The Age-Structured Population Models

A thesis presented in partial fulfilment of the requirements
for the degree of

Master of Science

in

Mathematics

at

Massey University

Norhayati Hamzah
1995

Preface

Mathematical theories of population dynamics have been derived and have been effectively used in the last two hundred years. These theories have appeared both implicitly and explicitly in many important studies of populations: human populations, as well as populations of animals, cells and viruses. The aim of this thesis is to understand how these models have developed with a view to an improved formulation. Nowadays, the structured model can be considered to be of great importance and use. Mathematicians have realised that in real biological and ecological situations, a model should be developed which is at least structured on age especially with higher order animals, for example human and possum populations, so in this thesis we pay much attention to these type of population models. We shall also be discussing the qualitative nature of the solutions to the model: such as the long-term behaviour, steady-age distribution and the stability of the solution in great details.

In chapter 1, we begin with the historical background of the unstructured population in which the properties of individuals are ignored and only the total population is considered. The Malthusian and Verhulst model are set as examples. We then proceed in chapter 2 with the simplest McKendrick's age-structured population model. In chapter 3, we shall show how Laplace transform can be used to solved the problem. We have also chosen some arbitrary functions for either one or both the birth and/or death rate, so that we can make deductions from the assumption of these special cases. Chapter 4, discusses the long-term behaviour: steady age distribution (s.a.d.) and the stability of the solution being analysed. We then generalise the linear age-dependent population model in chapter 5 to a non-linear age-dependent model where the limiting effects (overcrowding and limitation of resources) has an effect, on the specific age class only. Chapter 6 discusses the more realistic non-linear model similar to that described in chapter 5 but here the limiting effects have an effect on the whole population. Finally, we realise that since these models need to be tested, we shall, in chapter 7 test our model with possum populations on data collected from the Orongorongo Valley in Wellington. And then make suggestions for future work in Chapter 8.

Acknowledgments

I would like to particularly thank the following for their incomparable roles and help in preparing this thesis.

♥ Prof. G.C. Wake, who has taught me a great deal throughout the course and always there to give encouragement. For being patience and understanding with all of my problems and making me feel right at home. It has been a very good experience working with you.

♥ Aaron Parshotam, who has willingly spare a lot of his precious time, checking and re-checking my thesis in an attempt to make it better each time right from the begining. He has contributed a lot and partly responsible for the finish product.

♥ Anthony Cole, who has been a very patient tutor, teaching me MATLAB.

♥ Simon Watt, for his last minute role in correcting/checking the grammarical correctness of the thesis.

♥ Prof. Odo Diekmann from CWI, Netherland for his useful suggestions he gave during the Mathematical Modelling conference in Brunei.

♥ All the Mathematics Department Administration staffs, Gail and Vicki for being friendly and assisting me in any way necessary, especially in administrative matters.

♥ My husband Asrul, for his consistent support and effort in helping me to learn and like the computer, for otherwise up to now I would not be able to draw my own graphs.

Lastly, to everyone in Massey University who has contributed in making my stay and study in Palmerston North, New Zealand an enjoyable and a memorable one.

Contents

Chapter 1

Introduction to the early population models

1.1 Introduction

This chapter is concerned with a historical background of unstructured population models. We shall examine Malthusian and Verhulst population models.

1.2 The historical background of the unstructured population models.

Population models are an abstract representation of a situation regarding the population. These may have a purpose of control or to try and understand about the population dynamics, using mathematical concepts such as number, quantity, shape, variability, and so on. It is usually developed from a simple model and extended to a more realistic which will relate better to a real situation. It may be represented either as a single equation or as a system of equations.

Some of the earliest population models developed were the Malthusian model developed in the eighteenth century and the Verhulst model which was developed in the early nineteenth century. These models are unstructured in that they ignored the properties of individuals and considered only the total number of individuals in the population. The limitation of these models is that all members of the population are assumed to be equally likely to die or to reproduce. In a real biological situation however, the rates of breeding and survival are known to vary considerably with age and other properties. This could be related to the overall population health and can affect the overall growth rate of a population in ways that may not be predicted by either one of the above mentioned models. It has been only in the last two centuries that various other extensions of the logistic and alternative unstructured continuous-time populations models were developed which were modifications of the Malthusian model in order to make the model more representative of a real situation.

1.3 The Malthusian or Malthus population model

Malthus (1798) proposed a model of population dynamics in which the population growth rate was proportional to the size of the population. In this model, the properties of the individual were ignored. In mathematical terms, let us consider a small time interval δt and population size $N = N(t)$ in which the (total) births and (total) deaths are assumed to be proportional to the population size and to the time interval. It follows that

$$\textit{number of births}(B) = \beta N \delta t,$$

and

$$\textit{number of deaths}(D) = \mu N \delta t.$$

where β and μ are the birth and death rates *per capita* per unit time, respectively. Here, Malthus is considering the increase of the population size over a period of time to be the balance between the newly formed individuals (B) and the number eliminated (D). Thus we have :

$$\underset{\textit{over the time interval}\,\delta\, t}{\textit{The change in population size}} = \underset{(B)}{\textit{number of births}} - \underset{(D)}{\textit{number of deaths}}$$

This may be expressed as follows:

$$N(t+\delta t) - N(t) = \beta N \delta t - \mu N \delta t \tag{1.1}$$

By letting $\gamma = \beta - \mu$, dividing equation (1.1) by δt and taking the limit as $\delta \to 0$ in (1.1), one may obtain the following differential equation

$$\frac{dN}{dt} = \gamma N, \tag{1.2}$$

where γ is known as the *Malhusian parameter.*

The solution to (1.1) is given by:

$$N = N_0 \exp(\gamma t),$$

where N_0 is the initial population size at t = 0. Depending upon the sign of γ, there may be exponential growth for $\gamma > 0$, a constant population for $\gamma = 0$ or exponential decay for $\gamma < 0$. This is illustrated in Figure 1.1. We shall assume in this model and throughout this thesis that there is no immigration or emigration of individuals.

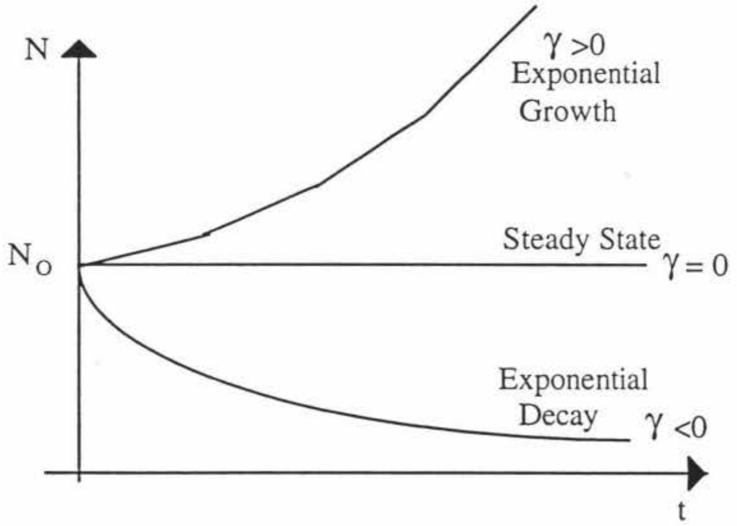


Figure 1.1: Malthusian population model : exponential growth or decay.

The quantities β and μ in (1.1) lend themselves to further analysis in terms of more fundamental characteristics of the aggregate. For example, suppose we have a model in which either one or both the quantities are dependent on age a of the organism. As such the model is made to consider the maximum birth rate to fall generally at some intermediate age while the maximum death rate is at some very young age or at an old age. In a qualitative way, the elimination of individual from a population by death are carried off in infancy, some in childhood, adolescence and maturity, until the remnant is finally eliminated in old age.

Malthus ignored the properties of individuals and considered only the total number of individuals in the population in which we nowadays called the human "population explosion". In a living species, such a simple life curve is usually not possible. It implies that the individual does not *age*, that his/her chance of living another year is just as good at ninety years of age as at fifty or at ten or at five; he/she can die, as it were, only by accident; he/she is perpetually young. Malthus also concluded that barring natural disasters, the world's population would grow exponentially, outgrow its resources and mass starvation would befall humanity. The Malthus model ignores the effects of overcrowding or the limitations of resources. Note that survival curves of this form do occur and play a significant role in the aggregates of atoms and molecules.

Suppose we extend this idea by allowing the Malthusian parameter, $\gamma = \beta - \mu$ to vary with time. For example, γ may be assumed to depend on the environment in some way, with the population growing at a given instant if $\gamma > 0$ and contracting if $\gamma < 0$. It is possible to look back at historical records and deduce the Malthusian parameter for any given periods in the history of a population. Not surprisingly, this turns out to be positive during the "good times" and negative during wars and famines!

1.4 The Verhulst population model

For a more realistic model of population growth, the Malthusian parameter γ may be assumed to be directly dependent on the size of the total population N, and therefore only indirectly dependent on t. Such a model was proposed by Verhulst (1838). The model of Verhulst is simply the modified model to the Malthus model that is achieved by adding a term (crowding effect or competition for resources term) to the right hand side of (1.2). This satisfies the differential equation of the form:

$$\frac{dN}{dt} = \gamma[1 - N / k]N, \tag{1.3}$$

where γ and k are positive constants and in this case we have assumed a linear effect for overcrowding. Then the solution to equation (1.3) with the initial condition N_0 is given by:

$$N(t) = \frac{k}{1 + [(k / N_0) - 1]\exp(-\gamma t)} \tag{1.4}$$

The logistic function suggests that if $N_0 < k$, the population size N simply increases monotonically in k while if $N_0 > k$, it decreases monotonically in k. In Figure 1.2, we can see that the graph curves are approaching the *environmental carrying capacity* k. Actually there are two *steady states* or *equilibrium states*, namely the unstable steady states at $N = 0$ and the stable one at $N = k$. Verhulst concludes that there are times when the rate of growth becomes depressed as the total population N becomes too large. This is a compensating effect of overcrowding which is not observed in the Malthusian population where the population approaches a nontrivial equilibrium state as time, t, approaches infinity.

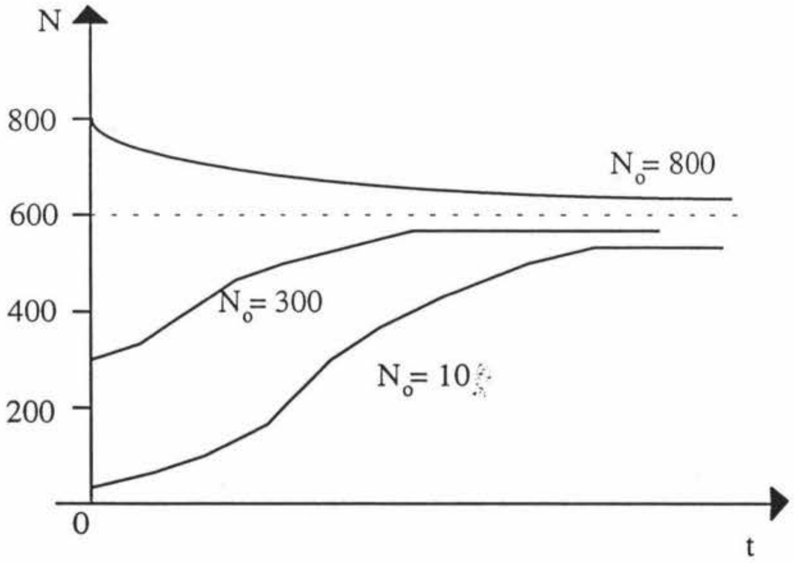


Figure 2.2: The population over time when a population is started with 10, 300 or 800 individuals with k=600.

A modification of this classical logistic form may occur in many other population models. For example: the population dynamics of the bud worm is predicted by the equation:

$$\frac{dN(t)}{dt} = \gamma_B[1 - N(t)/k_B]N(t) - p(N)$$

where γ_B, , k_B and $p(N)$ are the linear birth rate, the carrying capacity related to the density of the foliage available on the trees and the predation, respectively.

In general, the Malthusian, logistic and other unstructured population models are only useful when the individuals in a population are uniform or where the observed differences do not appear to influence the processes of birth and death. By observation this is rare, even though there are some situations where the theoretical curve closely approximates the observed change in population. For example, the population growth of a number of laboratory organisms such a Paramecium, Drosophila and yeast fit the logistic curve. This is because their spatial and age effects seem to be not so important that is the population growth is uniform. In the study of human populations, this is not seen to be true.

1.5 Conclusions

The 'Malthusian' model is the simplest model ever developed. It is far from the reality of most population growth. It has ignored the properties of individuals which implies that individuals do not age and consider only the total number of individuals present in the population. It has also ignored the effect of overcrowding or the limitation of resources. In other words, it assumes that the population will continue to grow exponentially, at good times unless there is some accident of something, for example, during war and famines then the population will continue to decay exponentially.

The Verhulst population model is a development from the Malthusian model which has to compensate with the crowding effects and the limitation of resources, in which the population approaches a non-trivial equilibrium state call the carrying capacity *k* as time, *t*, approaches infinity. In other words, the population becomes depressed as the total population becomes too large to compensate with the overcrowding factors and will continue to grow until it reaches the equilibrium state.

Overall, all the unstructured model are only useful for the populations in which the individuals growth is of the same behaviour and these differences therefore do not affect the birth and death processes. This is rare and may only occur to laboratory organisms.

Chapter 2

The age-structured population model

2.1 Introduction

This chapter is concerned with the historical development of the age-structured model where the population model is dependent on the age of the individuals. We will then develop an age-structured model that will be the subject of this thesis.

2.2 Historical development of the age-structured population model

The effect of the age of the individuals on the population growth had not been considered until relatively recently. Among the first 'continuous' population models incorporating age effects were those of Sharpe and Lotka (1911) and McKendrick (1926). Lotka formulated the basis of a population age dependent theory, while McKendrick modeled the growth of a population whose birth and death rates were age-dependent. Generally, in the models of Sharpe-Lotka-McKendrick the birth and mortality processes were linear functions of the population densities. In this early period, the theory of linear age-dependent population dynamics was extensively developed by mathematicians. As with the Malthusian models of age-independent population dynamics, the models of this theory were necessarily linear, and consequently, permitted no influence for crowding effects or environmental limitations.

Gurtin and MacCamy (1974) and Hoppensteadt (1975) introduced the first models of non-linear continuous age-dependent population dynamics. In the Gurtin-MacCamy study, the effects of crowding were incorporated into the model by allowing the birth and mortality processes to be nonlinear functions of the population densities. Consequently, the equations of their models, as in the case of the Verhulstian models, contained non-linear terms involving the unknown solutions. Analogously to the Verhulstian models of age-independent population dynamics, these non linearities provided a mechanism by which the population might stabilize to a nontrivial equilibrium state as time evolved.

The model of age-dependent population growth served as a basic building block of all population theories and in the study of contagious phenomena (such as epidemic disease) that was developed by Von Foerster. In this thesis we will only concentrate our discussion on the continuous age-structured model.

2.3 Which problems allow an age representation?

According to Diekmann and Metz (1986), there are two biological properties which allows an age representation that is not treated in any other previous population problems. These are that

(1) the population dynamical behavior of any individual is in no way directly related to that of its parent(s) or the state of the environment immediately preceding its birth;

(2) the average population dynamical properties of an individual, like the mean rate of giving birth or the probability of dying, does not depend on the circumstances it has experienced in its past.

Here, we are referring to what might be called *generalized* or *long term* population dynamically equivalent representations of the age type.

In this chapter, we will discuss the classical linear model of Sharpe-Lotka-McKendrick. We will then present a general formulation of age-dependent population dynamics which allows general birth and mortality processes.

2.4 The McKendrick-Von Foerster equation

The classical model of linear age-dependent population dynamics of Sharpe-Lotka-McKendrick is formulated as follows:

Let $n(a,t)$ be the population density (or *age distribution*) with respect to age a of a population at time t. The units of n(a,t) are given in units of population divided by units of time. Accordingly, the total number of individuals between ages a_1 and a_2 is given by

$$Q\int_{a_2}^{a_1} n(a,t)\mathrm{d}a$$

where Q is a scaling factor, for example, the population's size at $t=0$, $n(a,t)$ is taken to be a smooth function of (a,t). However, this is not necessarily a strong restriction: for example, if Q is a large number, a unit change in the population corresponds to a small change in $n(a,t)$ so that we can consider Q as unity. The total population at time t of all members of the population is given by

$$N=\int_{0}^{\infty} n(a,t)\mathrm{d}a.$$

The upper limit of chronological age of species is, of course, some finite number, but it will be assumed for convenience to be infinite with $n(\infty,t)=0$ and $N(t)$ is finite. This density function satisfies the so-called *balance law* (or aging process of the population).

There are *two* basic assumptions that has to be made about the population, which describes how individuals are included to or excluded from the population. The first specifies how individuals are removed. Note that during a very small time interval of size dt, chosen for convenience equal to da by Nisbet and Gurney (1982). In this thesis we are going to assume the same thing since it is obvious that age advances at the same rate as time.

Assumption 1

The change occurring in the population of age a at time t in a particular time interval of length dt is proportional to the size of population and dt.

Thus, we have

change in n over the time interval dt = rate of removal with respect to n

$$n(a+\mathrm{d}a,t+\mathrm{d}t)-n(a,t)=-\mu(a)n(a,t)\mathrm{d}t,$$

where $\mu(a)$ is the non-negative age-dependent death rate. By dividing this equation by $\mathrm{d}t$ and finding the limit at $\mathrm{d}t \to 0$, we have:

$$\frac{\partial n}{\partial t}+\frac{\partial n}{\partial a}=-\mu(a)n, \qquad t,a>0 \tag{2.1}$$

This is the equation for age-dependent population growth which is a linear first order hyperbolic partial differential equation. It is known as the McKendrick equation or somewhat unjustly known as "Von Foerster's equation". Here, only the death rate (removal) is considered and the birth rate is not involved in the equation because, when $a=0$, the individual is considered born. This is introduced to the population through the initial conditions.

Assumption 2:

The number of individuals introduced into the population aged between $a-\mathrm{d}t$ and a who survive, enter the age class a to $a+\mathrm{d}t$ is given by:

$$\int_0^\infty \beta(\mathrm{a})\mathrm{n}(\mathrm{a},\mathrm{t})\mathrm{d}a$$

where $\beta(a)$ gives the non-negative age-dependent birth rate and let $\beta(a)\mathrm{d}a$ be the average number of offspring produced per unit time by an individual of age a in time interval $(t,t+\mathrm{d}t)$.

2.5 *Initial and boundary condition*

The model is not complete without specifying the initial and boundary condition. From *Assumption 2*, it follows that the number of births into the population (or the input of population of age $a=0$) at any time t satisfies the so-called *birth law:*

$$n(0,t)=\int_0^\infty \beta(a)n(a,t)da, \tag{2.2}$$

This equation is usually called the *renewal equation*. Its units are given in units of population per units of time. Its value at any time t depends on the age-distribution of the population at that time, as determined by the integral of the density $n(a,t)$ weighted with the birth rate $\beta(a)$.

Finally, the *initial age-distribution* of the population is assumed to be known:

$$n(a,0)=n_0(a) \tag{2.3}$$

This is a known non-negative function of age, a. Notice that equation (2.2) is not required to hold at $t=0$. If (2.2) does hold at $t=0$, then (2.2) and (2.3) must be compatible in the sense that

$$\int_0^\infty \beta(a)n_0(a)da=n_0(0)$$

The above condition is called the *compatibility condition*, and it is not, in general, required of the initial age distribution.

Let us make some further simplifying assumptions:

1. The birth and death rates are functions of age only and not time.

2. Let us define R_0 to be the *net reproductive number*. This is expressed in terms of the given birth and death rates as

$$R_0=\int_0^\infty \beta(a)\exp\left(-\int_0^a \mu(\alpha)d\alpha\right)da$$

   Thus R_0 is the expected number of offspring produced in a lifetime by an individual. Therefore, for a population to grow in the absence of the disease, it is assumed that for growing population $R_0>1$.

The problem (2.1) , (2.2) and (2.3) constitutes the classical linear model of age-dependent population dynamics. The equation (2.1) is a linear first order hyperbolic partial differential equation with initial and a boundary condition. It can be reduced to a solvable ordinary differential equation by 'method of characteristics' along the characteristics lines which consists of straight lines parallel to the line t=a (see Figure 2.1) below.

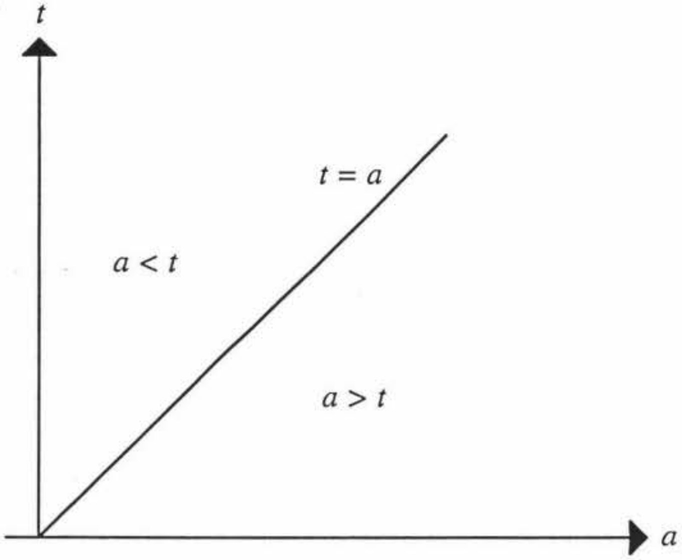


Figure 2.1: The sketch showing the two regions of interest along the characteristics lines.

2.6 Conclusions

The age-structured population model has at least provided an understanding of the differences between individuals which is more realistic. In this Chapter, the simplest model has been considered which consists of a linear first order hyperbolic partial differential equation known as "McKendrick equation" or sometimes called the "Von Foerster's equation". We can summarise the equation and conditions as follows:

i) $$\frac{\partial n}{\partial t}+\frac{\partial n}{\partial a}=-\mu(a)n \tag{2.1}$$

is the simplest equation of age-dependent population growth where $\mu(a)$ is the non-negative age-dependent death rate.

ii) The *boundary condition* is considered to be

$$n(0,t) = \int_0^\infty \beta(a) n(a,t) da, \qquad a \geq t \tag{2.2}$$

and

iii) the *initial age-distribution* of the population is assumed to be

$$n(a,0) = n_0(a), \qquad a < t \tag{2.3}$$

We also define the total population (*N*) to be as follows

$$N = \int_0^\infty n(a,t) da, \tag{2.4}$$

where the upper limit of the chronological age is of some finite number but it is assumed here for convenience to be infinite with $n(\infty,t) = 0$ and

$$R_0 = \int_0^\infty \beta(a) \exp(-\int_0^a \mu(a) da, \tag{2.5}$$

where R_0 is the expected number of offspring produced in a lifetime by an individual in the absence of the disease. Therefore, for a population to grow in the absence of the disease, it is assumed that for growing population, $R_0 > 1$.

This model will be modified and developed further in the following chapters.

Chapter 3

The general solutions to the McKendrick age-structured population model

3.1 Introduction

In this chapter, we shall obtain the general solution of the age-dependent population dynamics model developed by McKendrick. The formulation of this model has been discussed in Chapter 2.

The model equation is

$$\frac{\partial n}{\partial t}+\frac{\partial n}{\partial a}=-\mu(a)n(a,t), \tag{2.1}$$

with the following *renewal condition* given by

$$n(0,t)=\int_0^\infty \beta(a)n(a,t)da, \tag{2.2}$$

and the *initial-age distribution* given by

$$n(a,0)=n_0(a). \tag{2.3}$$

We shall use the method of characteristics at the early stage and then proceed with Laplace transform discussed elaborately by Zill in 1989 to solve equations (2.1) to (2.3) and then examine the solutions of the following cases:

a) CASE 1: both the birth and the death rate are constant, i.e. $\beta(a)\equiv\beta$ and $\mu(a)\equiv\mu$, respectively.

b) CASE 2: the birth rate is age-dependent and the death rate is a constant, i.e. $\beta(a)=\beta(a)$ and $\mu(a)\equiv\mu$, respectively.

c) CASE 3: both the birth and death rate are age-dependent, i.e. $\beta(a)$ and $\mu(a)$ respectively.

