

# **MATHEMATICAL MODELLING WITH CASE STUDIES**

## **A Differential Equations Approach Using Maple™ and MATLAB®**

*Second Edition*

**Belinda Barnes**

**Glenn Robert Fulford**



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# Preface

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## Aims and objectives

This book aims to provide the student with some basic modelling skills, which will have application to a wide variety of problems.

The focus is on those mathematical techniques which are applicable to models involving differential equations which describe rates of change. We consider models in three different areas: growth and decay processes, interacting populations and heating/cooling problems. The main mathematical technique used is that of solving differential equations. However, the range of applications and mathematical techniques presented should provide a broad appreciation of the scope of this type of modelling, while the skills developed are transferable to many other areas.

## *Layout*

The book is divided into three general sections: compartmental models, population models and heat transfer problems.

Within each of the modelling sections the process of constructing a model is carefully considered and presented in full detail. Because this is one of the most difficult and crucial aspects of modelling, we emphasise that the process followed is: start simple, evaluate and extend.

One very important skill is that of converting a seemingly complex problem into a much simpler one. To illustrate this, there is an emphasis on the development of simple models, where some reality may be sacrificed in order to gain a basic understanding of the problem being modelled. Flow diagrams and word equations are constructed, both to aid in the model building process and to develop the mathematical equations. The assumptions made and consequent limitations are discussed together with their ramifications in the interpretation of results. This structured and detailed approach has proved a successful learning strategy.

Analysis using a variety of techniques with theoretical, graphical and computational tools follows. Understanding the behaviour of the model under changing conditions (such as changes in the parameters and initial conditions) is part of this process. Graphical methods are encouraged and it is the intention of this course to provide an interactive use of software. To this end **Maple<sup>TM</sup>** and **MATLAB<sup>®</sup>** code and ensuing results are included within the text.

Validation of the model is discussed, using observations or prior knowledge, and extensions to the models are suggested and developed or incorporated into the exercises at the end of each chapter. There is an emphasis on identifying and recognising the strengths and limitations of a model, as well as its relevance in context. A more detailed overview of the layout is presented in Section 1.2.

## *Features*

Applications and case studies are integral to this text. Case studies have been included throughout to provide the reader with relevant applications of the skills learned and an understanding of how such skills are used and interpreted in current research. We have

aimed to include models from a diverse range of disciplines, environmental, biological, archaeological, etc. The authors strongly encourage students to read some of the research papers, for which references are provided.

An important feature of this book is the use of compartment diagrams and work equations as a way for students to help conceptualise the formulation of differential equations. In this book we require students to formulate variants of the various models as exercises. We believe it is important that a student attempts to formulate differential equations where they do not see the answer; this will be closer to real life. To this end we have sometimes organised material into a formulation chapter and an analysis chapter, particularly for the later chapters. Also we will usually explore a model numerically before attempting to solve symbolically or to use analytic techniques to analyze a model. This is sometimes the opposite way that models have been presented in traditional mathematics texts, but we think this is more beneficial to students studying mathematical modelling for the first time as it allows them to explore the models without getting too bogged down with algebra. Some of the simpler models introduced early in the text are further developed and extended and analysed in subsequent chapters of the book.

There are problems at the end of each chapter to practice the skills developed in formulating differential equation models as well as analysing and interpreting models. A solutions manual is available from the publishers for instructors.

### ***Prerequisites***

Some basic calculus, such as a first year modelling/calculus course or advanced school mathematics, as well as fundamental computing skills, are required to make optimal use of this text. We do expect that students will have some basic familiarity with differential equations.

This book is not intended to teach techniques for solving differential equations from the start; there are plenty of other books that do a good job of this. However, many details of the mathematics required for differential equations and their analysis are covered in the appendices, as a reminder for those who wish some revision of the basic techniques. Since much **Maple** and **MATLAB** code is included, prior detailed knowledge of any software package is not a prerequisite and basic computing skills should suffice.

### ***Course suggestions***

This book contains far more than was given by the authors in any one course. Chapters 2 and 3 provide a good introduction for students with little previous background in modelling. This could be followed by a choice in emphasis on either population models (Chapters 5, 6 and perhaps 8) or heat transport models (Chapters 9, 10 and perhaps 11).

The authors also suggest the inclusion of a project, to complement the course and contextualise the modelling process. This may involve an examination in depth of one of the case studies or other relevant research papers which incorporate the approaches and techniques of mathematical modelling learned through the various chapters of this book.

### ***Software integration***

The analysis of these models is carried out using a analytical approach as well as the integrated use of a software package, which provides both numerical solutions and an excellent means by which graphics are displayed. It allows us to obtain solutions to differential equations, which are not always possible analytically, and provides a valuable tool in the analysis process. **Maple** and **MATLAB** code are provided in the text so that students may reproduce the results exactly. Other software packages could replace **Maple** (such as **Mathematica**) where students are more familiar with these, as the principles are the same and their use would in no way detract from the thrust of the book. Many universities have a site licence

for Maple, or MATLAB or one of the other packages, with cheap student versions available. Electronic copies of the code used in this book are available from the publisher's web site.

Belinda Barnes is a Fellow at the National Centre for Epidemiology and Population Health at the Australian National University (ANU), Canberra. She has worked at a number of research schools at the ANU and as a lecturer in the Department of Mathematics, establishing courses in Mathematical Modelling and Bifurcation Theory. Her work has focussed on the formulation of models that capture biological, ecological and epidemiological processes, while remaining practical to use and with the facility for theoretical analysis. She has published work in a number of applied areas such as bifurcation theory, population dynamics, carbon sequestration and vegetation self-thinning, leaf water transpiration, pandemic influenza transmission and the dynamics of bacteria.

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most likely to be found in the same place as the *Leucosia* and *Leucostoma*, and it is also found in the same habitat as the *Leucostoma*. The most abundant species of *Leucostoma* in the collections from the *Leucostoma* area was *L. tenuis*, which was collected in great numbers in the same habitats as the *Leucostoma* and *Leucosia*.

குடியிருப்பு கூடம் என்று அழைகின்ற மலையில் காலத்திலே நீண்ட காலம் வரை வாழ்ந்த ஒரு மலையாகும்.

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APRIL 1940, 11 A.M. - 1940, 11 A.M.

在這裏，我們可以說，我們的社會主義者是沒有錯的。他們說：「我們的社會主義者是沒有錯的。」

卷之三

10. The following table gives the number of cases of smallpox in each of the 100 districts of the United States.

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## Acknowledgements

There are many friends and colleagues who have had an input into this book, with typing, technical support, suggestions and encouragement, and we would like to offer them all our warmest thanks.

We are extremely grateful to Jill Smith, Sharon Eldridge and Annette Hughes at the Australian National University, and Annabelle Lippiatt from University College, ADFA, who contributed significantly to the typing of this document. And to Tracey Hansen who undertook the copy editing. We would also like to thank James Gifford and Nick Guoth for the valuable technical advice they provided, as well as Harvinder Sidhu for his Maple code to generate the bifurcation diagram in Section 3.6. Furthermore, we thank Scott Rabuka and Waterloo Maple for their support.

One of the students taking the course, Cezary Niewiadomski, constructed some of the diagrams incorporated into the book, and we thank him warmly for this generous contribution. There are many other students who pointed out errors and provided suggestions, to all of whom we are most grateful. Willow Hart spent a large number of tedious hours compiling the index and updating files, to our great appreciation.

We are very grateful for information on alcohol and drug absorption which was so readily supplied to us by Kelly FitzGerald of Ainslie Pharmacy (Canberra, Australia) as well as the Alcohol and Other Drugs Council of Australia. Thanks are also due to Duck Australia who provided details of Australian standards for hot water heaters. Many thanks also to Tony Richings for his background information on land mines; we greatly admire your heroic task of clearing Cambodia of mines.

We extend our thanks to those colleagues who read and commented on sections of the book, particularly Harvinder Sidhu, David Rowland, Daryl Daley and Joe Gani. Your comments were a highly valued contribution in the construction of the text.

For the second edition of this book we are very grateful to Jen Pestana for her careful and enthusiastic work on producing a solutions manual. We would also like to thank Mark Nelson for pointing out some typographical errors and making some excellent suggestions and to thank Charisse Farr for commenting on the new case study on economic modelling.

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## 1.1 Mathematical models

Models of systems have become part of our everyday lives: they range from global decisions having a profound impact on our future, to local decisions about whether to cycle to university based on weather predictions. Together with their provision of a deeper understanding of the processes involved, this predictive nature of models, which aids in decision-making, is one of their key strengths.

In particular, many processes can be described with mathematical equations: that is, by mathematical models. Such models have a use in a diverse range of disciplines.

There is an aesthetic use, for example, in constructing perspective in paintings or etchings such as is seen in the paradoxical work of Escher. The proportions of the golden mean and the Fibonacci series of numbers, occurring in many natural phenomena such as the arrangement of seed spirals in sunflowers, have been applied to methods of information storage in computers. This well-known mathematical series is also applied in models describing the growth nodes on the stems of plants, as well as in aesthetically pleasing proportions in painting and sculpture and the design of musical instruments. From a philosophical perspective, mathematical logic and rigour provide a model for the construction of argument.

In a more practical and analytical mode there is a plethora of applications. Mathematical optimisation theory has been applied in the clothing industry to minimise the required cloth for the maximum number of garments, and to the arrangement of odd-shaped chocolates in a box to minimise the number required to give the impression that the box is full! The mathematics of fractals has allowed the successful development of fractal image compression techniques, requiring little storage for extremely precise images.

Some other areas of application include the physical sciences (such as astronomy), medicine (such as the absorption of medication), and the social sciences (such as patterns in election voting). Mathematical models are used extensively in biology and ecology to examine population fluctuations, water catchments, erosion and the spread of pollutants, to name just a few. Fluid mechanics is another extensive area of research, with applications ranging from the modelling of evolving tsunamis across the ocean, to the flow of lolly mixture into moulds. (Mathematicians were consulted to establish the best entry points for the mixture to the mould in order to ensure a filled nose for a Mickey Mouse lollipop!)

The use and versatility of such mathematical models has been heightened by the power of computers. This trend is likely to continue, as such modelling results in an efficient and economical way of understanding, analysing and designing processes. Furthermore, the diverse range of applications, where mathematical models are used, implicates an appeal to many areas of mathematics as well as to many types of models. Some models can be extremely accurate in their predictions, whereas others may be more susceptible to a range of interpretations, particularly in the case of large systems with many interacting mechanisms.

