UNCERTAINTY QUANTIFICATION IN POPULATION MODELS

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UNCERTAINTY QUANTIFICATION IN POPULATION MODELS

by

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LIST OF ABBREVIATIONS

SIR Susceptible Infected Recovered Model

SIS Susceptible Infected Susceptible Model

SI Susceptible Infected Model

SIRS Susceptible Infected Recovered Susceptible Model

PDF Probability Density Function

CDF Cumulative Density Function

ODEs Ordinary Differential Equations

IVPs Initial Value Problems

FIVPs Fuzzy Initial Value Problems

RIVPs Random Initial Value Problems

S-W Shapiro-Wilk Test

K-S Kolmogorov-Smirnov Test

AIDS Acquired Immunodeficiency Syndrome

HIV Human Immunodeficiency Virus

PENGKUANTIFAN KETIDAKPASTIAN DALAM MODEL POPULASI

ABSTRAK

Ketidakpastian pada umumnya, boleh dalam diungkapkan dalam bentuk berangka atau tak berangka dengan masing-masing diperihalkan sebagai kuantitatif dan kualitatif. Dalam kuantiti berangka, ketidakpastian boleh mengambil bentuk rawak dan di sini teori kebarangkalian adalah sesuai, atau ia boleh terhasil daripada maklumat yang tak jelas dan penggunaan teori set kabur adalah sesuai.

Pertimbangan kami di sini adalah pada ketidakpastian dalam model populasi, yang diperihalkan melalui persamaan pembezaan yang diselesaikan secara berangka. Kami memilih model pemangsa-mangsa dan model wabak dijangkiti-pulih untuk meneroka ketidakpastian dalam model populasi melalui syarat-syarat awal. Untuk model rawak, taburan normal dipilih untuk memperkenalkan ketidakpastian dalam model pemangsa-mangsa manakala taburan Beta digunakan untuk ketidakpastian dalam model wabak. Untuk pendekatan kabur, nombor kabur segi tiga digunakan untuk mengambil kira ketidakpastian maklumat dalam kedua-dua model.

Model yang dipilih diungkapkan sebagai satu sistem persamaan pembezaan tak linear. Untuk simulasi berangka, prosedur Runge-Kutta peringkat 4 diubahsuaikan untuk menyelesaikan sistem kedua-dua model apabila ketidaktentuan rawak dan kabur dipertimbangkan. Bagi persamaan pembezaan kabur, kaedah yang diubah suai digu-

nakan untuk menyelesaikan masalah pergantungan dalam pengiraan kabur. Pendekatan ini dibandingkan, melalui contoh berangka, dengan pendekatan yang lain dalam kesusasteraan di mana keputusan menunjukkan pendekatan kami lebih tepat dan berkesan.

Seterunnya, tingkah laku rawak dan kabur kesemua model diperhatikan dan dikaji untuk memahami dan memberi perbincangan yang berguna tentang kesan-kesan ketidakpastian pada interaksi antara komponen model.

UNCERTAINTY QUANTIFICATION IN POPULATION MODELS

ABSTRACT

Uncertainty in general can be in the form of numeric or non-numeric, where the latter is qualitative and the former quantitative in nature. In numerical quantities, uncertainty can be random in nature, in which case probability theory is appropriate, or it can be as a result of unclear information, whereby fuzzy set theory is useful.

Our concern will be on uncertainty in population models described by differential equations and solved numerically. We select the predator-prey model and susceptible-infected-recovered epidemic model to explore the uncertainty in the population models through the initial states. For randomness, the normal distribution is selected to introduce the uncertainty in the predator-prey model while we use the Beta distribution to insert the uncertainty in the epidemic model. For the fuzzy approach, we consider a triangular fuzzy number to treat the lack of information in the both models.

The selected models are each cast as a system of nonlinear ordinary differential equations. To carry out numerical simulations, we modified the Runge-Kutta of order 4 to solve the systems of both models when the random and fuzzy uncertainty is considered. For fuzzy differential equations, the modified procedure is adopted to solve the dependency problem in fuzzy computation. This approach is compared, via numerical examples, with other approaches in literature where the results are shown to

be more accurate and effective.

Further, the random and fuzzy behaviors of all models were observed and studied in order to understand and to give useful discussion about the effects of uncertainty on the interaction between the components of the models.

CHAPTER 1

INTRODUCTION

1.1 Overview

Richard Feynman believes that:

"It is in the admission of ignorance and the admission of uncertainty that there is a hope for the continuous motion of human beings..."(Feynman, 1998).