3.2 *The general solutions*

In Appendix A, we convert the first-order partial differential equation (equation 2.1) by the method of characteristics by introducing a set of new coordinates $r=a+t$ and $s=a-t$, and obtain the following ordinary differential equation

$$2\frac{dn}{dr}=-\mu(a)n. \tag{A.2}$$

This equation may be solved by separation of variables to give

$$n[r,s]=A(s)\exp\left(-\frac{1}{2}\int_{s}^{r}\mu[r,s]dr\right),$$

where *A(s)* is some arbitrary constant and by a change of coordinates are to be $(a,t)\to[r,s]$ and $\mu[r,s]=\mu(a,t)=\mu(a)$. We can then expressed the above equation as

$$n(a,t)=A(a-t)\exp\left(-\frac{1}{2}\int_{a-t}^{a}\mu(a,t)da\right),$$

or

$$n(a,t)=A(a-t)\exp\left(-\frac{1}{2}\int_{a-t}^{a}\mu(\alpha)d\alpha\right). \tag{3.1}$$

The equation (3.1) is the general solution for two regions shown in Figure 2.1. These have been defined in section 2.4.

Let us now investigate the solution (3.1) in the following regions:

i) $a \geq t$

The initial age distribution from (2.3) is known to be $n_0(a)$, so that the solution at region $a \geq t$ will be given by

$$n(a,t) = n_0(a-t)\exp\left(-\int_{a-t}^{a}\mu(\alpha)d\alpha\right). \tag{3.2}$$

This equation is equivalently

$$n(a,t) = n_0(a-t)\exp\left(\int_{0}^{t}\mu(a-t+\alpha)d\alpha\right), \tag{3.3}$$

by changing the limits of integration.

ii) $a < t$

In order to find the solution in this region, we need to make a change of coordinates. We will choose $s = t-a$ and $r = a+t$, so that equation (3.1) will become

$$n(a,t) = A(t-a)\exp\left(-\int_{t-a}^{a}\mu(\alpha)d\alpha\right),$$

where $A(t-a)$ is some arbitrary function. Putting a = 0, that is:

$$n(0,t) = A(t)\exp\left(-\int_{t}^{0}\mu(\alpha)d\alpha\right),$$

which we shall call $m(t)$. The function $A(t)$ can now be solved

$$A(t) = m(t)\exp\left(-\int_0^t \mu(\alpha)d\alpha\right),$$

or

$$A(t-a) = m(t-a)\exp\left(\int_0^{t-a} \mu(\alpha)d\alpha\right).$$

The general solution at region a<t is therefore

$$n(a,t) = m(t-a)\exp\left(-\int_0^a \mu(\alpha)d\alpha\right). \qquad (3.4)$$

The equations (3.2) to (3.4) allow for a simple interpretation of the population density function $n(a,t)$ in terms of the death function μ.

3.3 The interpretation of the equations (3.2) and (3.4)

To interpret equations (3.2) and (3.4) from the two regions discussed in section 3.1, let us first of all, suppose that the function

$$\Pi(b,a) = \exp\left(-\int_a^b \mu(s)ds\right) \qquad 0 \le a \le b \qquad (3.5)$$

where $\Pi(b,a)$ is the probability that a member of the population of age a survives to age b. In the region $a \ge t$, the equation (3.2) may be expressed as

$$n(a,t) = n_0(a-t)\Pi(a,a-t).$$

This equation represents those members of the population which were of age $a-t$ at the initial instant and which survived at age a at time t. In other words, this equation represents the dying off of the population present at $t=0$. In region $a < t$, the equation (3.4) may be expressed as

$$n(a,t) = n(0,t-a)\Pi(a,0),$$

which represents those members of the population born $t-a$ units of time which survive to age a at time t. This expression is of purely academic interest unless we can find some means of calculating $n(0,t-a)$, the number of newborn (a=0) individuals present at time $t-a$. This shall be discussed in the next section.

3.4 The expression for the population density n(a,t) in terms of the birth and death rate

From equations (3.2) and (3.4), we see that if the birth rate $n(0,t)$ or $m(t)$, can be determined as a function of t, then the population density function $n(a,t)$ becomes known. Equation (2.2) and (3.2) with (3.4) can be used to arrive at a single equation for the birth rate $n(0,t)$. Since we have defined $n(0,t)$ to be $m(t)$ then substituting (3.2) and (3.4) into (2.2) gives

$$m(t)=n(0,t)=\int_0^t \underbrace{\beta(a)n(a,t)da}_{a<t}+\int_t^\infty \underbrace{\beta(a)n(a,t)da}_{a\geq a} ,$$

or

$$m(t)=\int_0^t \beta(a)m(t-a)\exp\left(-\int_0^a \mu(\alpha)d\alpha\right)$$
$$+\int_t^\infty \beta(a)n_0(a-t)\exp\left(-\int_{a-t}^a \mu(\alpha)d\alpha\right). \tag{3.6}$$

The birth rate thus satisfies the integral equation

$$m(t)=\int_0^t m(t-a)G(a)da+F(t), \tag{3.7}$$

where

$$G(a)=\beta(a)\exp\left(-\int_0^a \mu(\alpha)d\alpha\right), \tag{3.8}$$

and

$$F(t)=\int_t^\infty \beta(a)n_0(a-t)\exp\left(-\int_{a-t}^a \mu(\alpha)d\alpha\right) \tag{3.9}$$

are known quantities.

The integral equation (3.7) is known as the *renewal equation* and is in the form of a *convolution equation* (see appendix B.2).

From the definition of the Laplace transform and the convolution theorem (Appendix B) as well as the conditions set on $F(t)$ and $G(a)$ for ensuring the Laplace transform of m(t) (which is $\bar{m}(p)$) is possible, we shall now conclude that equation (3.7) may be expressed as

$$\bar{m}(p) = \bar{m}(p)\bar{G}(p) + \bar{F}(p). \tag{3.10}$$

In particular, as long as $\bar{G}(p) \neq 1$, we have

$$\bar{m}(p) = \bar{F}(p)/[1 - \bar{G}(p)]. \tag{3.11}$$

Equation (3.11) can be solved by observing the contribution of the function $1 - \bar{G}(p)$ made by its zeros which we assumed it to be $z_1, z_2, \ldots\ldots$
If these are all real and distinct and we suppose that they can be enumerated in terms of the decreasing real part,

$$\mathrm{Re}(z_1) > \mathrm{Re}(z_2) \geq \ldots\ldots$$

and m(t) can be determined as an infinite series of exponential terms:

$$m(t) = m_0 \exp(p^* t) + \sum_1^\infty m_n \exp(z_n t),$$

where z_n are all the characteristics roots, all satisfying $\mathrm{Re}\, z_n < p^*$. The coefficients m_n in this expansion can be determined by calculating the residue of the integrand at the characteristic roots. It may happen that some of the complex roots are not simple, and then the problem becomes more difficult. Even in that case, we may still write

$$m(t) = m_0 \exp(p^* t) + \mathrm{o}[\exp(p^* t)]$$

where m_0 (given by B) is the residue calculated at $p = p^*$.

3.5 The expression for the population density n(a,t) for different values of birth and death rates : $\beta(a)$ and $\mu(a)$ respectively.

In this section we will examine at how the values of n(a,t) are affected by arbitrary birth and death rates. We will apply our solutions obtained by Laplace transforms discussed earlier in this chapter.

3.5.1 Case 1: Birth rates and deaths rates are constant ($\beta = \mu$ =constant)

In this case, our model (2.1) becomes:

$$\frac{\partial n}{\partial a}+\frac{\partial n}{\partial t}=-\mu n, \tag{3.12}$$

and the initial age distribution and the renewal equation are given respectively by:

i) $n(a,0)=n_0(a),$ (3.13)

ii) $n(0,t)=\beta\int_0^\infty n(a,t)da$

$$=\beta\int_0^t \underbrace{n(a,t)da}_{a\langle t}+\int_t^\infty \underbrace{n(a,t)da}_{a\geq t}. \tag{3.14}$$

i) In the region $a \geq t$, the solution may be obtained by direct substitution into equations (3.2) or (3.3) to give

$$n(a,t)=n_0(a-t)\exp(-\mu t). \tag{3.15}$$

ii) In the region $a \leq t$, we need to proceed with the method discussed in section 3.3. In order to find m(t) and to solve the problem in this region, we need to use the Laplace transform method.

Firstly, we need to find $G(a)$ as defined in (3.8) and thus its Laplace transform $\bar{G}(p)$. For this case we have the following result

$$\begin{aligned} G(a) &= \beta \exp(-\int_{\alpha=0}^{\alpha=a} \mu d\alpha) \\ &= \beta \exp(-\mu a) \end{aligned}$$

and

$$\begin{aligned} \bar{G}(p) &= \int_0^\infty \beta \exp(-\mu a) \exp(-pa) da \\ &= \beta \int_0^\infty \exp-(p+\mu) a da \\ &= \frac{\beta}{p+\mu} \end{aligned} \tag{3.16}$$

By substituting this value into the product of Laplace transforms (given by equation (3.10)), the equation

$$\begin{aligned} \bar{m}(p) &= \frac{\bar{F}(p)}{(1-\frac{\beta}{p+\mu})} \\ &= (\frac{p+\mu}{p+\mu-\beta}) \bar{F}(p) \\ &= \left\{ 1+\frac{\beta}{p-(\beta-\mu)} \right\} \bar{F}(p) \\ &= \bar{T}(p) \bar{F}(p) \end{aligned}$$

is obtained.

The value of F(t) is given by

$$F(t) = \beta \int_{a=t}^{a=\infty} n_0 \exp(\int_{a-t}^{a} \mu d\alpha) da$$

$$
\begin{aligned}
F(t) &= \beta \int_{a=t}^{a=\infty} n_0 \exp(-\mu t)da \\
&= \beta H \exp(-\mu t),
\end{aligned}
$$

by defining $H = \int_t^{\infty} n_0 da$.

Before one can find the integral resulting from inverting the Laplace transform of $\bar{m}(p)$, it may be better to find the solution of the equation $\bar{G}(p) = 1$ using the result in (3.16). This gives a simple unique real solution. The equation $T(t)$ may be expressed as an infinite series of exponential terms (see Appendix B).

$$T(t) = \beta \exp(\beta - \mu)t + \delta(t).$$

and the inversion of $\bar{m}(p)$ may be expressed as

$$
\begin{aligned}
m(t) &= \int_0^t \beta H e^{-\mu(t-s)}[\delta(s) + \beta e^{(\beta-\mu)s}]ds \\
&= \beta H e^{-\mu t} + \int_0^t \beta^2 H e^{-\mu t+\beta s} ds \\
&= \beta H e^{-\mu t} + \beta H[e^{-\mu t+\beta s}]_0^t \\
&= \beta H e^{-\mu t} + \beta H[e^{(\beta-\mu)t} - e^{-\mu t}] \\
&= \beta H e^{(\beta-\mu)t}.
\end{aligned}
$$

We may then be able to find *n(a,t)* in the region $a \le t$, by substituting *m(t)* into equation (3.4) and solving the problem:

$$
\begin{aligned}
n(a,t) &= \beta H e^{(\beta-\mu)(t-a)} e^{-\mu a} \\
&= \beta H e^{(\beta-\mu)t-\beta a}. \qquad (3.17)
\end{aligned}
$$

3.5.2 Case 2: Birth rate is some arbitrary function of age, *a* (=$\beta a e^{-\gamma a}$) and death rate is a constant.

In this case, our model (2.1) is the same as in Case 1:

$$\frac{\partial n}{\partial a}+\frac{\partial n}{\partial t}=-\mu n \tag{3.18}$$

and the initial age distribution and the renewal equation will be given by

i) $n(a,0)=n_0(a),$ (3.19)

ii) $n(0,t)=\beta\int\limits_0^\infty \exp(-\gamma a)n(a,t)da.$ (3.20)

i) The solution in the region $a \geq t$ is the same as the solution in case 1 because the solution is not affected by the birth rate but only upon the death rate. The equation is given by equation 3.15.

ii) In order to described the solution in region $a \leq t$, we use a similar procedure as those in section 3.4.2. We first of all need to find $G(a)$ and its Laplace transform. For this case, we have the following results.

$$\begin{aligned}G(a)&=\beta a\exp(-\gamma a)\exp(-\int\limits_{\alpha=0}^{\alpha=a}\mu d\alpha)\\&=\beta a\exp[-(\gamma+\mu)a]\end{aligned}$$

and

$$\begin{aligned}\bar{G}(p)&=\int\limits_0^\infty \beta a\exp[-(\gamma+\mu)a]\exp(-pa)da\\&=\beta\int\limits_0^\infty a\exp-[(p+\gamma+\mu)a]da\\&=\frac{\beta}{(p+\gamma+\mu)^2}.\end{aligned}$$

By substituting this value into the product of Laplace transforms given by equation (3.10), we have

$$\bar{m}(p)=\frac{\bar{F}(p)}{(1-\dfrac{\beta}{(p+\gamma+\mu)^2})}$$

$$\bar{m}(p) = \frac{(p+\gamma+\mu)^2}{(p+\gamma+\mu)^2-\beta}\bar{F}(p)$$

$$= \left\{1+\frac{\beta}{(p+\gamma+\mu)^2-\beta}\right\}\bar{F}(p).$$

In order to identify the characteristic roots we need to further simplify this result further by using partial fractions. Thus, we obtain

$$m(p) = \{1+\frac{\beta^{\frac{1}{2}}}{2[(p+\gamma+\mu)-\beta^{\frac{1}{2}}]}-\frac{\beta^{\frac{1}{2}}}{2[(p+\gamma+\mu)+\beta^{\frac{1}{2}}]}\}F(p) \qquad (3.21)$$

$$= \bar{T}(p)\,\bar{F}(p).$$

From the equation (3.21), we can determine the inverted value for $\bar{T}(p)$ and thus express it as an infinite series of exponential terms by looking at the roots of the characteristic equation. These are given by

$$T(t) = \frac{\beta^{\frac{1}{2}}}{2}e^{(-\gamma-\mu+\beta^{\frac{1}{2}})t}-\frac{\beta^{\frac{1}{2}}}{2}e^{(-\gamma-\mu-\beta^{\frac{1}{2}})t}+\delta(s).$$

The value of F(t) may be determined as

$$\begin{aligned} F(t) &= \beta\int_{a=t}^{a=\infty} an_0\exp(-\gamma a)\exp(-\int_{\alpha=a-t}^{\alpha=a}\mu d\alpha)da \\ &= \beta\int_{a=t}^{a=\infty} an_0\exp(-\gamma a)\exp(-\mu t)da \\ &= \beta H_1\exp(-\mu t), \end{aligned}$$

by defining $H_1 = \int_t^\infty an_0\exp(-\gamma a)da$.

The integral resulting from inverting the Laplace transform of $\bar{m}(p)$ may be expressed as

$$m(t)=\int_0^t \beta H_1 e^{-\mu(t-s)}[\delta(s)+\frac{\beta^{\frac{1}{2}}}{2}e^{(-\gamma-\mu+\beta^{\frac{1}{2}})s}-\frac{\beta^{\frac{1}{2}}}{2}e^{(-\gamma-\mu-\beta^{\frac{1}{2}})s}]ds$$

$$=\beta H_1\int_0^t e^{-\mu(t-s)}\delta(s)ds+\int_0^t\frac{\beta^{\frac{3}{2}}}{2}H_1e^{(-\mu-\gamma+\beta^{\frac{1}{2}})s-\mu t+\mu s}ds-\int_0^t\frac{\beta^{\frac{3}{2}}}{2}H_1e^{(-\mu-\gamma-\beta^{\frac{1}{2}})s-\mu t+\mu s}ds$$

$$=\beta H_1e^{-\mu t}+\frac{\beta^{\frac{3}{2}}H_1e^{-\mu t}}{2(-\gamma+\beta^{\frac{1}{2}})}[e^{(-\gamma+\beta^{\frac{1}{2}})s}]_0^t-\frac{\beta^{\frac{3}{2}}H_1e^{-\mu t}}{2(-\gamma-\beta^{\frac{1}{2}})}[e^{(-\gamma-\beta^{\frac{1}{2}})s}]_0^t$$

$$=\beta H_1e^{-\mu t}[1-\frac{\beta^{\frac{1}{2}}}{2(-\gamma+\beta^{\frac{1}{2}})}+\frac{\beta^{\frac{1}{2}}}{2(-\gamma-\beta^{\frac{1}{2}})}]+\frac{\beta^{\frac{3}{2}}H_1}{2}[\frac{e^{-(\mu+\gamma-\beta^{\frac{1}{2}})t}}{(-\gamma+\beta^{\frac{1}{2}})}-\frac{e^{-(\mu+\gamma+\beta^{\frac{1}{2}})t}}{(-\gamma-\beta^{\frac{1}{2}})}].$$

The solution in the region $a \leq t$ may be then be obtained by substituting this function *m(t)* into the equation (3.4) to give

$$\begin{aligned}n(a,t)=&\beta H_1e^{-\mu t}[1-\frac{\beta^{\frac{1}{2}}}{2(-\gamma+\beta^{\frac{1}{2}})}+\frac{\beta^{\frac{1}{2}}}{2(-\gamma-\beta^{\frac{1}{2}})}]\\&+\frac{\beta^{\frac{3}{2}}H_1}{2}[\frac{e^{-t(\mu+\gamma-\beta^{\frac{1}{2}})+a(\gamma-\beta^{\frac{1}{2}})}}{(-\gamma+\beta^{\frac{1}{2}})}-\frac{e^{-t(\mu+\gamma-\beta^{\frac{1}{2}})+a(\gamma+\beta^{\frac{1}{2}})}}{(-\gamma-\beta^{\frac{1}{2}})}].\end{aligned}\tag{3.22}$$

3.5.3 Case 3: Birth rates and death rates are a function of age, *a*.

In this section, we shall choose birth rate to be the arbitrary function $\beta a\exp(-\gamma a)$ and the death rate to be the arbitrary function $\mu\exp(ka)$. Thus our model (2.1) becomes:

$$\frac{\partial n}{\partial a}+\frac{\partial n}{\partial t}=-\mu\exp(ka)n,\tag{3.23}$$

and the initial age distribution and the renewal equation will be given by

i) $n(a,0) = n_0(a) = h(a),$ (3.24)

ii) $n(0,t) = \beta \int_0^\infty a \exp(-\gamma a) n(a,t) da.$ (3.25)

i) The solution in the region $a \geq t$ is different from cases 1 and 2, because the death rate in this case is some function of age a. By substituting the new age dependent death rate into equation, (3.2) or (3.3), we may obtain the solution

$$\begin{aligned} n(a,t) &= n_0(a-t)\exp\left(-\mu \int_{a-t}^{a} \exp(k\alpha) d\alpha\right) \\ &= n_0(a-t)\exp\left(-\frac{\mu}{k}\left[\exp(k\alpha)\right]_{a-t}^{a}\right) \\ &= n_0(a-t)\exp\left(\frac{\mu}{k} e^{ka}\left[e^{-kt} - 1)\right]\right). \end{aligned} \tag{3.26}$$

ii) In order to find the solution in the region $a \leq t$, we use a similar procedure as those in section 3.4.2. We first of all need to find $G(a)$ and its Laplace transform. For this case, we have the following:

$$\begin{aligned} G(a) &= \beta a \exp(-\gamma a)\exp(-\mu \int_{\alpha=0}^{\alpha=a} \exp(k\alpha) d\alpha) \\ &= \beta a \exp(-\gamma a)\exp(-\frac{\mu}{k}\left[\exp(k\alpha)\right]_0^a) \\ &= \beta a \exp(-\gamma a)\exp(\frac{\mu}{k}\left[1 - e^{ka}\right]) \end{aligned}$$

and

$$\begin{aligned} \overline{G}(p) &= \beta \int_0^\infty a \exp(-\gamma a)\exp(\frac{\mu}{k}\left[1 - e^{ka}\right])\exp(-pa) da \\ &= \beta \int_0^\infty a \exp(-\gamma a - pa - \frac{\mu}{k} e^{ka})\exp(\frac{\mu}{k}) da \\ &= \beta \exp(\frac{\mu}{k}) \int_0^\infty a \exp(-\gamma a - pa - \frac{\mu}{k} e^{ka}) da. \end{aligned}$$

This problem may not be solved easily as the integral is in a difficult form.

3.6 Conclusions

We conclude that the solution to equations (2.1) to (2.3) can be solved using the Laplace Transform method, since it can be simplified and expressed in the form of the *convolution equation*

$$\bar{m}(p) = \bar{F}(p) / [1 - \bar{G}(p)],$$

where $\bar{G}(p) \neq 1$. If we can solve for $F(t)$ and $1/[1 - \bar{G}(p)]$ can be inverted then this ensures that we can find the inversion of $\bar{m}(p)$ and thus be able to obtain an expression for the population density required.

Some special cases, where we have chosen only arbitrary functions, such as the age-dependent birth rate for cases 2 and 3 is chosen to be $\beta a e^{-\gamma a}$ are considered so that one can make deductions from the assumption of these special cases.

Chapter 4

Steady age distribution (s.a.d.)

4.1 Introduction

So far, we have discussed the existence and uniqueness of equations (2.1) to (2.3). In this chapter, we will discuss and observe the long-term behaviour of these solutions. We want to see how the size of the population is regulated and how the ages are distributed. In mathematical terms, we examine if our model admits the *steady age distribution (s.a.d)* and conclude whether or not these are stable. This will form the bulk of sections 4.2 and 4.3. The steady age distributions to be considered here are not the *stable age distributions* that are usually studied in age-dependent population growth where we assumed the solution of the separable variable type $n(a,t) = A(a)T(t)$ (e.g. in the book by Hoppensteadt (1975) and another by Lotka (1956)). In section 4.3, we will then apply our study of the s.a.d and its stability to the three cases mentioned in Chapter 2.

4.2 General discussion on the steady age distribution

We first define an equilibrium solution of the equations (2.1) to (2.3) as the solution $n(a,t) \rightarrow n_s(a)$ that is independent of time. The function $n_s(a)$ is the steady age distribution(s.a.d).

An equilibrium solution $n_s(a)$ will satisfy the equation:

$$\frac{dn_s}{da} = -\mu(a)n_s \tag{4.1}$$

and the renewal conditions (from 2.2) simplifies to

$$n_s(0) = \int_0^{\infty} \beta(a) n_s(a) da, \qquad (4.2)$$

where $n_s(0)$ is the (constant) birth rate at equilibrium. By separation of variables the solution to equation (4.1), satisfying the initial conditions (4.2) will be given by

$$n_s(a) = n_s(0) \exp(-\int_0^{a} \mu(\alpha) d\alpha) da \qquad (4.3)$$

On substituting (4.3) into (4.2), we obtain

$$n_s(0) = \int_0^{\infty} \beta(a) n_s(0) \exp(-\int_0^{a} \mu(\alpha) d\alpha) da$$

Upon cancellation of the similar term $n_s(a)$ we then have

$$R_0 = 1 = \int_0^{\infty} \beta(a) \exp(-\int_0^{a} \mu(\alpha) d\alpha) da \qquad (4.4)$$

Let us regard equation (4.4) to be R_0. Comparing with our assumption that we have made, represented by equation (2.5), our R_0 expected number of offspring produced in a life time by an individual in the absence of the disease s 1. Thus, a non trivial equilibrium solution of the problem (2.1) to (2.3) exists if and only if (4.4) holds, then a family of non-trivial equilibrium solution is given by the equation (4.3) as $n_s(0)$ ranges over all positive values. If (4.4) does not hold, then the zero solution is the only equilibrium solution of the problem. As often is the case that (4.4) does not hold, the nvestigators of the Sharpe-Lotka-McKendrick model turned their attention to ooking at the stability of the solution.

4.3 General discussion on the stability of the steady age distribution

n this section, we are concerned only with the simplest and most commonly considered notion of (Liapunov) stability for differential equation systems. Our approach will be the standard method of linearising the model about a solution (usually an equilibrium) whose stability or instability is of interest. We have denoted the equilibrium solution to be $n_s(a)$. This of course, yields stability results which are in general only local near the solution being considered. Although such local stability results are sometimes criticised as being too restrictive and inappropriate in general for the study of what should be a broader concept of 'ecological stability', we will justify this approach by saying that such a study surely contributes at least a first step towards understanding the qualitative nature of the models considered here.