The use of information from this modelling process to reach decisions is now very much in the public view, particularly in the case of environmental issues exemplified in the 1998 international meeting on Global Warming in Kyoto. We would hope that by encouraging the responsible use of models, we may improve public confidence in the role of science, which has been declining over recent years (Beck et al., 1993). It is well to remember that models are not reality and should not be promoted as such. They are considered by the authors to be a valuable and integral part of a multi-disciplinary approach towards decision-making on issues we face today and we encourage future modellers to adopt and promote this perspective.

## 1.2 An overview of the book

This course aims to provide the student with some basic modelling skills which have application to a wide variety of problems. There is an emphasis on the initial development of simple models, which are then extended and improved by incorporating further features.

As well, we have focused attention on the importance of declaring any assumptions made in the modelling process, and bearing these in mind when interpreting the predictions. We discuss various theoretical approaches as they arise, but the emphasis is on the modelling itself and the interpretation of the results.

### ***Layout of the book***

The analysis of these models is carried out using a theoretical approach as well as the integrated use of Maple or MATLAB (two mathematical software packages), both of which provide numerical solutions and an excellent means by which graphics are displayed. Maple and MATLAB code and output are presented throughout the text.

Furthermore, case studies have been included throughout to provide the reader with relevant applications of the skills learned and an understanding of how such skills are used and interpreted in current research. We have aimed to include models from a diverse range of subjects, environmental, biological, archaeological, etc. The authors strongly encourage students to read some of the research papers, for which references are provided.

In general, with such a diversity of modelling applications it is not surprising that many different areas of mathematics are used. These include differential and integral calculus, differential equations, matrices, statistics, probability, to name just a few.

This course focuses on those mathematical techniques which are applicable to differential equation models, in particular ordinary differential equations (ODEs) although partial differential equations (PDEs) are also briefly discussed. We consider models in three different areas: decay processes, interacting populations and heating/cooling problems. The main mathematical technique used is that of solving differential equations. However, this range of applications and the mathematical techniques presented should still provide an appreciation of the scope of this type of mathematical modelling, because the skills developed are transferable to many other areas.

The book is divided into three general parts: compartmental models, population models and heat transfer problems.

Within each of the modelling sections, the process of constructing a model is carefully considered, because this aspect is one of the most difficult and crucial parts of modelling. One very important skill is that of converting a seemingly complex problem into a much simpler one. There is an emphasis in this book on the development of simple models where some features of reality are sacrificed in order to gain a basic understanding of the underlying problem. With each model type the text covers this building process in detail, with a critical evaluation of the assumptions made and their subsequent limitations on interpretation. Flow diagrams aid the understanding of this process, and clarify any division of sub-sections within a model. Then 'word equations' are developed describing the process under consideration, and from these the differential equations follow. This structured approach has proved a successful learning strategy.

Once a model has been established it is analysed using a variety of techniques with theoretical, graphical and computational tools. Understanding the behaviour of the model under a variety of conditions (changes in the parameters and different initial conditions) is discussed, with an awareness of possible limitations on the interpretations (or misinterpretations) of the results. Graphical methods are encouraged, and it is the intention of this

These models can be extremely complicated, although this is not necessarily the case. They do have the advantage of incorporating a degree of uncertainty within them, and ideally should be used when there is a high degree of variability in the problem. This method is typically used for models of small populations when reproduction rates need to be predicted over a time interval. They also have valuable application in many other areas such as economic fluctuations, insurance problems, telecommunications and traffic theory, and biological models.

### ***Simulation models***

In a simulation model one writes a computer program which applies a set of rules, or possibly even physically builds a scale model. It is intended to produce a set of data which mimic a real outcome including extreme events. In a population model, the rules would apply to each member of the population. Usually a simulation will involve some random components. The computer program can be run many times and statistical information gained in the process.

Typically, such models are used in engineering applications as an aid to identifying problems which may arise during use or construction. They also provide a useful means by which data sets can be generated. One such example is rainfall data, which may be required as input to a model forecasting phosphorus concentrations in a stream network.

It might be argued that this simulation approach provides the most realistic models, but this does not mean it provides the best models. The best models are usually those which are simplest yet still provide results which are useful.

### ***Deterministic models***

Another approach to mathematical modelling is the deterministic approach. This is the approach we adopt in this book. Modelling in this manner we ignore random variation and try to formulate mathematical equations describing the basic fundamental relationships between the variables of the problem.

For instance, in the population model we would aim to obtain an equation relating birth rates and death rates which themselves are related through equations to the population size at any given time. In a sense we are constructing a model made of several empirical and inter-related sub-models, linking these sub-models together and then using the whole system to predict the outcome from a set of initial conditions.

This process is widely used and can be extremely accurate, such as in the case of predicting satellite orbits. It has the drawback that in other cases it is not possible to establish all the component mechanisms of a process or, even if this were possible, that including all known relationships renders the model unwieldy. However, as we shall see, even under these conditions this modelling technique can provide valuable insights into a process.

### ***Statistical models***

Statistical models concern the testing (referred to as hypothesis testing) of whether a set of empirical data is from one or another category. These categories are assumed to have particular distributions (with associated means and standard deviations) and the results suggest the data are drawn from one such category. This distribution can then be used to predict the outcome of further trials. In terms of our population such a model may test whether a sample of heights was taken from a population with an average height of six feet (say category A), or one with an average height of five feet and ten inches (say category B). Our results would indicate a percentage error margin with which we have made this prediction.

Statistical testing is used widely in psychology, paleontology and the biological sciences. One example application would be to establish spatial distributions of some ancient species

from sets of fossilised teeth found in different locations.

---

## 1.4 Modelling for decision-making

Currently modelling, and in particular mathematical modelling, provides a means by which many political and management planning decisions are made, both locally and globally. Such models have huge economic clout and wield social and environmental ramifications. There is a need to use these models wisely.

Modelling is an extremely powerful tool, a framework for research, debate and planning, which provides a valuable source of information for decision-making. However, while models aim to incorporate the main mechanisms of a process and have the capacity not only to describe and explain but to predict as well, they are not infallible, and should not be considered in isolation particularly in the light of the above remarks. Decision makers need to be made aware of the modelling process and its context-specific strengths and limitations, in order to make best use of the interpretations.

The main objectives of any model are twofold: first, to provide a deeper understanding of a system or process, and second, to use this knowledge for predictions and decision-making. In the first instance, mathematical modelling can be extremely successful with, in many cases, a combination of models providing the best insight into a problem. Of course, any model is, at best, merely a means of mimicking reality and as such at each stage of the process, there is the possibility of error or introduced limitations. This does not render the process useless, but rather suggests a need for an understanding of the complexities involved.

No part of the process is necessarily simple. For example, in the decision-making process individuals invariably have different interpretations of the results, and differ in opinion as to what might most benefit a situation. They may disagree on a 'safe' level of pollution in a local river, or how 'green' the Sydney Green Olympics should be, or what constitutes an endangered species, or even whether a population facing extinction warrants concern at all.

Furthermore, the model needs to be sufficiently simple so that the available equipment is adequate for sensible and useful predictions. If it took until next week to predict tomorrow's weather we might as well not bother: clearly accurate predictions are only useful before the event! Certain physical processes, such as the path of a satellite, can be accurately described while others, such as ecological systems or the process of global warming, are far more complex and require modelling and interpretation of a very different sort. Thus the modelling process is not necessarily simple and it needs to be well understood, with all its strengths, simplifications, assumptions and limitations to utilise the results optimally.

When involved in decision-making processes, to take the results of any single model as absolute would be short-sighted. It constitutes one part of a multi-dimensional field, far more complex in most cases than our single mathematical model can hope to represent. But, for their part, decision makers need to be made aware of the limitations of the model predictions, as well as their strengths. They need to recognise the assumptions on which the model is based and the rationale behind them. They should consider a variety of interpretations. They should be as well informed as possible.

Furthermore, beyond the mathematics there may be, for example, historical, legal or cultural issues involved which are integral to the planning process and should be acknowledged. It is the modellers' responsibility to provide the best information possible, not to

*of drugs into the bloodstream, using compartmental techniques.*

sell a ‘perfect’ model. It is well to remember that, ultimately, political and management decisions have an impact on us all.

In many instances, the reticence of scientists to work together with those in other ‘softer’ disciplines, and *vice versa*, has emphasised the distrust between them and the lack of respect

## 2.1 Introduction

Many processes may be considered as compartmental models: that is, the process has inputs to and outputs from a ‘compartment’ over time.

### Compartmental diagram

One example of this compartmental notion is the amount of carbon dioxide in the Earth’s atmosphere. The compartment is the atmosphere. The input of CO<sub>2</sub> occurs through many processes, such as burning, and the output occurs through processes such as plant respiration. This is illustrated in Figure 2.1 in a diagram known as a *compartmental diagram*.

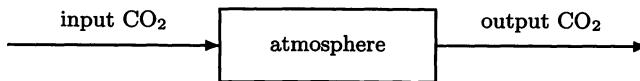


Figure 2.1: Input-output compartmental diagram for CO<sub>2</sub>.

What we are interested in is the amount of CO<sub>2</sub> in the compartment at any given time, or whether over long periods the levels are increasing or decreasing. Currently, the input of CO<sub>2</sub> into the Earth’s atmosphere appears to exceed the output, so that there is an overall increase in the level of CO<sub>2</sub> in the compartment.

### Balance law

Suppose we are modelling the amount of CO<sub>2</sub> as above, or the size of a population which is changing with time. We can think of the amount of a substance (CO<sub>2</sub> or the population) as occupying the compartment and the rate of change can be considered as the ‘rate in’ minus the ‘rate out’. Thus we have what is called the *balance law*. In words this is

$$\left\{ \begin{array}{l} \text{net rate} \\ \text{of change} \\ \text{of a substance} \end{array} \right\} = \left\{ \begin{array}{l} \text{rate} \\ \text{in} \end{array} \right\} - \left\{ \begin{array}{l} \text{rate} \\ \text{out} \end{array} \right\}. \quad (2.1)$$

It could describe, for example,

- the decay process of radioactive elements,
- births and deaths in a population,
- pollution into and out of a lake or river, or the atmosphere,
- drug assimilation into, and removal from, the bloodstream.

In the following sections, we use this balance law approach to formulate mathematical models of differential equations which describe such processes.