Feynman was of course talking about the incompleteness of our understanding of physics. However, in the context of our everyday life, this quote brings to mind many questions. Do we live in a world of certainty, or is it otherwise? Do our everyday decisions depend on complete and clear information? Does the available information represent the correct and complete information? When faced with unclear and incomplete information, are we able to decide or not? For example, if the sky is cloudy should we bring along an umbrella or not when we go out. This is an example of the uncertainty facing humans every day. Together with the sometimes unpredictability of human actions, predicting with certainty the course of actions of members of society can be an impossible task.

The idea of uncertainty has been around for some time within the statistics domain. However, it is only for the past few years that scientists and engineers have been thinking seriously about the implications of uncertainty in their respective fields. They have

come to realize that most real world phenomenon and physical experiments cannot be described fully 100%, partly because the full information is just not available.

One way to comprehend phenomena and ideas is through mathematical models. The development of most models depends on hypothesis about the system that is being studied. A criterion for the correctness of the model is the correspondence with available data. On the other hand, a particular model can be useful when there is no correspondence between model and data. This shows that some of the ideas used to build the model are not right. This does not mean that models are not useful. Among the usefulness is the ability to assess quantitative conjectures and to determine sensitivities to changes to parameter values.

Models describing real physical, chemical, or biological phenomena are normally deterministic models that take the form of differential equations. Input data for these models may have been measured, derived from remotely sensed imagery, or obtained from experts. The data are often pre-processed prior to submission to a model. As a result, uncertainty and errors are introduced. Users may or may not be aware that the uncertainty is propagateed through their models. However, this problem is rarely addressed. This is unfortunate since when the accuracy of the data is insufficient for the intended purpose, it will result in inaccurate solutions, wrong conclusions and poor decisions.

In population models such as the predator-prey model, uncertainty quantification generally happens when the initial state of population processes may be available but they cannot be defined with certainty due to low accuracy of the measurement process

and imprecise human knowledge as well as difficulties in assessing the actual population sizes. Similarly, in epidemic models, uncertainty can happen when the transmission rates are not known with certain or are approximated or when the simulation of an epidemic might require an educated guess for the initial state of infected individuals. In this situation, the mathematical model is not able to describe the dynamic behavior of the epidemic completely. Hence, mathematical descriptions of the model must be modified to account for uncertainty.

Now, this raises the question of how a mathematical model be modified can to accurately describe such a real phenomenon and what the impact of model uncertainty is (structural or parametric) on outputs from the model. Actually, understanding uncertainty is one of the great scientific and engineering challenges at the present time. It impacts on many crucial issues facing the world today. Some of the examples are, climate change prediction, economic, ecological and biological modeling, and the interpretation of medical data. Randomness and fuzziness are now well accepted as powerful and strong tools in dealing with such limitations. The former tool is a basic type of objective uncertainty, and in system theory, uncertainty is classically treated in probabilistic form by the theory of stochastic processes. However, when the underlying structure is not probabilistic, then it may be appropriate to use the latter tool which is the fuzzy theory instead of randomness.

The uncertainty quantification in principle is not a result of one part of the system but originates in the intrinsic uncertainty of all system. According to Diniz et al. (2001), the uncertainty can arise in the experimental part, the data collection, the measurement process, as well as when determining the initial conditions. Soong (1973)

considered the uncertainty in differential equation in different forms; the first is characterized by the presence of a random input term or source term, the second when the uncertainty enters through the parameters, and finally when the initial conditions are random. In population models, some research on uncertainty has been conducted. By way of example, Xu and Gertner (2009) introduced an uncertainty analysis technique, the general Fourier Amplitude Sensitivity Test (FAST), to study uncertainties in transient population dynamics. They found that the general FAST is able to identify the amount of uncertainty in transient dynamics and contributions by different demographic parameters. The general FAST is applied to a mountain goat (Oreamnos americanus) matrix population model to give a clear illustration of how uncertainty analysis can be conducted for transient dynamics arising from matrix population models. Pollett et al. (2010) presented a general method for incorporating random initial conditions in population models where a deterministic model is sufficient to describe the dynamics of the population. They observed that for a large class of stochastic models, the overall variation is the sum of variation due to random initial conditions and variation due to random dynamics.

Further, da Silva Peixoto et al. (2008) studied the fuzzy predator-prey population model. The authors create a model to study the interaction between aphids and ladybugs which represent a prey and its predator respectively by using fuzzy set theory by means of a fuzzy rule-based system. They compare the fuzzy model with the Holling-Tanner model by fitting some parameters of the latter model by the system of the new fuzzy model. Moreover, the stability of the critical points of the Holling-Tanner model is also studied. Ahmad and Bernard (2009), Ahmad and Hasan (2012) also addressed this issue by introducing the uncertainty through the initial states of the simple

prey predator model via assuming these initial states as interactive and non-interactive fuzzy intervals. The authors used a new computational approach to generate the fuzzy solution and to analyse the stability of the system.