Let us first of all assume that the solution to our equation model (3.1) is of the form

$$n(a,t) = n_s(a) + u(a,t). \tag{4.5}$$

Substitute this into equation (3.1) and linearising the resulting equations about $u = 0$ gives

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial a} = -\mu(a)u, \tag{4.6}$$

since

$$\frac{\partial n}{\partial a} = \frac{\partial ns}{\partial a} + \frac{\partial u}{\partial a} = n_s'(a) + \frac{\partial u}{\partial a}$$

and

$$\frac{\partial n}{\partial t} = \frac{\partial u}{\partial t}.$$

Let us try a solution of the form

$$u(a,t) = g(a)\exp(\lambda t),$$

where λ is a constant. Differentiating partially with respect of a, gives the following

$$\frac{\partial u}{\partial a} = g'(a)\exp(\lambda t)$$

$$\frac{\partial u}{\partial t} = \lambda g(a)\exp(\lambda t).$$

Substituting these into equation (4.6), gives

$$\begin{aligned}
&g'(a)\exp(\lambda t) + \lambda g(a)\exp(\lambda t) = -\mu(a)g(a)\exp(\lambda t)\\
&g'(a) + g(a)\lambda = -\mu(a)g(a)\\
&g'(a) = -[\mu(a)+\lambda]g(a)\\
&\frac{\partial g}{\partial a} = -[\mu(a)+\lambda]g(a)
\end{aligned}$$

Using the method of separation of variables, gives

$$g(a) = A\exp(-\int[\mu(\alpha)+\lambda]d\alpha) \tag{4.7}$$

where $g(0) = A$ is a constant and from the renewal condition (2.2), we have

$$g(0) = \int_0^\infty \beta(a)g(a)da. \tag{4.8}$$

By substituting (4.7) into (4.8) we obtain

$$g(0) = \int_0^\infty \beta(a)A\exp(-\int[\mu(\alpha)+\lambda]d\alpha)$$

and since $g(0) = A$, we obtain the following

$$\begin{aligned}
A &= \int_0^\infty \beta(a)A\exp(-\int_0^a[\mu(\alpha)d\alpha]da)\\
1 &= \int_0^\infty \beta(a)\exp(-\int_0^a[\mu(\alpha)+\lambda]d\alpha)\\
R(\lambda) = 1 &= \int_0^\infty \beta(a)\exp(-\lambda a)\exp(-\int_0^a \mu(\alpha)d\alpha).
\end{aligned} \tag{4.9}$$

The equation (4.9) is known as the *characteristic equation.* This equation was discovered by Lotka (1922). Under appropriate assumptions on the birth rate β and death rate μ, the right hand side of (4.9) is a strictly decreasing function of λ which assumes all values in $(0,\infty)$. In this case, (4.9) has a unique real solution λ^* and for this choice of λ^*, equation (4.9) describes the stability of the steady-age distribution for all value of A or $g(0)$ depending upon the sign of λ^*. Below is a proof of the proposition showing that there exists a unique solution.

THEOREM 1:

There is a unique solution to (4.9), say λ^*. All other solutions λ occur in complex conjugate pairs, with $\mathrm{Re}(\lambda) < \lambda^*$.

Proof:

Let $R(\lambda) = \int_0^\infty \beta(a)\exp(-\lambda a)\exp(-\int_0^a \mu(\alpha)d\alpha)$ and note that $R(\lambda) \to 0$ as $\lambda \to \infty$ and $R(\lambda) \to \infty$ as $\lambda \to -\infty$. It is then easy to show that $R(\lambda)$ is monotonic decreasing. Note that

$$\begin{aligned} &\lambda^* > 0 \text{ if } R(0) > 1 \\ &\lambda^* = 0 \text{ if } R(0) = 1 \\ &\lambda^* < 0 \text{ if } R(0) < 1 \end{aligned}$$

The graph of $R(\lambda)$ is shown in Figure 4.1 for cases $R(0) < 1$ and $R(0) > 1$.

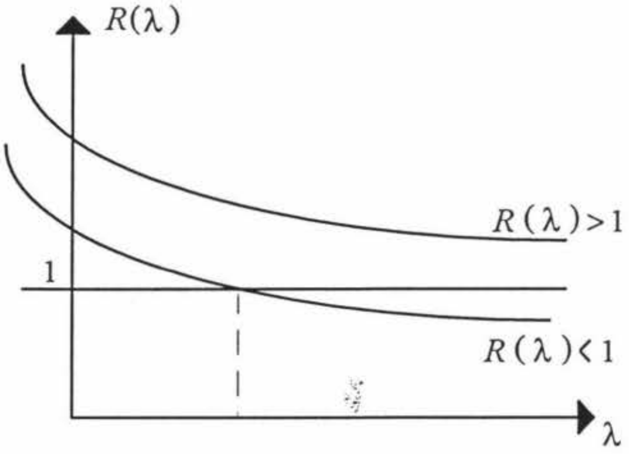


Figure 4.1: The graph of $R(\lambda)$ against λ.

Suppose $\lambda = \lambda_j$ are complex solutions. Let $\lambda_j = p_j + iq_j$ in (4.9) and let us equate the real and imaginary parts. This gives

$$\int_0^\infty \beta(a)\exp(-p_j a)\cos(q_j a)\exp(-\int_0^a \mu(\alpha)d\alpha)da = 0 \qquad (4.10)$$

$$\int_0^\infty \beta(a)\exp(-p_j a)\sin(q_j a)\exp(-\int_0^a \mu(\alpha)d\alpha)da = 0 \qquad (4.11)$$

Replacing q_j with $-q_j$ in (4.10), shows that the above equations are still satisfied, so that complex solutions occur in conjugate pairs. For some values of a it must be true that $\cos(q_j a) < 1$, so by comparing (5.8) with (5.7) it is obvious that $p_j < \lambda^*$ for all j. ■

From the above theorem, we have proved that the equation has exactly one real root, λ^*, which has a value greater than that of the real of any part of the complex roots. Thus eventually the population must grow or decay exponentially with a time constant $(\lambda^*)^{-1}$. Clearly the nature of its ultimate fate will be determined by the sign of λ^*, and we see from equation (4.9) that λ^* must be negative in order for the population to ultimately decay to extinction i.e. $R(\lambda) > 1$. Conversely λ^* will be positive and the population will ultimately grow without limit if $R(\lambda) > 1$. If again (as in section 3.2 (equation 3.2)), we are to assume

$$\Pi(a) = \exp\left(\int_0^a -\mu(\alpha)d\alpha\right)$$

to be the probability that a newly recruited individual will survive to age a, then the integral in equation (4.9) simply represents the total number of offspring produced, on average, by individual during its lifetime which is 1 in the absence of disease as described in the previous section.

We also have the result that the trivial steady age distribution is linearly *asymptotically stable* if $R(0) < 1$ and *unstable* if $R(0) > 1$. As we have assumed that the population is growing in the absence of the disease, $R(0) > 1$ and that the trivial steady age distribution is always unstable.

4.4 The Discussion of the steady age distribution and its stability for the three cases.

In Chapter 4 we have seen the solution for the three cases mentioned previously but in this chapter we will look at the long-term behaviour or the steady age distribution of the various values of birth and death rates used in the same three cases. We will also discuss the stability of the solution.

For all the three different cases we will obtain a bifurcation diagram using the characteristic equation for the steady age distribution (Equation 4.9) but here we take $\lambda = 0$ since we do not consider the influence of disease in our model.

4.4.1 Case 1: Birth rates and the death rates are constant

In the case where the birth and death rates are constant, our characteristic equation (4.9) becomes

$$\begin{aligned} R(0) = 1 &= \int_0^\infty \beta \exp(-\int_0^a \mu d\alpha)da \\ &= \int_0^\infty \beta \exp(-\mu a)da \\ &= \frac{\beta}{\mu} \end{aligned}$$

Following the proposition made earlier, if $R(0) < 1$, the solution is *asymptotically stable* and if $R(0) > 1$ the solution is *unstable*. Therefore when $\beta < \mu$, it is then asymptotically stable since $R(0) < 1$ and it is unstable when $\beta > \mu$ since $R(0) > 1$. Our bifurcation diagram is then shown in Figure 4.2.

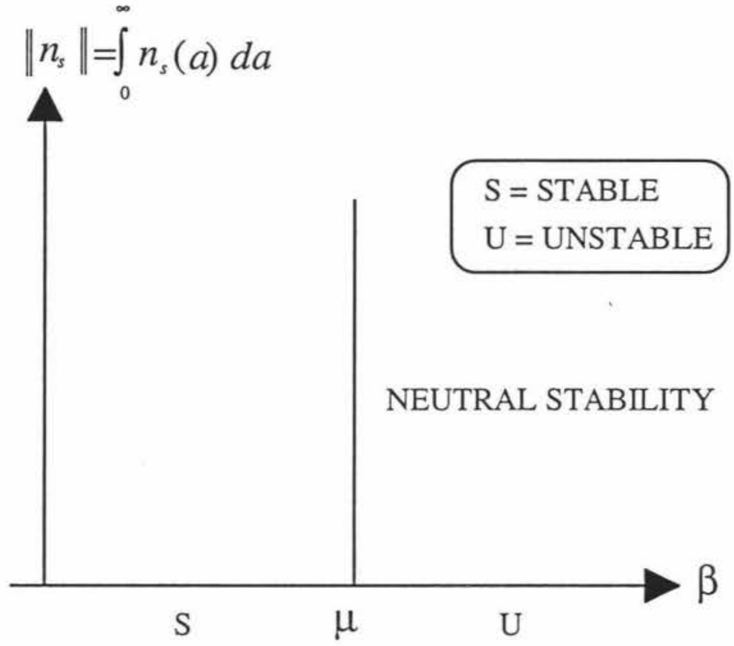


Figure 4.2: Bifurcation diagram for the case when the birth and death rates are constant.

4.4.2 Case 2: Birth rate is some arbitrary function of age *a* (=$\beta a \exp(-\gamma a)$) and the death rate is constant

For this particular case, our characteristic equation (4.9) then becomes:

$$\begin{aligned} R(0) = 1 &= \int_0^\infty B(a)\exp(-\int_0^a \mu(a)da \\ &= \beta\int_0^\infty a\exp(-\gamma a)\exp(-\int_0^a \mu)da \\ &= \beta\int_0^\infty a\exp(-\gamma a)\exp(-\mu a)da \end{aligned}$$

$$=\beta\int_0^\infty a\exp[-(\gamma+\mu)a]da.$$

Integrating by parts, gives

$$R(0)=\beta\left[\frac{a}{-(\gamma+\mu)}\exp[-(\gamma+\mu)a]+\frac{1}{(\gamma+\mu)^2}\exp[-(\gamma+\mu)a]\right]_0^\infty$$
$$1=\beta\left[\frac{1}{(\gamma+\mu)^2}\right],$$

so that

$$R(0)=1=\frac{\beta}{(\gamma+\mu)^2}.$$

Following our proposition made earlier, in this case, it is *asymptotically stable* when $\beta<(\gamma+\mu)^2$ and accordingly it is *unstable* when $\beta>(\gamma+\mu)^2$.

This is shown by Figure 4.3.

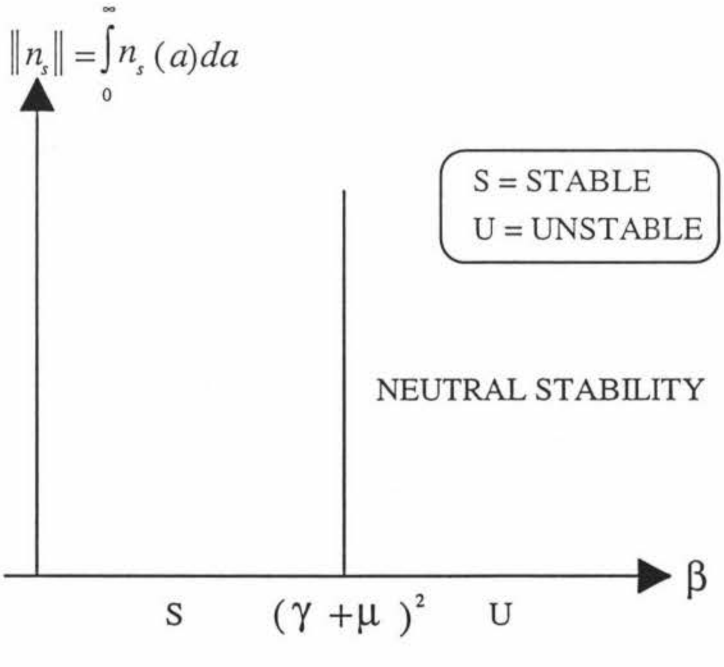


Figure 4.3: The bifurcation diagram for the case when the birth rate is some function of a and the death rate is a constant.

4.2.3 Case 3: Birth and death rates are some function of age a i.e. $\beta a e^{-\gamma a}$ and μe^{-ka} respectively

In the case where both the birth and death rates are some function of age a, our characteristics equation (4.9) becomes

$$\begin{aligned}
R(0) = 1 &= \int_0^\infty \beta a e^{-\gamma a} \exp(-\int_0^a \mu e^{k\alpha} d\alpha) da \\
&= \beta \int_0^\infty a e^{-\gamma a} \exp(-\frac{\mu}{k}[e^{ka} - 1]) \\
&= \beta \int_0^\infty a e^{-\gamma a} \exp(-\frac{\mu}{k}[e^{ka} - 1]) \\
&= \beta \int_0^\infty a e^{-\gamma a - \frac{\mu}{k}[e^{ka} - 1]} da \ .
\end{aligned}$$

This problem may not be solved easily as the integral is in a difficult form.

4.5 Conclusions

In this chapter, we discussed the steady age-distribution and its stability for our simplest age-dependent population model (equation 2.1). We obtained the *characteristic equation* which determines the stability of our steady age distribution as

$$R(\lambda) = 1 = \int_0^\infty \beta(a) \exp(-\lambda a) \exp(-\int_0^a \mu(\alpha) d\alpha),$$

where λ is a strictly decreasing function. If λ^* is the unique real solution, we can then determine the stability according to the sign of λ^*. The s.a.d. is linearly *asymptotically stable* if $R(0) < 1$ and *unstable* if $R(0) > 1$, assuming that the population is growing in the absence of disease.

For cases 1 and 2 that we considered, we have mentioned *neutral stability* at $\beta = \mu$ and $\beta = (\gamma + \mu)^2$ respectively which means that the stability is not defined at that point. This means that it is neither stable nor unstable. For case 3, the integral is too complicated to be solved.

Chapter 5

Non linear age-structured population

5.1 Introduction

In this chapter, we shall observe the solution to the non-linear age-structured population model by following a similar line of reasoning as that of the linear problem that has already been discussed in chapters 3 and 4. We shall also discuss the steady age distribution and its stability.

The non-linear model which we shall discussed in this chapter is

$$\frac{\partial n}{\partial t}+\frac{\partial n}{\partial a}=-\mu n(1+kn), \tag{5.1}$$

with the same renewal condition as given by (2.2) and initial-age distribution is given by (2.3). The terms $(1+kn)$ on the right hand side of equation (5.1) contribute to the limiting effects (these be due to crowding effects and limitations of resources affecting only a "specific age class") as in the Verhulst approach in the modification of Malthusian model, where k is a constant.

Under optimum conditions, most populations have a very high potential for growth. However, in spite of this potential, the numbers observed in population of many species appear to be *regulated* or *controlled* within certain limits. For example, the sheep population in Tasmania; after an initial period of very rapid growth the population has fluctuated around a mean of about $1\frac{1}{2}$ million for a century. The term $(1+kn)$ accounts for this. A better and a more well-defined model shall be discussed in chapter 6.

We shall look at the non-linearity effects because there is evidence that in most realistic models of a stable (or potentially stable) population, the total birth and death rates will vary with population in a non linear manner (see Nisbet and Gurney (1982)). Consequently, any presentation of the population dynamics will involve a non-linear mathematical equation of some type. This could be a differential equation, difference equation, integral equation or some combination of these. There are two situations in which we are forced to use non-linear kinetics as the basis for modelling, namely with models which have unstable steady states and with models which have two and more locally stable steady states.

Note that we shall use the term *robust* to characterise approximations which are useful over a much wider range of circumstances than those for which they were originally derived.

5.2 The general solutions

The general solution are obtained by methods similar to the one used in chapter 3 for solving the linear age-structured models. Here we shall again used the method of characteristics. The first order partial differential equation (5.1) may be converted into the following ordinary differential equation

$$2\frac{\partial n}{\partial r} = -\mu n(1+kn). \tag{5.2}$$

This equation may be solved by separable variables to give

$$\frac{n}{1+kn} = A(s)\exp(-\mu t)$$

where *A(s)* is some arbitrary function that may be expressed as

$$n[1-A(a-t)k\exp(-\mu t)] = A(a-t)\exp(-\mu t),$$

from which

$$n(a,t) = \frac{A(a-t)\exp(-\mu t)}{1 - A(a-t)k\exp(-\mu t)}. \qquad (5.3)$$

is obtained. The above equation is the general solution for the two regions shown in Figure 2.1. These have been defined in section 2.4.

Let us now investigate the equation (5.3) in the following regions

i) $a \geq t$

The initial age-distribution from (2.3) is known to be $n_0(a)$, so that the solution at this region will be given by

$$n(a,t) = \frac{n_0(a-t)\exp(-\mu t)}{1 - n_0(a-t)k\exp(-\mu t)}. \qquad (5.4)$$

ii) $a < t$

In order to find the solution in this region, we need to use the method of characteristics and make a change of coordinates. We will choose $s = t - a$ and $r = a + t$, so that equation (5.3) becomes

$$n(a,t) = \frac{A(t-a)\exp(-\mu t)}{1 - A(t-a)k\exp(-\mu t)},$$

where *A(t-a)* is some arbitrary function. Letting a=0, yields

$$n(0,t) = \frac{A(t)\exp(-\mu t)}{1 - A(t)k\exp(-\mu t)},$$

and we shall call this function $m(t)$.

The function *A(t)* may now be solved to give

$$A(t)=\frac{m(t)}{m(t)k\exp(-\mu t)+\exp(-\mu t)}$$

or

$$A(t-a)=\frac{m(t-a)}{m(t-a)k\exp(-\mu t)+\exp(-\mu t)}.$$

The general solution in the region $a<t$ is given by

$$n(a,t)=\frac{\dfrac{m(t-a)}{m(t-a)k-1}}{1-\dfrac{m(t-a)k}{[m(t-a)k-1]}},$$

which may be simplified to

$$n(a,t)=m(t-a). \tag{5.5}$$

5.3 *Finding the expression for the population density n(a,t) in terms of the birth and death rates*

From equations (5.4) and (5.5), we shall show that if the birth rate $n(0,t)$ or *m(t)* may be determined as a function of t, then the population density function $n(a,t)$ becomes known. Equation (2.2) and (5.4) with (5.5) may be used to arrive at a single equation for the birth rate $n(0,t)$. Since we have defined $n(0,t)$ to be *m(t)* by substituting (5.4) and (5.5) into (2.2) gives us the following

$$m(t)=n(0,t)=\underbrace{\int_0^t \beta(a)n(a,t)da}_{a<t}+\underbrace{\int_t^\infty \beta(a)n(a,t)da}_{a\geq t}$$

$$m(t)=\int_0^t \beta(a)m(t-a)da+\int_t^\infty \beta(a)\frac{n_0(a-t)\exp(-\mu t)}{1-n_0(a-t)\exp(-\mu t)}da.$$

The birth rate thus satisfies the integral equation

$$m(t)=\int_0^t \beta(a)m(t-a)da+F(t). \tag{5.6}$$

By letting $G(a)=\beta(a)$, the equation *m(t)* may be expressed as the following

$$m(t)=\int_0^t m(t-a)G(a)da+F(t)\ ,$$

where

$$F(t)=\int_t^\infty \beta(a)\frac{n_0(a-t)\exp(-\mu t)}{1-n_0(a-t)\exp(-\mu t)}da\ ,$$

is known, but cannot be evaluated unless n_0 is presented.

Equation (5.6) is the *renewal equation* for our non-linear model and this is linear. By the definition of Laplace transform (equation B1) and the convolution theorem (equation B2) given in Appendix B as well as the discussion upon the conditions set on $G(a)$ and $F(t)$ ensuring the Laplace transform of m(t): $\bar{m}(p)$ is possible, we can conclude that equation (3.10) and (3.11) are still applicable to equation (5.6), thus giving

$$\bar{m}(p)=\bar{F}(p)/[1-\bar{G}(p)] \tag{5.7}$$

In order to find the inverted value of $\bar{m}(p)$, we shall follow the same argument and conditions as described in section 3.3.

To see how this can be applied, let us take an example. By taking the birth rate to be a constant, i.e. as usual denoted as β, then our function *F(t)* becomes

$$F(t)=\beta\int_t^\infty \frac{n_0(a-t)\exp(-\mu t)}{1-n_0(a-t)\exp(-\mu t)}\,da.$$

Assuming that

$$n_0(a)=\alpha\exp(-\gamma a),$$

we obtain

$$F(t)=\beta\int_t^\infty \frac{\alpha e^{-\gamma(a-t)}\exp(-\mu t)}{1-\alpha e^{-\gamma(a-t)}\exp(-\mu t)}\,da$$

$$=\beta\int_t^\infty \frac{\alpha e^{-\gamma a}e^{(\gamma-\mu)t}}{1-\alpha e^{-\gamma a}e^{(\gamma-\mu)t}}\,da$$

$$=\beta\int_t^\infty \frac{\alpha e^{-\gamma(a-t)}}{e^{\mu t}-\alpha e^{-\gamma(a-t)}}\,da$$

$$=\beta e^{\gamma t}\int_t^\infty \frac{\alpha e^{-\gamma a}}{e^{\mu t}-\alpha e^{-\gamma(a-t)}}\,da.$$

To find the solution to $F(t)$, the denominator of the above value has to converge i.e. $e^{\mu t}>\alpha e^{\gamma t}$. And if we can find $F(t)$ and since $[1-\bar{G}(p)]^{-1}$ can be easily found and can be inverted then we can find $m(t)$ and thus $n(a,t)$ can be found.

5.4 Steady age distribution (s.a.d.)

We have discussed in great detail about the steady age distribution of the linear age-structured population in chapter 4 broadly. In this section we shall use the same procedure.

We first define an equilibrium solution of the equations (5.1, 2.2 and 2.3) as a solution $n(a,t) \to n_s(a)$ independent of time. $n_s(a)$ is the s.a.d.

At equilibrium solution $n_s(a)$ will then satisfy the equation

$$\frac{dn_s(a)}{da} = -\mu n_s(a)[1 + kn_s(a)] \tag{5.7}$$

and the renewal conditions (from 2.2) is then simplifies to

$$n_s(0) = \int_0^\infty \beta(a) n_s(a) da, \tag{5.8}$$

where $n_s(a)$ is the (constant) birth rate at equilibrium. By separable variable the solution to equation (5.7) is

$$n_s(a) = \frac{A\exp(-\mu a)}{1 - Ak\exp(-\mu a)}, \tag{5.9}$$

where A is some arbitrary function.

For $a = 0$, equation (5.9) becomes

$$n_s(0) = \frac{A}{1 - Ak},$$

and therefore

$$A = \frac{n_s(0)}{1 + n_s(0)k}.$$

On substituting the result back into equation (5.9), we obtain

$$n_s(a) = \frac{\dfrac{n_s(0)}{1+n_s(0)k}\exp(-\mu a)}{1-\dfrac{n_s(0)k}{1+n_s(0)k}\exp(-\mu a)} . \tag{5.10}$$

Let $n_s(0)$=C so that equation (5.10) becomes:

$$n_s(a) = \frac{C\exp(-\mu a)}{1+Ck[1-\exp(-\mu a)]} . \tag{5.11}$$

Substituting (5.11) into the renewal condition given by equation (5.8) considering $\beta(a) \equiv \beta$ is a constant, we obtain

$$C = C\beta\int_0^\infty \frac{\exp(-\mu a)}{1+Ck[1-\exp(-\mu a)]}da .$$

Upon cancellation of the similar term *C*, we have

$$1 = \beta\int_0^\infty \frac{\exp(-\mu a)}{1+Ck[1-\exp(-\mu a)]}da.$$

Let $s = \exp(-\mu a)$ such that $ds = -\mu\exp(-\mu a)da = -\mu s da$, then

$$\begin{aligned}
1 &= \frac{\beta}{-\mu}\int_0^\infty \frac{1}{1+Ck(1-s)}ds \\
1 &= \frac{\beta}{-\mu}\frac{1}{Ck}[\ln(1+Ck(1-s))]_0^1 \\
1 &= \frac{\beta}{\mu Ck}\ln(1+Ck) \\
\beta &= \frac{\mu Ck}{\ln(1+Ck)} \qquad (5.12)
\end{aligned}$$

By using equations 5.8 and 2.4, we can write $C = \beta N$. Substituting this value into the above equation gives

$$\beta = \frac{\mu(\beta N)k}{\ln(1+\beta Nk)}$$

$$\ln(1+\beta Nk) = \mu Nk$$

$$\beta Nk = e^{\mu Nk} - 1$$
$$\beta = \frac{e^{\mu Nk} - 1}{Nk}. \tag{5.13}$$

By L'Hôpital Rule $\lim\limits_{N\to 0}\frac{e^{\mu Nk}-1}{Nk} = \frac{\mu Nk}{Nk} = \mu$, so that the curves cut the β axis at μ. The overall diagram for both the cases when $k<0$ and $k>0$ is shown in Figure 5.1.

