21}(k) \left(\frac{a_1(k) - \alpha_{12}(k)N_2(k)}{\alpha_{11}(k)}\right) = 0$$
(474)

$$a_2(k) - \alpha_{22}(k)N_2(k) + \frac{a_1(k)\alpha_{21}(k)}{\alpha_{11}(k)} - \frac{\alpha_{12}(k)\alpha_{21}(k)}{\alpha_{11}(k)}N_2(k) = 0$$
(475)

$$-\alpha_{22}(k)N_2(k) - \frac{\alpha_{12}(k)\alpha_{21}(k)}{\alpha_{11}(k)}N_2(k) = -a_2(k) - \frac{a_1(k)\alpha_{21}(k)}{\alpha_{11}(k)}$$
(476)

$$\left(-\alpha_{22}(k) - \frac{\alpha_{12}(k)\alpha_{21}(k)}{\alpha_{11}(k)}\right)N_2(k) = \frac{-a_2(k)\alpha_{11}(k) - a_1(k)\alpha_{21}(k)}{\alpha_{11}(k)}$$
(477)

$$\left(\frac{-\alpha_{11}(k)\alpha_{22}(k) - \alpha_{12}(k)\alpha_{21}(k)}{\alpha_{11}(k)}\right)N_2(k) = \frac{-a_2(k)\alpha_{11}(k) - a_1(k)\alpha_{21}(k)}{\alpha_{11}(k)}$$
(478)

$$\therefore \qquad \bar{N}_2(k) = N_2(k) = \frac{a_2(k)\alpha_{11}(k) + a_1(k)\alpha_{21}(k)}{\alpha_{11}(k)\alpha_{22}(k) + \alpha_{12}(k)\alpha_{21}(k)}$$
(479)

Substituting (479) in (469) yields:

$$\bar{N}_1(k) = N_1(k) = \frac{a_1(k) - \alpha_{12}(k)N_2(k)}{\alpha_{11}(k)}$$
(480)

$$=\frac{a_1(k) - \alpha_{12}(k) \left(\frac{a_2(k)\alpha_{11}(k) + a_1(k)\alpha_{21}(k)}{\alpha_{11}(k)\alpha_{22}(k) + \alpha_{12}(k)\alpha_{21}(k)}\right)}{\alpha_{11}(k)}$$
(481)

$$= \frac{a_1(k)\alpha_{22}(k) - a_2(k)\alpha_{12}(k)}{\alpha_{11}(k)\alpha_{22}(k) + \alpha_{12}(k)\alpha_{21}(k)}$$
(482)

Therefore, assuming $\bar{N}_1(k)$ and $\bar{N}_2(k)$ are positive solutions of $N_1(k)$ and $N_2(k)$, then

$$\bar{N}_{1}(k) = \frac{a_{1}(k)\alpha_{22}(k) - a_{2}(k)\alpha_{12}(k)}{\alpha_{11}(k)\alpha_{22}(k) + \alpha_{12}(k)\alpha_{21}(k)} \quad \text{and} \quad \bar{N}_{2}(k) = \frac{a_{2}(k)\alpha_{11}(k) + a_{1}(k)\alpha_{21}(k)}{\alpha_{11}(k)\alpha_{22}(k) + \alpha_{12}(k)\alpha_{21}(k)}$$

$$(483)$$

where $\bar{N}_1(k)$ is positive provided that $a_1(k)\alpha_{22}(k) > a_2(k)\alpha_{12}(k)$.

In conclusion, we have the following equilibrium point in the absence of the second predator (S_3) :

$$(N_1(k), N_2(k), N_3(k)) = (N_1(k), N_2(k), 0) = E_2(\bar{N}_1(k), \bar{N}_2(k), 0)$$

Case 3

In the absence of the first predator (S_2) , we have $N_2(k) = 0$, hence system (450) becomes:

$$N_{1}(k+1) = N_{1}(k)e^{a_{1}(k)N_{1}(k) - \alpha_{11}(k)N_{1}^{2}(k) - \alpha_{13}(k)N_{1}(k)N_{3}(k)}$$

$$N_{3}(k+1) = N_{3}(k)e^{a_{3}(k)N_{3}(k) - \alpha_{33}(k)N_{3}^{2}(k) + \alpha_{31}(k)N_{1}(k)N_{3}(k)}$$
(484)

Finding the equilibrium points of (484), we have:

$$N_1(k)e^{a_1(k)N_1(k) - \alpha_{11}(k)N_1^2(k) - \alpha_{13}(k)N_1(k)N_3(k)} = 0$$
(485)

$$N_3(k)e^{a_3(k)N_3(k)-\alpha_{33}(k)N_3^2(k)+\alpha_{31}(k)N_1(k)N_3(k)} = 0$$
(486)

By using (485), we get

$$N_1(k)e^{a_1(k)N_1(k) - \alpha_{11}(k)N_1^2(k) - \alpha_{13}(k)N_1(k)N_3(k)} = 0$$
(487)

Therefore

$$N_1(k) = 0 \qquad \text{or} \qquad e^{a_1(k)N_1(k) - \alpha_{11}(k)N_1^2(k) - \alpha_{13}(k)N_1(k)N_3(k)} = 0 \tag{488}$$

Assuming a positive solution $N_1^{\phi}(k)$ of $N_1(k)$, we have:

$$e^{a_1(k)N_1(k) - \alpha_{11}(k)N_1^2(k) - \alpha_{13}(k)N_1(k)N_3(k)} = 0$$
(489)

$$a_1(k)N_1(k) - \alpha_{11}(k)N_1^2(k) - \alpha_{13}(k)N_1(k)N_3(k) = 0$$
(490)

$$N_1(k)[a_1(k) - \alpha_{11}(k)N_1(k) - \alpha_{13}(k)N_3(k)] = 0$$
(491)

$$a_1(k) - \alpha_{11}(k)N_1(k) - \alpha_{13}(k)N_3(k) = 0$$
(492)

$$-\alpha_{11}N_1(k) = -a_1(k) + \alpha_{13}(k)N_3(k)$$
(493)

$$\therefore \qquad N_1^{\phi}(k) = N_1(k) = \frac{a_1(k) - \alpha_{13}(k)N_3(k)}{\alpha_{11}(k)} \tag{494}$$

Substituting (494) in (486) and assuming a positive solution $N_3^{\phi}(k)$ of $N_3(k)$ yields:

$$N_3(k)e^{a_3(k)N_3(k)-\alpha_{33}(k)N_3^2(k)+\alpha_{31}(k)N_1(k)N_3(k)} = 0$$
(495)

Therefore

. .

$$N_{3}(k) = 0 \qquad \text{or} \qquad e^{a_{3}(k)N_{3}(k) - \alpha_{33}(k)N_{3}^{2}(k) + \alpha_{31}(k)N_{1}(k)N_{3}(k)} = 0 \tag{496}$$

$$e^{a_3(k)N_3(k) - \alpha_{33}(k)N_3^2(k) + \alpha_{31}(k)N_1(k)N_3(k)} = 0$$
(497)

$$a_{3}(k)N_{3}(k) - \alpha_{33}(k)N_{3}^{2}(k) + \alpha_{31}(k)N_{1}(k)N_{3}(k) = 0$$

$$N_{3}(k)[a_{3}(k) - \alpha_{33}(k)N_{3}(k) + \alpha_{31}(k)N_{1}(k)] = 0$$
(498)
(499)

$$N_{3}(k)[a_{3}(k) - \alpha_{33}(k)N_{3}(k) + \alpha_{31}(k)N_{1}(k)] = 0$$

$$a_{3}(k) - \alpha_{33}(k)N_{3}(k) + \alpha_{31}(k)N_{1}(k) = 0$$
(499)
(500)

$$a_{3}(k) - \alpha_{33}(k)N_{3}(k) + \alpha_{31}(k)\left(\frac{a_{1}(k) - \alpha_{13}(k)N_{3}(k)}{\alpha_{11}(k)}\right) = 0$$
(501)

$$a_{3}(k) - \alpha_{33}(k)N_{3}(k) + \frac{a_{1}(k)\alpha_{31}(k)}{\alpha_{11}(k)} - \frac{\alpha_{13}(k)\alpha_{31}(k)}{\alpha_{11}(k)}N_{3}(k) = 0$$
(502)

$$-\alpha_{33}(k)N_3(k) - \frac{\alpha_{13}(k)\alpha_{31}(k)}{\alpha_{11}(k)}N_3(k) = -a_3(k) - \frac{a_1(k)\alpha_{31}(k)}{\alpha_{11}(k)}$$
(503)

$$\left(-\alpha_{33}(k) - \frac{\alpha_{13}(k)\alpha_{31}(k)}{\alpha_{11}(k)}\right)N_3(k) = -a_3(k) - \frac{a_1(k)\alpha_{31}(k)}{\alpha_{11}(k)}$$

$$\frac{-\alpha_{11}(k)\alpha_{33}(k) - \alpha_{13}(k)\alpha_{31}(k)}{\alpha_{11}(k)}\right)N_3(k) = \frac{-a_3(k)\alpha_{11}(k) - a_1(k)\alpha_{31}(k)}{\alpha_{11}(k)}$$
(504)

$$\therefore \qquad N_3^{\phi}(k) = N_3(k) = \frac{a_3(k)\alpha_{11}(k) + a_1(k)\alpha_{31}(k)}{\alpha_{11}(k)\alpha_{33}(k) + \alpha_{13}(k)\alpha_{31}(k)}$$
(506)

Substituting (506) in (494) yields:

$$N_1^{\phi}(k) = N_1(k) = \frac{a_1(k) - \alpha_{13}(k)N_3(k)}{\alpha_{11}(k)}$$
(507)

$$=\frac{a_{1}(k) - \alpha_{13}(k) \left(\frac{a_{3}(k)\alpha_{11}(k) + a_{1}(k)\alpha_{31}(k)}{\alpha_{11}(k)\alpha_{33}(k) + \alpha_{13}(k)\alpha_{31}(k)}\right)}{\alpha_{11}(k)}$$
(508)

$$=\frac{a_1(k)\alpha_{33}(k) - a_3(k)\alpha_{13}(k)}{\alpha_{11}(k)\alpha_{33}(k) + \alpha_{13}(k)\alpha_{31}(k)}$$
(509)

Therefore, assuming $N_1^{\phi}(k)$ and $N_3^{\phi}(k)$ are positive solutions of $N_1(k)$ and $N_3(k)$, then

$$N_{1}^{\phi}(k) = \frac{a_{1}(k)\alpha_{33}(k) - a_{3}(k)\alpha_{13}(k)}{\alpha_{11}(k)\alpha_{33}(k) + \alpha_{13}(k)\alpha_{31}(k)} \quad \text{and} \quad N_{3}^{\phi}(k) = \frac{a_{3}(k)\alpha_{11}(k) + a_{1}(k)\alpha_{31}(k)}{\alpha_{11}(k)\alpha_{33}(k) + \alpha_{13}(k)\alpha_{31}(k)}$$
(510)

where $N_1^{\phi}(k)$ is positive provided that $a_1(k)\alpha_{33}(k) > a_3(k)\alpha_{13}(k)$.