In the epidemiological models, Kegan and West (2005) introduced the uncertainty in the simple susceptible-infectious epidemic model through their initial conditions. The authors investigated the effect of random initial conditions on the deterministic model for the epidemic by assuming a distribution on the initial proportion of the susceptible. A distribution for the proportion of the susceptible in time was developed and explored and they obtained the distribution of time until a given proportion of population remains susceptible. The author used an analytical technic to obtain the random solution and to compute some statistical properties of the solution. Enszer (2009) proposed an approach to verify the solution of a nonlinear dynamic model such as the SIRS model and other types of Kermack-McKendrick models. The approach useed Taylor models to present dependence on uncertain parameters and initial states, which means there is no information provided about the distribution of the uncertain values since only the upper and the lower bounded intervals are provided.

Several authors have used the fuzzy set theory to treat the uncertainty in the epidemiological models. Massad et al. (2008) worked on modeling the dynamics of rabies among a population of partially vaccinated dogs where the modeling process is based on fuzzy linguistic rules compared to the approach of crisp differential equations. The set of rules were chosen to have biological meaning to describe the system dynamics and the results were encouraging. de Oliveira (2002) considered the transmission and recuperation rates of the susceptible-infected-susceptible epidemiological model as a

fuzzy set. The authors presented more information about the disease based on the Basic Reproduction Value R_0, where they concluded that if the uncertainty is excluded before modeling, important parameters that manage and control the phenomenon will not be perfectly computed. Jafelice et al. (2004) addressed fuzziness in Anderson's model for AIDS through the transference rate of HIV. The process is based on the fuzzy rule base, which assumed dependence on the viral load and the level of $CD4+$. The results show that the fuzzy model provides a clearer and more meaningful characterization of the transference rate that is compatible with medical knowledge and perception.

The main concern of our research efforts is to focus on dynamical systems of differential equation of more complicated type for population models, where the initial conditions are described by randomness and fuzziness uncertainty. The effect of the uncertainty on the initial conditions on the interaction between a prey and its predator and the classes of the epidemic model is investigated for both models and both situations of uncertainty.

1.2 Problem Statement

Models such as the predator-prey model and the susceptible-infected-recovered epidemic model are described by differential equations. Naturally there will be differences between a mathematical model and reality due to inherent uncertainties in the model. Indeed, the uncertainty, for instance, in ecological and biological systems may force us to alter in radical ways our traditional (classical, crisp) approaches to the analysis of such systems. We therefore, may have to accept as unavoidable a substantial degree of probabilistic or fuzziness in the description of the behavior of ecological

and biological systems as well as in their characterization. As we mentioned in the previous section, the simple predator-prey model was studied when the initial population sizes were uncertain and some epidemic models were also discussed in the case when the values of the parameters/or initial conditions were unknown with certainty. The purpose of this study is to investigate the uncertainty in more complicated type of predator-prey models and epidemic models by using probability and fuzzy theories. Furthermore, we propose more accurate numerical methods that are able to eliminate, or at least reduce, uncertainty in the simulations for precise description of the models' behaviors.

1.3 Objectives

The major aims in this research are:

1. To introduce the uncertainty in the ratio-dependent predator-prey model and the susceptible-infected-recovered epidemic model through the initial conditions by assuming the normal distribution, Beta distribution and fuzzy numbers as the initial states of these models.

2. To propose accurate numerical methods for the random initial value problems and the fuzzy initial value problems that describe the studied models.

3. To analyse the effects of randomness on the behavior of the prey and their predator, and the behavior of epidemic disease as well.

4. To discuss the influences of fuzziness on the behavior of the populations and the disease.

1.4 Scope of the Study

The scope of the study in this thesis is to analyze uncertainty, generally in population models and especially in the ratio-dependent predator-prey model with Holling type III functional response and in the susceptible-infected-recovered epidemic model due to uncertainty in the initial conditions. Our primary interest will be to investigate efficient numerical approaches to carry out such analysis.

1.5 Significance of the Study

Uncertainty quantification in mathematical models has raised significant interest in recent years. One of the main challenges is to predict the natural course of a model in the absence of uncertainty and to compare what is going to happen to such a model after the proposed uncertainty. In the infectious diseases, for instance, the number of infected individuals involves several levels of imprecision and uncertainty because, for example, inability to obtain complete information about this number. This will force us to adapt the mathematical model in order to have helpful description of the disease's behavior that will assist us to get information about the disease during spread of the epidemic.