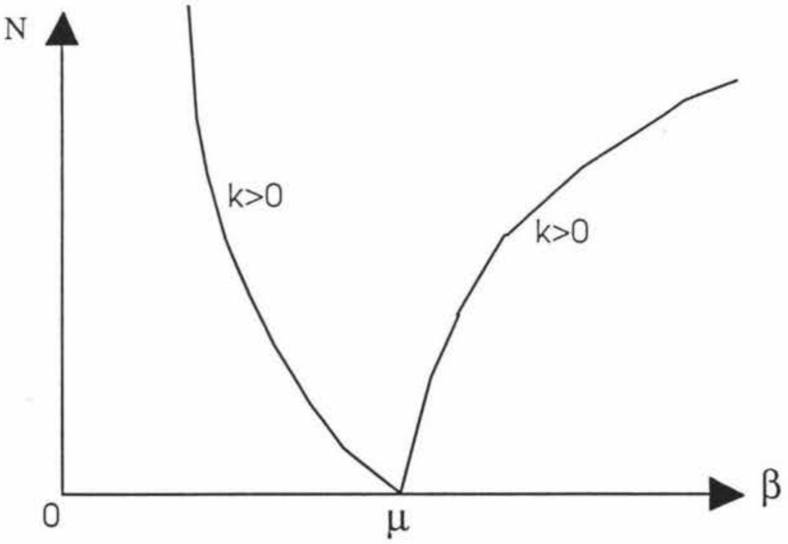


Figure 5.1: The Bifurcation diagram for the non-linear case that is represented by equation (5.1).

5.5 *Stability of the steady age distribution*

In this section, we are going to discuss the stability of the steady age distribution in which the bifurcation diagram is shown in the proceeding section. In section 4.3, we have discussed how to go about finding the stability of the s.a.d. In this section we are going to use the same method that is the method of Liapunov: linearisation of the model about a solution (usually the equilibrium) whose stability or instability is of interest.

Lets us first assume that the solution to our equation model (5.1) in the form

$$n(a,t) = n_s(a) + \varepsilon m(a)\exp(\lambda t), \tag{5.14}$$

such that *m(a)* is some function of age *a* and let equation (5.1) equal $F(n)$. Substituting this into equation (5.1), we have

$$\begin{aligned}&\varepsilon m(a)\lambda\exp(\lambda t) + n_s'(a) + \varepsilon m'(a)\exp(\lambda t) = F(n_s) + \\ &\varepsilon m(a)\exp(\lambda t)F'(n_s) + o(\varepsilon).\end{aligned}$$

This simplifies to

$$n_s'(a) + \varepsilon(\lambda m + m')\exp(\lambda t) = F(n_s) + \varepsilon m(a)\exp(\lambda t)F'(n_s) + o(\varepsilon),$$

such that $F'(n_s) = -\mu(1+2kn_s)$. By linearisation about *m(t)*, we have

$$\begin{aligned}m' + \lambda m &= -\mu(1+2kn_s)m \\ m' &= -(\mu + 2k\mu n_s + \lambda)m.\end{aligned}$$

Using the method of separable variables, we have

$$m(a) = A\int_0^\infty \exp\left(-(\lambda+\mu)a - 2k\mu\int_0^a n_s(a')da'\right)da, \tag{5.15}$$

where $m(0) = A$ is a constant and from the renewal condition, we have

$$m(0)=\beta\int_0^{\infty} m(a)da. \tag{5.16}$$

By substituting (5.15) into (5.16), we have

$$m(0)=A=\beta A\int_0^{\infty}\exp\left(-(\lambda+\mu)a-2k\mu\int_0^a n_s(a')da'\right)da$$

$1=\beta\int_0^{\infty}\exp$ $\left((-\lambda+\mu)a-2k\mu\int_0^a n_s(a')da'\right)da$

$$R(\lambda)=1=\beta\int_0^{\infty}\exp\left((-\lambda+\mu)a-2k\mu\int_0^a n_s(a')da'\right)da. \tag{5.17}$$

By equation (5.10) we know the value of $n_s(a)$, so the above equation becomes

$$R(\lambda)=\beta\int_0^{\infty}\exp\left(-(\lambda+\mu)a-2k\mu\int_{a'=0}^{a'=a}\frac{C\exp(-\mu a')}{1+Ck[1-\exp(-\mu a')]}da'\right)da.$$

Let $s=\exp(-\mu a')$ so that $ds=-\mu\exp(-\mu a')da'$ and thus $da'=\dfrac{ds}{-\mu s}$. The upper limit now becomes $s=\exp(0)=1$ while the lower limit is $s=\exp(-\mu a)$. Our equation now becomes

$$\begin{aligned}
R(\lambda)&=\beta\int_0^{\infty}\exp\left((-\lambda+\mu)a-2k\mu\int_{s=1}^{s=\exp(-\mu a)}\frac{C}{1+Ck(1-s)}\frac{ds}{-\mu s}\right)da\\
&=\beta\int_0^{\infty}\exp\left(-(\lambda+\mu)a-2\{\ln[1+Ck(1-s)]\}_{s=1}^{s=\exp(-\mu a)}\right)da\\
&=\beta\int_0^{\infty}\exp\left(-(\lambda+\mu)a-2\ln(1+Ck(1-e^{-\mu a}))-\ln 1\right)da\\
&=\beta\int_0^{\infty}\exp\left(-(\lambda+\mu)a-2\ln(1+Ck-Cke^{-\mu a})\right)da
\end{aligned}$$

$$R(\lambda)=\beta\int_0^{\infty}\exp(-(\lambda+\mu)a)-\exp[2\ln(1+Ck-Cke^{-\mu a})]da$$

$$=\beta\int_0^{\infty}\frac{e^{-(\lambda+\mu)a}}{(1+Ck-Cke^{-\mu a})^2}da.$$

By equation (5.8) and (2.4), we have $C=\beta N$ so the above equation then becomes

$$1=R(\lambda)=\beta\int_0^{\infty}\frac{e^{-(\lambda+\mu)a}}{(1+\beta Nk-\beta Nke^{-\mu a})^2}da \tag{5.18}$$

$$1=\beta\int_0^{\infty}\frac{e^{-\mu a(\frac{\lambda+\mu}{\mu})}}{[1+\beta Nk-\beta Nke^{-\mu a}]^2}da.$$

Let $\alpha=\beta kN$, then we have:

$$1=\beta\int_0^{\infty}\frac{e^{-\mu a(\frac{\lambda+\mu}{\mu})}}{[1+\alpha-\alpha e^{-\mu a}]^2}da$$

Let $s=e^{-\mu a}$ so that $da=\dfrac{ds}{-\mu s}$. The upper limit now becomes s=0 and the lower limit becomes s=1, our equation is then given by

$$1=\beta\int_1^{0}\frac{s^{\frac{\lambda}{\mu}+1}}{[1+\alpha-\alpha s]^2}\frac{ds}{-\mu s}$$

$$\frac{\mu}{\beta}=\int_0^{1}\frac{s^{\frac{\lambda}{\mu}}}{[1+\alpha-\alpha s]^2}ds=F(\lambda). \tag{5.19}$$

When $\lambda=0$ the equation (5.18) becomes the following:

$$R(0)=\beta\int_0^{\infty}\frac{e^{-\mu a}}{(1+\beta Nk-\beta Nke^{-\mu a})^2}da. \tag{5.20}$$

Let $s = e^{-\mu a}$ then equation (5.20) becomes:

$$\begin{aligned}
R(0) &= \frac{\beta}{\mu}\int_0^1 \frac{1}{(1+\beta Nk-\beta Nks)^2}ds \\
&= \frac{\beta}{\mu}\int_0^1 \frac{1}{(1+\beta Nk-\beta Nks)^2}ds \\
&= \frac{\beta}{\mu}\frac{1}{(\beta Nk)(1+\beta Nk-\beta Nks)}\Bigg]_0^1 \\
&= \frac{1}{\mu Nk}\left[\frac{1}{(1+\beta Nk-\beta Nk)}-\frac{1}{(1+\beta Nk)}\right] \\
&= \frac{1}{\mu Nk}\left[1-\frac{1}{1+\beta Nk}\right] \\
&= \frac{\beta Nk}{\mu Nk(1+\beta Nk)} \\
1 &= \frac{\beta}{\mu(1+\beta Nk)} = F(0).
\end{aligned} \tag{5.21}$$

5.5.1 The stability for the trivial solution

The *trivial* solution, can be obtained directly from equation (5.19). In this case $N = 0$, so that the equation becomes:

$$\begin{aligned}
\frac{\mu}{\beta} &= \int_0^1 s^{\frac{\lambda}{\mu}} ds \\
\frac{\mu}{\beta} &= \frac{1}{\frac{\lambda}{\mu}+1} \\
\lambda &= \beta-\mu
\end{aligned}$$

According to our assumption made earlier (in Chapter 4), when $\lambda < 0$ then it is *asymptotically stable* and if otherwise it is *unstable*. Therefore for our trivial solution, it is *asymptotically stable* when $\beta < \mu$ and *unstable* when $\beta > \mu$. Below is the bifurcation diagram showing the stability at the trivial branch.

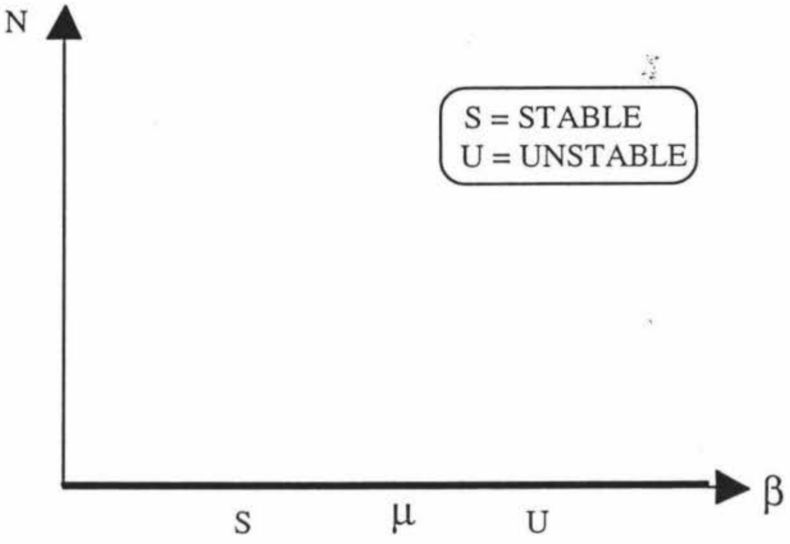


Figure 5.2: The bifurcation diagram for the trivial branch for non-linear model represented by equation (5.1).

5.5.2 The stability of the non-trivial solution

In order to find the stability for the non-trivial branch:

a) $k > 0$
b) $k < 0$,

let us first of all simplify equation (5.21). By substituting the value from equation (5.13) we obtain the following:

$$F(0)=\frac{\dfrac{e^{\mu Nk}-1}{Nk}}{\mu(1+[\dfrac{e^{\mu Nk}-1}{Nk}]Nk)}$$

$$F(0)=\frac{e^{\mu Nk}-1}{\mu Nk\,(e^{\mu Nk})}$$

$$=\frac{1-e^{-\mu Nk}}{\mu Nk}\ . \tag{5.22}$$

Letting $\theta=\mu Nk$, our equation (5.22) then becomes:

$$F(0)=\frac{1-e^{-\theta}}{\theta}. \tag{5.23}$$

Now we based our discussion on equation (5.23) in order to determine the stability for the trivial solution that is we need to know whether the above equation is less than or greater than 1. If $F(0)<1$ then it is *asymptotically stable* and for $F(0)>1$, it is *unstable*.

a) Let us first of all look into the case when $k>0$. We suspect that it is stable at that point so we need to show that (5.23) is less than 1 for $\theta>1$. Assuming this, we obtain

$$\begin{gathered}\frac{1-e^{-\theta}}{\theta}<1\\ 1-e^{-\theta}<\theta\\ 1-\theta<e^{-\theta}\\ 1<e^{-\theta}+\theta\end{gathered}$$

Let $g(\theta)=e^{-\theta}+\theta$ then $g^{'}(\theta)=1-e^{-\theta}>0$ since it is obvious that $e^{-\theta}$ is smaller than 1 and positive. Therefore $g(\theta)>g(0)=1$. Thus our assumption that $F(0)<1$ is true and hence it is *asymptotically stable* when $k>0$. Below

(Figure 6.3) is the sketch of $F(\lambda)$ against λ whereby we can see that if we look at the point when $F(\lambda)=1$, it is always less than 1.

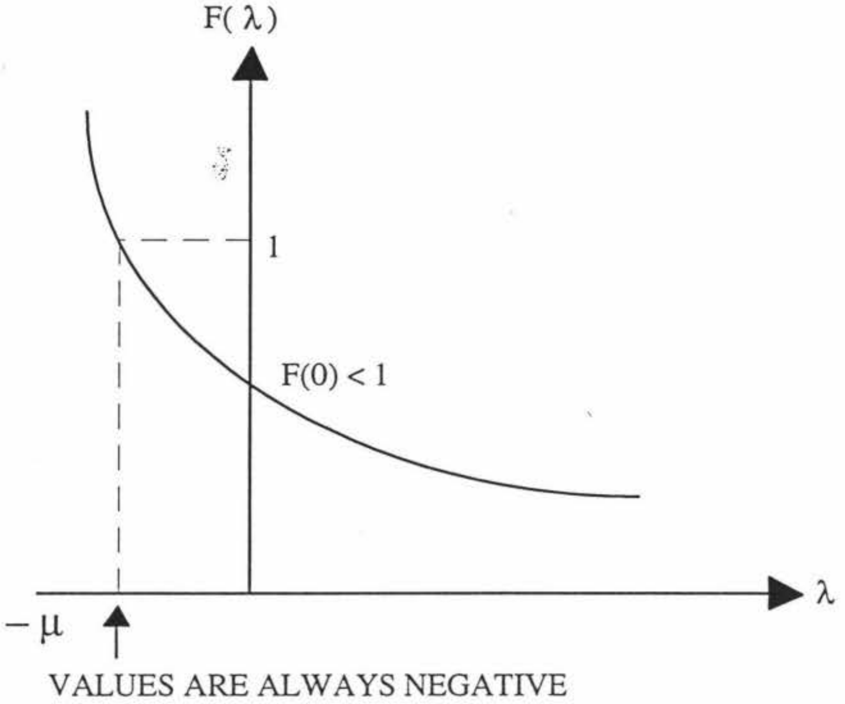


Figure 5.3: Sketch of $F(\lambda)$ against λ such that $F(0)<1$.

b) For the case when $k<0$, equation (5.22) becomes

$$F(0)=\frac{1-e^{\mu kN}}{-\mu Nk}\ . \tag{5.24}$$

Letting $\theta=\mu kN$, our equation (5.24) then becomes

$$F(0)=\frac{e^{\theta}-1}{\theta}\ . \tag{5.25}$$

Using the same procedure as when we look into the case when $k > 0$, let us investigate the stability at $k < 0$. We suspected that it is unstable at this point so we need to show that (5.25) is greater than 1 for $\theta < 1$. Assuming this, equation (5.25) becomes

$$\frac{e^{\theta} - 1}{\theta} > 1$$

so that,

$$e^{\theta} - 1 > \theta$$
$$1 > e^{\theta} - \theta$$

Let $g(\theta) = e^{\theta} - \theta$ then $g'(\theta) = e^{\theta} - 1 < 1$ since e^{θ} when $\theta < 1$ is always less than 1. Therefore $g(\theta) < g(0) = 1$. Thus our assumption that $F(0) > 1$ is true and hence it is *unstable* when $k < 0$. Below (Figure 6.4) is the sketch of $F(\lambda)$ against λ whereby we can see that if we look at the point when $F(\lambda) = 1$, it is always greater than 1.

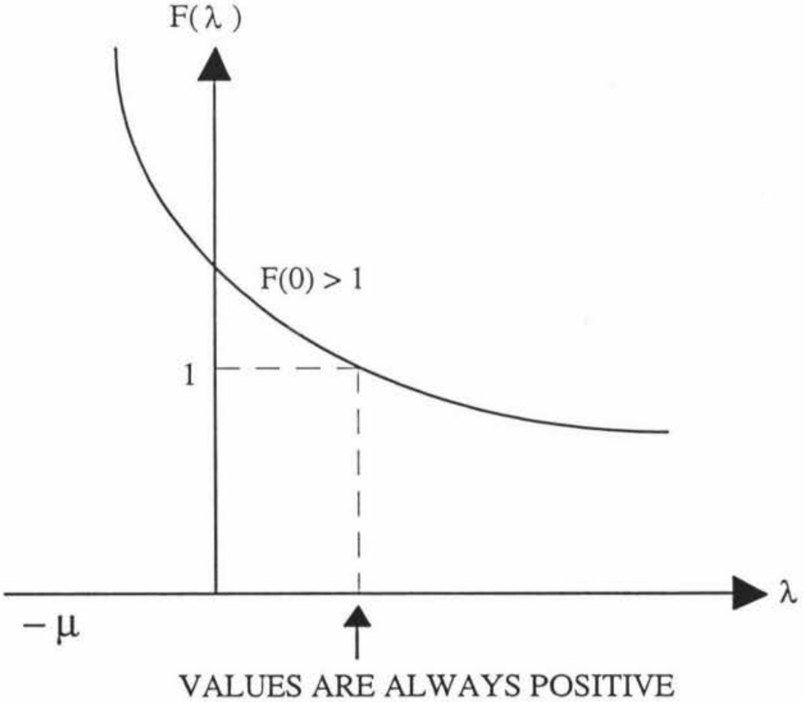


Figure 5.4: Sketch of $F(\lambda)$ against λ such that $F(0) > 1$.

In Figure 5.5 the overall representation of our bifurcation diagram with their stability: s-represent asymptotically stable and u-represent unstable.

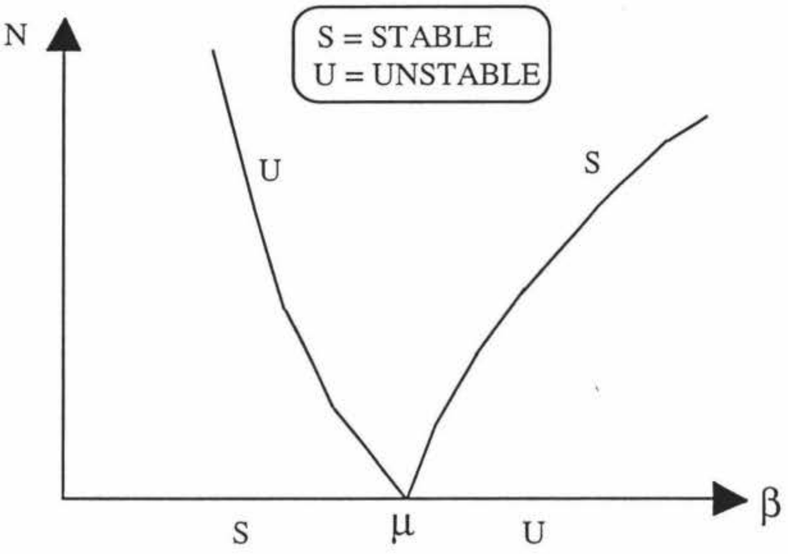


Figure 5.5: The overall representation of the bifurcation diagram with their stability.

5.6 Conclusions

The model that we considered in this chapter provides the effect of overcrowding or limitation of resources but to a certain extend that is, it only affects a specific age class only.

The s.a.d. is found to be :

i) at the trivial branch where it is *asymptotically stable* when $\beta < \mu$ and *unstable* when $\beta > \mu$.

and ii) at the non-trivial branch:

a) If $k > 0$ it is *stable.*
b) If $k < 0$ it is *unstable.*

Chapter 6

Another type of non linear age-structured population

6.1 Introduction

In this chapter, we progress with a more realistic nonlinear model. Here, our model suggests that the whole population will be affected in the case of overcrowding or limitations of resources. This is different from the model we have discussed in chapter 5, where the model suggests that only a specific age group will be affected. We will again look at the s.a.d and its stability using the method previously discussed in chapter 4 (linearisation about a solution: usually the equilibrium point) for a specific type of solution of the form $n(a,t)=e^{\lambda a}m(t)$ and for an arbitrary $n_0(a)$. We will then compare the solutions following the same argument regarding their stability.

The model we shall consider which makes (5.1) non-local is

$$\frac{\partial n}{\partial t}+\frac{\partial n}{\partial a}=-\mu n(1+kN), \qquad t,a>0 \tag{6.1}$$

with the same renewal condition as in (2.2) i.e.

$$n(0,t)=\beta\int_0^\infty n(a,t)da,$$

and initial age-distribution as in (2.3) i.e.

$$n(a,0)=n_0(a).$$

We also define the total population to be as follows

$$N(t) = \int_0^\infty n(a,t)da. \tag{6.2}$$

6.2 *The solutions to the non linear age-structured model*

In this section, we will look at the solutions of the form $n(a,t) = e^{\lambda a}m(t)$ and for general arbitrary function $n_0(a)$. We shall expect the solutions to be the same and thus we will show its relations.

6.2.1 The solution of a specific type

Let us, firstly assume the solution to our model is of the type

$$n(a,t) = e^{\lambda a}m(t), \tag{6.3}$$

where *m(t)* is some function of t.

Substituting this solution into (6.1), we obtain

$$\frac{m'(t)}{m(t)} + \lambda = -\mu(1+kN)$$
$$\frac{m'(t)}{m(t)} = -(\lambda+\mu) - \mu kN.$$

We can then find *m(t)* as follows

$$m(t) = Ce^{-(\lambda+\mu)t}\exp\left[\int_0^t(-\mu kN(s)ds)\right], \tag{6.4}$$

where *C* is some constant.