## 2.2 Exponential decay and radioactivity

The process of dating aspects of our environment is essential to the understanding of our history. From the formation of the earth through the evolution of life and the development of mankind historians, geologists, archaeologists, palaeontologists and many others use dating procedures to establish theories within their disciplines.

### Compartmental diagram

While certain elements are stable, others (or their isotopes) are not, and emit  $\alpha$ -particles,  $\beta$ -particles or photons while decaying into isotopes of other elements. Such elements are called *radioactive*.

The decay, or disintegration, of one nucleus is a random event and so for small numbers of nuclei one might apply probability functions. However, when dealing with large numbers of nuclei we can be reasonably certain that a proportion of the nuclei will decay in any time interval and thus we can model the process as continuous with some fixed rate of decay. We can consider the process in terms of a compartment without input but with output over time, as in Figure 2.2.

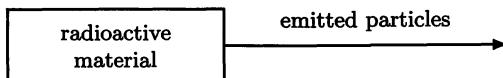


Figure 2.2: Input-output compartmental diagram for radioactive nuclei.

We make some assumptions and then, based on these, develop a model to describe the process.

- We assume that the amount of an element present is large enough so that we are justified in ignoring random fluctuations.
- We assume the process is continuous in time.
- We assume a fixed rate of decay for an element.
- We further assume there is no increase in mass of the body of material.

The first step is to determine an equation describing this disintegration process and, as with each subsequent model building in this book, we start with a word equation and then replace each 'word-term' with mathematical symbols. In a word equation we can express the above decay process as

$$\left\{ \begin{array}{l} \text{rate of change of} \\ \text{radioactive material} \\ \text{at time } t \end{array} \right\} = - \left\{ \begin{array}{l} \text{rate amount of} \\ \text{radioactive} \\ \text{material} \\ \text{decayed} \end{array} \right\}. \quad (2.2)$$

### Formulating the differential equation

To convert the terms in the word equation into symbols let  $N(t)$  be the number of radioactive nuclei at time  $t$  and let  $\Delta t$  be a small change in time. We know that the change in the number of nuclei is proportional to the number of nuclei at the start of the time period. Hence (2.2) translates to

$$\frac{dN}{dt} = -kN \quad (2.3)$$

where  $k$  is a positive constant of proportionality indicating the rate of decay per nucleus in unit time. We write  $N$  on the right-hand-side for  $N(t)$  as the dependence on  $t$  is implied by the derivative  $dN/dt$ . We assume  $k$  to be fixed although it will have a different value for different elements/isotopes.

Alternatively, we can obtain the differential equation from a limiting process of a consideration of the change in the number of particles in a small time interval  $\Delta t$ . Thus the number of particles at time  $t + \Delta t$  is the number at time  $t$  minus the number lost,

$$N(t + \Delta t) = N(t) - kN(t)\Delta t.$$

Diving through by  $\Delta t$ , and then letting  $\Delta t \rightarrow 0$  gives the instantaneous rate of change on the left-hand-side, and so we obtain

$$\frac{dN}{dt} = -kN.$$

Note that  $N(t)$  should be an integer (number of nuclei) while  $-kN(t)\Delta t$  may not be. However, if instead we consider  $N$  as a mass in grams (from which we can find the number of nuclei) then we can overcome this problem. Note that we then have an equation for  $N(t)$ , which assumes that  $N(t)$  is a continuous, differentiable function rather than an integer. This is an appropriate approximation, particularly when the number of nuclei is large.

Given a sample of a radioactive element at some initial time, say  $n_0$  nuclei at  $t_0$ , we may want to predict the mass of nuclei at some later time  $t$ . We require the value of  $k$  for the calculations: it is usually found through experimentation. Then, with known  $k$  and an initial condition  $N(0) = n_0$  we have an initial value problem (IVP)

$$\frac{dN}{dt} = -kN, \quad N(0) = n_0. \quad (2.4)$$

### Solving the differential equation

We can solve the differential equation numerically, using either MATLAB or Maple, and we can also solve this differential equation exactly by the technique of separation of variables. The techniques for numerical solutions are discussed in detail in Chapter 4. Firstly, the numerical solution can be obtained using the MATLAB code in Listing 2.1. The graph of the solution is shown in Figure 2.3.

Listing 2.1: MATLAB code: c\_cm\_expdecay.m

```
function c_cm_coldpills1
global k1;

k1=2.0; % set parameter value
tend=5; %end time in hours
x0=10^5;
[tsol, xsol] = ode45(@rhs, [0, tend], x0);
plot(tsol, xsol,'k');

function xdot = rhs(t, x)
global k1;
xdot = -k1*x;
```

A similar numerical solution can be also easily obtained using Maple, and in particular, the `detools` command. Some sample code is given in Listing 2.2.

Listing 2.2: Maple code: c\_cm\_expdecay.txt

```
> restart; with(plots): with(DEtools):
> de := diff(N(t),t) = -k*N(t);
> init := N(0) = 10^5;
> k := 2.0;
> plot1 := DEplot(de, N, t=0..5, [init], scene=[t, N]);
> display(plot1);
```

### Exact solution

We can also solve this equation theoretically using the separation of variables technique as in the following example. (See Appendix A.3 for a review of this technique for solving differential equations.)

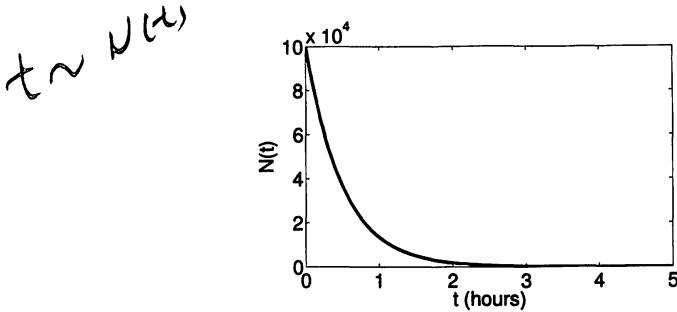


Figure 2.3: Numerical solution of the exponential decay differential equation with  $n_0 = 10^5$  and  $k = 2.0$ .

**Example 2.1:** Solve the initial value problem (IVP) in equation (2.4) with initial condition  $N(t_0) = n_0$ .

**Solution:** Since the differential equation is separable,

$$\int \frac{1}{N} \frac{dN}{dt} dt = \int -k dt,$$

$$\int \frac{1}{N} dN = -k \int dt,$$

and hence, since  $N$  is a positive quantity,

$$\ln N = -kt + C,$$

where  $C$  is an arbitrary constant. Taking exponentials of both sides we obtain

$$N(t) = Ae^{-kt}, \quad \text{where } A = e^C,$$

and note that  $N \geq 0$ .

Using the initial condition  $N(t_0) = n_0$  we get

$$n_0 = Ae^{-kt_0} \quad \text{and} \quad A = n_0 e^{kt_0}.$$

Thus

$$N(t) = n_0 e^{-k(t-t_0)}, \tag{2.5}$$

which is the solution of the IVP.

Note that above we have considered the indefinite integral, when technically we should specify the integral over a particular interval  $[0, t]$ . In the next example we show that this has no impact on the final solution, and thus for the many integrations carried out in this book the interval is often not given explicitly, but understood from the context.

**Example 2.2:** Solve the IVP in equation (2.4) on the interval  $[0, t]$ .

**Solution:** Since the differential equation is separable,

$$\int_0^t \frac{1}{N} \frac{dN}{dt} dt = \int_0^t -k dt,$$

$$\int_{n_0}^N \frac{1}{N} dN = -k \int_0^t dt,$$

and hence, since  $N$  and  $n_0$  are positive,

$$\begin{aligned}\ln N - \ln n_0 &= -kt + 0, \\ \ln \frac{N}{n_0} &= -kt.\end{aligned}$$

Taking exponentials of both sides, we obtain

$$N(t) = n_0 e^{-kt},$$

which is the solution of the initial value problem (IVP).

We can also obtain the analytic solution of the differential equation using **Maple**, or some other symbolic software package. We include many inserts of **Maple** code throughout the book, which are listed in the index, and which allow the reader to reproduce the analytic results and all illustrated graphs. For a brief introduction to **Maple** see Appendix C.1. The code to establish the analytic solution is given in Listing 2.3

Listing 2.3: Maple code: c\_cm\_expdecay\_sym.txt

---

```
> restart;
> de := diff(N(t),t) = -k*N(t);
> dsolve({de, N(0)=n0}, N(t));
```

---

**MATLAB**, with the symbolic toolbox, can also be used to obtain the exact symbolic solution. (The symbolic toolbox comes with the student version of **MATLAB** and is essentially a link to a version of **Maple**). The code to obtain the exact solution in **MATLAB** is given in Listing 2.4.

Listing 2.4: MATLAB code: c\_cm\_expdecay\_sym.m

---

```
dsolve('DN = -k*N', 'N(0)=N0', 't');
```

---

Consider a graph of the solution  $N = n_0 e^{-k(t-t_0)}$ , from (2.5). First, since  $t - t_0 > 0$ , we have that  $e^{-k(t-t_0)}$  is a negative exponential. We also have that

$$\lim_{t \rightarrow \infty} n_0 e^{-k(t-t_0)} = 0$$

and  $N' = -kN < 0$  (since  $N$  and  $k$  are positive). This implies that the function  $N(t)$  is monotonically decreasing and has no turning points. This information allows us to construct a graph of the solution illustrated in Figure 2.4.

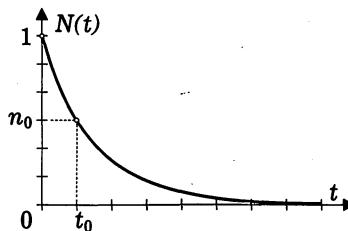


Figure 2.4: Graph of solution (2.5) showing exponential decay.

Equally, **Maple** could have been used to construct the graph with the following code in Listing 2.5.

Listing 2.5: Maple code: c\_cm\_expdecay\_symplot.txt

---

```
> restart;
> de := diff(N(t), t) = k*N(t);
> soln := dsolve({de, N(t0)=n0}, N(t));
> k:=-0.5; n0:=1.0; t0:=0;
> plot(rhs(soln), t=0..15);
```

---

Often experimental data provides information concerning  $N(t)$  at a given time  $t_1$  and what is required is to estimate the constant  $k$  and thus predict future or past values of  $N$ . This can be done algebraically, or using the substitution procedure of Maple (see Question 1 of the exercises) with code in Listing 2.6.