1.6 Outlines

This thesis is organized as seen in the flowchart 1.1 with the contributory chapters in blue color.

Chapter 2 offers a historical overview of the population models. This chapter starts with a discrete time simple model of a single species followed by a continuous time

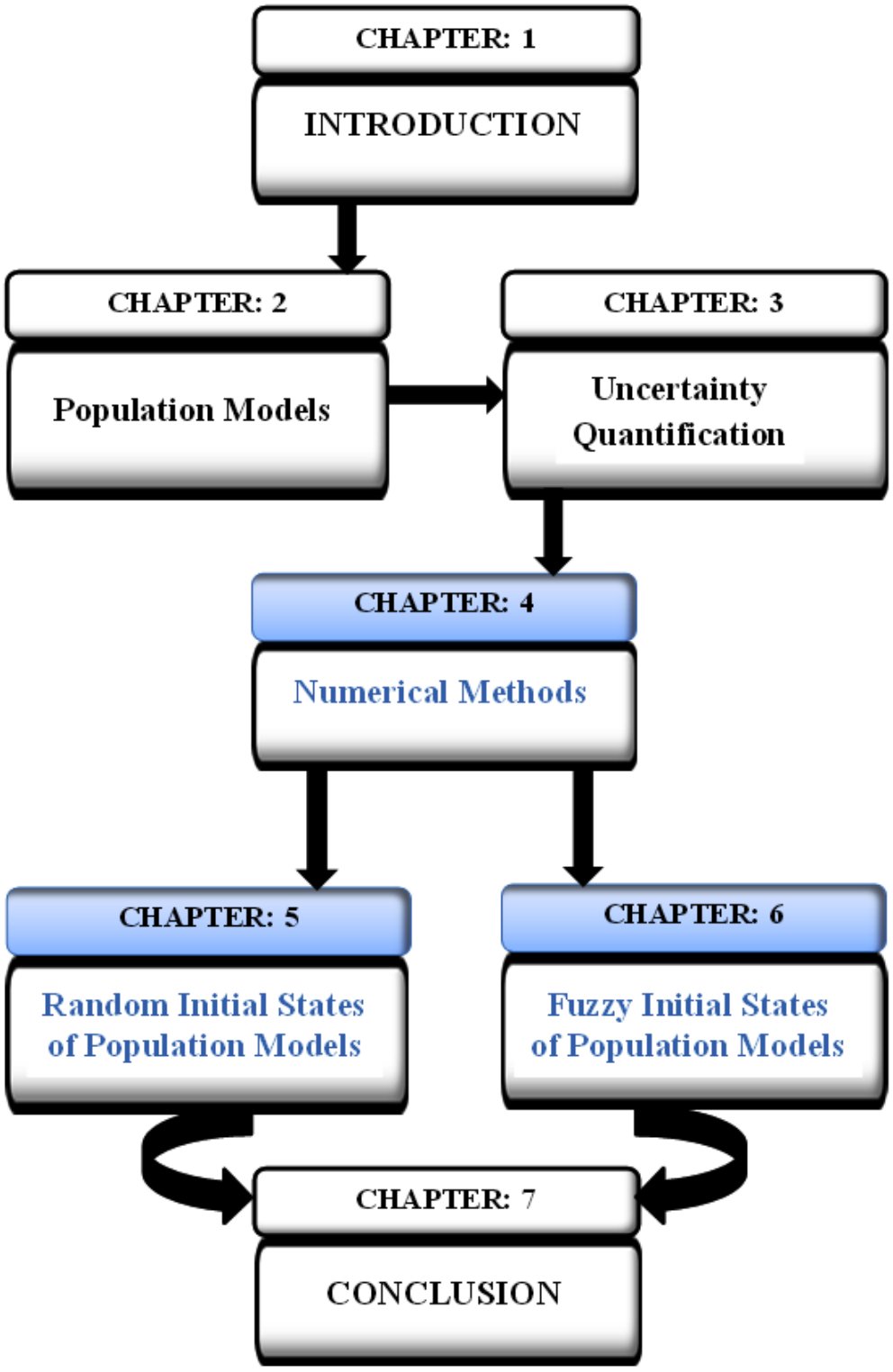

Figure 1.1: Organization of the thesis.

simple model of a single species and build up more sophisticated models as continuous time population models of two species. In the last two sections of the chapter,

we present the predator-prey model and the SIR epidemic model as examples of the interaction of continuous time population models of two species.