In conclusion, we have the following equilibrium point in the absence of the first predator (S_2) :

$$(N_1(k), N_2(k), N_3(k)) = (N_1(k), 0, N_3(k)) = E_3(N_1^{\phi}(k), 0, N_3^{\phi}(k))$$

Case 4

The interior equilibrium can be calculated, using the system (450), by the following:

$$N_1(k)e^{a_1(k)N_1(k)-\alpha_{11}(k)N_1^2(k)-\alpha_{12}(k)N_1(k)N_2(k)-\alpha_{13}(k)N_1(k)N_3(k)} = 0$$
(511)

$$N_2(k)e^{a_2(k)N_2(k) - \alpha_{22}(k)N_2^2(k) + \alpha_{21}(k)N_1(k)N_2(k) + \alpha_{23}(k)N_2(k)N_3(k)} = 0$$
(512)

$$N_3(k)e^{a_3(k)N_3(k)-\alpha_{33}(k)N_3^2(k)+\alpha_{31}(k)N_1(k)N_3(k)+\alpha_{32}(k)N_2(k)N_3(k)} = 0$$
(513)

By using (511), we get:

$$N_1(k)e^{a_1(k)N_1(k) - \alpha_{11}(k)N_1^2(k) - \alpha_{12}(k)N_1(k)N_2(k) - \alpha_{13}(k)N_1(k)N_3(k)} = 0$$
(514)

Therefore

$$N_1(k) = 0 \qquad \text{or} \qquad e^{a_1(k)N_1(k) - \alpha_{11}(k)N_1^2(k) - \alpha_{12}(k)N_1(k)N_2(k) - \alpha_{13}(k)N_1(k)N_3(k))} = 0 \tag{515}$$

Assuming a positive solution N_1^* of N_1 , we have:

$$e^{a_1(k)N_1(k) - \alpha_{11}(k)N_1^2(k) - \alpha_{12}(k)N_1(k)N_2(k) - \alpha_{13}(k)N_1(k)N_3(k)} = 0$$
 (516)

$$a_1(k)N_1(k) - \alpha_{11}(k)N_1^2(k) - \alpha_{12}(k)N_1(k)N_2(k) - \alpha_{13}(k)N_1(k)N_3(k) = 0$$
(517)

$$N_1(k)[a_1(k) - \alpha_{11}(k)N_1(k) - \alpha_{12}(k)N_2(k) - \alpha_{13}(k)N_3(k)] = 0$$
(518)

$$a_1(k) - \alpha_{11}(k)N_1(k) - \alpha_{12}(k)N_2(k) - \alpha_{13}(k)N_3(k) = 0$$
(519)

$$-\alpha_{11}(k)N_1(k) = -a_1(k) + \alpha_{12}(k)N_2(k) + \alpha_{13}(k)N_3(k)$$
(520)

$$\therefore \qquad N_1^*(k) = N_1(k) = \frac{a_1(k) - \alpha_{12}(k)N_2(k) - \alpha_{13}(k)N_3(k)}{\alpha_{11}(k)} \tag{521}$$

Substituting (521) in (512) and assuming a positive solution N_2^* of N_2 yields:

$$N_2(k)e^{a_2(k)N_2(k) - \alpha_{22}(k)N_2^2(k) + \alpha_{21}(k)N_1(k)N_2(k) + \alpha_{23}(k)N_2(k)N_3(k)} = 0$$
(522)

Therefore

$$N_{2}(k) = 0 \quad \text{or} \quad e^{a_{2}(k)N_{2}(k) - \alpha_{22}(k)N_{2}^{2}(k) + \alpha_{21}(k)N_{1}(k)N_{2}(k) + \alpha_{23}(k)N_{2}(k)N_{3}(k)} = 0 \quad (523)$$
$$e^{a_{2}(k)N_{2}(k) - \alpha_{22}(k)N_{2}^{2}(k) + \alpha_{21}(k)N_{1}(k)N_{2}(k) + \alpha_{23}(k)N_{2}(k)N_{3}(k)} = 0$$

$$a_{2}(k)N_{2}(k) - \alpha_{22}(k)N_{2}^{2}(k) + \alpha_{21}(k)N_{1}(k)N_{2}(k) + \alpha_{23}(k)N_{2}(k)N_{3}(k) = 0$$

$$N_{2}(k)[a_{2}(k) - \alpha_{22}(k)N_{2}(k) + \alpha_{21}(k)N_{1}(k) + \alpha_{23}(k)N_{3}(k)] = 0$$

$$a_{2}(k) - \alpha_{22}(k)N_{2}(k) + \alpha_{21}(k)N_{1}(k) + \alpha_{23}(k)N_{3}(k) = 0$$
(524)

$$\therefore \quad a_2(k) - \alpha_{22}(k)N_2(k) + \alpha_{21}(k)N_1(k) + \alpha_{23}(k)N_3(k) = 0$$
(525)

$$a_{2}(k) - \alpha_{22}(k)N_{2}(k) + \alpha_{21}(k) \left(\frac{a_{1}(k) - \alpha_{12}(k)N_{2}(k) - \alpha_{13}(k)N_{3}(k)}{\alpha_{11}(k)}\right) + \alpha_{23}(k)N_{3}(k) = 0 \quad (526)$$

$$a_{2}(k) - \alpha_{22}(k)N_{2}(k) + \frac{a_{1}(k)\alpha_{21}(k)}{\alpha_{11}(k)} - \frac{\alpha_{12}(k)\alpha_{21}(k)}{\alpha_{11}(k)}N_{2}(k) - \frac{\alpha_{13}(k)\alpha_{21}(k)}{\alpha_{11}(k)}N_{3}(k) + \alpha_{23}(k)N_{3}(k) = 0 \quad (527)$$

$$-\alpha_{22}(k)N_{2}(k) - \frac{\alpha_{12}(k)\alpha_{21}(k)}{\alpha_{11}(k)}N_{2}(k) = -a_{2}(k) - \frac{a_{1}(k)\alpha_{21}(k)}{\alpha_{11}(k)} + \frac{\alpha_{13}(k)\alpha_{21}(k)}{\alpha_{11}(k)}N_{3}(k) + \alpha_{23}(k)N_{3}(k)$$
(528)

$$\left(-\alpha_{22}(k) - \frac{\alpha_{12}(k)\alpha_{21}(k)}{\alpha_{11}(k)}\right)N_2(k) = \frac{-a_2(k)\alpha_{11}(k) - a_1(k)\alpha_{21}(k)}{\alpha_{11}(k)} + \left(\alpha_{23}(k) + \frac{\alpha_{13}(k)\alpha_{21}(k)}{\alpha_{11}(k)}\right)N_3(k) \quad (529)$$

$$\left(\frac{-\alpha_{11}(k)\alpha_{22}(k) - \alpha_{12}(k)\alpha_{21}(k)}{\alpha_{11}(k)}\right)N_2(k) = -\frac{a_2(k)\alpha_{11}(k) - a_1\alpha_{21}(k)}{\alpha_{11}(k)} + \left(\frac{\alpha_{11}(k)\alpha_{23}(k) + \alpha_{13}(k)\alpha_{21}(k)}{\alpha_{11}(k)}\right)N_3(k) \quad (530)$$

$$\therefore \qquad N_2^*(k) = N_2(k) = \frac{a_2(k)\alpha_{11}(k)a_1(k)\alpha_{21}(k)}{\alpha_{11}(k)\alpha_{22}(k) + \alpha_{12}(k)\alpha_{21}(k)} \\ + \left(\frac{\alpha_{11}(k)\alpha_{23}(k) + \alpha_{13}(k)\alpha_{21}(k)}{-\alpha_{22}(k)\alpha_{11}(k) - \alpha_{12}(k)\alpha_{21}(k)}\right) N_3(k) \quad (531)$$

Substituting (531) and (521) in (513) and assuming a positive solution $N_3^*(k)$ of $N_3(k)$ yields:

$$N_3(k)e^{a_3(k)N_3(k)-\alpha_{33}(k)N_3^2(k)+\alpha_{31}(k)N_1(k)N_3(k)+\alpha_{32}(k)N_2(k)N_3(k)} = 0$$
(532)

Therefore

$$N_3(k) = 0 \qquad \text{or} \qquad e^{a_3(k)N_3(k) - \alpha_{33}(k)N_3^2(k) + \alpha_{31}(k)N_1(k)N_3(k) + \alpha_{32}(k)N_2(k)N_3(k)} = 0 \tag{533}$$

$$e^{a_3(k)N_3(k) - \alpha_{33}(k)N_3^2(k) + \alpha_{31}(k)N_1(k)N_3(k) + \alpha_{32}(k)N_2(k)N_3(k)} = 0$$
(534)

$$a_3(k)N_3(k) - \alpha_{33}(k)N_3^2(k) + \alpha_{31}(k)N_1(k)N_3(k) + \alpha_{32}(k)N_2(k)N_3(k) = 0$$
(535)

$$N_3(k)[a_3(k) - \alpha_{33}(k)N_3(k) + \alpha_{31}(k)N_1(k) + \alpha_{32}(k)N_2(k)] = 0$$
(536)

$$a_3(k) - \alpha_{33}(k)N_3(k) + \alpha_{31}(k)N_1(k) + \alpha_{32}(k)N_2(k) = 0$$
(537)

$$a_{3}(k) - \alpha_{33}(k)N_{3}(k) + \alpha_{31}(k)\left(\frac{a_{1}(k) - \alpha_{12}(k)N_{2}(k) - \alpha_{13}(k)N_{3}(k)}{a_{11}(k)}\right) + \alpha_{32}(k)\left(\frac{a_{2}(k)\alpha_{11}(k)a_{1}(k)\alpha_{21}(k)}{\alpha_{11}(k)\alpha_{22}(k) + \alpha_{12}(k)\alpha_{21}(k)} + \left(\frac{\alpha_{11}(k)\alpha_{23}(k) + \alpha_{13}(k)\alpha_{21}(k)}{-\alpha_{22}(k)\alpha_{11}(k) - \alpha_{12}(k)\alpha_{21}(k)}\right)N_{3}(k)\right) = 0 \quad (538)$$