Listing 2.6: Maple code: c\_cm\_expdecay\_findt.txt

---

```
> restart;
> de:=diff(N(t),t)=k*N(t);
> soln:=n0->dsolve({de, N(t0)=n0}, N(t));
> t0:=0;n0:=1;
> ans:=soln(n0);
> get_k:=solve(subs(t=2,N(2)=1/4,ans),k);
> evalf(get_k);
```

---

The *half-life*  $\tau$  of the radioactive nuclei can be used to determine  $k$ , where  $\tau$  is the time required for half of the nuclei to decay. The half-life  $\tau$  is more commonly known than the value of the rate constant  $k$  for radioactive elements.

---

**Example 2.3:** If the half-life is  $\tau$  then find  $k$  in terms of  $\tau$ .

**Solution:** Using the solution (2.5), and setting  $N(t + \tau) = N(t)/2$ , we have

$$\frac{N(t + \tau)}{N(t)} = \frac{1}{2} \quad (2.6)$$

which gives

$$\frac{n_0 e^{-k(t+\tau-t_0)}}{n_0 e^{-k(t-t_0)}} = \frac{1}{2}.$$

This simplifies to

$$e^{-k\tau} = \frac{1}{2}.$$

Taking logarithms of both sides gives  $\ln(1/2) = -k\tau$ . Hence

$$k = \frac{\ln(2)}{\tau}. \quad (2.7)$$

Note that both  $\tau$  and  $k$  are independent of  $n_0$  and  $t_0$ .

---

### Residence time

Similar to the idea of half-life is the concept of residence time. This is defined to be the mean time that a individual particle is in the compartment. A nice interpretation is that the residence time for a single compartment is  $k^{-1}$  where  $k$  is the rate constant in the differential equation

$$\frac{dN}{dt} = -kN.$$

To see how to deduce this result we think of particles leaving the compartment randomly and find the probability density function for the random variable  $T$ , the time each particle spends inside the compartment before leaving.

If we start with  $n_0$  particles then it is easy to compute the fraction of particles remaining in the compartment at time  $t$ . Since  $N(t) = n_0 e^{-kt}$  then this fraction is given by  $e^{-kt}$ . This can be given a probabilistic interpretation. Since  $e^{-kt}$  is the fraction of particles left in the compartment at time  $t$ , then the quantity  $F(t) = 1 - e^{-kt}$  represents the probability an individual particle has left the compartment by time  $t$ . This is the cumulative probability function for the time each particle was in the compartment, i.e.,  $T$  is the random variable representing the time for each particle, then

$$F(t) = \Pr\{T < t\}$$

is the cumulative probability of the time of each particle in the compartment. The probability density function (pdf),  $f(t)$  is given as the derivative of the cumulative probability function, so the random variable corresponding to the time a particle stays in the compartment is

$$f(t) = -ke^{-kt},$$

which shows that the time in the compartment  $T$  has an exponential distribution. We can calculate the mean of this distribution as the integral

$$\int_0^\infty t \times -ke^{-kt} dt = \frac{1}{k}.$$

Hence we have the interpretation *the reciprocal of the rate constant,  $k^{-1}$ , is the mean time that an individual particle spends in the compartment.*

### **Radiocarbon dating**

We can apply the above theory to the problem of dating artifacts and paintings by considering the decay process of certain radioactive elements in each.

The following description and example are adapted from Borelli and Coleman (1996). All living organisms absorb carbon from carbon dioxide ( $\text{CO}_2$ ) in the air, and thus all contain some radioactive carbon nuclei. This follows since  $\text{CO}_2$  is composed of a radioactive form of carbon  $^{14}\text{C}$ , as well as the common  $^{12}\text{C}$ . ( $^{14}\text{C}$  is produced by the collisions of cosmic rays (neutrons) with nitrogen in the atmosphere and the  $^{14}\text{C}$  nuclei decay back to nitrogen atoms by emitting  $\beta$  particles.) Nobel Prize winner Willard Libby, during the late 1940s, established how the known decay rate and half-life of  $^{14}\text{C}$ , together with the carbon remaining in fragments of bones or other dead tissue, could be used to determine the year of its death. Because of the particular half-life of carbon, internationally agreed upon as  $5568 \pm 30$  years for  $^{14}\text{C}$ , this process is most effective with material between 200 and 70 000 years old.

Carbon dating depends on the fact that for any living organism the ratio of the amount of  $^{14}\text{C}$  to the total amount of carbon in the cells is the same as that ratio in the surroundings. Assuming the ratio in air is constant, then so is the ratio in living organisms. However, when an organism dies,  $\text{CO}_2$  from the air is no longer absorbed although  $^{14}\text{C}$  within the organism continues to undergo radioactive decay.

In the Cave of Lascaux in France there are some ancient wall paintings, believed to be prehistoric. Using a Geiger counter the current decay rate of  $^{14}\text{C}$  in charcoal fragments collected from the cave was measured as approximately 1.69 disintegrations per minute per gram of carbon. In comparison, for living tissue in 1950 the measurement was 13.5 disintegrations per minute per gram of carbon.

**Example 2.4:** How long ago was the radioactive carbon formed and, within an error margin, the Lascaux Cave paintings painted?

**Solution:** Let  $N(t)$  be the amount of  $^{14}\text{C}$  per gram in the charcoal at time  $t$ . We apply the model of exponential decay,  $N' = -kN$ . We know  $\tau = 5568 \pm 30$  years (the half-life of  $^{14}\text{C}$ ). From equation (2.7)  $k \simeq 0.0001245$  per year.

Let  $t = t_0 = 0$  be the current time. Let  $T$  be the time that the charcoal was formed, and thus  $T < 0$ . For  $t > T$ ,  $^{14}\text{C}$  decays at the rate

$$\frac{dN}{dt} = -kN \quad \text{with} \quad N(0) = n_0$$

and

$$N(T) = n_0 e^{-kT}$$

or

$$T = -\frac{1}{k} \ln \left( \frac{N(T)}{n_0} \right).$$

But we do not know  $N(T)$  or  $n_0$ . However,

$$\frac{N'(T)}{N'(0)} = \frac{-kN(T)}{-kN(0)} = \frac{N(T)}{n_0}$$

and we do have  $N'(T)$  and  $N'(0)$ . Thus

$$T = -\frac{1}{k} \ln \left( \frac{N(T)}{n_0} \right) = -16690 \pm 94 \text{ years.}$$

The accuracy of this process depends on having prior knowledge of the exact ratio of  $^{14}\text{C}$  to the total C in the atmosphere, but this has changed over the years. There is a basic sinusoidal variation with an 8000-year period (approximately) to consider. Further, volcanic eruptions and industrial smoke emit only  $^{12}\text{C}$  (from tissue older than 100 000 years) into the atmosphere and decrease the ratio, while nuclear testing has resulted in a 100% increase of the ratio in certain parts of the northern hemisphere! These are now factored into dating calculations (see Borelli and Coleman (1996)).

As previously mentioned, radiocarbon dating is inaccurate for the recent past and for very long time periods. Thus the lead isotope with a relatively short half-life ( $\simeq 22$  years) is used for the dating of paintings in our recent history, while at the other extreme, radioactive substances (such as Uranium-238) with half-lives of billions of years are used to date the earth.



#### Summary of skills developed here:

- Understand the concept of modelling with compartments and the balance law.
- Find the constant of proportionality from the half-life for radioactive elements.
- Generate a solution, using Maple or analytical methods, to simple separable differential equations.

## 2.3 Case Study: Detecting art forgeries

This case study is based on an article in Braun (1979).

After World War II, Europe was in turmoil. Some well-known artworks had disappeared, others had turned up miles from the galleries to which they belonged, and some new ones had appeared! The Dutch Field Security uncovered a firm which, acting through a banker, had been involved in selling artworks to the Nazi leader, Goering. In particular in the case of a painting by the seventeenth century artist Jan Vermeer, "Woman taken in adultery", the banker claimed that he had been acting on behalf of Van Meegeren, a third rate painter, who was duly imprisoned for the crime of collaboration. However, shortly after his arrest Van Meegeren announced that he had never sold this painting to Goering and that it was in fact a forgery. He claimed that, together with "Disciples at Emmaus" and several others, he himself had painted them. In order to prove this claim he began to forge a further work by Vermeer while in prison. When he learned that his charge had been changed from that of collaboration to one of forgery, he refused to finish the work as it would provide evidence against himself and reveal the means by which he had 'aged' the paintings.

A team of art historians, chemists and physicists was employed to settle the dispute. They took X-rays to establish what paintings might lie underneath, analysed pigments in the paints and looked for chemical and physical signs of old age authenticity. They found traces of modern pigment in the cobalt blue, although Van Meegeren had been very careful, in all other cases, to use pigments which the artists themselves might have used. Further examination indicated Van Meegeren had scraped old canvases which he had used as a base for the forgeries. The discovery of phenoformaldehyde, which he had cleverly mixed into the paints and then baked in the oven so that it would harden to bakelite as was typical of old paint, finally sealed his fate and he was convicted in October 1947 and sentenced to a year in prison. (He died of a heart attack while in prison in December of that year.)

But the controversy was not over. Art lovers claimed that "Disciples at Emmaus" was far too beautifully painted to be a forgery and was in quite a different class from the other forgeries. They demanded more scientific evidence to prove it a fake. Besides, a noted art historian A. Bredius had previously certified it as authentic and it had been bought by the Rembrandt Society for a sizeable sum of money. Reputations and money were at stake here.

A scientific study was undertaken with the results based on the notion of radioactive decay. The atoms of certain elements are unstable, or radioactive, and within a given time (which depends on the element involved) a number of the atoms disintegrate. This rate of disintegration has been shown to be proportional to the number of atoms present at that time,  $N(t)$ . So, starting from  $N(t_0) = n_0$ , where  $n_0$  is the original amount of material,

$$\frac{dN}{dt} = -\lambda N, \quad \text{with} \quad N = n_0 e^{-\lambda(t-t_0)},$$

where  $\lambda$ , the decay constant, is chosen positive.

From here, if the initial formation of the substance was at time  $t_0$  then its age is  $(1/\lambda) \ln(n_0/N)$ .  $N$  can be measured, but  $n_0$ , the original amount of the material, is harder to find.