From the equations (6.4) and (6.3), it then follows that

$$n(a,t) = Ce^{\lambda a} e^{-(\lambda+\mu)t} \exp[\int_0^t (-\mu k N(s) ds)]. \tag{6.5}$$

When $a = 0$, equation (6.5) then becomes

$$n(0,t) = Ce^{-(\lambda+\mu)t} \exp[\int_0^t (-\mu k N(s) ds)]. \tag{6.6}$$

By substituting (6.5) and (6.6) into the renewal condition: (2.2), we have

$$\begin{aligned} 1 &= \beta \int_0^\infty e^{\lambda a} da \\ &= -\frac{\beta}{\lambda} \end{aligned}$$

Therefore $\lambda = -\beta$ and equation (6.5) can be expressed as

$$n(a,t) = Ce^{-\beta a + (\beta-\mu)t} \exp[\int_0^t (-\mu k N(s) ds)]. \tag{6.7}$$

From the above equation, it follows that the initial conditions

$$n(a,0) = n_0(a) = Ce^{-\beta a} .$$

Therefore the total population *N*(*t*) can be calculated, using equation (6.2) and (6.7) which is given by

$$N(t) = \frac{C}{\beta} e^{(\beta-\mu)t} \exp(-\mu k \int_0^t N(s) ds).$$

Let us now differentiate *N*(*t*)

$$N'(t) = [\beta - \mu - \mu k N(t)] N(t), \tag{6.8}$$

with

$$N(0)=\frac{C}{\beta}$$

Then by writing

$$P(t)=\frac{1}{N(t)}, \tag{6.9}$$

it then follows that

$$N^{'}(t)=-\frac{1}{P^{2}}P^{'}(t). \tag{6.10}$$

Substituting the value of (6.9) and (6.10) into equation (6.8), we have

$$P^{'}(t)=\mu k-(\beta-\mu)P(t)$$

which has the solution

$$P(t)=Ke^{-(\beta-\mu)t}+\frac{\mu k}{(\beta-\mu)}.$$

Therefore

$$N(t)=\frac{1}{Ke^{-(\beta-\mu)t}+\dfrac{\mu k}{(\beta-\mu)}}$$

and from the initial conditions $N(0)=\dfrac{C}{\beta}$, we obtain

$$\frac{C}{\beta}=\frac{1}{\frac{\mu k}{\beta-\mu}+K},$$

so that

$$K=\frac{\beta}{C}-\frac{\mu k}{\beta-\mu}.$$

We then represent $N(t)$ as follows

$$\boxed{N(t)=\frac{1}{\frac{\mu k}{(\beta-\mu)}\left(1-e^{-(\beta-\mu)t}\right)+\frac{\beta}{C}e^{-(\beta-\mu)t}}} \tag{6.11}$$

We can now substitute the value (6.11) into the population density equation (6.7), which gives

$$n(a,t)=Ce^{-\beta a+(\beta-\mu)t}\exp(-\mu k\int_{0}^{t}\frac{1}{\frac{\mu k}{(\beta-\mu)}\left(1-e^{-(\beta-\mu)s}\right)+\frac{\beta}{C}e^{-(\beta-\mu)s}}ds). \tag{6.12}$$

Let $x=e^{-(\beta-\mu)s}$ so that $ds=\frac{dx}{-(\beta-\mu)x}$. The upper and lower limit is thus given by $x=e^{-(\beta-\mu)t}$ and $x=1$ respectively. The equation (6.12) can then be written as :

$$n(a,t)=Ce^{-\beta a+(\beta-\mu)t}\exp(\mu k\int_{x=1}^{x=e^{-(\beta-\mu)t}}\frac{1}{x[C\mu x-(C\mu x-\beta^{2}+\beta\mu)x}dx)$$

$$=Ce^{-\beta a+(\beta-\mu)t}\exp(\mu k\left[\frac{1}{-C\mu k}\ln(\frac{C\mu x-(C\mu x-\beta^{2}+\beta\mu)x}{x})\right]_{x=1}^{x=e^{-(\beta-\mu)t}}$$

$$= Ce^{-\beta a+(\beta-\mu)t}\exp(\frac{1}{-C}\ln(\frac{C\mu - C\mu e^{-(\beta-\mu)t} - \beta^2 + \beta\mu}{\mu - C\mu + \beta^2 + \beta\mu}))$$

$$n(a,t) = \left[\frac{C\mu - C\mu e^{-(\beta-\mu)t} - \beta^2 + \beta\mu}{\mu - C\mu + \beta^2 + \beta\mu})\right] Ce^{-\beta a+(\beta-\mu)t+1/-C}. \qquad (6.13)$$

This is the solution to our model (6.1) for the type (6.3).

6.2.2 The solution to the arbitrary $n_0(a)$.

Next, we would like to see whether our equation model could cope with the arbitrary $n_0(a)$. In this case let us take the Laplace transform in a for $n(t,a)$, which is given by:

$$\bar{n}(p,t) = \int_0^\infty e^{-pa} n(a,t)da.$$

Then our model becomes:

$$\frac{d\bar{n}}{dt} + p\bar{n} - n(t,0) = -\mu\bar{n}(1 + kN(t),$$

but by equation (2.2)

$$n(0,t) = \beta N(t),$$

so that

$$\frac{d\bar{n}}{dt} + \bar{n}[p + \mu(1 + kN(t))] = \beta N(t) \qquad (6.14)$$

Since the lefthand side of the above equation can be written as

$$e^{(pt+\mu t+\mu k\int_0^t N(s)ds)} \frac{\partial}{\partial t}[\bar{n}\exp(pt + \mu t + \mu k\int_0^t N(s)ds)],$$

our equation (6.14) then becomes

$$e^{(pt+\mu t+\mu k\int_0^t N(s)ds)}\frac{\partial}{\partial t}[\bar{n}\exp(pt+\mu t+\mu k\int_0^t N(s)ds)]=\beta N(t).$$

Therefore we can thus find $\bar{n}(t,p)$ as:

$$\bar{n}(t,p)=\left[\exp(-pt-\mu t-\mu k\int_0^t N(s)ds)\right]$$
$$\beta\int_0^t N(r)\exp(-pr-\mu r-\mu k\int_0^r N(s)ds)ds+\bar{n}(0,p)$$

so that

$$n(a,t)=\beta\int_0^t e^{-p(t-x)}e^{-\mu(t-x)}e^{-\mu k\int_r^t N(s)ds}N(r)dr+$$
$$\bar{n}_0(p)e^{-pt}e^{-\mu t}e^{-\mu k\int_0^t N(s)ds}$$

From the Laplace transform $\bar{f}(p)=e^{-pt}$ and $\bar{f}(p)=e^{-p(t-r)}$, we have $f(a)=\delta(a-t)$ and $f(a)=\delta(a-t+r)$ respectively.

So that we may obtain the value of $n(t,a)$ in terms of N(t) to give

$$n(a,t)=\beta\int_0^t \delta(a-t+r)e^{-\mu(t-r)}e^{-\mu k\int_r^t N(s)ds}N(r)dr+$$
$$n_0(a)*\delta(a-t)e^{-\mu t}e^{-\mu k\int_r^t N(s)ds}.$$

Now since

$$
\begin{aligned}
\int_0^t \delta(a-t+r)F(t,r)dr &= F(t,t-a), && t \geq a \\
&= 0, && t \leq a \\
&= F(t,t-a)H(t-a)
\end{aligned}
$$

and

$$
\begin{aligned}
n_0(a)*\delta(a-t) &= \int_0^a n_0(\alpha)\delta(a-\alpha-t)d\alpha \\
&= \int_0^a n_0(\alpha)\delta(\alpha-(a-t))d\alpha \\
&= n_0(a-t), a \geq t \\
&= 0 \qquad ,a \leq t \\
&= n_0(a-t)H(a-t),
\end{aligned}
$$

the solution falls on the 2 different regions discussed in chapter 2 (see Figure 2.1)

$$
\begin{aligned}
n(a,t) = &\underbrace{\beta e^{-\mu a} e^{-\mu k \int_{t-a}^{t} N(s)ds} N(t-a)H(t-a)}_{a<t}. \\
&\underbrace{+n_0(a-t)H(a-t)e^{-\mu t} e^{-\mu k \int_{r}^{t} N(s)ds}}_{a \geq t}
\end{aligned}
\tag{6.15}
$$

Equation (6.15) satisfies the equation $n(0,t) = \beta N(t)$ trivially.

From equation (6.2) we have that

$$
N(t) = \int_0^\infty n(t,a)da = \int_0^t \underbrace{n(a,t)da}_{a<t} + \int_t^\infty \underbrace{n(a,t)da}_{a \geq t}.
$$

Therefore, our equation becomes

$$\begin{aligned} N(t) &= \beta\int_0^t e^{-\mu a} e^{-\mu k\int_{t-a}^{t} N(s)ds} N(t-a)da + \int_t^{\infty} n_0(a-t)e^{-\mu t} e^{-\mu k\int_0^t N(s)ds} da \\ &= \beta e^{-\mu k\int_0^t N(s)ds} \int_0^t e^{-\mu a} e^{\mu k\int_0^{t-a} N(s)ds} N(t-a)da + e^{-\mu t} e^{-\mu k\int_0^t N(s)ds} \int_t^{\infty} n_0(a-t)da. \end{aligned}$$

But $\int_t^{\infty} n_0(a-t)da = \int_0^{\infty} n_0(r)dr \equiv N_0$, where N_0 is the total number of individuals present at $t = 0$. The above equation becomes:

$$\begin{aligned} N(t) &= \beta e^{-\mu k\int_0^t N(s)ds} \int_0^t N(a) e^{\mu k\int_0^a N(s)ds} e^{-\mu(t-a)}da + N_0 e^{-\mu t-\mu k\int_0^t N(s)ds} \\ &= e^{-\mu k\int_0^t N(s)ds} e^{-\mu t}\{N_0 + \beta\int_0^t N(a) e^{\mu k\int_0^a N(s)ds} e^{\mu a}da\}. \end{aligned} \tag{6.16}$$

Taking the derivative of, equation (6.16) with respective to *t* gives

$$\begin{aligned} N^{'}(t) &= [-\mu - \mu k N(t)]N(t) + \beta N(t) \\ &= N(t)[(\beta-\mu) - \mu k N(t)]. \end{aligned}$$

By separable variables, we then have:

$$\frac{1}{(\mu-\beta)}\ln\left|\frac{-\mu k N(t) + \beta - \mu}{N(t)}\right| = t + C$$

where C is a constant.

The simplified equation can now be expressed as

$$N(t) = \frac{(\beta-\mu)}{Ae^{(\mu-\beta)t} + \mu k},$$

where A is the constant obtained by redefining C. At $t = 0$,

$$N(t) = N_0.$$

The value of the constant A is then given by

$$A = \frac{(\beta - \mu)}{N_0} - \mu k.$$

Thus we can find N(t) for arbitrary $n_0(a)$ as:

$$N(t) = \frac{(\beta - \mu)}{\left[\frac{(\beta - \mu)}{N_0} - \mu k\right] e^{(\mu - \beta)t} + \mu k}$$

or

$$N(t) = \frac{(\beta - \mu) N_0}{\left[(\beta - \mu) - \mu k N_0\right] e^{(\mu - \beta)t} + \mu k N_0} \tag{6.17}$$

6.2.3 Comparison of the solutions of the specific type $n(a,t) = e^{\lambda a} m(t)$ with the arbitrary $n_0(a)$

The solutions to both the specific type and the arbitrary functions are summarised in Table 6.1.

	The solutions	
	Total population N(t)	Population density n(a,t)
specific solution $n(a,t) = e^{\lambda a} m(t)$	$\dfrac{1}{\dfrac{\mu k}{(\beta-\mu)}\left(1-e^{-(\beta-\mu)t}\right)+\dfrac{\beta}{C}e^{-(\beta-\mu)t}}$	$\left[\dfrac{C\mu - C\mu e^{-(\beta-\mu)t} - \beta^2 + \beta\mu}{\mu - C\mu + \beta^2 + \beta\mu})\right] C e^{-\beta a+(\beta-\mu)t+1/-C}$
arbitrary function $n_0(a)$	$\dfrac{(\beta-\mu)N_0}{\left[(\beta-\mu)-\mu k N_0\right]e^{(\mu-\beta)t}+\mu k N_0}$	$n(a,t) = \underbrace{\beta e^{-\mu a} e^{-\mu k \int_{t-a}^{t} N(s)ds} N(t-a) H(t-a)}_{a<t}$ $\underbrace{+n_0(a-t)H(a-t)e^{-\mu t}e^{-\mu k \int^{t} N(s)ds}}_{a\geq t}$

Table 6.1: Summary of the solutions to the specific type with the arbitrary function mentioned in sections 6.2.1 and 6.2.2.

Basically, the solutions to the specific type and the arbitrary function are equal to one another. There are of different forms. The solution to the arbitrary function is the general solution to the problem.

6.3 The steady age-distribution (s.a.d.) and its stability

In chapter 4, we have discussed elaborately about steady ages-distribution (s.a.d) and the stability argument of how we are going to go about obtaining the result. Here, we shall follow the same procedure. We shall observe the steady age-distribution for the specific form using the equation (6.11) and for the arbitrary $n_0(a)$, we shall use the equation (6.17). Before we begin with our investigation, we may assume that there exists a critical C, which we hereby represents as C_{cr}. This is said to represent the edge of the stable manifold of $n_s \equiv 0$.

Let us first define an equilibrium solution to the equation (6.1, 2.2 and 2.3) as the solution $n(a,t) \to n_s(a)$ that is independent of time. The function $n_s(a)$ is the steady age-distribution (s.a.d.).

An equilibrium solution $n_s(a)$ will satisfy the equation

$$\frac{dn_s}{da} = -\mu n_s(1 + kN_s)$$

and the renewal conditions (from 2.2) is then simplifies to

$$n_s(0) = \int_0^\infty \beta(a) n_s(a) da,$$

where $n_s(0)$ is the (constant) birth rate at equilibrium. By separation of variables, the solution to the above equation then becomes

$$n_s(a) = L\exp[-\mu a(1 + kN_s)], \tag{6.18}$$

where $n_s(0) = L$.

For $a = 0$, equation (6.18) becomes

$$n_s(0) = L,$$

and substituting the above results and equation (6.18) into the renewal condition, we obtain

$$L = \beta L \int_0^\infty \exp[-\mu a(1 + kN_s)]da$$

$$1 = \frac{\beta}{\mu(1 + kN_s)} \tag{6.19}$$

$$N_s = \frac{\beta - \mu}{\mu k}. \tag{6.20}$$

We have defined earlier the expression for the total population to be

$$N_s = \int_0^\infty n_s(a)da.$$

Substituting (6.18) into the above equation gives

$$N_s = \frac{L}{\mu(1+kN_s)}.$$

To find the value for the arbitrary constant L, we need to use the equation (6.19) substituted into the expression (6.20) as demonstrated below:

$$\begin{aligned} L &= \mu(N_s + kN_s^2) \\ &= \mu\left(\frac{\beta-\mu}{\mu k} + k\left(\frac{\beta-\mu}{\mu k}\right)^2\right). \end{aligned}$$

Simplifying the above expression we have:

$$L = \frac{\beta(\beta-\mu)}{\mu k}.$$

By using the equation (6.19) and the above result, equation (6.18) becomes

$$\boxed{n_s(a) = \frac{\beta(\beta-\mu)}{\mu k}\exp(-\beta a)} \tag{6.21}$$

This is the equation of the steady age-distribution (s.a.d.) for our model.

6.3.1 The stability for the specific solution of the form represented by equation (6.3)

In subsection 6.2.1, we have found the expression for the total population to be represented by (6.11)

$$N(t)=\frac{1}{\frac{\mu k}{(\beta-\mu)}\left(1-e^{-(\beta-\mu)t}\right)+\frac{\beta}{C}e^{-(\beta-\mu)t}}.$$

We shall use this equation inorder to investigate the stability of the following:

a) trivial solution (when *N*(*t*)=*0*)

b) the two non-trivial branches, which are:
  i) when $\beta>\mu$ and $k>0$ and
  ii) when $\beta<\mu$ and $k<0$

a) For the trivial solution ($N_s\equiv 0$), we define equation (6.19) as

$$R(0)=1=\frac{\beta}{\mu(1+kN_s)}$$

$$=\frac{\beta}{\mu}$$

Following the proposition made earlier, if $R(0)<1$, the trivial solution ($N_s\equiv 0$) is *asymptotically stable* and if $R(0)>1$, it is *unstable*. Therefore, if $\beta<\mu$, then it is *asymptotically stable* and if $\beta>\mu$, then it is *unstable*.

b i) If $\beta>\mu$ and $k>0$ then from equation (6.11) the term $e^{-(\beta-\mu)t}$ is too small and vanishes and therefore we have

$$N(t)\rightarrow\frac{1}{\frac{\mu k}{\beta-\mu}}\text{for all } C\neq 0.$$

Argument:

At this branch, $\frac{(\beta-\mu)}{\mu k}$ is known as the *global attractor*. This means that whatever value of N(t) we start with (greater or less than this expression), it will always tends to this expression. We can then conclude that at this branch it is *asymptotically stable*. This result means that the area below the graph $n_0(a)$ plotted against a i.e. the long term behaviour N_0 will be the same regardless of the shape of the graph it takes, i.e. it is robust. This is demonstrated by the bifurcation diagram of *N(t)* against β in Figure 6.1 and its population-time graph (transient diagram) in Figure 6.2.

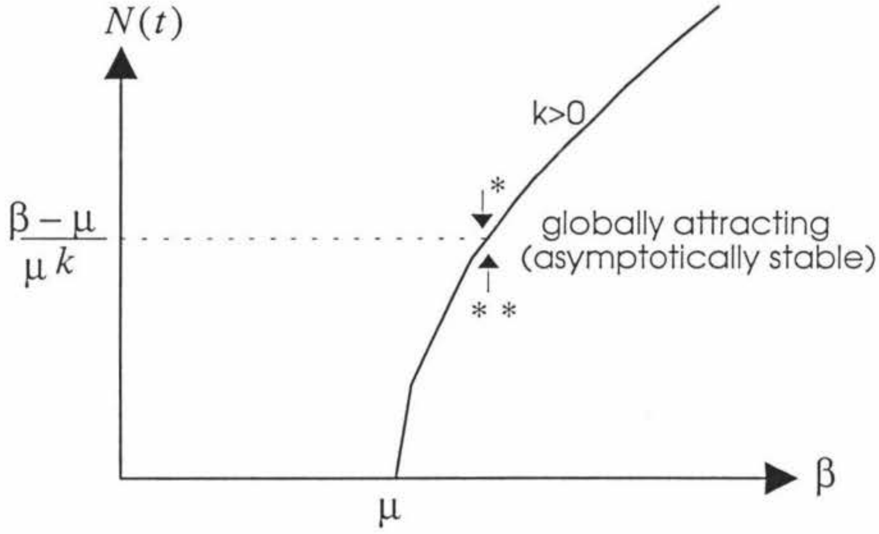


Figure 6.1: The sketch of bifurcation diagram *N(t)* against β when $\beta > \mu$ and $k > 0$ for the case when the solution is assumed to be of the type $n = e^{\lambda a} m(t)$.

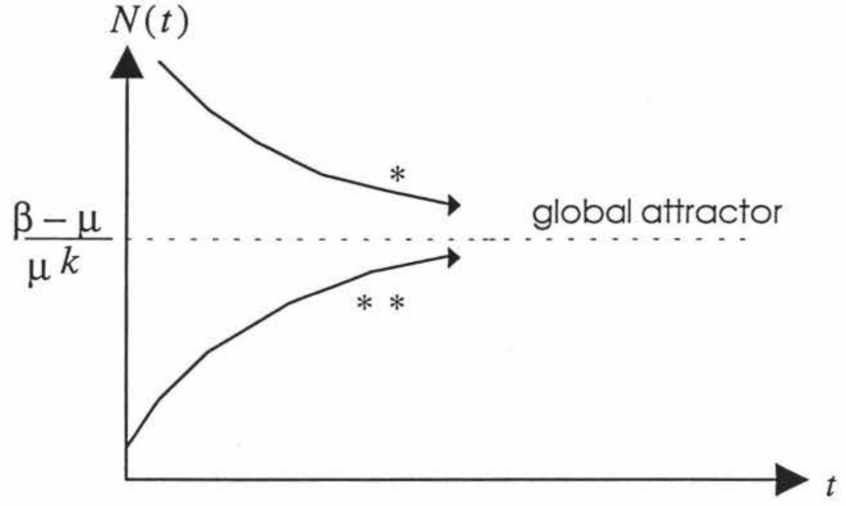


Figure 6.2: The population-time graph (transient diagram) when $\beta > \mu$ and $k > 0$ showing the global attraction for the type $n = e^{\lambda a}m(t)$.

b ii) If $\beta < \mu$ and $k < 0$, then the expression (6.11) becomes:

$$N(t) = \frac{1}{-\frac{\mu k}{\mu-\beta}(e^{(\mu-\beta)t}-1)+\frac{\beta}{C}e^{(\mu-\beta)t}}\,. \qquad (6.22)$$

Let us now look at the denominator of the above equation in order to determined whether

i) $N(t) \to 0$ as $t \to \infty$ (that is when C is sufficiently small) or
ii) if C is large is it possible that $\exists t^{*}: N(t) \to \infty$ as $t \to t^{*}$.

i) If we want $N(t) \to 0$ as $t \to \infty$, then the denominator of equation (6.22) must get to infinity but in order for this to happen the denominator of the denominator that is $(\mu-\beta)$ or C has to be small. However, since $\beta < \mu$, then $\mu - \beta$ is large so that C should be small, small enough to be dominated by the factor $e^{(\mu-\beta)t}$ because this factor tends to be large as $t \to \infty$. In other words, we need

$$-\frac{\mu k}{\mu-\beta}(e^{(\mu-\beta)t}-1)<\frac{\beta}{C}e^{(\mu-\beta)t}$$

How small should C be?

$$e^{(\mu-\beta)t}\left[\frac{\beta}{C}+\frac{\mu k}{\mu-\beta}\right]<0$$

$$-\frac{\mu k}{\mu-\beta}<\frac{\beta}{C}$$

$$C<\frac{\beta(\beta-\mu)}{\mu k}$$

and since $N(0)=N_0=\dfrac{C}{\beta}$, then we have

$$N_0<\frac{\beta-\mu}{\mu k}.$$

Therefore C has to be smaller than $\dfrac{\beta(\beta-\mu)}{\mu k}$ and we can say that the critical value for C i.e. C_{cr} is given by $C_{cr}=\dfrac{\beta(\beta-\mu)}{\mu k}$ or the critical value of N_0 i.e. $N_{0,cr}$ is given by $N_{o,cr}=\dfrac{(\beta-\mu)}{\mu k}$.

ii) For the equation (6.22) to tend to infinity, the denominator has to tend to zero that is we need

$$\frac{\mu k}{\mu-\beta}(e^{(\mu-\beta)t}-1)=\frac{\beta}{C}e^{(\mu-\beta)t}.$$

This is to determine the time at which the denominator will tend to infinity, we shall proceed further as follows:

$$\left[\frac{\mu k}{\mu-\beta}-\frac{\beta}{C}\right]e^{(\mu-\beta)t}=\frac{\mu k}{\mu-\beta}$$

$$e^{(\mu-\beta)t}=\frac{\mu kC}{\mu kC-\beta\mu+\beta^2}$$

$$t^*=\frac{1}{(\mu-\beta)}\ln\left[\frac{\mu kC}{\mu kC-\beta\mu+\beta^2}\right].$$

Argument:

From 6.3.1 b ii) this means that if we start with the value of *N(t)* below the critical value $N_{0,cr}$, the total population will dies out and if we start with value of *N(t)* above the critical value, the population will explodes that is *N(t)* will go to infinity at the time given by t^*, such that $N_{o,cr}=\frac{(\beta-\mu)}{\mu k}$. At this branch we can say that it is *unstable* and there is a *watershed* at that point. This is best demonstrated by Figure 6.3 and the population-time graph (transient diagram) is shown in Figure 6.4. This is then followed by the overall bifurcation diagram for this problem which will be shown by Figure 6.5.

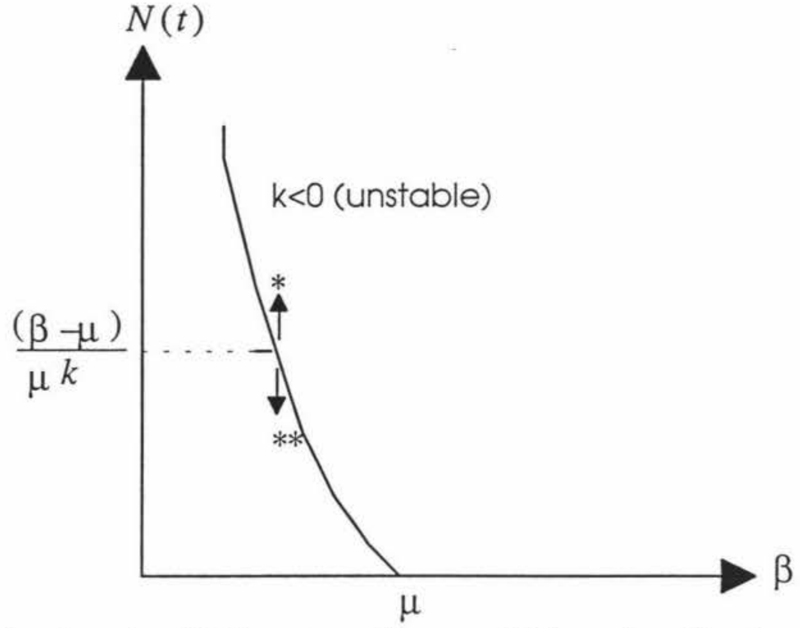


Figure 6.3: The sketch of bifurcation diagram *N(t)* against β when $\beta < \mu$ and $k < 0$ for the case when the solution is assumed to be of the type $n = e^{\lambda a} m(t)$ showing the *water shed* at the point $N_{o,cr} = \dfrac{(\beta - \mu)}{\mu k}$.