$$a_{3}(k) - \alpha_{33}(k)N_{3}(k) + \alpha_{33}(k)N_{3}(k) + \alpha_{31}(k) - \alpha_{12}(k) \left(\frac{a_{2}(k)\alpha_{11}(k)a_{1}(k)\alpha_{21}(k)}{\alpha_{11}(k)\alpha_{22}(k) + \alpha_{12}(k)\alpha_{21}(k)} + \left(\frac{\alpha_{11}(k)\alpha_{23}(k) + \alpha_{13}(k)\alpha_{21}(k)}{-\alpha_{22}(k)\alpha_{11}(k) - \alpha_{12}(k)\alpha_{21}(k)}\right)N_{3}(k)\right) - \alpha_{13}(k)N_{3}(k)\right) + \alpha_{32}(k) \left(\frac{a_{2}(k)\alpha_{11}(k)a_{1}(k)\alpha_{21}(k)}{\alpha_{11}(k)\alpha_{22}(k) + \alpha_{12}(k)\alpha_{21}(k)} + \left(\frac{\alpha_{11}(k)\alpha_{23}(k) + \alpha_{13}(k)\alpha_{21}(k)}{-\alpha_{22}(k)\alpha_{11}(k) - \alpha_{12}(k)\alpha_{21}(k)}\right)N_{3}(k)\right) = 0$$
(539)

$$\therefore N_3^*(k) = N_3(k) = \frac{\rho_3}{D}$$
(540)

where

$$\rho_{3} = a_{1}(k)[\alpha_{21}(k)\alpha_{33}(k) + \alpha_{31}(k)\alpha_{23}(k)] + a_{2}(k)[\alpha_{11}(k)\alpha_{33}(k) + \alpha_{13}(k)\alpha_{31}(k)] + a_{3}(k)[\alpha_{11}(k)\alpha_{23}(k) - \alpha_{13}(k)\alpha_{21}(k)]$$

$$D = \alpha_{11}(k)[\alpha_{22}(k)\alpha_{33}(k) - \alpha_{23}(k)\alpha_{32}(k)] + \alpha_{12}(k)[\alpha_{21}(k)\alpha_{33}(k) + \alpha_{31}(k)\alpha_{23}(k)] + \alpha_{13}(k)[\alpha_{31}(k)\alpha_{32}(k) + \alpha_{31}(k)\alpha_{22}(k)]$$

Substituting (540) in (531) yields:

$$N_2^*(k) = N_2(k) = \frac{\rho_2}{D}$$
(541)

where

$$\rho_{2} = a_{1}(k)[\alpha_{21}(k)\alpha_{33}(k) + \alpha_{31}(k)\alpha_{23}(k)] + a_{2}(k)[\alpha_{11}(k)\alpha_{33}(k) + \alpha_{13}(k)\alpha_{31}(k)] + a_{3}(k)[\alpha_{11}(k)\alpha_{23}(k) - \alpha_{13}(k)\alpha_{21}(k)]$$

$$D = \alpha_{11}(k) [\alpha_{22}(k)\alpha_{33}(k) - \alpha_{23}(k)\alpha_{32}(k)] + \alpha_{12}(k) [\alpha_{21}(k)\alpha_{33}(k) + \alpha_{31}(k)\alpha_{23}(k)] + \alpha_{13}(k) [\alpha_{31}(k)\alpha_{32}(k) + \alpha_{31}(k)\alpha_{22}(k)]$$

Substituting (540) and (541) in (521) yields:

$$N_1^*(k) = N_1(k) = \frac{\rho_1}{D}$$
(542)

where

$$\rho_{1} = a_{1}[\alpha_{22}(k)\alpha_{33}(k) - \alpha_{23}(k)\alpha_{32}(k)] - a_{2}(k)[\alpha_{12}(k)\alpha_{33}(k) + \alpha_{13}(k)\alpha_{32}(k)] - a_{3}(k)[\alpha_{12}(k)\alpha_{23}(k) + \alpha_{13}(k)\alpha_{22}(k)]$$
(543)

$$D = \alpha_{11}(k) [\alpha_{22}(k)\alpha_{33}(k) - \alpha_{23}(k)\alpha_{32}(k)] + \alpha_{12}(k) [\alpha_{21}(k)\alpha_{33}(k) + \alpha_{31}(k)\alpha_{23}(k)] + \alpha_{13}(k) [\alpha_{31}(k)\alpha_{32}(k) + \alpha_{31}(k)\alpha_{22}(k)]$$
(544)

Therefore

$$N_1^*(k) = \frac{\rho_1}{D} \qquad N_2^*(k) = \frac{\rho_2}{D} \qquad N_3^*(k) = \frac{\rho_3}{D}$$
 (545)

where

$$\rho_{1} = a_{1}[\alpha_{22}(k)\alpha_{33}(k) - \alpha_{23}(k)\alpha_{32}(k)] - a_{2}(k)[\alpha_{12}(k)\alpha_{33}(k) + \alpha_{13}(k)\alpha_{32}(k)] - a_{3}(k)[\alpha_{12}(k)\alpha_{23}(k) + \alpha_{13}(k)\alpha_{22}(k)]$$
(546)

$$\rho_{2} = a_{1}(k)[\alpha_{21}(k)\alpha_{33}(k) + \alpha_{31}(k)\alpha_{23}(k)] + a_{2}(k)[\alpha_{11}(k)\alpha_{33}(k) + \alpha_{13}(k)\alpha_{31}(k)] + a_{3}(k)[\alpha_{11}(k)\alpha_{23}(k) - \alpha_{13}(k)\alpha_{21}(k)]$$
(547)

$$\rho_{3} = a_{1}(k)[\alpha_{21}(k)\alpha_{33}(k) + \alpha_{31}(k)\alpha_{23}(k)] + a_{2}(k)[\alpha_{11}(k)\alpha_{33}(k) + \alpha_{13}(k)\alpha_{31}(k)] + a_{3}(k)[\alpha_{11}(k)\alpha_{23}(k) - \alpha_{13}(k)\alpha_{21}(k)]$$
(548)

$$D = \alpha_{11}(k) [\alpha_{22}(k)\alpha_{33}(k) - \alpha_{23}(k)\alpha_{32}(k)] + \alpha_{12}(k) [\alpha_{21}(k)\alpha_{33}(k) + \alpha_{31}(k)\alpha_{23}(k)] + \alpha_{13}(k) [\alpha_{31}(k)\alpha_{32}(k) + \alpha_{31}(k)\alpha_{22}(k)]$$
(549)

provided that the following expressions hold:

$$\{ a_2(k) [\alpha_{12}(k)\alpha_{33}(k) + \alpha_{13}(k)\alpha_{32}(k)] + a_3(k) [\alpha_{12}(k)\alpha_{23}(k) + \alpha_{13}(k)\alpha_{22}(k)] \}$$

$$< a_1(k) [\alpha_{22}(k)\alpha_{33}(k) - \alpha_{23}(k)\alpha_{32}(k)]$$

$$\begin{aligned} &\alpha_{11}(k)\alpha_{23}(k) > \alpha_{13}(k)\alpha_{21}(k) \\ &\alpha_{11}(k)\alpha_{32}(k) > \alpha_{12}(k)\alpha_{31}(k) \\ &\alpha_{22}(k)\alpha_{33}(k) > \alpha_{23}(k)\alpha_{32}(k) \end{aligned}$$

In conclusion, we have the following equilibrium point for the interior equilibrium:

$$(N_1(k), N_2(k), N_3(k)) = E_4(N_1^*(k), N_2^*(k), N_3^*(k))$$

17 Stability

17.1 Discrete Form of System Using Euler's Method

Consider the following discrete non-linear autonomous time-invariant system of difference equations:

$$N(k+1) = N(k) + h \begin{pmatrix} a_1 N_1(k) - \alpha_{11} N_1^2(k) - \alpha_{12} N_1(k) N_2(k) - \alpha_{13} N_1(k) N_3(k) \\ a_2 N_2(k) - \alpha_{22} N_2^2(k) + \alpha_{21} N_1(k) N_2(k) + \alpha_{23} N_2(k) N_3(k) \\ a_3 N_3(k) - \alpha_{33} N_3^2(k) + \alpha_{31} N_1(k) N_3(k) + \alpha_{32} N_2(k) N_3(k) \end{pmatrix}$$
(550)

where $N(k+1) = \begin{pmatrix} N_1(k+1) \\ N_2(k+1) \\ N_3(k+1) \end{pmatrix}$, $N(k) = \begin{pmatrix} N_1(k) \\ N_2(k) \\ N_3(k) \end{pmatrix}$ and $k = 0, 1, 2, \dots$

17.1.1 Linearisation Method

1. Applying a linearisation method to system (550) at equilibrium point $(N_1, N_2, N_3) = (0, 0, 0)$, let $f = (f_1, f_2, f_3)^T$ where

$$f_1 = h[a_1 N_1(k) - \alpha_{11} N_1^2(k) - \alpha_{12} N_1(k) N_2(k) - \alpha_{13} N_1(k) N_3(k)]$$
(551)

$$f_2 = h[a_2 N_2(k) - \alpha_{22} N_2^2(k) + \alpha_{21} N_1(k) N_2(k) + \alpha_{23} N_2(k) N_3(k)]$$
(552)

$$f_3 = h[a_3N_3(k) - \alpha_{33}N_3^2(k) + \alpha_{31}N_1(k)N_3(k) + \alpha_{32}N_2(k)N_3(k)]$$
(553)

2. Then, the Jacobian matrix of system (550) is:

$$J_{(0,0,0)} = \frac{\partial f}{\partial N}\Big|_{(0,0,0)} = \left(\begin{array}{ccc} \frac{\partial f_1(0,0,0)}{\partial N_1} & \frac{\partial f_1(0,0,0)}{\partial N_2} & \frac{\partial f_1(0,0,0)}{\partial N_3} \\ \frac{\partial f_2(0,0,0)}{\partial N_1} & \frac{\partial f_2(0,0,0)}{\partial N_2} & \frac{\partial f_2(0,0,0)}{\partial N_3} \\ \frac{\partial f_3(0,0,0)}{\partial N_1} & \frac{\partial f_3(0,0,0)}{\partial N_2} & \frac{\partial f_3(0,0,0)}{\partial N_3} \end{array}\right) = \left(\begin{array}{ccc} ha_1 & 0 & 0 \\ 0 & ha_2 & 0 \\ 0 & 0 & ha_3 \end{array}\right)$$
(554)