A useful quantity to know is the half-life of an element, the time taken for the number of atoms present at a particular time to halve. Now if  $N = \frac{1}{2}n_0$  then, rearranging the above gives

$$\text{half-life} = \frac{\ln 2}{\lambda} \simeq \frac{0.69}{\lambda}.$$

The half-lives of many radioactive substances are well known: for Uranium-238 it is 4.5 billion years, for Carbon-14 is 5568 years, for Lead-210 it is 22 years and for Polonium-214 it is less than 1 second.

All paintings contain small amounts of radioactive Lead-210 which we know to decay with a half-life of 22 years, as this is contained in lead white which has been used by artists

as a pigment for over 2000 years. Lead white contains lead metal (which is smelted from rocks) which in turn contains small amounts of Lead-210 and extremely small amounts of Radium-226 (mostly removed in the smelting process). There is no further supply of lead due to the absence of Radium-226 which decays to Lead-210 in a series of steps, and so Lead-210 initially decays rapidly. Radium-226 has a half-life of 1600 years and since it exists in very small amounts in lead white, eventually the process of lead decay stabilises when the amount disintegrating balances with the amount produced by radium disintegration.

Let  $N(t)$  be the amount of Lead-210, and then, as before,

$$\frac{dN}{dt} = -\lambda N + R(t), \quad n_0 = N(t_0),$$

where  $R(t)$  is the rate of disintegration of Radium-226 per minute per gram of white lead. Since we are interested in a time period of 300 years at the most, and the half-life of Radium-226 is 1600 years, and the amount present is so small, we can consider  $R(t) = R$  to be a constant. Solving the equation, using an integrating factor of  $e^{\lambda t}$ , we conclude that

$$N(t) = \frac{R}{\lambda} \left( 1 - e^{-\lambda(t-t_0)} \right) + n_0 e^{-\lambda(t-t_0)}.$$

$R$  and  $N$  can be measured easily and  $\lambda$  is known; however  $n_0$  is more difficult and is dealt with in the following way. The above equation can be rearranged to give

$$\lambda n_0 = \lambda N e^{\lambda(t-t_0)} - R(e^{\lambda(t-t_0)} - 1)$$

where  $\lambda n_0$  is the disintegration rate when the white lead was extracted from the ore at time  $t_0$ . A good estimate of a reasonable size for this disintegration rate can be obtained by taking current measurements for such ore, and they provide a range from 0.18 to 140 disintegrations per minute per gram. In exceptional circumstances the rate has been measured as 30 000 disintegrations (per minute per gram). This gives a very wide range and thus excludes any possibility of predicting the age of the painting with much accuracy. However, an exact date is not required. What is needed is to establish if the painting is old (about 300 years old) or modern (painted within the last 30 to 50 years).

Suppose it were 300 years old, then  $\lambda n_0$  as expressed above should provide an original (at  $t_0$ ) disintegration rate of much less than 30 000. Alternatively, if it is a modern forgery then  $\lambda n_0$  should be ridiculously large, or far greater than 30 000 disintegrations per minute per gram.

Using the half-life formula to find  $\lambda$  ( $\lambda = (\ln 2)/22$ ) it follows that  $e^{300\lambda} = 2^{150/11}$ . The current disintegration rate can be measured, and since it is the same as for Polonium-210 after a few years, and as the latter is easier to measure in white lead, it is taken as 8.5 disintegrations ( $\text{min}^{-1} \text{g}^{-1}$ ) (measured from  $^{210}\text{Po}$ ) for the painting "Disciples of Emmaus". Now, with  $R = 0.8$ , the equation gives

$$\lambda n_0 = 8.5 \times 2^{150/11} - 0.8(2^{150/11} - 1) > 98\,000.$$

This painting was definitely not painted by Vermeer in the seventeenth century.

## 2.4 Case Study: Pacific rats colonise New Zealand

The case study which follows emphasises the care with which such models should be adopted when applying this dating procedure as 'proof' of a proposed theory. This case study is based on an article by Anderson (1996).

Opinions are divided as to when humans first occupied New Zealand. Some, due to changes in the vegetation, favour an arrival date of 1400BP (where BP means before present) or earlier, while others argue, based on archaeological evidence, a date of 900BP or later. Anderson (Anderson (1996)) discusses the dating of Pacific rats (*rattus exulans*) as an indicator of human arrival as they would have arrived as 'stowaways' with the first Polynesians. The advantage of this means of establishing an arrival time is that the rat population would have expanded rapidly and thus evidence of them should be easy to find.

To ensure the least contamination of the material by other carbon sources, clean hard bones were carefully selected from dry shelters and dunes in the Shag River Mouth. The idea was to use the bone protein (collagen) for obtaining the age as it would hold no inbuilt age, a potential problem associated with marine reservoir effects. (Some shell exposed only to water from deep in the ocean is exposed to a very different ratio, a lower ratio, of carbon to  $^{14}\text{C}$  than that in air. Thus different dates can result. These are marine reservoir effects.)

The AMS (accelerator mass spectroscopy) radiocarbon dating method was used since it only requires very tiny amounts of carbon and the Institute of Geological and Nuclear Sciences, Ltd. (IGNS) produced a range with dates as early as 2000BP. This suggested that the rats were in existence in NZ at least a millennium earlier than previously thought. By 1996 this date had been accepted as 'fact'.

Anderson proposes that these 'facts' and dates are questionable. Such dates are not consistent with the carbon chronologies associated with moa eggshell, charcoal and bones using non-protein (non-collagen) samples. He suggests that there are further factors which contribute to carbon levels. There is a considerable likelihood and evidence that the rats ate insects living in rotting wood, in which case the radiocarbon activity in the rats may have been depleted to levels approaching the age of the old logs — possibly a thousand or thousands of years older than the rats.

Thus, in the case of the NZ rat bones, the radiocarbon dating procedure was in fact dating these ancient NZ logs and not the rats which, 1000 or so years later, arrived with the first New Zealanders and set about eating the insects which were eating the rotten old logs! All this in spite of the extreme care taken in avoiding any possible contamination of the samples.

## 2.5 Lake pollution models

First we consider the simple example of the concentration of salt in a tank of water. We then apply this method to model the changing concentration of pollution in a lake system.

### *Background*

Pollution in our lakes and rivers has become a major problem particularly over the last 50 years. In order to improve this situation in the future it is necessary to gain a good understanding of the processes involved. Some way of predicting how the situation may improve (or decline) as a result of current management practices is vital. To this end we need to be able to predict how pollutant amounts or concentrations vary over time and under different management strategies.

### *General compartmental model*

This problem can be considered as a compartmental model with a single compartment, the lake, as is illustrated in Figure 2.5. Applying the balance law there is an input of polluted

water from the river(s) flowing into the lake, or due to a pollution dump into the lake, and an output as water flows from the lake carrying some pollution with it.

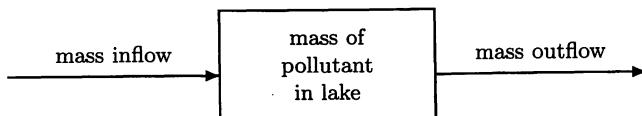


Figure 2.5: Input-output compartmental diagram for pollution in a lake.

This leads us to the word equation, for the mass of pollutant in the lake,

$$\left\{ \begin{array}{l} \text{rate of change} \\ \text{of mass} \\ \text{in lake} \end{array} \right\} = \left\{ \begin{array}{l} \text{rate} \\ \text{mass} \\ \text{enters lake} \end{array} \right\} - \left\{ \begin{array}{l} \text{rate} \\ \text{mass} \\ \text{leaves lake} \end{array} \right\}. \quad (2.8)$$

Before developing the differential equations describing this process, we examine the simple model of a salt solution in a tank.

### An example problem of salt dissolved in a tank

(The following example is adapted from Borelli and Coleman (1996).) As an example problem involving concentrations let us consider how to model the concentration of salt dissolved in a tank of water. The solution of water and salt is sometimes called brine. A large tank contains 100 litres of salt water. Initially  $s_0$  kg of salt is dissolved. Salt water flows into the tank at the rate of 10 litres per minute, and the concentration  $c_{\text{in}}(t)$  (kg of salt/litre) of this incoming water-salt mixture varies with time. We assume that the solution in the tank is thoroughly mixed and that the salt solution flows out at the same rate at which it flows in: that is, the volume of water-salt mixture in the tank remains constant.

*Example 2.5:* Find a differential equation for the amount of salt in the tank at any time  $t$ . (Note that concentration can be defined as the mass of salt per unit volume of mixture.)

*Solution:* The tank is the ‘compartment’. Let  $S(t)$  be the amount (mass) of salt in the tank at time  $t$ .  $S(t)$  is what we want to find. First we draw a diagram of the situation as in Figure 2.6.

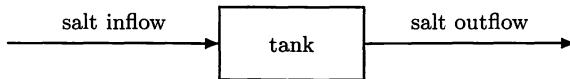


Figure 2.6: Input-output compartmental diagram for salt solution in tank.

Then, applying the balance law to the mass of salt, this can be described by the word equation

$$\left\{ \begin{array}{l} \text{rate of change} \\ \text{of mass of salt} \\ \text{in tank} \end{array} \right\} = \left\{ \begin{array}{l} \text{rate} \\ \text{mass of salt} \\ \text{enters tank} \end{array} \right\} - \left\{ \begin{array}{l} \text{rate} \\ \text{mass of salt} \\ \text{leaves tank} \end{array} \right\}. \quad (2.9)$$

The rate at which the mass of salt is added is the flow rate 10 (litres) multiplied by the concentration of the incoming mixture  $c_{\text{in}}(t)$  (in kg/litre),

$$\left\{ \begin{array}{l} \text{rate} \\ \text{salt} \\ \text{enters tank} \end{array} \right\} = 10c_{\text{in}}(t).$$

$$W = Q c$$

The rate at which the salt is leaving the tank is the flow rate out multiplied by the concentration of salt in the tank,  $S(t)/100$ , so

$$\left\{ \begin{array}{c} \text{rate} \\ \text{salt} \\ \text{leaves tank} \end{array} \right\} = 10 \times \frac{S(t)}{100} = \frac{S(t)}{10},$$

again measured in kg/min.

So the differential equation describing the rate of change in the mass of salt in the tank is given by

$$\frac{dS}{dt} = 10c_{\text{in}}(t) - \frac{S(t)}{10}.$$

To solve the differential equation we also need an initial condition. At time  $t = 0$  we assume the amount of salt dissolved in the tank is  $s_0$  (measured in kg). Hence we are required to solve IVP

$$\frac{dS}{dt} = 10c_{\text{in}}(t) - \frac{1}{10}S(t), \quad S(0) = s_0. \quad (2.10)$$

This is a linear, first-order ODE (ordinary differential equation). It is not a separable equation, but we can solve it using the technique of integrating factors (see Appendix A.4 on integrating factors). We obtain a solution for an arbitrary function for input concentration  $c_{\text{in}}(t)$  and then later investigate different functional forms of  $c_{\text{in}}(t)$ .