In Chapter 3, we provide literature reviews of the uncertainty quantification and its relation with the probability theory and fuzzy set (possibility) theory. Some statistical and fuzzy notations used in this thesis are displayed, and the normal and the Beta distribution are also given in this chapter.

Chapter 4 is divided into two main sections. In the first section, we review methods to obtain the analytical solutions of the random and the fuzzy initial value problems as well as give some illustrative examples. In the first subsection of the second main section, we modify the 4th order Runge-Kutta to solve the random initial value problem, whilst in the second subsection we modify the same method to evaluate the fuzzy solution of the fuzzy initial value problem. The latter modified method is an important contribution of our research efforts. Unlike previous approaches found in the literature, the proposed method takes into account the dependency problem in the fuzzy computation, which is also introduced in this section.

In Chapter 5, the random solutions of the predator-prey model and the SIR model are numerically obtained, and the effect of assuming the initial states of the predator-prey model and the SIR model as random variables having particular distribution function, are studied. Moreover, some statistical properties of the random solutions are also discussed.

In Chapter 6, the fuzzy sets are assumed to be the initial states of the predator-prey model and the SIR model. The numerical approximated fuzzy solutions are evaluated

for both models. The effect of the fuzziness on the models' behavior is investigated. Furthermore, some numerical simulations are carried out.

Finally, conclusions and suggestions for further research are drawn in Chapter 7.

1.7 Outline of Contributions

Several contributions have been supplied in this research

1. Developing a new numerical method for solving the fuzzy initial value problems with the dependency problem. (Chapter 4)
2. Studying the effect of quantity randomness on the ratio-dependent predator-prey model. (Chapter 5)
3. Showing the influence of random uncertainty on the susceptible-infected-recovered epidemic model. (Chapter 5)
4. Investigating the impact of introducing uncertainty into the ratio-dependent predator-prey model using the fuzzy sets concept. (Chapter 6)
5. Offering a discussion that considers the initial states of the susceptible-infected-recovered epidemic model as a fuzzy number. (Chapter 6)

These contributions are further elaborated in the following sub-sections

1.7.1 Developing a New Numerical Method for Solving the Fuzzy Initial Value Problems with the Dependency Problem.

As a graduate student at the University of Toronto, Lee Rozema, who led a new study of the uncertainty principle said

"*You do not have to add more uncertainty to a quantum system by measuring it*"

(Rozema, 18/7/2013; Rozema et al., 2012).

Unfortunately, most established methods for solving the fuzzy initial value problems have not taken into account the dependency problem that increase the uncertainty through the computation via the overestimation. A few who addressed this issue applied the Euler method to compute the fuzzy solution of the model; which, the process of trying to address the overestimation issue, will increase the errors in the computation. In Chapter 4, we develop a new numerical method by modifying the 4th order Runge-Kutta method to solve the fuzzy initial value problem when the dependency problem is included. The new approach is then compared with some established methods via numerical examples, where the result shows that our approach is accurate, capable, and effective in obtaining the solution of fuzzy differential equations. Furthermore, the proposed method is also able to produce good results even when the dependency problem is not included.

1.7.2 Studying the Effect of Quantity Randomness on the Ratio Dependent predator-prey Model.

The uncertainty is introduced in the nondimensional ratio-dependent predator-prey model in Chapter 5. The initial populations sizes are assumed to be random variables that take the form of normal distribution. The random solution is obtained numerically by using a modified 4th order Runge-Kutta, where the simulation allows us to determine the probability distribution functions of the two population at every instance, which have different shapes over time. The distribution functions are tested for normality by using the *Shapiro Wilk* and *Kolmogorov-Smirnov* tests. The outputs illustrate the function will lose the normality after a short time as a result of the influence of the nonlinearity of the system. Stability of the equilibrium points of the model is discussed and some of statistical properties of the random behavior of the model are investigated. The effects of the size of the initial random sample on determining the confidence intervals of the mean and the variance are displayed. The result shows that, the confidence interval decreases as the sample size increases. We observe that, when the initial states of the population begin with uncertainty, the size of this population remains uncertain as the behavior of the variance shows.