3. Hence, the system (550) can be rewritten as:

$$N(k+1) = AN(k) + g(N(k))$$
(555)

where

$$N(k+1) = \begin{pmatrix} N_1(k+1) \\ N_2(k+1) \\ N_3(k+1) \end{pmatrix}, A = \begin{pmatrix} ha_1 & 0 & 0 \\ 0 & ha_2 & 0 \\ 0 & 0 & ha_3 \end{pmatrix}, N(k) = \begin{pmatrix} N_1(k) \\ N_2(k) \\ N_3(k) \end{pmatrix}$$
(556)

and

$$g(N(k)) = -h \begin{pmatrix} a_1 N_1(k) - \alpha_{11} N_1^2(k) - \alpha_{12} N_1(k) N_2(k) - \alpha_{13} N_1(k) N_3(k) \\ a_2 N_2(k) - \alpha_{22} N_2^2(k) + \alpha_{21} N_1(k) N_2(k) + \alpha_{23} N_2(k) N_3(k) \\ a_3 N_3(k) - \alpha_{33} N_3^2(k) + \alpha_{31} N_1(k) N_3(k) + \alpha_{32} N_2(k) N_3(k) \end{pmatrix}$$
(557)

4. Calculating the eigenvalues of A:

$$|A - \lambda I| = \begin{vmatrix} ha_1 - \lambda & 0 & 0 \\ 0 & ha_2 - \lambda & 0 \\ 0 & 0 & ha_3 - \lambda \end{vmatrix}$$
$$= ha_1 - \lambda \begin{vmatrix} ha_2 - \lambda & 0 \\ 0 & ha_3 - \lambda \end{vmatrix}$$
$$= (ha_1 - \lambda)(ha_2 - \lambda)(ha_3 - \lambda)$$
(558)

Therefore

$$\lambda_1 = ha_1 \qquad \lambda_2 = ha_2 \qquad \lambda_3 = ha_3 \tag{559}$$

If:

- ha₁, ha₂, ha₃ < 0
 ⇒ The equilibrium solution (0, 0, 0) of system (550) is Stable.
- Otherwise \Rightarrow The equilibrium solution (0, 0, 0) of system (550) is Unstable.

17.2 Discrete Form of System Using Method of Piecewise Constant Arguments

Consider the following discrete non-linear autonomous time-invariant system of difference equations: $N_{k}(k) = N_{k}(k)N_{k}(k) - \alpha_{k}(k)N_{k}(k) - \alpha_{k}(k)N_{k}(k) - \alpha_{k}(k)N_{k}(k)N_{k}(k) - \alpha_{k}(k)N_{k}(k) - \alpha_{k}(k)N_{k}$

$$N_{1}(k+1) = N_{1}(k)e^{a_{1}(k)N_{1}(k) - \alpha_{11}(k)N_{1}^{2}(k) - \alpha_{12}(k)N_{1}(k)N_{2}(k) - \alpha_{13}(k)N_{1}(k)N_{3}(k)}$$

$$N_{2}(k+1) = N_{2}(k)e^{a_{2}(k)N_{2}(k) - \alpha_{22}(k)N_{2}^{2}(k) + \alpha_{21}(k)N_{1}(k)N_{2}(k) + \alpha_{23}(k)N_{2}(k)N_{3}(k)}$$

$$N_{3}(k+1) = N_{3}(k)e^{a_{3}(k)N_{3}(k) - \alpha_{33}(k)N_{3}^{2}(k) + \alpha_{31}(k)N_{1}(k)N_{3}(k) + \alpha_{32}(k)N_{2}(k)N_{3}(k)}$$
(560)

17.2.1 Linearisation Method

1. Applying a linearisation method to system (560) at equilibrium point $(N_1, N_2, N_3) = (0, 0, 0)$, let $f = (f_1, f_2, f_3)^T$ where

$$f_1 = N_1(k)e^{a_1(k)N_1(k) - \alpha_{11}(k)N_1^2(k) - \alpha_{12}(k)N_1(k)N_2(k) - \alpha_{13}(k)N_1(k)N_3(k)}$$
(561)

$$f_2 = N_2(k)e^{a_2(k)N_2(k) - \alpha_{22}(k)N_2^2(k) + \alpha_{21}(k)N_1(k)N_2(k) + \alpha_{23}(k)N_2(k)N_3(k)}$$
(562)

$$f_3 = N_3(k)e^{a_3(k)N_3(k) - \alpha_{33}(k)N_3^2(k) + \alpha_{31}(k)N_1(k)N_3(k) + \alpha_{32}(k)N_2(k)N_3(k)}$$
(563)

2. Then, the Jacobian matrix of system (560) is:

$$J_{(0,0,0)} = \frac{\partial f}{\partial N}\Big|_{(0,0,0)} = \left(\begin{array}{ccc} \frac{\partial f_1(0,0,0)}{\partial N_1} & \frac{\partial f_1(0,0,0)}{\partial N_2} & \frac{\partial f_1(0,0,0)}{\partial N_3} \\ \frac{\partial f_2(0,0,0)}{\partial N_1} & \frac{\partial f_2(0,0,0)}{\partial N_2} & \frac{\partial f_2(0,0,0)}{\partial N_3} \\ \frac{\partial f_3(0,0,0)}{\partial N_1} & \frac{\partial f_3(0,0,0)}{\partial N_2} & \frac{\partial f_3(0,0,0)}{\partial N_3} \end{array}\right) = \left(\begin{array}{ccc} 1 & 1 & 1 \\ 1 & 1 & 1 \\ 1 & 1 & 1 \end{array}\right)$$
(564)

3. Hence, the system (560) can be rewritten as:

$$N(k+1) = AN(k) + g(N(k))$$
(565)

where

$$N(k+1) = \begin{pmatrix} N_1(k+1) \\ N_2(k+1) \\ N_3(k+1) \end{pmatrix}, A = \begin{pmatrix} 1 & 1 & 1 \\ 1 & 1 & 1 \\ 1 & 1 & 1 \end{pmatrix}, N(k) = \begin{pmatrix} N_1(k) \\ N_2(k) \\ N_3(k) \end{pmatrix}$$
(566)

and

$$g(N(k)) = - \begin{pmatrix} N_1(k)e^{a_1(k)N_1(k) - \alpha_{11}(k)N_1^2(k) - \alpha_{12}(k)N_1(k)N_2(k) - \alpha_{13}(k)N_1(k)N_3(k)} \\ N_2(k)e^{a_2(k)N_2(k) - \alpha_{22}(k)N_2^2(k) + \alpha_{21}(k)N_1(k)N_2(k) + \alpha_{23}(k)N_2(k)N_3(k)} \\ N_3(k)e^{a_3(k)N_3(k) - \alpha_{33}(k)N_3^2(k) + \alpha_{31}(k)N_1(k)N_3(k) + \alpha_{32}(k)N_2(k)N_3(k)} \end{pmatrix}$$
(567)

4. Calculating the eigenvalues of A:

$$|A - \lambda I| = \begin{vmatrix} 1 - \lambda & 1 & 1 \\ 1 & 1 - \lambda & 1 \\ 1 & 1 & 1 - \lambda \end{vmatrix}$$

= $1 - \lambda \begin{vmatrix} 1 - \lambda & 1 \\ 1 & 1 - \lambda \end{vmatrix} - \begin{vmatrix} 1 & 1 \\ 1 & 1 - \lambda \end{vmatrix} + \begin{vmatrix} 1 & 1 - \lambda \\ 1 & 1 \end{vmatrix}$
= $1 - \lambda[(1 - \lambda)(1 - \lambda) - 1] - [1 - \lambda - 1] + [1 - (1 - \lambda)]$
= $1 - \lambda[\lambda^2 - 2\lambda] + \lambda + \lambda$
= $-\lambda^3 + \lambda^2 + 2\lambda$
= $-\lambda(\lambda - 1)(\lambda + 2)$ (568)

Therefore

$$\lambda_1 = 0 \qquad \lambda_2 = 1 \qquad \lambda_3 = -2 \tag{569}$$

Since

$$\lambda_1 \le 0 \qquad \lambda_2 > 0 \qquad \lambda_3 < 0 \tag{570}$$

 \Rightarrow The equilibrium solution (0,0,0) of system (560) is Unstable.

18 Numerical Examples

18.1 Discrete Form of System Using Euler's Method

Example 1

Modifying values from Example 1 (with corrections) from Chapter 4, for a discrete autonomous time-invariant system, we have:

 $\begin{array}{rrrr} a_1 = 3 & a_2 = 1 & a_3 = 1 \\ \alpha_{11} = 0.01 & \alpha_{21} = 0.1 & \alpha_{31} = 0.1 \\ \alpha_{12} = 0.1 & \alpha_{22} = 0.2 & \alpha_{32} = 0.1 \\ \alpha_{13} = 0.1 & \alpha_{23} = 0.1 & \alpha_{33} = 0.3 \end{array}$

with initial values:

 $N_1 = 0.5$ $N_2 = 0.75$ $N_3 = 0.6$

and step size h = 0.05 for the k interval 0 < k < 20.

Hence, we have the following MATLAB script for solving the system by using a k-iterate loop as well as plotting the results on a 2D and 3D plane:

```
a1 = 3;
a2 = 1;
a3 = 1;
alpha11 = 0.01;
alpha12 = 0.1;
alpha13 = 0.1;
alpha21 = 0.1;
alpha22 = 0.2;
alpha23 = 0.1;
alpha31 = 0.1;
alpha32 = 0.1;
alpha33 = 0.3;
h=0.05;
N1zero = 0.5;
N2zero = 0.75;
N3zero = 0.6;
N1 = zeros(21, 1);
N2 = zeros(21, 1);
N3 = zeros(21,1);
N1(1) = N1zero;
N2(1) = N2zero;
N3(1) = N3zero;
```

```
n=0:20;
for k=1:20
    N1(k+1) = N1(k)+h*(a1*N1(k)-alpha11*N1(k).^{2}-alpha12*N1(k)*N2(k)
    -alpha13*N1(k)*N3(k));
    N2(k+1) = N2(k)+h*(a2*N2(k)-alpha22*N2(k).^{2}+alpha21*N1(k)*N2(k)
    +alpha23*N2(k)*N3(k));
    N3(k+1) = N3(k)+h*(a3*N3(k)-alpha33*N3(k).^2+alpha31*N1(k)*N3(k)
    +alpha32*N2(k)*N3(k));
end
%2D Plot
plot(n,N1,'-o',n,N2,'-.',n,N3,'--')
title('Example 1')
xlabel('Time'), ylabel('Population')
%3D Plot
plot3(N1,N2,N3)
title('Example 1')
xlabel('Prey Population'), ylabel('Predator 1 Population'),
zlabel('Predator 2 Population')
```

which yields the following 2D and 3D plots:



Figure 9: Example 1 2D Plot



Figure 10: Example 1 3D Plot

Example 2

Modifying values from Example 1 (with corrections) from Chapter 4, for a discrete autonomous time-invariant system, we have:

 $\begin{array}{rrrr} a_1 = 3 & a_2 = 1 & a_3 = 1 \\ \alpha_{11} = 0.01 & \alpha_{21} = 0.1 & \alpha_{31} = 0.1 \\ \alpha_{12} = 0.1 & \alpha_{22} = 0.2 & \alpha_{32} = 0.1 \\ \alpha_{13} = 0.1 & \alpha_{23} = 0.1 & \alpha_{33} = 0.3 \end{array}$

with initial values:

 $N_1 = 10$ $N_2 = 10$ $N_3 = 10$

and step size h = 0.05 for the k interval 0 < k < 20.