**Example 2.6:** Using the technique of integrating factors, solve the IVP (2.10) on the interval  $[0, t]$ , in terms of an arbitrary function  $c_{\text{in}}(t)$ .

**Solution:** Multiplying equation (2.10) by the integrating factor (IF)  $e^{\int_0^t \frac{1}{10} ds} = e^{(t-0)/10} = e^{t/10}$  we get

$$\frac{d}{dt} \left( S(t) \times e^{t/10} \right) = 10c_{\text{in}}(t)e^{t/10},$$

whence, integrating over  $[0, t]$ , gives

$$S(t)e^{t/10} - s_0e^{0/10} = 10 \int_0^t c_{\text{in}}(s)e^{s/10} ds.$$

Hence,

$$S(t) = s_0e^{-t/10} + 10e^{-t/10} \int_0^t c_{\text{in}}(s)e^{s/10} ds. \quad (2.11)$$

Note that the initial condition  $S(0) = s_0$  was included when applying the boundaries of the given interval of integration. Alternatively, for the more general case of indefinite integrals see Appendix A.4.

The original question was: How much salt is in the tank at time  $t$ ? To answer this we need to know  $c_{\text{in}}(t)$ , the concentration of the incoming salt solution. Suppose  $c_{\text{in}}(t) = c_1$ , a constant, then (2.11) gives

$$S(t) = s_0e^{-t/10} + 100c_1(1 - e^{-t/10}). \quad (2.12)$$

Suppose, instead,  $c_{\text{in}}$  is a sinusoidal function, say  $c_{\text{in}}(t) = 0.2 + 0.1 \sin t$ , then evaluating the integral (either by tables or by using Maple) gives

$$S(t) = s_0e^{-t/10} + 20 + \frac{10}{101}(\sin t - 10 \cos t + 192e^{-t/10}). \quad (2.13)$$

Note that in equations (2.11), (2.12) and (2.13), as  $t \rightarrow \infty$  the effect of the initial condition on the solution decreases and becomes negligible. Also, these solutions have two parts: one which is the response to the initial data and one which is the response to the input. We discuss this further in Section 2.10 where we cover some general theory about first-order linear differential equations.

### A lake pollution model

We return now to the problem of pollution in a lake. We apply the above theory to investigate the changing concentration of a pollutant.

As usual we need to make some assumptions while developing the model and to this end we assume that the lake has a constant volume  $V$ , and that it is continuously well mixed so that the pollution is uniform throughout.

Let  $C(t)$  be the concentration of the pollutant in the lake at time  $t$ . Let  $F$  be the rate at which water flows out of the lake in  $\text{m}^3/\text{day}$ . Since the volume is constant we have

$$\left\{ \begin{array}{l} \text{flow of} \\ \text{mixture} \\ \text{into lake} \end{array} \right\} = \left\{ \begin{array}{l} \text{flow of} \\ \text{mixture} \\ \text{out of lake} \end{array} \right\} = F.$$

Applying the balance law to the mass of the pollutant  $M(t)$  we can describe the process in words

$$\left\{ \begin{array}{l} \text{rate of} \\ \text{change of} \\ \text{mass of} \\ \text{pollutant} \\ \text{in lake} \end{array} \right\} = \left\{ \begin{array}{l} \text{rate at} \\ \text{which the} \\ \text{pollutant enters} \\ \text{the lake} \end{array} \right\} - \left\{ \begin{array}{l} \text{rate at} \\ \text{which the} \\ \text{pollutant leaves} \\ \text{the lake} \end{array} \right\}.$$

This translates into the differential equation for the changing mass

$$M'(t) = Fc_{\text{in}} - F \frac{M(t)}{V}, \quad (2.14)$$

where  $c_{\text{in}}$  is the concentration (in units of mass per unit of volume, such as  $\text{g}/\text{m}^3$ ) of the pollutant in the flow entering the lake.

Now, since  $M(t) = C(t)V$  we have that  $M'(t) = C'(t)V$  (since  $V$  is constant) and hence that  $C'(t) = M'(t)/V$ . With this change of variable the differential equation (2.14) for the mass is transformed to a differential for the concentration of the pollutant in the lake,

$$\frac{dC}{dt} = \frac{F}{V}c_{\text{in}} - \frac{F}{V}C. \quad (2.15)$$

If the flow rate  $F$  is constant with time then we can use the technique of separating the variables to solve the equation, as in the following example.

**Example 2.7:** Solve the differential equation (2.15) with the initial condition  $C(0) = c_0$ .

**Solution:** Separating the variables,

$$\int \frac{1}{c_{\text{in}} - C} dC = \int \frac{F}{V} dt.$$

Integrating gives

$$-\ln |c_{\text{in}} - C| = \frac{F}{V}t + K \quad (K \text{ an arbitrary constant}),$$

and thus

$$C(t) = c_{\text{in}} - e^{-K} e^{-Ft/V}.$$

Using the initial condition  $C(0) = c_0$ , we obtain

$$C(t) = c_{\text{in}} - (c_{\text{in}} - c_0)e^{-Ft/V}. \quad (2.16)$$

Note again that the solution can be divided into two parts:  $c_0e^{-Ft/V}$  which is the contribution from the initial data, and  $(c_{\text{in}} - c_{\text{in}}e^{-Ft/V})$  which is the contribution from the pollution inflow to the system. Also note that as  $t \rightarrow \infty$ , then  $C(t) \rightarrow c_{\text{in}}$ . That is,

$$\lim_{t \rightarrow \infty} (c_{\text{in}} - (c_{\text{in}} - c_0)e^{-Ft/V}) = c_{\text{in}}$$

and the concentration in the lake increases/decreases steadily to this limit.

Maple or MATLAB could have been used to establish the solution and plot the results. The following code (see Listing 2.7 and Listing 2.8) provides the time-dependent plot for a variety of initial pollution concentrations where the safety threshold for the level of pollution is illustrated with a line.

Listing 2.7: Maple code: c\_cm\_lake.txt

```
> restart:with(plots):
> cin:=3;V:=28;F:=4*12;threshold:=4;init_c:=10;
> de1:=diff(C(t),t)=F/V*(cin-C(t));
> soln:=c0->dsolve({de1,C(0)=c0},C(t),numeric):
> plot1:=c0->odeplot(soln(c0),[t,C(t)],0..8):
> list1:=seq(plot1(i/2),i=1..12):
> line1:=plot([[0,threshold],[8,threshold]]):
> display(list1,line1);
```

Listing 2.8: MATLAB code: c\_cm\_lake.m

```
function c_cm_lake
global F V cin %set global variables
N = 100;
cin=3; V=28; F=4*12; c0=10; tend=4;
t = linspace(0,1,N);
[tsol, ysol] = ode45( @derhs, [0, tend], c0 );
plot(tsol, ysol)

function ydot = derhs(t, c)
global F V cin %set global variables
ydot = F/V*(cin - c);
```

Suppose we start with a polluted lake, with initial concentration  $c_0$ , but subsequently only fresh water enters the lake. We are interested in calculating the time for the pollution level in the lake to reduce to a specified value.

**Example 2.8:** How long will it take for the lake's pollution level to reach 5% of its initial level, if only fresh water flows into the lake.

**Solution:** From the solution (2.16), and setting  $c_{\text{in}} = 0$ , we have

$$C(t) = c_0 e^{-Ft/V}. \quad (2.17)$$

Rearranging to solve for  $t$ ,

$$t = -\frac{V}{F} \ln \left( \frac{C}{c_0} \right).$$

Since  $C = 0.05c_0$ , we find  $t$  given by

$$t = -\ln(0.05) \times \frac{V}{F} \simeq \frac{3V}{F}.$$

### Application to American lakes

Consider two American lakes where Lake Erie flows into Lake Ontario (Mesterton-Gibbons (1989)). Lake Erie has  $V = 458 \times 10^9 \text{ m}^3$  and  $F = 480 \times 10^6 \text{ m}^3/\text{day} = 1.75 \times 10^{11} \text{ m}^3/\text{year}$ . Thus if  $t_{0.05}$  is the time it takes for the pollution level to reach 5% of its current level, then from above  $t_{0.05} \approx 7.8$  years.

Similarly, Lake Ontario has  $V = 1636 \times 10^9 \text{ m}^3$ ,  $F = 572 \times 10^6 \text{ m}^3/\text{day} = 2.089 \times 10^{11} \text{ m}^3/\text{year}$  and we calculate  $t_{0.05} \approx 23.5$  years, if only fresh water flows into Lake Ontario. Although the flow rate in and out of Lake Ontario is similar to Lake Erie, it takes significantly longer to clear the pollution from Lake Ontario due to the larger volume water in Lake Ontario.

Maple provides a method of substitution which can be used to find this time. The Maple code, in Listing 2.9, with  $c_0 = 10$  in the above example, shows how to do this.

Listing 2.9: Maple code: c\_cm\_lake\_subs.txt

---

```
> restart:
> de1:=diff(C(t),t)=(F/V)*(cin-C(t));
> soln:=c0->dsolve({de1,C(0)=c0},C(t)):
> cin:=0;c0:=10:
> ans:=soln(c0):
> get_t:=solve(subs(C(t)=(0.05*c0),ans),t):
> evalf(get_t);
```

---

We have made some assumptions in this model. First, we assumed the lake to be well mixed. However, if the lake were not well mixed then the time taken to flush the lake is likely to be longer since poor mixing will prolong the process. We have also assumed the flow rate  $F$  to be constant.