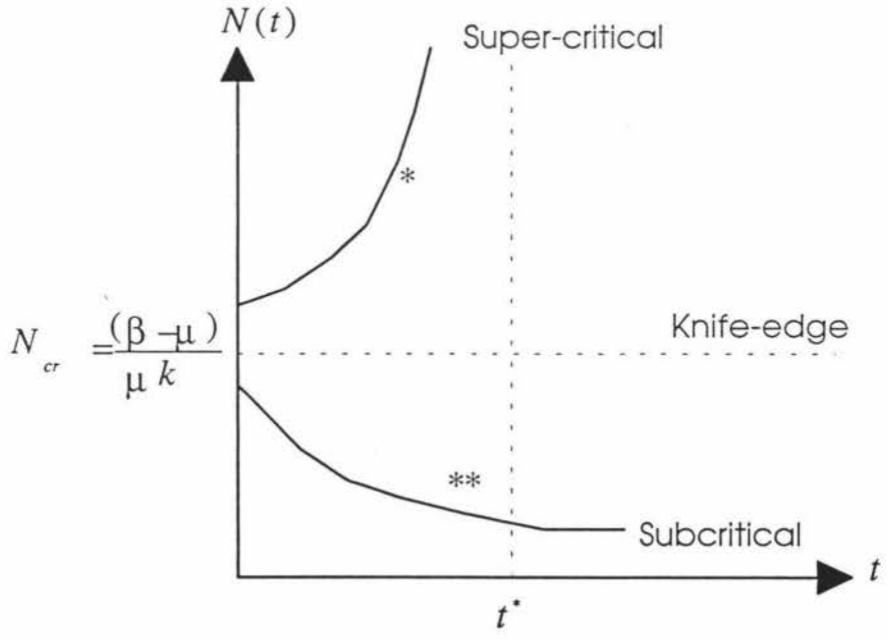


Figure 6.4: The population-time graph (Transient diagram) for the case if $\beta < \mu$ and $k < 0$ when the solution is assumed to be of the type $n = e^{\lambda a} m(t)$

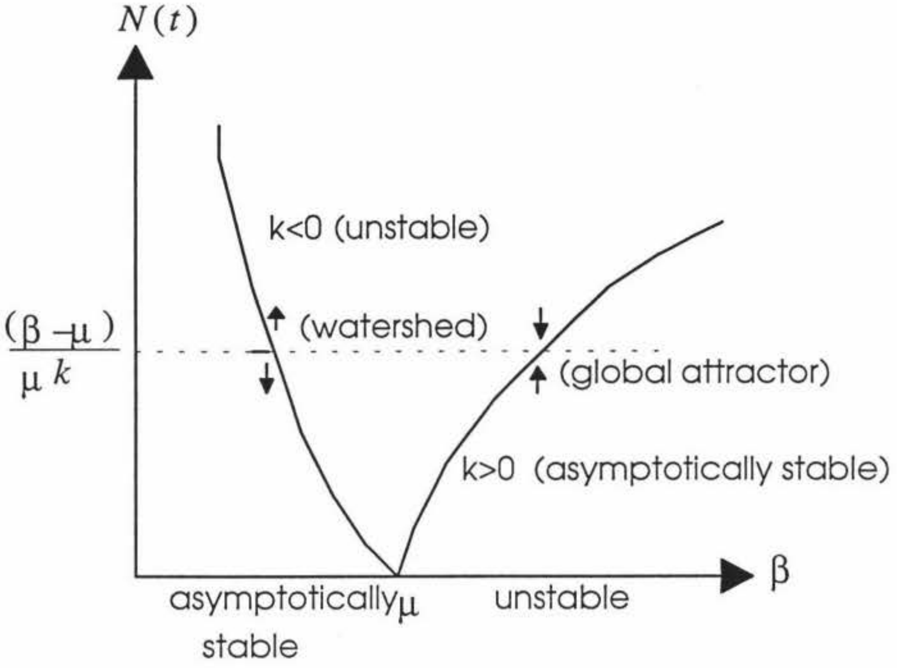


Figure 6.5: The overall bifurcation diagram for the case when the solution is assumed to be of the type $n = e^{\lambda a} m(t)$

6.3.2 The stability of the steady age-distribution for the arbitrary $n_0(a)$

In subsection 6.2.2, we have found the expression for the total population to be given by equation (6.17)

$$N(t) = \frac{(\beta - \mu) N_0}{[(\beta - \mu) - \mu k N_0] e^{(\mu - \beta)t} + \mu k N_0}. \tag{6.17}$$

Let us now look at the stability at the following:

a) the trivial solution ($N(t) \equiv 0$),

b) the two non-trivial branches. The two branches are:
  i) when $\beta > \mu$ and $k > 0$ and
  ii) when $\beta < \mu$ and $k < 0$

a) For the trivial solution, we have the same argument for the specific type. We first of all define the equation (6.19)

$$R(0) = 1 = \frac{\beta}{\mu(1 + kN_s)}.$$

When $N_s \equiv 0$, we have

$$R(0) = \frac{\beta}{\mu}.$$

Following the proposition made earlier in Chapter4, if $R(0) < 1$, it is *asymptotically stable*, and if $R(0) > 1$, it is *unstable*. Therefore, if $\beta < \mu$, then it is *asymptotically stable* and if $\beta > \mu$, then it is *unstable*.

b i) If $\beta > \mu$ and $k > 0$, then the term in the denominator which dominates is $\mu k N_0$ because the exponential term is too small so that $N(t) \to \frac{\beta - \mu}{\mu k}$. It means that at this branch it will always tend to the value $\frac{\beta - \mu}{\mu k}$. The expression $\frac{\beta - \mu}{\mu k}$ is said to be the *global attractor* and it is *asymptotically stable* at this point and it does not depends on the value of N(t). This suggest that the the area below the graph $n_0(a)$ plotted against a i.e the long-term behaviour N_0 will be the same regardless of the shape of the graph it takes. This is robust. The bifurcation diagram Figure 6.1 and transient diagram Figure 6.2 still applies for this problem.

b ii) For $\beta < \mu$ and $k < 0$, then the expression (6.17) can be simplifies as

$$N(t) = \frac{1}{\left[\frac{1}{N_0} + \frac{\mu k}{\mu - \beta}\right] e^{(\mu-\beta)t} + \frac{\mu k}{\mu - \beta}}.$$

We shall now consider the following cases in conjunction with the above equation, in order to determine whether

i) $N(t) \to 0$ as $t \to \infty$ (that is when N_0 is sufficiently small) or
ii) if N_0 is large is it possible that $\exists t^*: N(t) \to \infty$ as $t \to t^*$.

i) For $N(t) \to 0$, we need the denominator to gets to infinity. When $t \to \infty$, it is obvious that the term $e^{(\mu-\beta)t} \to +\infty$, but the terms μk is less than zero, so that the term

$$\left[\frac{1}{N_0} + \frac{\mu k}{\mu - \beta}\right] e^{(\mu-\beta)t}$$

will dominate. For this terms to get to infinity, we must have this condition

$$\left[\frac{1}{N_0} + \frac{\mu k}{\mu - \beta}\right] > 0.$$

Therefore, we obtain the critical value for the total population, $N_{0,cr}$ to be given by

$$N_{0,cr} < \frac{\beta - \mu}{\mu k}.$$

ii) For $N(t) \to \infty$, we need the denominator to be zero.

$$\left[\frac{1}{N_0}+\frac{\mu k}{\mu-\beta}\right]e^{(\mu-\beta)t}=\frac{\mu k}{\mu-\beta}$$

$$t^{*}=\frac{1}{\mu-\beta}\ln\left\{\frac{\mu k N_0}{\beta-\mu+\mu k N_0}\right\} \tag{6.23}$$

From 6.3.2 b ii) this explains that if we are to start with a total population *N(t)* below the critical value $N_{0,cr}=\dfrac{\beta-\mu}{\mu k}$, the population will dies out and if we are to start with value of *N(t)* above the critical value then the population will explodes that is *N(t)* will go to infinity at the time given by t^{*}. At this point there is a *watershed* effect which means that the value always avoids $\dfrac{\beta-\mu}{\mu k}$. At this branch we can say that it is *unstable*. The diagram is the same as the case when we are considering the specific type so that we can refer to Figure 6.3 for the bifurcation diagram and Figure 6.4 for the population-time graph. The overall bifurcation diagram will be demonstrated by Figure 6.6.

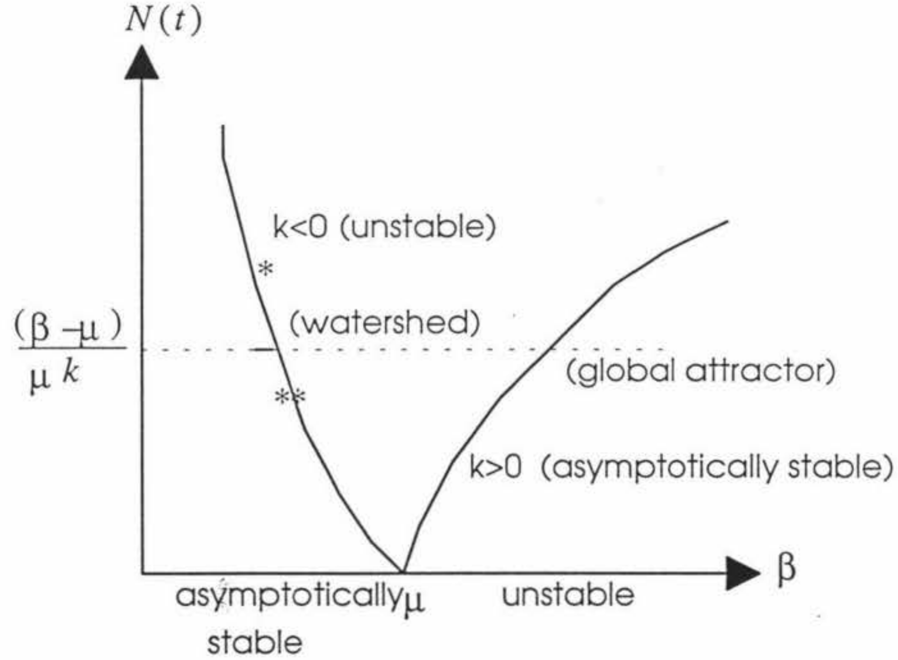


Figure 6.6: The sketch of the overall bifurcation diagram for the case when the solution is the arbitrary $n_0(a)$.

6.4 Conclusions

The non-linear population model that we consider in this chapter is expected to be the more realistic compared to the model discussed in chapter 3 and 5. It allows the effect of overcrowding or limitation resources which have the possibility to affect the whole population and not only a certain age group.

The model considered is of the form:

$$\frac{\partial n}{\partial t}+\frac{\partial n}{\partial a}=-\mu n(1+kN).$$

The solutions can be summarised in Table 6.1 below.

Solutions	solution of the form $n(a,t)=e^{\lambda a}m(t)$	arbitrary function $n_o(a)$
Total population $N(t)$	$\dfrac{1}{\dfrac{\mu k}{(\beta-\mu)}\left(1-e^{-(\beta-\mu)t}\right)+\dfrac{\beta}{C}e^{-(\beta-\mu)t}}$	$\dfrac{(\beta-\mu)N_0}{\left[(\beta-\mu)-\mu kN_0\right]e^{(\mu-\beta)t}+\mu kN_0}$
Population density $n(a,t)$	$\left[\dfrac{C\mu-C\mu e^{-(\beta-\mu)t}-\beta^2+\beta\mu}{\mu-C\mu+\beta^2+\beta\mu})\right]Ce^{-\beta a+(\beta-\mu)t+\mu-C}$	$\underbrace{\beta e^{-\mu a}e^{-\mu k\int_{t-a}^{t}N(s)ds}N(t-a)H(t-a)}_{a<t}$ $+\underbrace{n_0(a-t)H(a-t)e^{-\mu t}e^{-\mu k\int_{t}^{t}N(s)ds}}_{a\geq t}$

The s.a.d. for the model is given by

$$n_s(a)=\frac{\beta(\beta-\mu)}{\mu k}\exp(-\beta a)$$

The summary of the stability of solution of the type $n(a,t)=e^{\lambda a}m(t)$ and the arbitrary function $n_o(a)$ is given by Table 6.2 below.

	$n(a,t)=e^{\lambda a}m(t)$	$n_o(a)$
Critical value of $N_{0,cr}$	$\frac{(\beta-\mu)}{\mu k}$	$\frac{(\beta-\mu)}{\mu k}$
t^{*}	$\frac{1}{(\mu-\beta)}\ln\left[\frac{\mu kC}{\mu kC-\beta\mu+\beta^{2}}\right]$	$\frac{1}{\mu-\beta}\ln\left\{\frac{-\mu kN_0}{\beta-\mu-\mu kN_0}\right\}$
stability at trivial branch	when $\beta>\mu$, it is asymptotically stable and when $\beta>\mu$ it is unstable.	when $\beta>\mu$, it is asymptotically stable and when $\beta>\mu$ it is unstable.
stability at branch when $\beta>\mu$ and $k>0$	Whatever the value that N(t) starts with will always tend to the critical value $N_{0,cr}$. We said that $N_{0,cr}$ is the global attractor and it is *asymptotically stable* at this branch.	Whatever the value that N(t) starts with will always tend to the critical value $N_{0,cr}$. We said that $N_{0,cr}$ is the global attractor and it is *asymptotically stable* at this branch.
stability at branch when $\beta<\mu$ and $k<0$,	If we start with a value of N(t) below the $N_{0,cr}$ then the total population will dies out and if we start with the value of N(t) above $N_{0,cr}$ then the total population will explodes that is N(t) will tends to t^{*}. There is a watershed effect and it is unstable.	If we start with a value of N(t) below the $N_{0,cr}$ then the total population will dies out and if we start with the value of N(t) above $N_{0,cr}$ then the total population will explodes that is N(t) will tends to t^{*}. There is a watershed effect and it is unstable.

Basically, there is a similar argument can be said regarding the stability of the specific type and the arbitrary $n_o(a)$. And the argument which says that the area below the graph $n_0(a)$ plotted against a that is the long term behaviour N_0, will be the same regardless of the shape of the graph. This is robust.

Chapter 7

Example of an age-structured population model : Possums

7.1 Introduction : possums

According to Wodzicki (1950), in America, the name "possums" applies to a Family Didelphidae which belongs to the polyprotodont sub-order of marsupials. Similar animals are found in Australia (Family Phalanggeridae) which are however diprotodont i.e. have a two-incisored condition of the lower jaw. In Australia and New Zealand those animals are popularly known by the same name "possums". Dead animals, killed by motor vehicles, are a common sight on roads. In fact, possums are 'flat' animals and live on roads.

One of the best known of the introduced possums in New Zealand belongs to the tree-dwellers of the genus *Trichosurus vulpecula (Brush-Tailed Possums)*. This genus derives its name from "thick bushy tail" which, in association with the pointed snout and long ears, suggested the name of "vulpine" or foxlike possums to the naturalists who described the first one sent home. Today, they exist as different types of subspecies.

In this chapter, we will discuss factors such as liberation, effect on plantation, how much of a nuisance this animals is and other indirect damages. We shall then discuss the general aspects which should be considered in the study of the possums populations and control: in which we will explain the observation made by trappers and scientists on the fecundity: breeding period and movement. We shall compile the various methods used to measure possum populations. We limit our discussion to the observations on possum populations based on the research made by Bell (1981).

7.2 Liberation of possums in New Zealand

The possums were introduced for a set purpose-'material profit'. It was thought until a few years ago, that the value of the New Zealand bush would be considerably enhanced by the introduction of possums. This "advantage might be made enormously greater by the sale of skins" as quoted by Troughton (1946) from the speech made by the Tripp, President of the Wellington Acclamation Society. The most common brush-tailed possums, the "*trichosurus Vulpecula*" which is a native of Australia has a number of varieties, differing in colour, size and commercial value are recognised here. The first recorded successful liberation in New Zealand was made near Australian mainland and Tasmania peaked between 1890 and 1898 but continued until 1924. Introductions consisted predominantly of black possums from Tasmania with the remainder being grey animals from mainland Australia.

However, the species found in New Zealand nowadays, is a compound one in that it contains animals that vary in colour and size and it has been described that there are eight subspecies or varieties (Refer to Appendix F for pictures of some of these species). This resulted in having a range of fur colour. Brown and grey populations still predominates in many localities (see Figure 7.1 showing the picture of a silver-grey possums).

Figure 7.1: Silver-grey possums, Orongorongo Valley, Wellington, September, 1946.

Liberation of New Zealand-bred stock continued until 1952. In 1922 the department of Internal Affairs refused any further request for liberation. Many introduction between 1910 and 1922 were illegal releases by trappers and private individuals, as were the releases made after 1922. The trend of public opinion once prevailed regarding the possums may well be illustrated by the following quotation from the Annual Report, Auckland acclimatisation Society, 1916-17: " We shall be doing a great service to the country in stocking these areas [of rough bush tail hills] with this valuable and harmless animals." The effect of the extensive possums liberation has resulted in this country at present to face with serious problem of possums control.

According to John and Mac Gibbon (1986), the taking of possum skin has been permitted in 1921: most hunting is by professional trappers who trap, snare or poison the animals and between 1970 and 1983, twenty-four million skins were exported. During that period of the first time the possum population reduction are noticeable. However, nowadays trappers activity are declining so there is an increase in the possums population.

7.3 The possums as a pest and its effect on forest, vegetation, orchards and garden.

In the past, when Kirk (1920) examined certain types of native forests, he came to a conclusion that the damage done by possums to the forest is negligible in compare to the advantage that already accures to the community. With the exception of the Wainui-o-mata plantation, no other serious damage was reported, but in view of reports from Australia, Kirk suggested that possums should not be liberated in districts with exotic plantations. He also advocated the destruction of possums in plants and animals sanctuaries because of possible competition with native birds in the matter of food. However, later in his final report, he had hope that with organised trapping, the districts with orchards would soon be cleared of the pest. This is due to his observation when a considerable damage has been done to orchards in Albany near Auckland. Possums are also damaging leaves and young shoots of apple trees, of peach trees and all other stone-fruits, Lemon trees were also eaten. In garden, bud and shoots of roses and of many shrubs were bitten off, while peas, beet and other vegetables were also attacked.

Possums is found to damage native timber quite a great deal. Their main food are leaves and persistent defoliation kill trees. Results might not be immediate in which it may takes five to ten years for some trees to be completely dead. These of course depend upon the number of possums present. Not only that, possums feed on almost every parts of native trees: berries, leaves and stem of the leaves are consumed seasonally.

Trees which were extensively used for control of erosion were greatly affected by possums activities. Marks caused by bark- biting were observed which resulted in damaging adult trees.

Mason (1949) reported that several plants which are poisonous to other animals are also eaten by this animal.

The damage reported occurs in many districts and number of complaints has been steadily increasing in the last few years. The number of complaints received from each districts seems to vary in proportion to the possums population.

7.4 Nuisance Damage

Other annoying possums activities are the entering of premises at night, pollution of the water supply, and noise at night. Power interruption has also been reported. There were an average of five interruptions in 1945 as was reported by the Taranaki and New Plymouth Electric Power Boards, while Opunake in 1943 registered as many as 105 failures caused by possums. In several places, e.g. the Grey districts, metal plates need to be fixed to power poles in order to prevent possums climbing up and reaching the wires.

7.5 Indirect Damage

The damage suffered by natives trees through trapping activities was first reported by Yerex (1933) during his visit to Mount Egmont National Park. (unpublished report, Department of Internal Affairs, 1933)

In order to mark a trap line and to indicate the exact spot where each trap is set, trees are blazed, the type of blazing indicates the number of traps in the line (see Figure 7.2). Trees are blazed to attract possums while ponga fern stems are even cut down for this purpose. Yerex observed one tree with as many as 10 new blazes to indicate the trap number while another tree carried 26 blazes made apparently for the purpose of attracting possums. Unfortunately, blazed trees often develop disease and dies out as a result of the blazing.

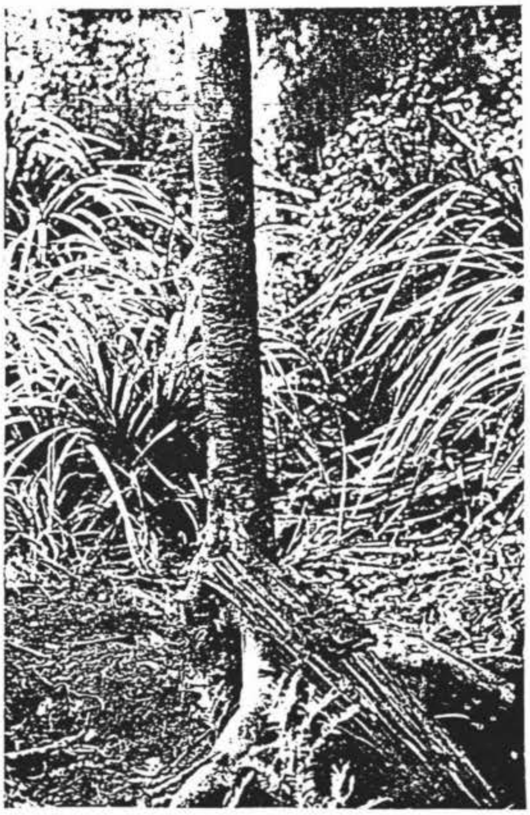


Figure 7.2 : possums trap set on "run" against "playing" tree, Orongorongo Valley, September, 1946. Note possum bark biting.

7.6 *Other problem caused by possums*

According to John and Mac Gibbon (1986), possums affected the health of many farm animals. These animals can be infected by and carry the disease tuberculosis. Since 1970, research and intensive possum control programs have been undertaken to reduce this problem.

7.7 *Possums Population*

Scientific control of any animal population depends on a knowledge of its distribution, rate of replacement (fecundity: breeding period and number of young and the mortality rate), population density and movement.

Here, we are not going to discuss the distribution because basically at present day possums are found throughout New Zealand except for the very top of the North Island and the south-western corner of Fiordland. The map showing the distribution can be observed in Appendix C.

7.71 Fecundity Rate: Breeding Period and Number of young

Troughton (1946) discovered that possums "begin to breed in the year following that of birth" and "the breeding season is in May or June and normally occurs only once a year though it is commonly believed to be twice annually". Any if there is second breeding would likely to occur between August to October.

Perham (unpublished report, State Forest Service, 1924), claims that "quite seventy to eighty percent of the females have young in the pouch from May to September" and "suggest that certain females which have missed mating in the usual season may breed during any part of the year". He also reports a most unusual occurrence of possums having two kittens of different size in the pouch of one female. Parcy (1946), Department of Internal Affairs, stated that "the mating season is about the end of April, and is general throughout

New Zealand forests". After a gestation period of about three or four weeks, the young possums is found in the pouch " about the end of May or beginning of June". If the climate is mild according to the investigation of Pracy, there is a possibility of second breeding. He also has confirmed the rarity of twins, having only once recorded such an occurrence amongst the thousands of female possums he handled.

Very little if anything is known regarding the breeding age and the average age attained by opossums. Since opossums seems to have one young at the time, this suggest that it has early breeding age. Pracy(1946) suggested claims that the minimum breeding age of a female opossums is one year. No observation have been made regarding the average age attained by opossums. According to him the tape length (from base of skull, excluding tail) of particular large opossums is up to 16 inches and such animals are estimated to be about four years old. This depends on the area under observation. In section 7.8, we are going to look at a specific area that is Orongorongo in Wellington which is by research paper of Bell (1981).

7.72 Mortality rate and the limiting factors that could affect the growth of possums.

Efford (1991b) observed that the common pattern for a mortality rate is to be very high in early life, to decline abruptly and remain low for several years and then to increase in old age, forming a typical 'U'-shaped curve and long-term monitoring of possums in New Zealand forests shows that the populations approach and vary about an equilibrium usually known as the carrying capacity (*k*) even as they continue to modify the vegetation. At a descriptive level, this implies that the population seems to increase when density is low and to decrease when density is high, at least at some times or in some places. Regarding the method of measuring mortality rate, Caughly(1966)'s critique suggests that it will seldom be feasible to reliably estimate age-specific mortality from kill samples.