Hence, we have the following MATLAB script for solving the system by using a k-iterate loop as well as plotting the results on a 2D and 3D plane:

```
a1 = 3;
a2 = 1;
a3 = 1;
alpha11 = 0.01;
alpha12 = 0.1;
alpha13 = 0.1;
alpha21 = 0.1;
alpha22 = 0.2;
alpha23 = 0.1;
alpha31 = 0.1;
alpha32 = 0.1;
alpha33 = 0.3;
h=0.05;
N1zero = 0.1;
N2zero = 0.1;
N3zero = 0.1;
N1 = zeros(21,1);
N2 = zeros(21, 1);
N3 = zeros(21, 1);
N1(1) = N1zero;
N2(1) = N2zero;
N3(1) = N3zero;
n=0:20;
```

```
for k=1:20
    N1(k+1) = N1(k)+h*(a1*N1(k)-alpha11*N1(k).^{2}-alpha12*N1(k)*N2(k)
    -alpha13*N1(k)*N3(k));
    N2(k+1) = N2(k)+h*(a2*N2(k)-alpha22*N2(k).^{2}+alpha21*N1(k)*N2(k)
    +alpha23*N2(k)*N3(k));
    N3(k+1) = N3(k)+h*(a3*N3(k)-alpha33*N3(k).^2+alpha31*N1(k)*N3(k)
    +alpha32*N2(k)*N3(k));
end
%2D Plot
plot(n,N1,'-o',n,N2,'-.',n,N3,'--')
title('Example 2')
xlabel('Time'), ylabel('Population')
%3D Plot
plot3(N1,N2,N3)
title('Example 2')
xlabel('Prey Population'), ylabel('Predator 1 Population'),
zlabel('Predator 2 Population')
```

which yields the following 2D and 3D plots:



Figure 11: Example 1 2D Plot



Figure 12: Example 1 3D Plot

18.2 Discrete Form of System Using Method of Piecewise Constant Arguments

Example 1

Modifying values from Example 1 (with corrections) from Chapter 4, for a discrete autonomous time-invariant system, we have:

 $\begin{array}{ll} a_1 = 0.3 & a_2 = 0.1 & a_3 = 0.1 \\ \alpha_{11} = 0.001 & \alpha_{21} = 0.01 & \alpha_{31} = 0.01 \\ \alpha_{12} = 0.01 & \alpha_{22} = 0.02 & \alpha_{32} = 0.01 \\ \alpha_{13} = 0.01 & \alpha_{23} = 0.01 & \alpha_{33} = 0.03 \end{array}$

with initial values:

 $N_1 = 0.05$ $N_2 = 0.075$ $N_3 = 0.06$

and step size h = 0.05 for the k interval 0 < k < 20.

Hence, we have the following MATLAB script for solving the system by using a k-iterate loop as well as plotting the results on a 2D and 3D plane:

```
a1 = 0.3;
a2 = 0.1;
a3 = 0.1;
alpha11 = 0.001;
alpha12 = 0.01;
alpha13 = 0.01;
alpha21 = 0.01;
alpha22 = 0.02;
alpha23 = 0.01;
alpha31 = 0.01;
alpha32 = 0.01;
alpha33 = 0.03;
N1zero = 0.05;
N2zero = 0.075;
N3zero = 0.06;
N1 = zeros(21, 1);
N2 = zeros(21, 1);
N3 = zeros(21, 1);
N1(1) = N1zero;
N2(1) = N2zero;
N3(1) = N3zero;
n=0:20;
```

```
for k=1:20
    N1(k+1) = N1(k) \exp(a1*N1(k)-alpha11*N1(k).^2-alpha12*N1(k)*N2(k)
    -alpha13*N1(k)*N3(k));
    N2(k+1) = N2(k) * exp(a2*N2(k)-alpha22*N2(k).^{2}+alpha21*N1(k)*N2(k)
    +alpha23*N2(k)*N3(k));
    N3(k+1) = N3(k) * exp(a3*N3(k)-alpha33*N3(k).^{2}+alpha31*N1(k)*N3(k)
    +alpha32*N2(k)*N3(k));
end
%2D Plot
plot(n,N1,'-o',n,N2,'-.',n,N3,'--')
title('Example 1')
xlabel('Time'), ylabel('Population')
%3D Plot
plot3(N1,N2,N3)
title('Example 1')
xlabel('Prey Population'), ylabel('Predator 1 Population'),
zlabel('Predator 2 Population')
```

which yields the following 2D and 3D plots:



Figure 13: Example 1 2D Plot



Figure 14: Example 1 3D Plot

Example 2

Modifying values from Example 2 (with corrections) from Chapter 4, for a discrete autonomous time-invariant system, we have:

 $\begin{array}{ll} a_1 = 0.3 & a_2 = 0.1 & a_3 = 0.1 \\ \alpha_{11} = 0.001 & \alpha_{21} = 0.01 & \alpha_{31} = 0.01 \\ \alpha_{12} = 0.01 & \alpha_{22} = 0.02 & \alpha_{32} = 0.01 \\ \alpha_{13} = 0.01 & \alpha_{23} = 0.01 & \alpha_{33} = 0.03 \end{array}$

with initial values:

 $\begin{array}{l} N_1 = 0.01 \\ N_2 = 0.01 \\ N_3 = 0.01 \end{array}$

and step size h = 0.05 for the k interval 0 < k < 20.

Hence, we have the following MATLAB script for solving the system by using a k-iterate loop as well as plotting the results on a 2D and 3D plane:

```
a1 = 0.3;
a2 = 0.1;
a3 = 0.1;
alpha11 = 0.001;
alpha12 = 0.01;
alpha13 = 0.01;
alpha21 = 0.01;
alpha22 = 0.02;
alpha23 = 0.01;
alpha31 = 0.01;
alpha32 = 0.01;
alpha33 = 0.03;
N1zero = 0.01;
N2zero = 0.01;
N3zero = 0.01;
N1 = zeros(21, 1);
N2 = zeros(21,1);
N3 = zeros(21, 1);
N1(1) = N1zero;
N2(1) = N2zero;
N3(1) = N3zero;
n=0:20;
for k=1:20
```

```
N1(k+1) = N1(k)*exp(a1*N1(k)-alpha11*N1(k).^2-alpha12*N1(k)*N2(k)
```

```
-alpha13*N1(k)*N3(k));
N2(k+1) = N2(k)*exp(a2*N2(k)-alpha22*N2(k).^2+alpha21*N1(k)*N2(k)
+alpha23*N2(k)*N3(k));
N3(k+1) = N3(k)*exp(a3*N3(k)-alpha33*N3(k).^2+alpha31*N1(k)*N3(k)
+alpha32*N2(k)*N3(k));
end
%2D Plot
plot(n,N1,'-o',n,N2,'-.',n,N3,'--')
title('Example 2')
xlabel('Time'), ylabel('Population')
%3D Plot
plot3(N1,N2,N3)
title('Example 2')
xlabel('Prey Population'), ylabel('Predator 1 Population'),
zlabel('Predator 2 Population')
```

which yields the following 2D and 3D plots:



Figure 15: Example 1 2D Plot



Figure 16: Example 1 3D Plot

18.3 Comparison of Both Methods

Here, we compare results for both methods using the same constants and initial values:

Case 1

Using values from Example 1 of the Discrete Form of System Using Euler's Method, we have

 $\begin{array}{ll} a_1 = 3 & a_2 = 1 & a_3 = 1 \\ \alpha_{11} = 0.01 & \alpha_{21} = 0.1 & \alpha_{31} = 0.1 \\ \alpha_{12} = 0.1 & \alpha_{22} = 0.2 & \alpha_{32} = 0.1 \\ \alpha_{13} = 0.1 & \alpha_{23} = 0.1 & \alpha_{33} = 0.3 \end{array}$

with initial values:

 $N_1 = 0.5$ $N_2 = 0.75$ $N_3 = 0.6$

and step size h = 0.05 for the k interval 0 < k < 100.

Hence, results for both discrete schemes produce the following plot of results:



Figure 17: Example 1 2D Plot

Here, we can see that values for N_1 , N_2 and N_3 , using Euler's method, increase over time until approximately k = 40 for N_1 and k = 45 for N_2 and N_3 where they all decrease. Values for N_1 , N_2 and N_3 , using the method of piecewise constant arguments tend very quickly to infinity before tending very quickly to zero. Therefore, there is a great difference between results produced by both methods.

Case 2

Using values from Example 2 of the Discrete Form of System Using Euler's Method, we have

 $\begin{array}{ll} a_1 = 3 & a_2 = 1 & a_3 = 1 \\ \alpha_{11} = 0.01 & \alpha_{21} = 0.1 & \alpha_{31} = 0.1 \\ \alpha_{12} = 0.1 & \alpha_{22} = 0.2 & \alpha_{32} = 0.1 \\ \alpha_{13} = 0.1 & \alpha_{23} = 0.1 & \alpha_{33} = 0.3 \end{array}$ with initial values:

 $N_1 = 0.1$ $N_2 = 0.1$ $N_3 = 0.1$

and step size h = 0.05 for the k interval 0 < k < 100.

Hence, results for both discrete schemes produce the following plots of results:



Figure 18: Example 1 2D Plot
Similar to Case 1, here we can see that values for N_1 , N_2 and N_3 , using Euler's method, until approximately k = 40 for N_1 and k = 45 for N_2 and N_3 where they all decrease, whilst reaching smaller numbers of population at their highest values. Again, values for N_1 , using the method of piecewise constant arguments tend very quickly to infinity whilst values for N_2 and N_3 gradually increase over time. Therefore, as in Case 1, there is a great difference between results produced by both methods.