### Seasonal flow rate

Suppose that the flow rate into and out of the lake,  $F(t)$ , varied seasonally. We could let  $F(t) = F_0(1 + \epsilon \sin(2\pi t))$  where  $F_0$  is the mean in/out flow and  $|\epsilon| < 1$  so that  $F \geq 0$ . Here  $2\epsilon$  is the maximum variation (maximum-minimum) of the flow rate, and we assume this to be small compared to the overall flow rate  $F$ . Let us look at the modified equation for the concentration:

$$\frac{dC}{dt} = -\frac{F_0}{V} (1 + \epsilon \cos(2\pi t)) C.$$

Separating the variables and integrating gives

$$\ln |C(t)| = \frac{-F_0}{V} t - \frac{F_0}{V} \frac{\epsilon}{2\pi} \sin(2\pi t) + K,$$

with  $K$  some arbitrary constant, and applying the initial condition and solving for  $C(t)$

$$C(t) = c_0 e^{-F_0(t + \frac{\epsilon}{2\pi} \sin(2\pi t))/V}.$$

Since  $\sin(2\pi t) \leq 1$ , and  $\epsilon$  is small, we have

$$\begin{aligned} C(t) &\leq c_0 e^{-F_0(t + \frac{\epsilon}{2\pi})/V} \\ &\leq c_0 e^{-F_0(t + \frac{1}{2\pi})/V} \end{aligned} \tag{2.18}$$

since  $\epsilon < 1$ . For large  $t$  and small  $\epsilon$ , there is little difference between the predictions from this solution and that of the simpler model as given in (2.17), concerning the time taken for the lake to purify. Thus, from (2.18) and (2.17), we can be reasonably sure that the times we estimated applying the previous very simple model will provide a lower bound for the purification time.

### **Further extensions**

This model can easily be extended to encompass a system of lakes (one lake flowing into another) by setting the inflow in the model of the downstream lake equal to the outflow of the upstream lake. Clearly, there may be several lakes/rivers feeding into the downstream lake at any time, and a single upstream lake may only be a fraction of the flow feeding the lower lake.

#### **Summary of skills developed here:**

- Apply the concept of modelling with compartments and the balance law.
- Extend the model developed in this section to a system of lakes, or the addition of further pollution sources into a single lake.
- Sketch graphs of pollution levels over time.
- Generate solutions, using Maple or analytical methods, to the model and its extensions.

## **2.6 Case Study: Lake Burley Griffin**

The information for the case study is adapted from the research paper Burgess and Olive (1975).

Lake Burley Griffin in Canberra, the capital city of Australia, was created artificially in 1962 for both recreational and aesthetic purposes. In 1974 the public health authorities indicated that pollution standards set down for safe recreational use were being violated and that this was attributable to the sewage works in Queanbeyan upstream (or rather the discharge of untreated sewage into the lake's feeder river).

After extensive measurements of pollution levels taken in the 1970s it was established that, while the sewage plants (of which there are three above the lake) certainly exacerbated the problem, there were significant contributions from rural and urban runoff as well, particularly during summer rainstorms. These contributed to dramatic increases in pollution levels and at times were totally responsible for lifting the concentration levels above the safety limits. As a point of interest Queanbeyan (where the sewage plants are situated) is in the state of New South Wales (NSW), while the lake is in the Australian Capital Territory, and although they are a ten-minute drive apart the safety levels/standards for those who swim in NSW are different from the standards for those who swim in the Capital Territory!

In 1974 the mean concentration of the bacteria faecal coliform count was approximately  $10^7$  bacteria per  $\text{m}^3$  at the point where the river feeds into the lake. The safety threshold for this faecal coliform count in the water is such that for contact recreational sports no more than 10% of total samples over a 30-day period should exceed  $4 \times 10^6$  bacteria per  $\text{m}^3$ .

Given that the lake was polluted it is of interest to examine how, if sewage management were improved, the lake would flush out and if and when the pollution levels would drop below the safety threshold.

The system can be modelled, very simply, under a few assumptions. Flow ( $F$ ) into the lake is assumed equal to flow out of the lake and the volume ( $V$ ) of the lake will be

considered constant and is approximately  $28 \times 10^6 \text{ m}^3$ . Further, the lake can be considered as well mixed in the sense that the pollution concentration throughout will be taken as constant. Under these assumptions a suitable differential equation model for the pollutant concentration is

$$\frac{dC}{dt} = \frac{F}{V} c_{\text{in}} - \frac{F}{V} C, \quad (2.19)$$

where  $c_{\text{in}}$  is the concentration of the pollutant entering the lake. With the initial concentration taken as  $c_0$  the solution is

$$C(t) = c_{\text{in}} - (c_{\text{in}} - c_0)e^{-Ft/V}. \quad (2.20)$$

With only fresh water entering the lake ( $c_{\text{in}} = 0$ ), with a mean monthly flow of  $4 \times 10^6 \text{ m}^3/\text{month}$  and with the initial faecal coliform count of  $10^7$  bacteria per  $\text{m}^3$  (as was measured in 1974) the lake will take approximately 6 months for the pollution level to drop below the safety threshold. However, pure water entering the lake is not a very realistic scenario with three sewage plants and much farmland upstream, and so including the entrance of polluted river water into the lake model is essential.

From the solution (2.20), as time increases so the concentration of a pollutant in the lake will approach the concentration of the polluted water entering the lake. This level is independent of the initial pollution level in the lake and if  $c_0 > c_{\text{in}}$  then the level of pollution in the lake decreases monotonically to  $c_{\text{in}}$ , while if  $c_0 < c_{\text{in}}$  then the level increases steadily until it reaches  $c_{\text{in}}$ . Thus with the faecal coliform entering the lake at a count of  $3 \times 10^6$  bacteria per  $\text{m}^3$  the concentration of the pollutant in the lake will approach this level with time. This is evident in Figure 2.7, where Maple has been used to solve the differential equation (2.19) and plot the results, for a number of different initial concentrations.

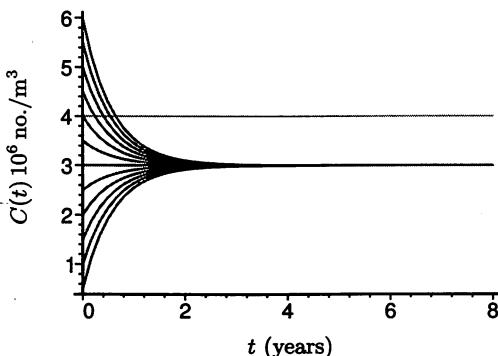


Figure 2.7: Pollution levels in Lake Burley Griffin over time with constant rates of flow and pollution. A range of initial concentrations has been used. The grey line is the pollution threshold level.

However, the model is still simplistic. Flow rates change over the year with on average a seasonal pattern, while the amount of pollution reaching the lake will itself be seasonal. Assuming a sinusoidal pattern over the year, a rough estimate of the inflow concentration from the available data in the 1970s is  $c_{\text{in}}(t) = 10^6(10 + 10 \cos(2\pi t))$  bacteria  $\text{m}^{-3}$  and for the flow rate,  $F(t) = 10^6(1 + 6 \sin(2\pi t)) \text{ m}^3/\text{year}$ . Note here that the concentration of the pollutant increases when the flow is low. We need to re-solve the differential equation (2.19) with  $F$  no longer constant. Using Maple to determine the solution and plot the concentration of pollution in the lake over time, the results are displayed in Figure 2.8.

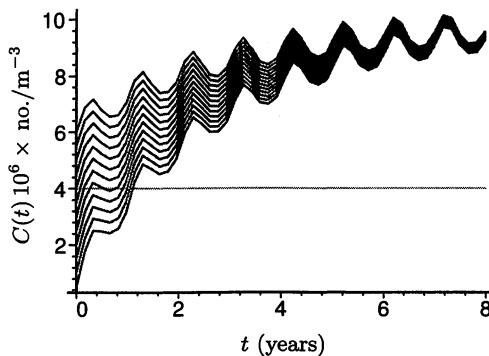


Figure 2.8: Pollution levels in Lake Burley Griffin over time with seasonal incoming flows and pollutant concentrations. A range of initial concentrations has been used. The grey line is the pollution threshold level.

*It should be noted that this model for Lake Burley Griffin is still simplistic in its assumption of a well mixed body of water. If the concentration decreased from the point of river entry to the point of outflow then the flushing time could take considerably longer. Further, in most lakes there is a main channel of water flow which flushes regularly, and adjacent to this channel are areas of trapped water which flush less frequently and through a very different process. The process is that of diffusion which operates at a microscopic level and is extremely gradual. Thus pockets of the lake may have a much higher (or lower) pollution concentration than others and these may also be the protected bays where swimming is most likely to take place.*

## 2.7 Drug assimilation into the blood

We investigate two simple models of cold pill assimilation into the bloodstream which are adapted from Borelli and Coleman (1996). In the first model we consider a single cold pill and in the second a course of cold pills. The basic idea of using a compartmental diagram to build the models is used.

### Background

We readily take pills or drink alcohol, without necessarily having a good understanding of how these drugs are absorbed into the bloodstream or for how long they have an effect on us. The warnings on the packaging list some of the effects and are intended to ensure safety for all users. In the following example and case study we see that different drugs are absorbed into, and extracted from, the blood at very different rates. Some may affect us for many hours after the medication has ceased. Further, in the case study on alcohol absorption, we see how different body mass and the sex of an individual can radically modify the effects of alcohol.

The drug dissolves in the gastrointestinal tract (GI-tract) and each ingredient is diffused into the bloodstream. They are carried to the locations in which they act and are removed from the blood by the kidneys and the liver. The assimilation and removal may occur at different rates for the different ingredients of the same pill.



### General compartmental model

We can consider this problem as a compartmental model with two compartments, corresponding to the GI-tract and the bloodstream. This is illustrated in Figure 2.9. The GI-tract compartment has a single input and output and the bloodstream compartment has a single input and output.

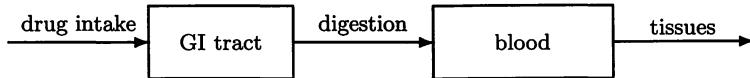


Figure 2.9: Input-output compartmental diagram for drug assimilation.

This application of the balance law gives us two word equation, one for each compartment. We have

$$\begin{aligned} \left\{ \begin{array}{l} \text{rate of change} \\ \text{of drug} \\ \text{in GI tract} \end{array} \right\} &= \left\{ \begin{array}{l} \text{rate of} \\ \text{drug} \end{array} \right\} - \left\{ \begin{array}{l} \text{rate} \\ \text{drug} \\ \text{leaves GI-tract} \end{array} \right\}, \\ \left\{ \begin{array}{l} \text{rate of change} \\ \text{of drug} \\ \text{in blood} \end{array} \right\} &= \left\{ \begin{array}{l} \text{rate} \\ \text{drug} \\ \text{enters blood} \end{array} \right\} - \left\{ \begin{array}{l} \text{rate} \\ \text{drug} \\ \text{leaves blood} \end{array} \right\}. \end{aligned} \quad (2.21)$$

We let  $x(t)$  be the amount of a drug in the GI-tract at time  $t$  and  $y(t)$  the amount in the bloodstream at time  $t$ . We consider two models: a single cold pill where there is no ingestion of the drug except that which occurs initially, and a course of cold pills where the drug intake is assumed to occur continuously.