1.7.3 Showing the Influence of Random Uncertainty on the Susceptible-Infected-Recovered Epidemic Model.

In Chapter 5, we consider the random uncertainty through the initial states of the susceptible-infected-recovered epidemic model. In this model we assume the random variables to have the Beta distribution form. The random solution is computed as obtaining the probability distribution function at any time, and the effect of random-

ness of the epidemic size is also discussed. The probability density functions initially take different shapes depending on the parameters of the Beta distribution, the shapes change over time depending on the behavior of the epidemic. The variances and the means of all epidemic classes are obtained with 95% confidence intervals; where the results that illustrate the widths of these intervals also depend on the initial sample size. The influence of choosing a variety of the parameters of the Beta distribution on the variances, the means and the interquartile ranges is also discussed. We have clearly observed that when the initial states of the epidemic are not clearly known and start with random uncertainty, that will affect the whole process of the model, which will also be random uncertainty that will still be deterministic within bounded range.

1.7.4 Investigating the Impact of Introducing the Uncertainty into the Ratio Dependent Predator-Prey Model Using the Fuzzy Sets Concept.

In Chapter 6, we use the fuzzy theory to introduce the uncertainty in the dimensional ratio-dependent predator-prey model. The initial populations sizes are considered as fuzzy numbers, and the proposed numerical method (in Chapter 4) is used to compute the fuzzy approximated solution. From the fuzzy solutions obtained we remark some observations.

1. The crisp solution can be obtained when the possibility degree is equal to one.

2. The behavior of the lower and upper bounds of fuzzy intervals that represent the fuzzy solution is similar to the crisp behavior for every possibility degree.

3. Unlikely the diameter of the interval of the fuzzy solution of predators, the diameter of fuzzy solution of preys has non-increasing fuzzy interval over time,

whilst the uncertainty in the population size of predators decreases and increases over time.

The stability of the equilibrium points of the fuzzy model is also studied. The result of the fuzzy simulation illustrates that the coexistence fuzzy equilibrium is unstable because the fuzzy model moves away from this fuzzy equilibrium point.

1.7.5 Offering a Discussion that Considers the Initial States of Susceptible-Infected-Recovered Epidemic Model as a Fuzzy Number.

Similar to the previous contributions, the uncertainty is introduced in the susceptible-infected-recovered epidemic model through the initial states of the epidemic using triangular fuzzy numbers. The fuzzy solution is obtained using the modified 4th order Runge-Kutta method. Every epidemic class has different degrees of fuzziness; when the infected class starts with uncertainty, this uncertainty increases over time and reaches its maximum when the crisp behavior does. Moreover, it approaches zero at the end of the epidemic. On the other hand, when the class of the susceptible begins with uncertainty; the uncertainty will shortly decrease and will never increase during the epidemic. At first, the recovered class is set as zero uncertainty because the number of recovered individuals is assumed to be crisp and equal to zero. After one unit of time, it will be affected by the fuzzy consideration in the other classes and the uncertainty will decrease as time increases.

CHAPTER 2

POPULATION MODELS

2.1 Introduction

Interaction between mathematical science and the other sciences have been increasing rapidly and will continue unabated in the coming years. The application of mathematical principles to biological and ecological processes have made topics such as population dynamics an exciting field. The creation of a mathematical model for the dynamic behavior of any population is equivalent to determining and to investigating how this population is going to change in the near or distant future, taking into account the environmental conditions that the population is exposed to. If we consider the population as individuals, and we ignore any differences in the individuals comprising the group (i.e., male-female differences, age differences), then formulating population model for determining the changes in the population abundance, is simply based on three components of population change, which are birth, death and movement (immigration, emigration and spatial distribution). In this thesis, we shall only consider changes with respect to time. We start with a simple model of a single species and build up more sophisticated models from here.

2.2 Discrete Time Population Models of a Single Species

The rate at which a population increases or decreases discretely can be mathematically expressed as

$$x(t+\Delta t) = x(t) + B(\Delta t) - D(\Delta t) + I(\Delta t) - E(\Delta t). \tag{2.1}$$

This equation is called a *population balance equation*, where x denotes population size, B is births, D is deaths, I the immigration and E the emigration with a small time-step interval Δt, such that, the births and immigration help to increase the population abundance, while both death and emigration of any individual decrease this abundance. The population is assumed to be constrained to a finite region.

Existence and movement of both immigration and emigration in equation (2.1) can be interpreted as individuals having the freedom or ability to move from and into the region of the population. If these components are omitted or ignored, then the region will be closed to any type of movements. Therefore the balance equation (2.1) becomes

$$x(t+\Delta t) = x(t) + B(\Delta t) - D(\Delta t). \tag{2.2}$$

Rearrange the equation (2.2) to get

$$x(t+\Delta t) - x(t) = B(\Delta t) - D(\Delta t). \tag{2.3}$$

where the difference in the right side of the equation (2.3) represents the change in the population state which is equal to the difference between the number of individuals that have been born during the time-step interval Δt and the number that have died during that interval. Notice that equation (2.3) signifies a discrete-time population change. *Discrete-time model* has been considered by many scientists to formulate population dynamics, especially when the goal of the formulation is to model populations where changes only occur once a year or once a season. An example is the population of annual plants that reproduce by producing seeds which over winter germinate in the

year following their cultivation.