Case 3

Using values from Example 1 of the Discrete Form of System Using Method of Piecewise Constant Arguments, we have

| $a_1 = 0.3$ | $a_2 = 0.1$ | $a_3 = 0.1$ |
|-----------------------|----------------------|----------------------|
| $\alpha_{11} = 0.001$ | $\alpha_{21} = 0.01$ | $\alpha_{31} = 0.01$ |
| $\alpha_{12} = 0.01$ | $\alpha_{22} = 0.02$ | $\alpha_{32} = 0.01$ |
| $\alpha_{13} = 0.01$ | $\alpha_{23} = 0.01$ | $\alpha_{33} = 0.03$ |
| | | |

with initial values:

 $N_1 = 0.05$ $N_2 = 0.075$ $N_3 = 0.06$

and step size h = 0.05 for the k interval 0 < k < 100.

Hence, results for both discrete schemes produce the following plots of results:



Figure 19: Example 1 2D Plot

Case 3 shows a better correlation between results for both Euler and piecewise constant argument methods. Here, values for N_1 , N_2 and N_3 for both methods all gradually increase over time, with N_1 values using the method of piecewise constant arguments rapidly increasing between the interval 60 < k < 70 before tending very quickly to zero after k = 70.

Case 4

Using values from Example 2 of the Discrete Form of System Using Method of Piecewise Constant Arguments, we have

 $\begin{array}{ll} a_1 = 0.3 & a_2 = 0.1 & a_3 = 0.1 \\ \alpha_{11} = 0.001 & \alpha_{21} = 0.01 & \alpha_{31} = 0.01 \\ \alpha_{12} = 0.01 & \alpha_{22} = 0.02 & \alpha_{32} = 0.01 \\ \alpha_{13} = 0.01 & \alpha_{23} = 0.01 & \alpha_{33} = 0.03 \end{array}$ with initial values:

 $N_1 = 0.01$ $N_2 = 0.01$ $N_3 = 0.01$

and step size h = 0.05 for the k interval 0 < k < 100.

Hence, results for both discrete schemes produce the following plots of results:



Figure 20: Example 1 2D Plot

Case 4 shows the strongest relationship between both methods. Here, N_1 , N_2 and N_3 values for both methods display a positive correlation, continuously increasing in the interval 0 < k < 100.

19 Existence and Uniqueness of The System

In order to study the existence and uniqueness of systems (370) and (374), we use the following definition and theorem:

Definition 7 (Existence of a Unique Continuous Solution of a Autonomous Time-Invariant System[5]).

Let
$$x(n) = f^n(x_0)$$
 and $x(0) = f^0(x_0) = x_0$.

Hence:

$$x(n+1) = f^{n+1}(x_0) = f[f^n(x_0)] = f(x(n))$$
(571)

If $f^n(x_0) \to 0$ as $n \to \infty$, then there exists a unique continuous solution of the Autonomous Time-Invariant system:

$$x(n+1) = f(x(n))$$
(572)

Theorem 11 (Unique Continuous Solution of a Discrete System of Difference Equations [41]). *The vector difference equation*

$$EX = F(X, t) \tag{573}$$

where $X = [x_1(t), x_2(t), \dots, x_n(t)]$, has a solution X defined for $t_0 \le t \le t_0 + k$, where k is a positive integer or zero, provided that F exists for all X and t, and that for $t_0 \le t \le t_0 + 1$:

$$X(t) = X_0 = [f_1(t), f_2(t), \dots, f_n(t)]$$
(574)

where the functions $f_j(t)$, j = 1, 2, ..., n, are defined for $t_0 \le t \le t_0 + k$.

Hence, the existence of the solution X is unique and continuous.

Proof. Assuming that the function F is defined for all t and X, we look for a solution X such that, for $t = t_0$:

$$X = X_0 = [x_1(t_0), x_2(t_0), \dots, x_n(t_0)]$$
(575)

Since $EX_0 = F(X_0, t)$, and F is determined for all X and t, we have

$$EX_0 = [x_1(t+1), x_2(t+1), \dots, x_n(t+1)] = X_1 = F(X_0, t_0)$$
(576)

so that X_1 is determined.

But

$$EX_1 = [x_1(t_0+2), x_2(t_0+2), \dots, x_n(t_0+2)] = X_2 = F(X_1, t_0+1)$$
(577)

so that X_2 is determined.

To complete the proof by induction, we assume that

$$EX_k = [x_1(t_0 + k + 1), x_2(t_0 + k + 1), \dots, x_n(t_0 + k + 1)] = X_{k+1}$$

= $F(X_k, t_0 + k)$ (578)

so that X_{k+1} is determined.

(588)

In conclusion, we can see that X is determined for $t_0 + k$, where k is an arbitrary positive integer or zero. This however does not prove that X exists for any t since we have limited ourselves to values $t_0 + k$, where k is a positive integer or zero. To determine X for any value of t we need more specific initial conditions.

Assume that, for $t_0 \leq t \leq t_0 + 1$:

$$X = X_0 = [f_1(t), f_2(t), \dots, f_n(t)]$$
(579)

where the $f_j(t), j = 1, 2, ..., n$ and thus the vector X_0 , are defined for $t_0 \le t \le t_0 + 1$.

Then

$$EX_0 = F(X_0, t) = X_1 = [x_1(t), x_2(t), \dots, x_n(t)]$$
(580)

which defines X for $t_0 + 1 \le t \le t_0 + 2$,

$$EX_1 = F(X_1, t+1) = X_2 = [x_1(t), x_2(t), \dots, x_n(t)]$$
(581)

which defines X for $t_0 + 2 \le t \le t_0 + 3$,

: Assuming that:

$$X_k = [x_1(t), x_2(t), \dots, x_n(t)]$$
(582)

for $t_0 + k \le t \le t_0 + k + 1$, then:

$$EX_k = F(X_k, t+k) = X_{k+1}$$
(583)

which defines X for the interval $t_0 + k + 1 \le t \le t_0 + k + 2$.

Thus, X is determined for $t_0 \le t \le t_0 + k$, where k is an arbitrary positive integer or zero.

Proving uniqueness, suppose that (573) has two solutions X and Y satisfying the conditions of Theorem 11, then:

$$EY = F(Y,t) \tag{584}$$

$$EX = F(X, t) \tag{585}$$

with $Y = X_0(t) = X$ for $t_0 \le t \le t_0 + 1$. It follows that:

$$EX = F(X,t) = F(Y,t) = EY, \qquad t_0 \le t \le t_0 + 1$$
(586)

$$E^{2}X = F(FX, t+1) = F(EY, t+1) = E^{2}Y, \qquad t_{0} + 1 \le t \le t_{0} + 2$$
(587)

Assuming that $E^k X = E^k Y$ for $t_0 + k - 1 \le t \le t_0 + k$, then:

$$E^{k+1}X = F(E^kX, t+k) = F(E^kY, t+k) = E^{k+1}Y$$
(589)

for $t_0 + k \le t \le t_0 + k + 1$.

19.1 Proving Existence and Uniqueness of The System

19.1.1 Discrete Form of System Using Euler's Method

Consider the following discrete non-linear autonomous time-invariant system of difference equations:

$$N(k+1) = N(k) + h \begin{pmatrix} a_1 N_1(k) - \alpha_{11} N_1^2(k) - \alpha_{12} N_1(k) N_2(k) - \alpha_{13} N_1(k) N_3(k) \\ a_2 N_2(k) - \alpha_{22} N_2^2(k) + \alpha_{21} N_1(k) N_2(k) + \alpha_{23} N_2(k) N_3(k) \\ a_3 N_3(k) - \alpha_{33} N_3^2(k) + \alpha_{31} N_1(k) N_3(k) + \alpha_{32} N_2(k) N_3(k) \end{pmatrix}$$
(590)

where
$$N(k+1) = \begin{pmatrix} N_1(k+1) \\ N_2(k+1) \\ N_3(k+1) \end{pmatrix}$$
, $N(k) = \begin{pmatrix} N_1(k) \\ N_2(k) \\ N_3(k) \end{pmatrix}$ and $k = 0, 1, 2, \dots$

By Definition 7, let:

$$N(k+1) = f^{n+1}(x_0)$$
 and $N(k) = f^n(x_0)$ (591)

Hence, system (590) becomes:

$$f^{n+1}(x_0) = f^n(x_0) + h \begin{pmatrix} a_1 f_1^n(x_0) - \alpha_{11} f_1^{n^2}(x_0) - \alpha_{12} f_1^n(x_0) f_2^n(x_0) - \alpha_{13} f_1^n(x_0) f_3^n(x_0) \\ a_2 f_2^n(x_0) - \alpha_{22} f_2^{n^2}(x_0) + \alpha_{21} f_1^n(x_0) f_2^n(x_0) + \alpha_{23} f_2^n(x_0) f_3^n(x_0) \\ a_3 f_3^n(x_0) - \alpha_{33} f_3^{n^2}(x_0) + \alpha_{31} f_1^n(x_0) f_3^n(x_0) + \alpha_{32} f_2^n(x_0) f_3^n(x_0) \end{pmatrix}$$
(592)

given initial conditions:

$$x_1(0) = f_1^0(x_0) = x_1^0 \tag{593}$$

$$x_2(0) = f_2^0(x_0) = x_2^0 \tag{594}$$

$$x_3(0) = f_3^0(x_0) = x_3^0 \tag{595}$$

If $f^{n+1}(x_0) \to 0$ as $n \to \infty$.

 \Rightarrow There exists a unique and continuous solution of system (590).

