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The Age-Structured Population Models

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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.

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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

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

and

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

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 :

$$\begin{array}{l} \text{The change in population size} = \text{number of births} - \text{number of deaths} \\ \text{over the time interval } \delta t \qquad \qquad \qquad (B) \qquad \qquad \qquad (D) \end{array}$$

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 $\delta \rightarrow 0$ in (1.1), one may obtain the following differential equation

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

where γ is known as the *Malthusian 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.

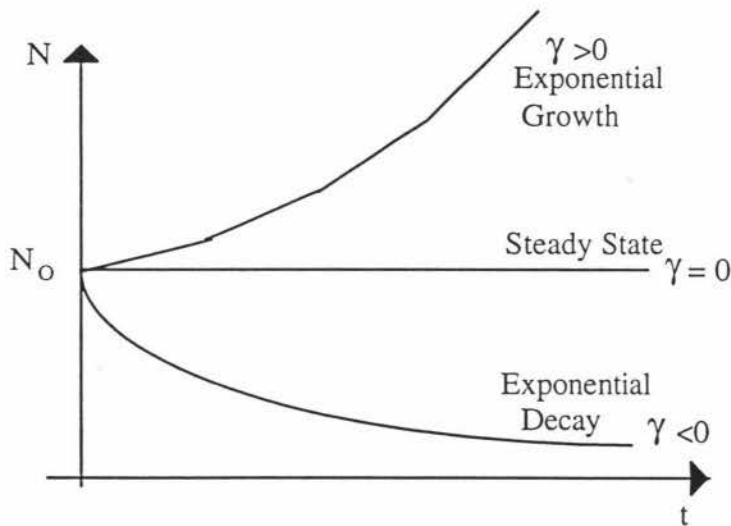


Figure 1.1: Malthusian population model : exponential growth or decay.

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.

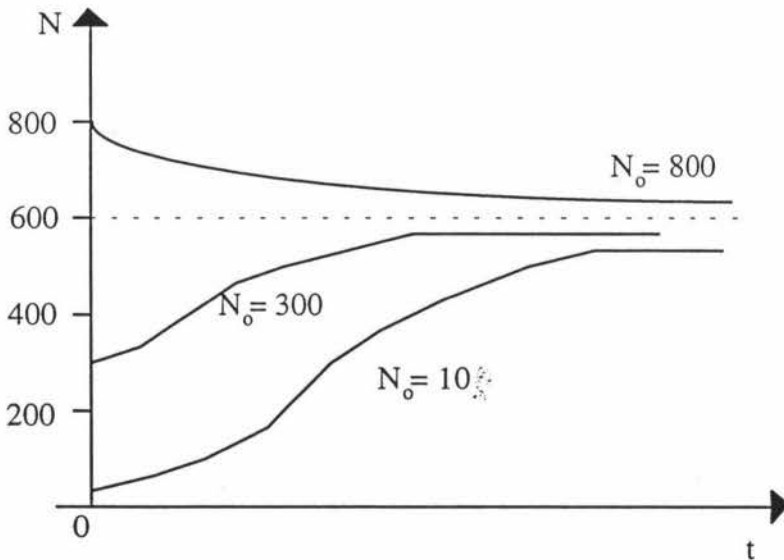


Figure 2.2: The population over time when a population is started with 10, 300 or 800 individuals with $k=600$.

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 as 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.