2.3 Continuous Time Models of a Single Species

Usually, the populations data might be observed in a laboratory discontinuously over time. The number of the population can only be an integer and therefore the change in the population occurs in integral units. However, it is reasonable to use continuous functions of time to represent the population sizes if the sizes are large enough. To turn to a *continuous-time model*; first, we divide both sides of the balance equation (2.3) by Δt

$$\frac{x(t+\Delta t)-x(t)}{\Delta t} = \frac{B(\Delta t)}{\Delta t} - \frac{D(\Delta t)}{\Delta t}. \tag{2.4}$$

Let Δt approach to 0 on both sides of equation (2.4) as

$$\lim_{\Delta t \to 0} \frac{x(t+\Delta t)-x(t)}{\Delta t} = \lim_{\Delta t \to 0} \frac{B(\Delta t)}{\Delta t} - \lim_{\Delta t \to 0} \frac{D(\Delta t)}{\Delta t}. \tag{2.5}$$

we get

$$\frac{dx(t)}{dt} = B(x) - D(x). \tag{2.6}$$

Equation (2.6) is an ordinary differential equation, where the left hand side represents the derivative of $x(t)$ with respect to time t, while the first part of the right-hand side represents the birth rate of the individuals into the population, and the second part represents the death rate of disappearing individuals from the population.

Since all individuals in the population are supposedly identical, it is often useful to express population parameters such as birth and death rates on the so-called per capita birth rate and per capita death rate, respectively. This is helpful in comparing what

is going on in populations of differing sizes. To determine per capita birth and per capita death rates, we simply divide the rate of births $B(x)$ and the rate of deaths $D(x)$ respectively by the number of the population N as follows

$$b(x) = \frac{B(x)}{x}. \tag{2.7}$$

and

$$d(x) = \frac{D(x)}{x}. \tag{2.8}$$

Therefore, the balance equation (2.9) can be written as

$$\frac{dx(t)}{dt} = b(x)x - d(x)x. \tag{2.9}$$

which is a general continuous-time population balance equation for changes in the population abundance. This equation needs an initial state of a population to specify a whole population dynamic model. Without specifying any initial state, equation (2.9) is not able to determine explicitly how the population abundance is going to change over time. Commonly, this initial state is chosen to be equal to the population size presents at some prior time. Usually we assume that at $t = 0$ the population size is a known value

$$x(0) = x_0. \tag{2.10}$$

2.3.1 Exponential Growth

The earliest appearance of a theoretical relationship between population growth and economic development was presented by Malthus (1798), when he introduced his es-

say on *Principle of Population*. He observed, by looking at the birth and death register, that the population of his parish increased and doubled every 30 years. He assumed the following ordinary differential

$$\frac{dx(t)}{dt} = \beta x - \delta x. \tag{2.11}$$

as the population balance equation, where β and δ were chosen to replace the per capita birth $b(x)$ and death $d(x)$ rates respectively. Malthus (1798) assumed β and δ to be independent of x by considering both as constants which will give the autonomous differential equation for density-independent population growth,

$$\frac{dx(t)}{dt} = rx. \tag{2.12}$$

where

$$r = \beta - \delta. \tag{2.13}$$

where r is known as the population growth rate. By using the initial state in equation (2.10), the separation of variables method can be applied to solve equation (2.12) as

$$\ln \frac{x}{x_0} = rt. \tag{2.14}$$

or

$$x = x_0 e^{rt}. \tag{2.15}$$

The behavior of this solution has two situations. First, is *the exponential growth* without bound which occurs when $r > 0$ (more births than deaths) and the second situation

is *the exponential decay* which occurs once $r < 0$ (more deaths than births). Population growth as described by equation (2.15) is often a reasonable description for the initial growth of populations in the absence of any limiting factor. However, it fails as a long time description since no population can ever grow unboundedly. The resources are limited, hence modification would have to be made to improve the model (2.12).