19.1.2 Discrete Form of System Using Method of Piecewise Constant Arguments

Consider the following discrete non-linear autonomous time-invariant system of difference equations: (1)N(l) = (1)N(l)N(l) = (1)N(l)N(l)

$$N_{1}(k+1) = N_{1}(k)e^{a_{1}(k)N_{1}(k) - \alpha_{11}(k)N_{1}^{2}(k) - \alpha_{12}(k)N_{1}(k)N_{2}(k) - \alpha_{13}(k)N_{1}(k)N_{3}(k)}$$

$$N_{2}(k+1) = N_{2}(k)e^{a_{2}(k)N_{2}(k) - \alpha_{22}(k)N_{2}^{2}(k) + \alpha_{21}(k)N_{1}(k)N_{2}(k) + \alpha_{23}(k)N_{2}(k)N_{3}(k)}$$

$$N_{3}(k+1) = N_{3}(k)e^{a_{3}(k)N_{3}(k) - \alpha_{33}(k)N_{3}^{2}(k) + \alpha_{31}(k)N_{1}(k)N_{3}(k) + \alpha_{32}(k)N_{2}(k)N_{3}(k)}$$
(596)

By Definition 7, let:

$$N_i(k+1) = f^{n+1}(x_0)$$
 for $i = 1, 2, 3, ...$ and $N_i(k) = f^n(x_0)$ for $i = 1, 2, 3, ...$ (597)

Hence, system (596) becomes:

$$f_1^{n+1}(x_0) = f_1^n(x_0)e^{a_1(k)f_1^n(x_0) - \alpha_{11}(k)f_1^{n2}(x_0) - \alpha_{12}(k)f_1^n(x_0)f_2^n(x_0) - \alpha_{13}(k)f_1^n(x_0)f_3^n(x_0)}$$

$$f_2^{n+1}(x_0) = f_2^n(x_0)e^{a_2(k)f_2^n(x_0) - \alpha_{22}(k)f_2^{n2}(x_0) + \alpha_{21}(k)f_1^n(x_0)f_2^n(x_0) + \alpha_{23}(k)f_2^n(x_0)f_3^n(x_0)}$$

$$f_3^{n+1}(x_0) = f_3^n(x_0)e^{a_3(k)f_3^n(x_0) - \alpha_{33}(k)f_3^{n2}(x_0) + \alpha_{31}(k)f_1^n(x_0)f_3^n(x_0) + \alpha_{32}(k)f_2^n(x_0)f_3^n(x_0)}$$
(598)

given initial conditions:

$$x_1(0) = f_1^0(x_0) = x_1^0 \tag{599}$$

$$x_2(0) = f_2^0(x_0) = x_2^0 \tag{600}$$

$$x_3(0) = f_3^0(x_0) = x_3^0 \tag{601}$$

If $f^{n+1}(x_0) \to 0$ as $n \to \infty$. \Rightarrow There exists a unique and continuous solution of system (596).

$\mathbf{20}$ Permanence

Discrete Form of System Using Euler's Method 20.1

Considering the following non-linear discrete autonomous time-invariant system of difference equations:

$$N_1(k+1) = N_1(k) + h[a_1N_1(k) - \alpha_{11}N_1^2(k) - \alpha_{12}N_1(k)N_2(k) - \alpha_{13}N_1(k)N_3(k)]$$
(602)

$$N_2(k+1) = N_2(k) + h[a_2N_2(k) - \alpha_{22}N_2^2(k) + \alpha_{21}N_1(k)N_2(k) + \alpha_{23}N_2(k)N_3(k)]$$
(603)

$$N_3(k+1) = N_2(k) + h[a_3N_3(k) - \alpha_{33}N_3^2(k) + \alpha_{31}N_1(k)N_3(k) + \alpha_{32}N_2(k)N_3(k)]$$
(604)

Here, we prove that the system is persistent. Hence, we prove that:

$$\liminf_{t \to \infty} N_1(k+1) > 0 \tag{605}$$

$$\liminf_{t \to \infty} N_2(k+1) > 0 \tag{606}$$

$$\liminf_{t \to \infty} N_3(k+1) > 0 \tag{607}$$

Here, we assume that the parameters $N_i(k) > 0$ and the constants $a_i, \alpha_{ij} > 0$ for i = 1, 2, 3 and j = 1, 2, 3.

1. Considering equation (602):

$$N_1(k+1) = N_1(k) + h[a_1N_1(k) - \alpha_{11}N_1^2(k) - \alpha_{12}N_1(k)N_2(k) - \alpha_{13}N_1(k)N_3(k)]$$
(608)

If:

$$a_1 N_1(k) > \alpha_{11} N_1^2(k) + \alpha_{12} N_1(k) N_2(k) + \alpha_{13} N_1(k) N_3(k)$$
(609)

or

•

$$a_1 N_1(k) < \alpha_{11} N_1^2(k) + \alpha_{12} N_1(k) N_2(k) + \alpha_{13} N_1(k) N_3(k)$$

and
(610)

and

$$N_1(k) > h[a_1N_1(k) - \alpha_{11}N_1^2(k) - \alpha_{12}N_1(k)N_2(k) - \alpha_{13}N_1(k)N_3(k)]$$

then:

$$\liminf_{t \to \infty} N_1(k+1) > 0 \tag{611}$$

and equation (602)/(608) is said to be persistent.

2. Considering equation (603):

$$N_2(k+1) = N_2(k) + h[a_2N_2(k) - \alpha_{22}N_2^2(k) + \alpha_{21}N_1(k)N_2(k) + \alpha_{23}N_2(k)N_3(k)]$$
(612)

If:

$$\alpha_{22}N_2^2(k) < a_2N_2(k) + \alpha_{21}N_1(k)N_2(k) + \alpha_{23}N_2(k)N_3(k)$$
(613)

or

•

$$\alpha_{22}N_2^2(k) > a_2N_2(k) + \alpha_{21}N_1(k)N_2(k) + \alpha_{23}N_2(k)N_3(k)$$
and
(614)

$$N_2(k) > h[a_2N_2(k) - \alpha_{22}N_2^2(k) + \alpha_{21}N_1(k)N_2(k) + \alpha_{23}N_2(k)N_3(k)]$$

then:

$$\liminf_{t \to \infty} N_2(k+1) > 0 \tag{615}$$

and equation (603)/(612) is said to be persistent.

3. Considering equation (604):

$$N_3(k+1) = N_2(k) + h[a_3N_3(k) - \alpha_{33}N_3^2(k) + \alpha_{31}N_1(k)N_3(k) + \alpha_{32}N_2(k)N_3(k)]$$
(616)

If:

$$\alpha_{33}N_3^2(k) < a_3N_3(k) + \alpha_{31}N_1(k)N_3(k) + \alpha_{32}N_2(k)N_3(k)$$
(617)

or

•

$$\alpha_{33}N_3^2(k) > a_3N_3(k) + \alpha_{31}N_1(k)N_3(k) + \alpha_{32}N_2(k)N_3(k)$$

and (618)

and

$$N_2(k) > h[a_3N_3(k) - \alpha_{33}N_3^2(k) + \alpha_{31}N_1(k)N_3(k) + \alpha_{32}N_2(k)N_3(k)]$$

then:

$$\liminf_{t \to \infty} N_3(k+1) > 0 \tag{619}$$

and equation (604)/(616) is said to be Persistent.

Therefore, if:

1.

$$\liminf_{t \to \infty} N_1(k+1) > 0 \tag{620}$$

$$\liminf_{t \to \infty} N_2(k+1) > 0 \tag{621}$$

$$\liminf_{t \to \infty} N_3(k+1) > 0 \tag{622}$$

2. Conditions (609), (610), (613), (614), (617) and (618) are true.

 \Rightarrow The system of equations (370) is Persistent.

20.2 Discrete Form of System Using Method of Piecewise Constant Arguments

Consider the following discrete non-linear autonomous time-invariant system of difference equations:

$$N_1(k+1) = N_1(k)e^{a_1(k)N_1(k) - \alpha_{11}(k)N_1^2(k) - \alpha_{12}(k)N_1(k)N_2(k) - \alpha_{13}(k)N_1(k)N_3(k)}$$
(623)

$$N_2(k+1) = N_2(k)e^{a_2(k)N_2(k) - \alpha_{22}(k)N_2^2(k) + \alpha_{21}(k)N_1(k)N_2(k) + \alpha_{23}(k)N_2(k)N_3(k)}$$
(624)

$$N_3(k+1) = N_3(k)e^{a_3(k)N_3(k) - \alpha_{33}(k)N_3^2(k) + \alpha_{31}(k)N_1(k)N_3(k) + \alpha_{32}(k)N_2(k)N_3(k)}$$
(625)

Here, we prove that the system is persistent. Hence, we prove that:

$$\liminf_{t \to \infty} N_1(k+1) > 0 \tag{626}$$

$$\liminf_{t \to \infty} N_2(k+1) > 0 \tag{627}$$

$$\liminf_{t \to \infty} N_3(k+1) > 0 \tag{628}$$

Here, we assume that the parameters $N_i(k) > 0$ and the constants $a_i(k)$, $\alpha_{ij}(k) > 0$ for i = 1, 2, 3 and j = 1, 2, 3.

1. Considering equation (623):

$$N_1(k+1) = N_1(k)e^{a_1(k)N_1(k) - \alpha_{11}(k)N_1^2(k) - \alpha_{12}(k)N_1(k)N_2(k) - \alpha_{13}(k)N_1(k)N_3(k)}$$
(629)

Since

$$N_1(k) > 0$$
 (630)

and

$$e^{a_1(k)N_1(k) - \alpha_{11}(k)N_1^2(k) - \alpha_{12}(k)N_1(k)N_2(k) - \alpha_{13}(k)N_1(k)N_3(k)} > 0$$
(631)

then:

$$\liminf_{t \to \infty} N_1(k+1) > 0 \tag{632}$$

and equation (623)/(629) is said to be Persistent.

2. Considering equation (624):

$$N_2(k+1) = N_2(k)e^{a_2(k)N_2(k) - \alpha_{22}(k)N_2^2(k) + \alpha_{21}(k)N_1(k)N_2(k) + \alpha_{23}(k)N_2(k)N_3(k)}$$
(633)

Since

$$N_2(k) > 0$$
 (634)

and

$$e^{a_2(k)N_2(k) - \alpha_{22}(k)N_2^2(k) + \alpha_{21}(k)N_1(k)N_2(k) + \alpha_{23}(k)N_2(k)N_3(k)} > 0$$
(635)

then:

$$\liminf_{t \to \infty} N_2(k+1) > 0 \tag{636}$$

and equation (624)/(633) is said to be Persistent.

3. Considering equation (625):

$$N_3(k+1) = N_3(k)e^{a_3(k)N_3(k) - \alpha_{33}(k)N_3^2(k) + \alpha_{31}(k)N_1(k)N_3(k) + \alpha_{32}(k)N_2(k)N_3(k)}$$
(637)

Since

$$N_3(k) > 0$$
 (638)

and

$$e^{a_3(k)N_3(k) - \alpha_{33}(k)N_3^2(k) + \alpha_{31}(k)N_1(k)N_3(k) + \alpha_{32}(k)N_2(k)N_3(k)} > 0$$
(639)

then:

$$\liminf_{t \to \infty} N_3(k+1) > 0 \tag{640}$$

and equation (625)/(637) is said to be Persistent.

Therefore, since

$$\liminf_{t \to \infty} N_1(k+1) > 0 \tag{641}$$

$$\liminf_{t \to \infty} N_2(k+1) > 0 \tag{642}$$

$$\liminf_{t \to \infty} N_3(k+1) > 0 \tag{643}$$

 \Rightarrow The system of equations (374) is Persistent.