In the natural control of populations of wild animals, disease plays a role. This has been stressed by Elton (1931). Epidemics are one of the commonest factors responsible for fluctuations in number of animals and occur generally when the population has become unusually dense. However, there is no information on the incidence of disease among possums in New Zealand has been placed on record except for a skin disease which was reported to affect the base of the tail amongst possums of the Wellington province which was reported by Woodland and Hopkirk (1946) of the Wallanceville Laboratory who examined some of these possums suspected small Acari (a skin disease similar to those which affect rabbit). The Department of internal Affairs, found in winter, in the Poverty Bay district that many, possibly 25% of possums killed "are poor conditioned and scurvy, old and young alike". In this area, however, the defoliation and destruction of plants and trees on which possums feed was far advanced. This disease seemed to be similar to mange in dogs but did not penetrate the flesh. Although the appearance of entrails was normal there was evidence of constipation. Many dead or dying possums were found, and in one small area of five acres of bush as many as 17 possums were found dead after a belt of particularly cold weather. After 10 percent of the 60 replies received to a questionnaire sent to possums trappers, reported possums showing signs of disease of being in very poor condition. Disease was described as follows: scabies, "big joints", "wasting disease", "mange or pus sore on base of tail" and "skin disease".

In spite of all those skin problems, it may be stated that no epidemics which could seriously check the number of possums in this country have so far been reported. Man's activities (e.g. trappings) seem to be the only known factor in possums control.

The presence of predators is another factor which could reduce the population naturally. For, example in Australia, the possum has enemies which have an effect on the possums population but no such animals exists in New Zealand. Therefore, trapping is the only factor.

7.73 Migration and population density

The distribution and density of an animal population is largely influenced by colonisation, i.e., their spread within a limited area, or migration, i.e., moving to new districts, and by cyclic variations in numbers.

There is very little information concerning colonisation or migration of possums in New Zealand. Possums live in colonies which do not move a great deal. Supporting this statement is the fact that possums of certain colour varieties are trapped for years in particular blocks. It seems likely, however that opossums migrate from areas which carry a heavy population to those where the population has been thinned by trapping.

In the absence of further data it seems likely that possums' movements are rather of the nature of extending an occupied territory, i.e. colonisation rather than migration.

There has always been a problem in trying to distinguish between mortality and emigration but consideration of the sex and age pattern of emigration allows the problem to be minimised. According to Clout and Efford (1984) and Efford (1991a), female possums rarely disperse, and dispersal is concentrated in the youngest age classes. Estimates of immigration suggest that one third of breeding females were born elsewhere (Efford 1991a). Assuming that all migration occurs in the first year of independence, and that emigration equals immigration, the mortality series may be corrected by increasing the apparent survival rate (1-q) in the first years by a factor of $(\frac{1}{1-1/3})$, where we assume q to be the mortality rate. Efford (1991a) suggested that the assumptions do not strictly hold but the overall effect turns out to be about right (the observed stability of the population is reproduced by an age-structured model based on the estimates).

7.8 Methods used to measure possum populations and thus to class them into different ages

There are many methods that could be used in order to measure the possums populations. D.J. Bell from the Forest Research Institute of Christchurch discussed 4 methods which have been or are used to assess the effectiveness of possum control operations.

They are:-

a) spotlight counts. This is a relatively untried techniques.

b) gin-graping. This method provides an index of animal density based on the numbers caught on successive nights.

c) non-toxic baits. This method is used to establish the relative levels of pasture utilisation at increasing intervals from the main bush margin. Baits stations consists of a small length of alkathene pipe attached to a reinforcing rod, into which is forced a plastic cap to contain the bait. These are placed at 50 m intervals along the lines and filled with a flour and soya bean oil paste.

d) Faecal pellets. This method is used to estimate the number of possums by calculating the number of pellets accumulating each day in a given area and dividing this by the average number of pellets voided each day by one animal.

However, there are problems associated with all those techniques and more research is required before it can be unconditionally recommended.

On the other hand, Pekelharing (1970) has developed another more reliable method for allotting possums to annual age classes based on the deposition of cementum layers of the molars. Earlier techniques could be misleading (B.D. Bell, A.J.White, unpublished).

He classed the possums in the following manner: animal without an inner cementum layer on the lower first molar are classed as 0-1 year olds. The one with 1 cementum layer as 1-2 years old and 2 cementum layer as 2-3 years old and so on.

Some author group their results on another basis, e.g Bamford (1972) divided his sample into "pivotal " age classes - a pivotal age of 1 including animals between six and eighteen months old, a pivotal age of 2 including animals between eighteen and thirty months old, and so on while Kean (1953) under a sample of 1449 possums used tooth wear and skull sutures as an aging technique .

7.9 The analysis of sample taken from Orongorongo in Wellington based on the survey made by Ben D.Bell in June, 1981.

One of the sample surveyed by Ben (1981) which was of interest in this thesis is the one taken from Orongorongo Valley, southern Rimutaka Range, 16 km east of Wellington based on the tracking of the opossums from 1970 to 1973. 103 opossums were found dead on the ground or dying in cage traps were collected from broadleaf-podocarp forest near the mouths of Greens stream and Woottons Stream (see Crawley (1970)). These animals were found during a capture-recapture study running since 1966 and are presumed to have died of natural causes.

The method used in this survey, in order to group the population into different classes was by grounding, staining and examining under an X40 microscope a molar tooth taken from the lower jaw of each opossums found in order to reveal the annual layers of cementum which was suggested by Pekelharing (1970).

In table 1 of Appendix F, are the summary of the age structure of samples collected in the area of interest.

7.9.1 Life expectancy and mortality rate of the data

The 103 possums found dead or dying in the Orongorongo Valley between 1966 and 1974 form a useful mortality series. In Table 1, it reveals that, of 1000 animals which left the pouch, 47 could be expected to survive until their 13th year. The mean life expectancy on leaving on leaving the pouch was 6.2 years. At 3 to 4 years of age, the animals could expect to live another 5 years.

The *mean annual mortality rate* for all the animals which left the pouch is 14.9%. The mortality rate varied with age, however, 0-2 years old suffering a 11.1% to 12.6%; 2-4 years old a 3.9% to 5.0% loss; and animals over 4 years old losing 10.3% to 45.3% of their age class annually.

7.9.2 Observable Annual and seasonal difference in mortality of the data

Those resident adult possums known to have died or disappeared from the 14 ha study area of Orongorongo Valley between 1966 and 1973 are listed in Appendix E. Deaths and disappearances occurred more frequently in 1967 and 1968 than in the other years while very few animals died or disappearing from the study area fluctuated 15-fold (from 4 to 62) between the best and worst years.

Over the eight year period, the greatest number of deaths occurred in July and fewest in March. Seasonally, 44.5% of deaths and disappearances occurred in winter, 20% in spring, 19% in summer and 16.5% in autumn.

7.9.3 Estimation of the parameter from the data in Appendix D

The parameter that we need to figure out from the data in Appendix D are the birth rate (β), mortality or death rate (μ) and the death rate density dependent parameter k. The annual mortality rate has been found for us from the data analysis in Appendix D is 14.9% or 0.149 per year per capita. The annual birth rate can be easily obtained from column 3 and row 1 of Appendix D (under the number of survivors at the beginning of age, of the 1000 born), since we define it as the number of individuals being born at age 0 out of the total population, thus it is given by 1000/6710 = 0.14903 per year per capita. We are unable to find or estimate the value of k directly from the data. One method is to use equation (6.20) in Chapter 6. Since we know that the total population (N_s) is 6710, then we can carry out the method as follows:

$$N_s = \frac{\beta - \mu}{\mu k} \tag{6.20}$$

$$k = \frac{0.14903 - 0.149}{0.149(6710)}$$

$$= 3 \times 10^{-8}$$

The parameter can be summarised as in Table 7.1 below:

Parameters	Value estimated from given data
β	0.14903 per year per capita
μ	0.14900 per year per capita
k	3×10^{-8} per capita

Table 7.1 : Summary of the parameter estimated from the data given.

7.9.4 Comparison of the long term population density $n_s(a)$ of the data, calculated values and the non-linear regression values

First of all we need to defined the different values of population density we are going to considered so that it will be easy for us to refer to each of them from the Graph 7.1. There are:

a) Values from the data given in Appendix D is denoted by D
b) Values calculated from the model is denoted by R
c) Values from the non-linear regression is denoted by Q

Obviously, the data values seems to be linear (see Graph 7.1) such that the best line (linear regression) is given by

$$N = n_s(a) = -73.13a + 954.6, \quad r = -0.995$$

This is not what we have been expected for a normal population graph which is supposed to be non-linear and is given by the equation (6.21):

$$R = n_s(a) = \frac{\beta(\beta-\mu)}{\mu k}\exp(-\beta a). \qquad (6.21)$$

Using the three parameters already found summarised in Table 7.1, we can simplify equation (6.21) as

$$R = 999.99\exp(-0.14903a).$$

When trying to obtain a good estimate of the value of the three parameters using a non-linear regression, we minimise the residual sum of squares

$$S(\beta,\mu,k) = \sum_{0}^{13}(R-D)^{2},$$

we obtained the three parameters as is summarised in Table 7.2 below:

Parameters	Value estimated using non-linear regression
β	0.14458 per year per capita
μ	0.13195 per year per capita
k	1.30722×10^{-5} per capita

Table 7.2 : Summary of the three parameter obtained by the non-linear regression.

Our long term behaviour population density is now given by

$$Q = 1059\exp(-0.14458a).$$

To see the difference in values of the age-dependent population densities of D, R and Q, we shall summarise the results and their residue sum of squares in Table 7.3.

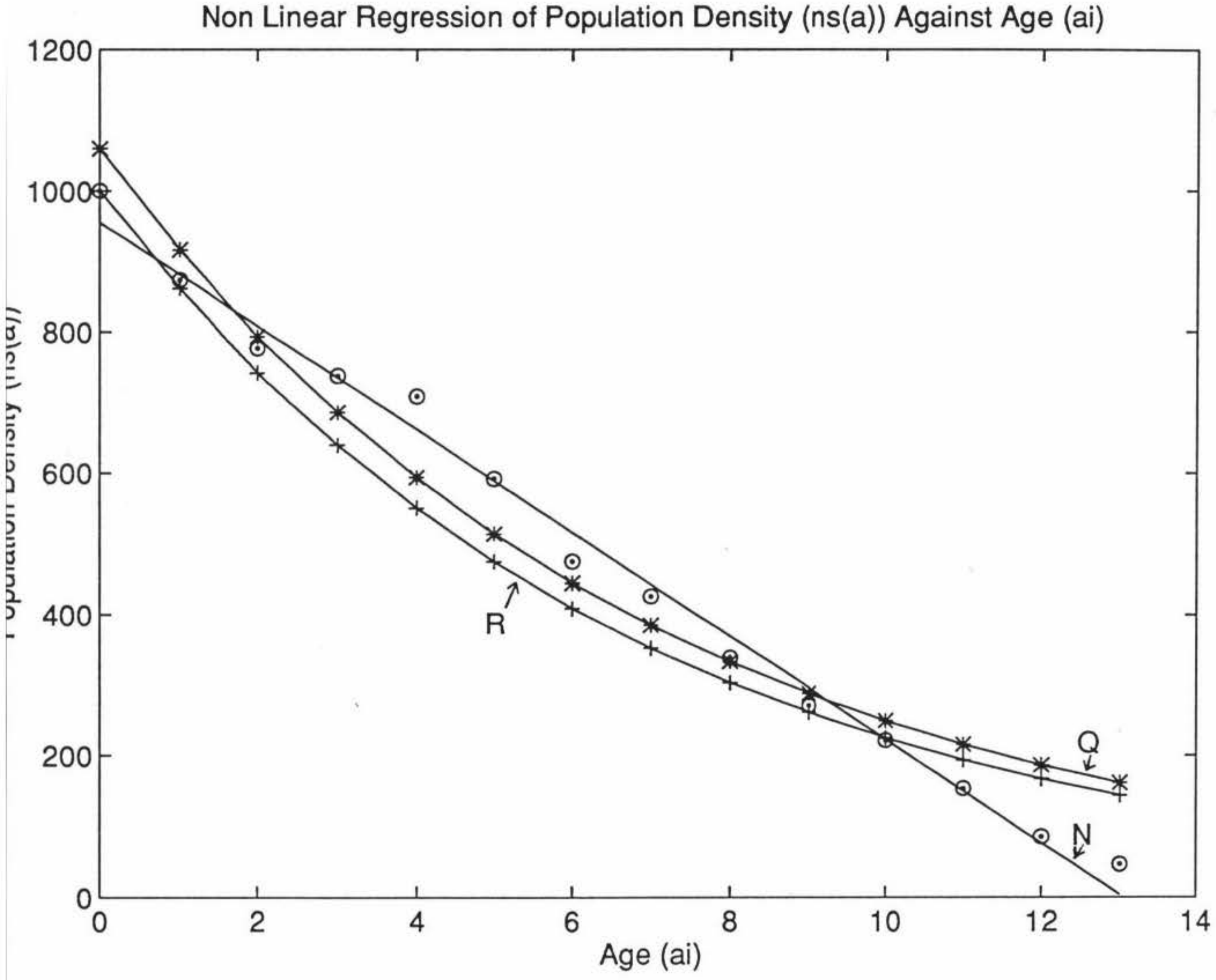
a_i	D	N	R	Q	$(R-D)^2$	$(Q-D)^2$
0	1000	955	1000	1059	0	3.5×10^3
1	874	882	862	916	1.4×10^3	1.8×10^3
2	777	808	742	793	1.2×10^3	2.6×10^3
3	738	735	640	686	9.6×10^3	2.7×10^3
4	709	662	551	594	2.5×10^4	1.3×10^4
5	592	589	475	514	1.4×10^4	6.1×10^3
6	475	516	409	445	4.4×10^3	9.0×10^2
7	426	443	352	385	5.5×10^3	1.7×10^3
8	339	370	304	333	1.2×10^3	3.6×10^1
9	271	296	262	288	8.1×10^1	2.9×10^2
10	222	223	225	250	9.0×10^0	7.8×10^2
11	154	150	194	216	1.6×10^3	3.8×10^3
12	86	77	167	187	6.6×10^3	1.0×10^4
13	47	4	144	162	9.4×10^3	1.3×10^4
TOTAL	6710	6750	6326	6828	$\sum_0^{13}(R-D)^2 =$ 7.9×10^4	$\sum_0^{13}(Q-D)^2 =$ 5.8×10^4

Table 7.3 : Table to show the summary of the values of the population density from the data D, linear regression N, model values R and non-linear regression *Q*.

We can then determined the *mean sum of squares* of the following:

a) Data D and model values R is $7.9\times10^4/13 = 6.1\times10^3$

b) Data values and non-linear regression is $5.8\times10^4/13 = 4.5\times10^3$



Graph 7.1: Graph showing the plots of the linear regression (N) of data (D), model values R and the non-linear regression *Q* against age *a*.

7.9.5 Observations and arguments on the results in section 7.9.4

The results from the data seems to be linear than expected. We have a better estimate for the best value of β, μ and k using linear regression rather than with the non-linear regression. This is because the value of k obtain from the data is so small (3×10^{-8}) which is almost negligible which makes our model i.e. the model considered by McKendrick which we discussed in Chapter 2 and 3. The value is not suitable for an evaluation using our non linear model. Values of the data obtained depends on the area being investigated and other various reasons or problems experiences during the data collection which shall be discussed in the next sub-section based on the discussion made by the researcher.

7.9.6 Possible reasons for inaccuracy in data collection

Bell (1981) has argued in his research papers the following difficulties and possibilities for inaccuracy in his data:

1) The samples are collected in many ways and for various purposes. The data is suggested to present a heterogeneous base on which to build any sort of speculative analysis and thus little or nothing is known of the stability or instability of the populations. In our calculated values, we are assuming that it is stable.

2) The researcher has a problem in estimating or distinguishing between mortality and dispersal.

3) Traps or cyanide, the poison used to killed this animals tends to kill some age classes more than others.

4) Older age classes may be under-represented in samples aged from cementum rings. A similar cumulative bias has been reported for horn rings in female Dall sheep, and according to Pekelharing (1970) and Clout (1982) the tooth ring method has been checked against few known-age older female only.

5) Some may survive the poisoning, so that we do not know the exact number of possums present and thus our estimation regarding their age structure may be under estimated.

6) According to the frequency of the 103 possums found dead (see Appendix D), it is predicted that there are more possums aged 4 for example than aged 3. There is an inconsistency in the number of possums found dead and that the data is just an estimation and it is a bad assumption to estimate the population density from these data.

7) The data (Appendix D) is based on the 103 possums found dead. This is used just a 'prediction' and not assumed to be accurate.

7.10 Conclusions

The data collected does not agree well with the calculated value that is our non linear model because the data seems to be more linear than expected. There might be a problem with the data collection since the data is collected for other reasons and some of these reasons has been discussed in section 7.9.6 and that data collected varies depending upon the areas under investigation; history of the area, that is whether the area has been under reattach previously or in fact this could lead to migration of these animals and they tend to produce more due to a depression of population; and population varies throughout the seasons, or our model is simply not suitable for this particular sample.

We also must concur with Caughley (1974) that the age-structure of possum populations are of little value in estimating whether a population is increasing or decreasing. It is just a way of predicting the characteristic of the population. Age-specific birth and death rates, the incidence of double breeding and spring births, the migration or dispersal of certain age classes, overwhelming degradation or improvements in the habitat, control operations, food crop successes or failures, and perhaps predation and disease, all these shape the pattern of age-structure. Add to these factor the bias of most sampling methods and the usual demographic changes which overtake an animal population from month to month, and most of all, in spite of all those the interpretation of data becomes hazardous. However, despite all those difficulties, age estimation is nevertheless a valuable exercise as it throws light on the age of maturity, age-specific reproductive performance and mortality, the potential and actual rates of increase, the age-specific effects of diseases and control operations.

Chapter 8

Conclusions and suggestions for future work

The unstructured models are only useful for the population in which the rate of growth of the individuals is uniform and that the differences do not affect the birth and death processes. This is suspected to be rare and usually happens only with laboratory organisms.

The age-structured models has provided better correlations with the real biological situations especially for a higher structured animals and better still if we encounter the effect of overcrowding and the limitations of the resources which have the potential to have an effect not only to a specific age group but to the whole population. Together with the study of steady age distribution (s.a.d.) and their stability, we have a better understanding upon the long-term behaviour of the solutions in which we can judge whether the behaviour of a population is stable or otherwise at a certain stage or conditions. For example, in chapter 6, we have concluded that we have an effect of a watershed and unstable when the birth rate is less than the death rate and the death rate density dependent parameter k is less than zero, there is a critical value (the initial population); and when the birth rate is greater than the death rate, then there is a global attracting effect about the steady or survival population.

Despite the heated philosophical debate over the role which mathematics should to play in the life- sciences, we then realise that on some grounds, our models need to be tested. In chapter 7, we are using the data collected by Bell (1981) in Orongorongo, Wellington. We try to fit the data to the models and it seems that the data does not go well with our results in the models. The data appears to be linear while our model is a non-linear case. There are various possibilities which could have an effect on this results. Obviously, the value of the death rate density dependent parameter *k* estimated from the data is too small (3×10^{-8}) which implies that it does not have an overcrowding or limitation of resources effect. The model is simply the 'linear' first order hyperbolic partial differential equation developed by McKendrick discussed in Chapter 2 and 3. That is why it does not fit our non-linear model. There are a few other reasons. Some of which have been discussed in sub-section 7.9.6 and section 7.10 which could led to a bias estimation of the data, which is a usual problem that encounters since this is not a closed system. Migration, seasons, breeding of possums are not exactly understood and they tend to vary with different areas under investigation, which might be some of the reasons. An area which has been under reattachment previously could in fact lead to migration of these animals and they tend to produce more due to depression of population. One might get a better estimation if we were to use other data from other area. Furthermore, the data collected is based on the 103 dead possums found dead in the area and it may not be a good idea to predict age-structure based on that data alone.

The age-structure of possum populations is of a little value in estimating whether a population is on the increase or decrease. It is just a method of predicting the population. As a result of all these problems and uncertainties, interpretation of the data becomes extremely difficult.

Despite of all these difficulties, age estimation is nevertheless a valuable exercise as it throws light on the age of maturity, age-specific reproductive performance and mortality, the potential and actual rates of increase, the age-specific effects of diseases and control operations.

Suggestions

For further developments on the study of the possum populations and control, permanent sterilisation would be a better approach than poisoning or trapping which could only gives an immediate relief from damage because the survivors will have an increased reproductive and survival rate immediately after the animals are reduced because of a reduction in density-dependent regulating factors. Inhibition of reproduction (or sterilisation) or both sexes leaves animals alive to compete for mates, nesting sites and other resources and therefore does not result in increasing reproductive and survival rates of non-sterilised animals. If the sterilised animals are fully competitive and equally distributed they are theoretically capable of suppressing reproduction in non-sterilised members of the population to a degree equal to the percentage of the population sterilised. This will perhaps agree with our non-linear model which we had encounter for the overcrowding effect.

Another suggestions is that our model can be extended to the case where we are considering the effect of susceptibility of a person or animals being affected by a disease where we have a systems of partial differential equations.

Our model can be tested perhaps using human demographic data instead of possums where the population considered must be overcrowded (since our model assume an overcrowding effect and limitation of resources), like India and China.

APPENDICES

APPENDIX A
The method of characteristics

APPENDIX B
Laplace Transform

APPENDIX C
Expanding possum distribution

APPENDIX D
Life table of Orongorongo possums, based on 103 animals found dead or dying 1966 - 1974

APPENDIX E
Possum mortality. Seasonal and annual distribution of possums found dead or dying and resident animals known to have disappeared permanently from trapping grids in the Orongorongo Valley, Wellington

APPENDIX F
Pictures of different species of possums

Appendix A

THE METHOD OF CHARACTERISTICS

Any linear first order hyperbolic partial differential equation may be reduced to a solvable ordinary differential equation by the method of characteristics. For example, consider the age-dependent populaton model developed by McKendrick given by equation (2.1), in order to obtain the solution to the model, we shall proceed with the following method.

Let us introduce a new set of coordinates s and r, where the charac-teristics can be expressed as s=constant. Thus, a possible choice is $s = a - t$. The other coordinate r must be selected so that to a given point (s,r) there corresponds only one point in the a-axis and t-axis coordinates. In other words, we want the curve r = constant to intersect s = constant in the (a,t) plane in one and only one point. Now, in Figure A1 below the line r=a+t meets a characteristic in one and only one point. Therefore we can make the change of coordinates as

$$s = a - t \quad \text{and} \quad r = a + t \tag{A.1}$$

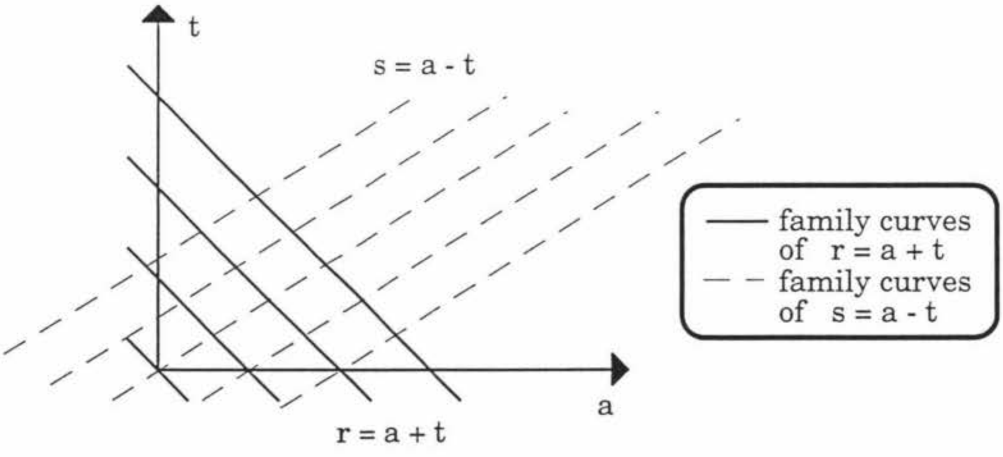


Figure A1: Graph showing the family curves of $s = a - t$ intersecting the family curves of $r = a + t$ (characteristic lines).