2.3.2 Logistic Growth

From the viewpoint of Verhulst (1838), the model in equation (2.12) proposed by Malthus (1798) was quite modest as it was just described by linear expressions. He hence formulated a principle and inserted it into the following equation that was constructed for single-species population dynamics

$$\frac{dx(t)}{dt} = ax - bx^2. \tag{2.16}$$

where a and b are positive constants. For most populations, as the population abundance increases the per capita birth rate decreases, due largely to crowding and privation of the individuals in the population. In other words, there is dependency between the population abundance and the per capita birth rate. To realize this dependency, the following balance equation was considered

$$\frac{dx(t)}{dt} = \beta x\left(1 - \frac{x}{F}\right) - \delta x. \tag{2.17}$$

where the parameter β in Malthus' balance equation (2.11) was chosen as the actual per capita birth rate once the population abundance is quite low, and with high values of the population abundance x, it is also chosen to be a linear decreasing value and

reach zero at some population abundance F. The parameter δ is the per capita death rate which is assumed to be density independent.

By some mathematical substituting, the equation (2.17) may be written in a common formula as

$$\frac{dx(t)}{dt} = rx\left(1 - \frac{x}{K}\right). \tag{2.18}$$

Equation (2.18) is called *logistic growth equation* or *Verhulst equation*, where r represents the rate of growth of the population while K is the carrying capacity for the same population. The both parameters were substituted the parameters β, δ and F of equation (2.17) as

$$r = \beta - \delta. \tag{2.19}$$

$$K = \frac{\beta - \delta}{\beta} F. \tag{2.20}$$

The solution of the ordinary differential equation (2.18) with the initial state $x(0) = x_0$ is

$$x(t) = \frac{x_0 e^{rt}}{1 + \frac{x_0}{K}(e^{rt} - 1)}. \tag{2.21}$$

It is called the *sigmoid function*. When K goes to infinity, the dynamical behavior of this solution behaves the same way as the dynamical behavior of (2.15). For finite carrying capacity K, the solution (2.21) has three cases:

Case 1. If $x_0 < K$, the population starts with slow growth, enters a rapid growth phase and then levels off when the carrying capacity for that population has been reached. It asymptotically approaches to K as $t \to \infty$, which requires the per capita birth rate to decline and the per capita death rate to increase.

Case 2. When $x_0 > K$, the behavior is opposite of **Case 1**, where the population in this case decreases and again approaches asymptotically to K as t goes to infinity.

Case 3. If $x_0 = K$ then $x(t) = K$ for all t which means the population stays constant.

As is clearly seen in the logistic model (2.18), the carrying capacity K is a limiting factor on the growth of the population abundance. It is the maximum (minimum) number of individuals which a population abundance can reach when it is initially small (large).

Analyzing the solutions of (2.15) and (2.21) of the exponential and logistic growth respectively, help the modeler to get the needed information on the dynamical behavior of the model. Generally, finding the solution for some models by solving the differential equation is not an easy task, maybe even not possible. In this situation, a method such *Stability Analysis* is provided to deal with analyzing and interpreting the model without finding its solution.

2.3.3 The Stability Analysis

The stability analysis procedure generally depends on two major concepts. First is to locate the *equilibrium population* which is a situation in which the population stays at the same level; that is, the number of births would offset the number of deaths. The equilibrium populations can be estimated by setting the change of those populations to zero. In other words, equilibrium occurs when $dx/dt = 0$. The second concept is to check *the stability* which is the investigation of the trajectories of the solutions in the neighbourhood of the equilibrium. If the trajectories always return (attract) to the

equilibrium point after small disturbances, then this equilibrium is said to be *stable*. If the trajectories move away (repel) from that equilibrium, then the equilibrium is *unstable*.

Referring to the logistic model (2.18), the equilibrium populations are

$$x = 0 \qquad \text{and} \qquad x = K. \tag{2.22}$$

The zero equilibrium population is unstable. This means that after a small deviation of population numbers from $N = 0$, the population never returns back to this equilibrium point. However, the major interest is in the case in which $N = K$. To analyze the solution in the neighborhood of this equilibrium population, let $x = x^* + \varepsilon$ (In this case $x^* = K$) and substitute in the logistic model (2.18) to get

$$\frac{dx}{dt} = \frac{d(x^* + \varepsilon)}{dt} = \frac{dx^*}{dt} + \frac{d\varepsilon}{dt}. \tag{2.23}$$

Since x^* is an equilibrium population then

$$\frac{dx^*}{dt} = 0. \tag{2.24}$$

hence

$$\frac{dx}{dt} = \frac{d\varepsilon}{dt}. \tag{2.25}$$

To approximate an expression for $d\varepsilon/dt$ at all time, we substitute x by $x^* + \varepsilon$ in the right hand side of the logistic model $g(x) = rx(1 - x/K)$ as