Conclusion

To summarise what this investigation has discovered, In Chapter 1 we studied basic concepts of population modelling. These included single equations of continuous nature such as the Malthus [27] and Verhulst [45] models and the example of Monod's Nightmare [20], [31] associated with the growth of E. coli. We also examined single equations of a discrete nature involving difference equations, focusing on density-dependent and density-independent growth and examples that simulated growth of rabbit, cell and insect populations [4], [30]. Next we looked at systems of equations and how they can be solved. For continuous type systems, this involved the elimination and eigenvalue-eigenvector method whilst the discrete case of equations required the classification of autonomous time-invariant or non-autonomous time-variant types of systems as well as linear and non-linear cases. Following the classification of systems of a continuous or discrete nature, we examined interacting populations including predator-prey, competition and mutualism or symbiosis relationships. Here, we investigated the Lotka-Volterra Model [25], [26], [30], [47] and how it could be modified for each type of interaction. We also studied examples of these interactions including the Canadian lynx and snowshoe hare [30], a host-parasitoid system [4] and the spread of and introduced pest in the form of the red and black fire and [22], [46].

Chapters 2 and 3 introduced stability analysis of both continuous and discrete systems. Here we studied theorems and examples of linear problems involving calculating equilibrium solutions and non-linear problems including eigenvalue, linearisation and Lyapunov methods [2], [5], [42].

In Chapter 4 we studied the research paper - A Model of a Three Species Ecosystem with Mutualism Between The Predators by K. S. Reddy and N. C. Pattabhiramacharyulu [32]. Here, we looked at the basic definitions and assumptions of the model, examined different cases for equilibrium solutions, proved global stability of the system and implemented numerical examples for the model before reviewing existence and uniqueness and permanence properties.

Chapter 5 involved constructing a discrete scheme of the model from Chapter 4. We were able to do this in two ways, by using Euler's method to create one autonomous time-invariant form of the system, and utilising the method of piecewise constant arguments implemented in the research paper Periodic Solutions of a DIscrete Time Nonautonomous Ratio-Dependent Predator-Prey System by M Fan and K Wang [6] to establish another autonomous timeinvariant form of the system. For both discretisations, we studied equilibrium solutions, stability using the linearisation method, numerical examples and existence and uniqueness, and permanence properties.

In future, this investigation could be taken further in a number of ways. Many examples in Chapters 1 and 3 could be developed by studying stability, existence and uniqueness and permanence properties as studied for systems in Chapters 4 and 5. These examples could also be implemented in mathematical software such as MATLAB in order to integrate numerical examples that produce quantitative results and behaviours for each model or system. The continuous and discrete models in Chapters 4 and 5 are bases for implementing further concepts such as delay-differential equations. They can also be studied further in terms of stability analysis. For systems (211), (370) and (374) we used the linearisation method to determine stability. The Lyapunov method for a given Lyapunov function could also be used as well as additional stability methods. For Euler's method and the method of piecewise constant arguments, we created two numerical examples each. Here, additional examples could be used, incorporating different values of a_i, α_{ij} and $N_i(0)$ for i = 1, 2, 3 as well as different step sizes hfor the scheme using Euler's method.

Bibliography

- [1] Beverton RJH, Holt SJ. On the dynamics of exploited fish populations. *Fishery Investigations*. Series II. 19:1-533. 1957.
- [2] Braun M. Differential Equations and their Applications: An Introduction to Applied Mathematics, 4th ed. New York: Springer-Verlag. 1993.
- [3] Burden RL, Faires JD. Numerical Analysis. 8th ed. Belmont, CA; London: Thomson Brooks/Cole. 2005.
- [4] Edelstein-Keshet L. Mathematical Models in Biology. Random House: New York. 1988.
- [5] Elaydi SN. An Introduction to Difference Equations, 2nd ed. New York: Springer. 1999.
- [6] Fan M, Wang K. Periodic Solutions of a Discrete Time Nonautonomous Ratio-Dependent Predator-Prey System. Mathematical and Computer Modelling. 35. 951-961. 2002.
- [7] Finch CE. Longevity, Senescence, and the Genome. University of Chicago Press, Chicago. 1990.
- [8] Gompertz B. On the Nature of the Function Expressive of the Law of Human Mortality, and on a New Mode of Determining the Value of Life Contingencies. *Philosophical Transactions* of the Royal Society of London. 115:513-83. 1825.
- [9] Gopalsamy K. Stability and Oscillations in Delay Differential Equations of Population Dynamics. AA Dordrecht, Netherlands: Kluwer Academic. 1992.
- [10] Gross LJ. Ecology: an idiosyncratic overview. In Biomathematics. Mathematical Ecology. Ed. Hallam TG & Levin SA. Berlin: Springer-Verlag. 17:3-15. 1986.
- [11] Hale JK, Waltman P. Persistence in Infinite-dimensional Systems. SIAM Journal on Mathematical Analysis. Society for Industrial and Applied Mathematics: Philadelphia, PA, USA. 20(2): 388-395. 1989.
- [12] Hassell MP. The Dynamics of Arthropod Predator-Prey Systems. Princeton University Press, NJ, Princeton, 1978.
- [13] Hastings A. Population Biology (1st edition 1997). New York, Springer-Verlag. 2000.
- [14] Hillis W D. Why physicists like models and why biologists should. Current Biology. Vol. 3(2): 79-81. 1993.
- [15] Hoppensteadt FC & Peskin CS. Mathematics in Medicine and the Life Sciences. Springer-Verlag, Berlin-Heidelberg-New York. 1992.

- [16] Hsu SB, Hubbell SP, Waltman P. A contribution to the theory of competing predators. *Ecological Monographs.* 48:337349. 1979.
- [17] Istas J. Mathematical Modeling for the Life Sciences. Berlin: Springer. 2005.
- [18] Jordan DW, Smith P. Nonlinear Ordinary Differential Equations: An Introduction for Scientists and Engineers, 4th ed. Oxford: Oxford University Press. 2007.
- [19] Kirlinger G. Permanence of some ecological systems with several predator and one prey species. *Journal of Mathematical Biology*. 26(2): 217-232. 1988.
- [20] Kot M. Elements of Mathematical Ecology. Cambridge: Cambridge University Press. 2001.
- [21] Kuang Y. Delay Differential Equations: with Applications in Population Dynamics. Boston: Academic Press; 1993.
- [22] Lockley TC. Imported fire ants. In Radcliffes IPM World Textbook. University of Minnesota. http://ipmworld.umn.edu/lockley.
- [23] Logan JD, Wolesensky WR. Mathematical Methods in Biology. Oxford: Wiley. 2009.
- [24] Lomen D, Mark J. Differential Equations. Englewood Cliffs, NJ; London: Prentice Hall International. 1988.
- [25] Lotka AJ. *Elements of Physical Biology*. Williams and Wilkins, Baltimore. 1925.
- [26] Lotka AJ. Undamped oscillations derived from the law of mass action. *Journal of the American Chemical Society.* 42:15951599. 1920.
- [27] Malthus TR. An Essay on the Principle of Population. Anonymously published. 1798 (reprinted by Cosimo Classics, 2007).
- [28] May RM. Stability and Complexity in Model Ecosystems, 2nd ed. Princeton: University Press. 1974.
- [29] McClure FA. The Bamboos a Fresh Perspective. Harvard University Press, Cambridge, MA. 1967.
- [30] Murray JD. Mathematical Biology. New York: Springer. 2002.
- [31] Panikov NS. Microbial Growth Kinetics. Chapman Hall: London. 1995.
- [32] Reddy KS, Pattabhiramacharyulu NC. A Model of a Three Species Ecosystem with Mutualism Between the Predators. *International Journal of Mathematics and Scientific Computing*. Vol 1. No 2. 87-90. 2011.
- [33] Renshaw E. Modelling Biological Populations in Space and Time, New. ed. Cambridge U.P: ; 1993.
- [34] Richards FJ. A Flexible Growth Function for Empirical Use. Journal of Experimental Botany. 1959. 10(2):290-301.
- [35] Segel LA, Edelstein-Keshet L. A Primer on Mathematical Models in Biology. Philadelphia, PA: Society for Industrial and Applied Mathematics; 2013.

- [36] Shonkwiler RW. Mathematical Biology: An Introduction with Maple and Matlab, 2nd ed. New York; London;: Springer; 2007.
- [37] Sirovich L. Introduction to Applied Mathematics. Springer Verlag. 1988.
- [38] Smith HL. An Introduction to Delay Differential Equations with Applications to the Life Sciences. New York: Springer; 2010.
- [39] Smith JM. Models in Ecology. Cambridge University Press. 1974.
- [40] Suli E, Mayers DF. An Introduction to Numerical Analysis. Cambridge; New York; Cambridge University Press. 2003.
- [41] Tauber S. Existence and Uniqueness Theorems for Solutions of Difference Equations. The American Mathematical Monthly. 71(8): 859-62. 1964.
- [42] Taubes CH. Modeling Differential Equations in Biology, 2nd ed. Cambridge: Cambridge University Press. 2008.
- [43] Thorp JH, Covich AP. Ecology and Classification of North American Freshwater Invertebrates. Academic Press, San Diego, CA. 1991.
- [44] Tikhonov AN, Vasil'eva AB, Sveshnikov AG. Differential Equations. Springer Verlag. 1984.
- [45] Verhulst PF. Notice sur la loi que la population poursuit dans son accroissement. Correspondance mathematique et physique. 1838. 10: 113-121.
- [46] Voit EO. A First Course in Systems Biology. Abingdon; New York;: Garland Science; 2013.
- [47] Volterra V. Variazioni e fluttuazioni del numero d'individui in specie d'animali conviventi. Accademia Nazionale dei Lincei. 2:31-113. 1926.
- [48] Waltman PE. Competition Models in Population Biology. Philadelphia, Pa: Society for Industrial and Applied Mathematics; 1983.
- [49] Whitham TG. The theory of habitat selection: examined and extended using Pemphigus aphids. American Naturalist. 115:449-466. 1980.
- [50] Wiener J. Differential Equations with Piecewise Constant Delays. Trends in Theory and Practice of Nonlinear Differential Equations. *Journal of Pure and Applied Mathematics*. Marcel Dekker, New York. 90:547-552. 1984.
- [51] Yeargers EK, Shonkwiler RW, Herod JV. An Introduction to the Mathematics of Biology: With Computer Algebra Models. Boston: Birkhauser; 1996.
- [52] Zhang L, Teng Z, Jiang H. Permanence for General Nonautonomous Impulsive Population Systems of Functional Differential Equations and Its Applications. Acta Applicandae Mathematicae. 110(3): 1169-97. 2010.