There may be other possibilities for choosing the family curves, providing that they meet the criterion that the curve s = constant and intersects r = constant once and once only.

By the chain rule for partial derivatives, we have

$$\frac{\partial n}{\partial a} = \frac{\partial n}{\partial s}\cdot\frac{\partial s}{\partial a} + \frac{\partial n}{\partial r}\cdot\frac{\partial r}{\partial a} = \frac{\partial n}{\partial s} + \frac{\partial n}{\partial r}$$

since from equation A1, we have: $\frac{\partial s}{\partial a} = 1$ and $\frac{\partial r}{\partial a} = 1$

and therefore

$$\frac{\partial n}{\partial t} = \frac{\partial n}{\partial s}\cdot\frac{\partial s}{\partial t} + \frac{\partial n}{\partial r}\cdot\frac{\partial r}{\partial t} = -\frac{\partial n}{\partial s} + \frac{\partial n}{\partial r}$$

since $\frac{\partial s}{\partial t} = -1$ and $\frac{\partial r}{\partial t} = 1$. Thus by substitution in equation(2.1), we obtain the solvable ordinary differential equation as given below :

$$2\frac{dn}{dr} = -\mu n \qquad \text{(A.2)}$$

Appendix B

Laplace Transform

B.1 Definition of Laplace Transform

Let $f(t)$ be defined for $t \geq 0$; then the integral

$$\int_0^\infty e^{-pt} f(t)dt = \lim_{b \to \infty} \int_0^b e^{-pt} f(t)dt \tag{B.1}$$

is said to be the *Laplace transform* of f, provided the limit exists.

Symbolically, the Laplace transform of f is denoted by $L\{f(t)\}$ and this depends on p. This is usually expressed by

$$L\{f(t)\} = \bar{F}(p).$$

We may say that $f(t)$ is the *inverse Laplace transform* of $\bar{F}(p)$ and expressed this as

$$f(t) = L^{-1}\left\{\bar{F}(p)\right\}.$$

B.2 The convolution theorem

If functions *f* and *g* are piecewise continuous on $[0,\infty)$, then the convolution of *f* and *g*, (denoted by $f*g$), is given by the integral

$$f*g=\int_{0}^{t} f(\tau)g(t-\tau)d\tau \tag{B.2}$$

It is possible to find the Laplace transform of the convolution of the two functions, without evaluating the integral. The result that follows is known as the *convolution theorem.*

Theorem B1

Let *f(t)* and *g(t)* be piecewise continuous on $[0,\infty)$ and of exponential order; then

$$\begin{aligned} L\{f*g\} &= L\{f(t)\}L\{g(t)\} \\ &\bar{F}(p)\bar{G}(p). \end{aligned} \tag{B.3}$$

Proof:

Let $\bar{F}(p)=L\{f(t)\}=\int_{0}^{\infty} e^{-p\tau}f(\tau)d\tau$

$$\bar{G}(p)=L\{g(t)\}=\int_{0}^{\infty} e^{-p\beta}g(\beta)d\beta$$

proceeding formally, we have:

$$\begin{aligned} \bar{F}(p)\bar{G}(p) &= \left(\int_{0}^{\infty} e^{-p\tau}f(\tau)d\tau\right)\left(\int_{0}^{\infty} e^{-p\beta}g(\beta)d\beta\right) \\ &= \int_{0}^{\infty}\int_{0}^{\infty} e^{-s(\tau+\beta)}f(\tau)g(\beta)d\tau d\beta \\ &= \int_{0}^{\infty} f(\tau)d\tau\int_{0}^{\infty} e^{-s(\tau+\beta)}g(\beta)d\beta \end{aligned}$$

Holding τ fixed, we let $t=\tau+\beta$, $dt=d\beta$ so that

B.2 The convolution theorem

If functions *f* and *g* are piecewise continuous on $[0,\infty)$, then the convolution of *f* and *g*, (denoted by $f*g$), is given by the integral

$$f*g=\int_0^t f(\tau)g(t-\tau)d\tau \tag{B.2}$$

It is possible to find the Laplace transform of the convolution of the two functions, without evaluating the integral. The result that follows is known as the *convolution theorem.*

Theorem B1

Let *f(t)* and *g(t)* be piecewise continuous on $[0,\infty)$ and of exponential order; then

$$\begin{aligned} L\{f*g\} &= L\{f(t)\}L\{g(t)\} \\ &\bar{F}(p)\bar{G}(p). \end{aligned} \tag{B.3}$$

Proof:

Let
$$\bar{F}(p)=L\{f(t)\}=\int_0^\infty e^{-p\tau}f(\tau)d\tau$$
$$\bar{G}(p)=L\{g(t)\}=\int_0^\infty e^{-p\beta}g(\beta)d\beta$$

proceeding formally, we have:

$$\begin{aligned} \bar{F}(p)\bar{G}(p) &= \left(\int_0^\infty e^{-p\tau}f(\tau)d\tau\right)\left(\int_0^\infty e^{-p\beta}g(\beta)d\beta\right) \\ &= \int_0^\infty\int_0^\infty e^{-s(\tau+\beta)}f(\tau)g(\beta)d\tau d\beta \\ &= \int_0^\infty f(\tau)d\tau\int_0^\infty e^{-s(\tau+\beta)}g(\beta)d\beta \end{aligned}$$

Holding τ fixed, we let $t=\tau+\beta$, $dt=d\beta$ so that

$$\bar{F}(s)\,\bar{G}(s)=\int_0^\infty f(\tau)d\tau\int_0^\infty e^{-pt}g(t-\tau)dt$$

In the $t\tau$ plane we are integrating over the shaded region in Figure B1. Since f and g are piecewise continuous on $[0,\infty)$ and of exponential order. it is possible to interchange the order of integration:

$$\begin{aligned}\bar{F}(p)\,\bar{G}(p)&=\int_0^\infty e^{-pt}dt\int_0^t f(\tau)g(t-\tau)d\tau\\&=\int_0^\infty e^{-pt}\left\{\int_0^t f(\tau)g(t-\tau)d\tau\right\}dt\\&=L\{f*g\}.\end{aligned}$$

The convolution theorem is sometimes useful in finding the inverse Laplace transform of a product of two Laplace transforms. From our convolution theorem discussed above, it follows immediately:

$$f*g=L^{-1}\left\{\bar{F}(p)\,\bar{G}(p)\right\} \tag{B.4}$$

In section 3.3, we defined equation 3.10 to be the Laplace of the birth rate $m(t)$ of the form:

$$\bar{m}(p)=\bar{m}(p)\,\bar{G}(p)+\bar{F}(p). \tag{3.10}$$

As long as $\bar{G}(p)\neq 1$, we have

$$\bar{m}(p)=\bar{F}(p)/[1-\bar{G}(p)]. \tag{B.5}$$

The equation

$$\bar{G}(p)\equiv\int_0^\infty e^{-pa}G(a)da=1$$

is exactly Lotka's characteristic equation. The above conditions for $\bar{G}(p)$ are sufficient to ensure that equation B5 has a unique real solution say $p=p^*$.

Hence, we suspect that with appropriate conditions imposed upon f and g, we will have the explicit solution

$$m(t) = \frac{1}{2\pi i}\int_{c-i\infty}^{c+i\infty} \frac{e^{-pt}\,\bar{F}(p)dp}{\left[1-\bar{G}(p)\right]} \tag{B.6}$$

where c is chosen so that all the singular points lie to the left of the line Re(p)=c in the complex p plane.

Next, we need to establish and derive some conditions which allows this approach.

B.3 Exponential Bounds for m(t)

Let us establish the following lemma. The use of this result is that to show $m(t)$ is bounded by an exponential whenever $F(t)$ and $G(t)$ are. This condition is met in all important applications. It follows that $\bar{m}(p)$ will be analytic function of p for $\mathrm{Re}(p)\rangle p^{*}$.

Lemma B2:

If for $t \geq 0$ and some $\mathrm{Re}(P)$, we have

a) $|F(t)| \leq c_1 e^{\mathrm{Re}(p)t}$,

b) $\int_0^\infty e^{-\mathrm{Re}(p)a}|G(a)|da = c_2 \langle 1$

then

$$|m(t)| \leq \frac{c_1 e^{\mathrm{Re}(p)t}}{1-c_2}$$

Using the foregoing result, we readily establish the following theorem.

Theorem B3

If for $t \geq 0$ and some $\mathrm{Re}(P)$, we have

a) $|F(t)| \leq c_1 e^{p^* t}$,

b) $\int_0^\infty e^{-p^* a}|G(a)|da = c_2 \langle 1$

then the laplace transform of *m(t):* $\bar{m}(p)$ is given by

$$m(p) = \frac{\bar{F}(p)}{1-\bar{G}(p)}$$

$\mathrm{for}\,\mathrm{Re}(p)\rangle p^*$.

At every point t, where m is continuous and of bounded variation in some interval containing t, we have

$$\bar{m}(p) = \int_b \frac{\bar{F}(p)}{1-\bar{G}(p)} e^{pt} dp \qquad \text{(B.7)}$$

for $b \rangle p^*$.

The proof of the Lemma B.2 and Theorem B.3 and a full discussion on the simple conditions upon *F*(*t*) and *G*(*a*) which permitted us to conclude that *m*(*t*) is continuous and is of bounded variation is extensively discussed by author Bellmann and Cooke (1963): p224-225.

B.4 Use of the Contour Integral Representation

Referring to the representation of B.7:

$$m(t) = \frac{1}{2\pi i} \int_{c-i\infty}^{c+i\infty} \frac{e^{-pt}\,\bar{F}(p)dp}{\left[1-\bar{G}(p)\right]}$$

let us employ some simple complex variable techniques. Suppose initially that the function

$$\bar{F}(p)=\int_{0}^{\infty} e^{-pt} f(t)dt$$

is a mereomorphic function of p, that is, possessing only poles of finite order in the p-plane, and that $\bar{G}(p)$ is a function with similar properties.

Since $1-\bar{G}(p)$ is a mereomorphic function of p, by assumption, its singularities will play no role, except in cancelling those of $\bar{F}(p)$. The important contribution of the function $1-\bar{G}(p)$ will be made by its zeros Let these be $z_{1,}z_2,\ldots,$ and suppose that they can be enumerated in terms of decreasing real part,

$$b\rangle \operatorname{Re}(z_1)\rangle \operatorname{Re}(z_2)\geq.... \qquad \text{(B.8)}$$

If we shift the contour of integration (discussed elaborately by author Bellmann and Cooke (1963): p233-234) from the line $b+ir$ to the line b_1+ir where $\operatorname{Re}(z_1)\rangle b_1\rangle \operatorname{Re}(z_2)$, we pick up a residue term at z_1 due to the denominator $1-\bar{G}(p)$, and possibly some residues from poles of $\bar{F}(p)$. Suppose, as is often the case, that $\bar{F}(p)$ has no singularities in the region. Then B.7 yeilds

$$m(t)=m_0e^{z_1t}+\int_{(b_1)}\frac{\bar{F}(p)}{1-\bar{G}(p)}e^{pt}dp$$

where m_0 is a constant given, if z_1 is simple, by

$$m_0=\frac{\int_{0}^{\infty}e^{-z_1t}F(t)dt}{\int_{0}^{\infty}ae^{-z_1a}G(a)da}$$

Under reasonable conditions, we would suspect that

$$m(t) = m_0 e^{z_1 t} + \mathrm{o}(e^{b_1 t}). \qquad \text{(B.9)}$$

Depending upon the assumptions that are made, relations of this type are relatively easy or relatively difficult to establish.
The error $\mathrm{o}[\exp(b_1 t)]$ indicates terms which approach zero as $t \to \infty$ when divided by $\exp(b_1 t)$. These terms are therefore negligible compared to $m_0 \exp(b_1 t)$ for large time.

In the important case where *g(a)* is a positive function, we establish the fact that z_1 is *real* and *simple*. Consider the Lotka's characteristic equation

$$1 = \int_0^\infty e^{-pa} g(a)da \qquad \text{(B.10)}$$

and suppose, without loss generality, that

$$\int_0^\infty g(a)da = \infty$$

but that

$$\int_0^\infty e^{-ba} g(a)da \langle \infty$$

for some $b \rangle 0$.

In this case, (B.10) is a sufficient condition to ensure that equation (B.5) has a unique positive real solution, say $p = p_0 \neq p^*$. Then we have:

$$1 = \left| \int_0^\infty e^{-\mathrm{Re}(p_0)a} g(a)da \right| \langle \int_0^\infty e^{-\mathrm{Re}(p_0)a} g(a)da \qquad \text{(B.11)}$$

and hence Re $p_0 \langle$ Re $p*$.

One result of this is that if the characteristic roots are all distinct, m(t) can be determined as an infinite series of exponential terms:

$$m(t) = m_0 \exp(p^* t) + \sum_{0}^{\infty} m_n \exp(p_n t)$$

where p_n are the characteristics roots, all satisfying $\operatorname{Re} p_n < p^*$. The coefficients in this expansion can be determined by calculating the residue of the integrand at the characteristic roots.

"Taken from Bellmann and Cooke (1963)."

APPENDIX C : EXPANDING POSSUM DISTRIBUTION

N.Z.F.S. map Base information from Department of Lands and Survey maps

Appendix D : Life table of Orongorongo possums, based on 103 animals found dead or dying 1966 - 1974

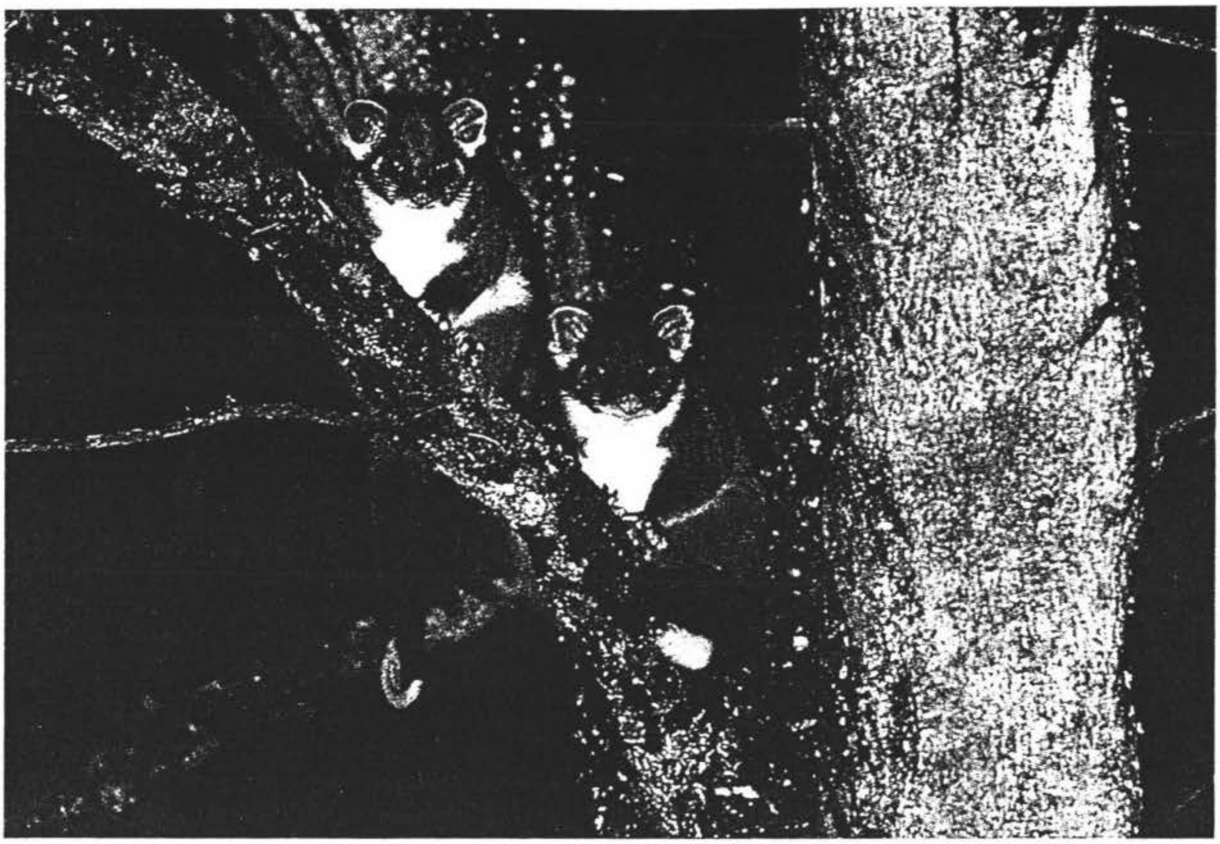
AGE IN YEARS	FREQUENCY OF OCCURANCE	NO. OF SURVIVORS AT BEGINNING OF AGE INTERVAL OF 1000 BORN lx	MORTALITY RATE NO. DYING IN 1 YEAR OF 1000 BORN	YEARS LIVED BY ALL POSSUMS IN AGE GROUP	YEARS LIVED AFTER x	EXPECTION OF LIFE OR MEAN LIFETIME REMAINING TO THOSE ATTAINING AGE INTERVAL	% ANNUAL MORTALITY
0 - 1	13	1000	126	937	6210	6.2	12.6
1 - 2	10	874	97	825.5	5273	6.0	11.1
2 - 3	4	777	39	757.5	4447.5	5.7	5.0
3 - 4	3	738	29	723.5	3690	5.0	3.9
4 - 5	12	709	117	650.5	2966.5	4.2	16.5
5 - 6	12	592	117	533.5	2316	3.9	19.8
6 - 7	5	475	49	450.5	1782.5	3.8	10.3
7 - 8	9	426	87	382.5	1332	3.1	20.4
8 - 9	7	339	68	305	949.5	2.8	20.1
9 - 10	5	271	49	246.5	644.5	2.4	18.1
10 - 11	7	222	68	188	398	1.8	30.6
11 - 12	7	154	68	120	210	1.4	44.2
12 - 13	4	86	39	66.5	90	1.0	45.3
13 - 14	5	47	47	23.5	23.5	0.5	-
TOTAL	103	6710	1000	6210			

Appendix E : Possum Mortality. Seasonal and annual distribution of possums found dead or dying and resident animals known to have disappeared permanently from trapping grids in the Orongorongo Valley, Wellington.

YEAR		J	F	M	A	M	J	J	A	S	O	N	D	TOTAL	
1966	M									2	1	1	2	6	8
	F											1	1	2	
1967	M	1	2	1	6	2	3	3	3	1	1	3	2		46
	F	1	3		3	1		2	3	2	1	2			
1968	M	3	3	1	3		3	10		3	1	1			62
	F	3	2		5		6	5	6	2	2	2	1		
1969	M	2			1			2	1	1			1		17
	F	1		2	1				3	1			1		
1970	M					2	1	1	2	3					16
	F				1	2	2				1		1		
1971	M						1			1					4
	F	1					1								
1972	M		2			2	4	2	2			1			33
	F		1				3	7	3	4	1		1		
1973	M						1	2	2				1		14
	F		1				1	3	1	1			1		
TOTAL	M	6	7	2	10	6	13	20	10	11	3	6	6	100	
	F	6	7	2	10	3	13	17	16	10	5	5	6	100	
TOTAL		12	14	4	20	9	26	37	26	21	8	11	12	200	
	SUMMER (DEC - FEB)				AUTUMN (MAR - MAY)				WINTER (JUN - AUG)			SPRING (SEP - NOV)			
	M-19			F-19	M-18		F-15		M-43		F-46	M-20		F-20	
			38			33				89			40		

Common Brushtail Possum *(Trichosurus vulpecula)*, Australia's best known possum, an invader of urban homes and gardens. Photography by E. Beaton (National Photographic Index).

Mountain Brushtail Possum *(Trichosurus caninus)* an inhabitant of rainforest and wet sclerophyll eucalypt forest. Photography by R. and A. Williams.



Common Ringtail Possums *(Pseudocheirus peregrinus)* in natural habitat in South Gippsland, Victoria.
Photography by Andrew Smith.

Green Ringtail Possum *(Pseudocheirus archeri)* an inhabitant of upland tropical rainforest.
Photography by R. and A. Williams.

Mountain Brushtail Possum *(Trichosurus caninus)* an inhabitant of rainforest and wet sclerophyll eucalypt forest. Photography by R. and A. Williams.

Bibliography

Bamford, J.M., "The dynamics of the possum (Trichosurus vulpecula Kerr) populations controlled by aerial poisoning", Unpublished Ph.D. thesis, Zoology Department, University of Canterbury. (1972)

Bell, B.D., "Breeding and condition of possums *Trichosurus vulpecula* in the Orongorongo Valley, near Wellington, New Zealand, 1966-1975". In Bell, B.D. (Ed.),"Proccedings of the first symposium on marsupials in New Zealand", *Zoological publications from Victoria University of Wellington*, **74**, 87-139. (1981)

Bellman, R. and Cooke, K.L., "Differential-difference equations", Academic Press, U.S.A. (1963)

Caughley, G., "Mortality patterns in mammals", *Ecology*, **47**, 906-918. (1966)

Caughley, G., "Interpretation of age ratios", *Journal of wildlife Management*, **38**, 557-562. (1974)

Clout, M.N. and Efford, M.G., "Sex differences in the dispersal and settlement of brushtail possums (*Trichosurus vulpecula*)", *Journal of animal Ecology* **53,** 737-749. (1984)

Efford, M.G., "A review of possum dispersal", *DSIR Land Resources Scientific Report* **23**, 70. (1991a)

Efford, M.G., "The ecology of an unindected forest possum population. In: Proceedings of a Symposium on Tuberculosis. Publication No. 132 Veterinary Continuing Education", Massey University, Palmerston North, 41-51. (1991b)

Gurtin, M.E. and Mac Camy, R.C., "Non-linear age-dependent population dynamics", *Arch. Rat. Mech. Anal.* **5**, 281-300. (1974)

Hoppensteadt, F.C., "Mathematical theories of populations: Demographics, Genetics and Epidemics", Society for Industrial and Applied Mathematics, Arrowsmith, England. (1975)

John, J.H. and Mac Gibbon, R.J., "Wild animals in New Zealand", Reed methuen, Auckland. (1986)

Kean, R.I., "Growth of opossums(*Trichosurus Vulpecula*) in the Orongorongo Valley, Wellington, New Zealand, 1953-61", *New Zealand Journal of zoology* **2**, 435-44. (1975)

Kirk, H.B., "Opossums in New Zealand: Appendix to Journals", House of Representatives, New Zealand, H-28. (1920)

Lotka, A.J., "Elements of Mathematical Biology", Dover Publication, New York. (1956)

Malthus, T.R., "An essay on the principle of population", St. Paul's, London (1798); reprinted in: Malthus, T.R., "An essay on the principle of population *and* A summary view of the principle of population", Harmondsworth, England Penguin. (1970)

Mason, R., "Food of Australian opossums in nature bush in Orongorongo Valley", *New Zealand Journal Sci. and Tech.* (1949) (in the press)

Mc'Kendrick, A.G., "Applications of mathematics to medical problems", *Proc. Edinburgh Math. Soc.* **44**, 98-130. (1926)

Metz, J.A.J and Diekmann, O., "The dynamics of physiologically structured populations", Springer-verlag, Berlin. (1986)

Nisbet, R.M. and Gurney, W.S.C., "Modelling fluctuating populations", Wiley-interscience, New York. (1982)

Pekelharing, C.J., "Cementum deposition as an age indicator in the brush-tailed possums Trichosurus vulpecula Kerr (marsupialia) in New Zealand", *Australian Journal of zoology* **18,** 71-76. (1970)

Sharpe, F.R. and Lotka, A.J., " A problem in age distributions", *Phil. Mag.* **21**, 435-438. (1911)

Troughton, E., "Furred animals of Australia", Angus and Robertson, Sydney (1946)

Verhulst, P.F., "Notice sur la loi que population suit dans son accroisement", *Correspondence mathematique et physique publiee parA. Quetelet* **10**, 112-121. (1838)

Webb, G.F., "Theory of non linear age-dependent population dynamics" Marcel Dekker, New York. (1985)

Wodzicki, K.A., "Introduced mammals in New Zealand", Department of Scientific and Industrial Research, Wellington. (1950)

Zill, D.G., "A first course in Differential Equations with applications", 4 th Ed., PWS-kent, Boston. (1989)