The common cold remains without a cure. However, there are pills which can be taken to relieve some of the congestion and symptoms, such as watering eyes and a running nose, through the action of a decongestant and an antihistamine. The cold pills we consider in the following two models consist of these two drugs.

#### **Model I: Case of a single cold pill**

In the GI-tract we consider the pill to have been swallowed, and so after this event (over subsequent time) we have nothing more entering the GI-tract. The pill dissolves and diffuses into the bloodstream from the GI-tract. So, for the GI-tract there is only an output term. Assuming the output rate is proportional to the GI-tract drug concentration, which is therefore proportional to the amount of drug in the bloodstream, then

$$\frac{dx}{dt} = -k_1 x, \quad x(0) = x_0, \quad (2.22)$$

where  $x_0$  is the amount of a drug in the pill, our initial condition, and  $k_1$  is a positive coefficient of proportionality (the rate constant).

In the bloodstream the initial amount of the drug is zero, so  $y(0) = 0$ . The level increases as the drug diffuses from the GI-tract and decreases as the kidneys and liver remove it. Thus

$$\frac{dy}{dt} = k_1 x - k_2 y, \quad y(0) = 0, \quad (2.23)$$

with  $k_2$  another positive constant of proportionality. The cold pill is made up of a decongestant and an antihistamine, and the coefficients of proportionality,  $k_1$  and  $k_2$ , are different for the different component drugs in the pill.

As expected, as  $t$  increases both  $x$  and  $y$  approach zero although the rate at which this occurs depends on the coefficients  $k_1$  and  $k_2$  associated with each drug. Some values are given in Table 2.1.

Table 2.1: Values of constants for decongestant and antihistamine in cold pills, from Borelli and Coleman (1996).

	Decongestant	Antihistamine
$k_1$	1.3860/hr	0.6931/hr
$k_2$	0.1386/hr	0.0231/hr

Using these values we easily solve the differential equations numerically, with MATLAB or Maple, and we can graph the changing values for  $x$  and  $y$  in each of the two ‘compartments’. Some sample MATLAB code is given in Listing 2.10 to graph the amounts of decongestant as a function of time. In Figure 2.10 the solutions are plotted for both decongestant and anti-histimine. The Maple code used to produce this is given in Listing 2.11.

Listing 2.10: MATLAB code: c\_cm.coldpills.m

```
function c_cm_coldpills1
global k1 k2;
k1=1.386; k2=0.1386;
tend=15; %end time in hours
x0=1; y0=0; u0 = [x0; y0];
[tsol; usol] = ode45(@rhs, [0, tend], u0);
xsol = usol(:,1);
ysol = usol(:,2);
plot(tsol, xsol,'k'); hold on
plot(tsol, ysol,'r:'); hold off

function udot = rhs(t, u)
global k1 k2
x = u(1); y=u(2);
xdot = -k1*x;
ydot = k1*x - k2*y;
udot = [xdot; ydot];
```

Listing 2.11: Maple code: c\_cm.coldpills.txt

```
> restart:with(plots):with(DEtools):
> k1:=1.386;k2:=0.1386;k3:=0.6931;k4:=0.0231;
> I1:=0;I2:=0;hours:=15;initx:=1;inity:=0;initw:=1;initz:=0;
> de1:=diff(x(t),t)=I1-k1*x(t);
> de2:=diff(y(t),t)=k1*x(t)-k2*y(t);
> pair1:=[de1,de2]:
> plot1:=DEplot(pair1,[x,y],t=0..hours,{{0,initx,inity}});
  stepsize=0.1,scene=[t,x],linecolour=gray,arrows=NONE):
> plot2:=DEplot(pair1,[x,y],t=0..hours,{{0,initx,inity}});
  stepsize=0.1,scene=[t,y],linecolour=gray,arrows=NONE):
> de3:=diff(w(t),t)=I1-k3*w(t);
> de4:=diff(z(t),t)=k3*w(t)-k4*z(t);
> pair2:=[de3,de4]:
> plot3:=DEplot(pair2,[w,z],t=0..hours,{{0,initw,initz}});
  stepsize=0.1,scene=[t,w],linecolour=black,arrows=NONE):
> plot4:=DEplot(pair2,[w,z],t=0..hours,{{0,initw,initz}});
  stepsize=0.1,scene=[t,z],linecolour=black,arrows=NONE):
```

```
> display(plot1,plot3);display(plot2,plot4);
```

---

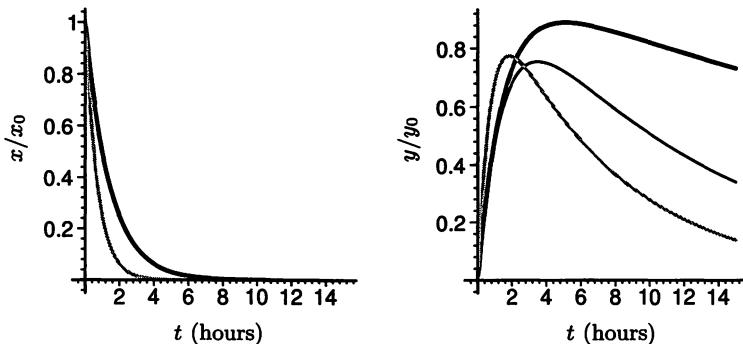


Figure 2.10: Single cold pill. The graph on the left represents the GI-tract and that on the right the bloodstream. The levels of antihistamine are illustrated with black lines ( $k_2 = 0.0231$  thick line,  $k_2 = 0.08$  thin line) and the decongestant with a grey line. The other parameter values are given in Table 2.1, with typical initial values for the antihistamine and decongestant, 4 mg and 60 mg.

The coefficients also depend on the age and health of the person involved, and the concentration of a drug may also depend on the persons' body mass, which means that for some people the doses may peak higher and/or faster than for the average person, and of course this may be potentially dangerous. The coefficients also depend on the age and health of the person involved, and the concentration of a drug may also depend on the persons' body mass, which means that for some people the doses may peak higher and/or faster than for the average person, and of course this may be potentially dangerous.

### ***Exact solution for Model I***

The differential equations (2.22) and (2.23) are not coupled because the first equation is totally independent of  $y$ . So we can solve it independently of the second equation. The solution to this first differential equation is (see Exercises, Question 10)

$$x = x_0 e^{-k_1 t}.$$

Using this solution the second differential equation (2.23) becomes

$$\frac{dy}{dt} = k_1 x_0 e^{-k_1 t} - k_2 y.$$

This equation is a first-order linear differential equation whose solution when  $k_1 \neq k_2$  is (see Exercises, Question 10)

$$y = \frac{k_1 x_0}{k_1 - k_2} (e^{-k_2 t} - e^{-k_1 t}).$$

(Note that a different solution is valid when  $k_1 = k_2$ .)

### ***Model II: A course of cold pills***

In reality, particularly for a cold, we take a course of pills rather than just one. In this way there is a continuous flow of drugs into the GI-tract. We adjust our model of the previous

section to give

$$\begin{aligned}\frac{dx}{dt} &= I - k_1 x, & x(0) &= 0, \\ \frac{dy}{dt} &= k_1 x - k_2 y, & y(0) &= 0,\end{aligned}\tag{2.24}$$

where  $I$  is a positive constant representing the rate of ingestion of the drug (in grams per unit of time).

Once again we have a sequence (cascade) of linear equations which are not coupled and thus can be exactly solved sequentially. For

$$\frac{dx}{dt} = I - k_1 x$$

the solution is (see Exercises, Question 11)

$$x(t) = \frac{I}{k_1} (1 - e^{-k_1 t}).$$

Then solving for  $y(t)$  in the second equation gives (see Exercises, Question 11)

$$y(t) = \frac{I}{k_2} \left[ 1 - \frac{1}{k_2 - k_1} (k_2 e^{-k_1 t} - k_1 e^{-k_2 t}) \right].$$

(Note again that this solution is valid only if  $k_1 \neq k_2$ .)

As usual we are interested in what happens over time; in this case as  $t \rightarrow \infty$  then  $x \rightarrow I/k_1$  and  $y \rightarrow I/k_2$ . Now we draw the graphs of these functions to establish the accumulating levels of the decongestant and antihistamine in the GI-tract and the bloodstream over a time period where pills are taken each hour and the value of  $I$  is constant.

With Maple or MATLAB, we can easily explore the effects of the antihistamine in the bloodstream as  $k_2$  increases/decreases and determine how sensitive the system is to changes in the parameter  $k_2$ ; see Figure 2.10.

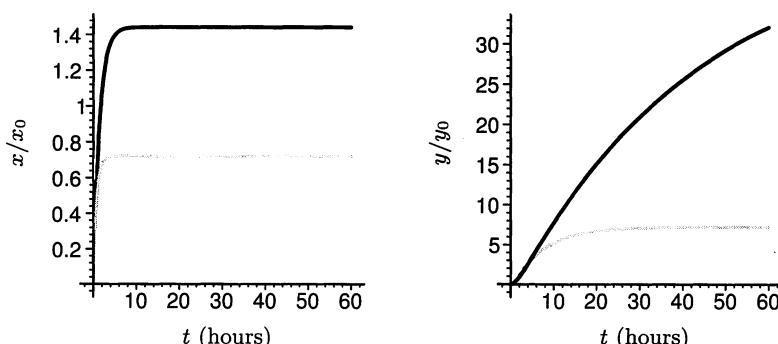


Figure 2.11: Course of cold pills. The graph on the left represents the GI-tract and that on the right the bloodstream. The levels of antihistamine are illustrated with black lines and the decongestant with a grey line. The parameter values are given in Table 2.1, with typical initial values for the antihistamine and decongestant, 0.5 mg and 15 mg.

Note that the level of the antihistamine (which makes you sleepy) is slow to rise, but settles to a high level, while that of the decongestant is faster to rise but settles to a lesser level with time. This is illustrated in Figure 2.11.

Our assumption of  $I$  constant holds in the case where drugs are embedded in resins which dissolve at constant rates, allowing the drug to be released slowly and evenly over a period of hours. In reality some pills dissolve quickly and thus  $I(t)$  should be a pulsing function, possibly a sinusoidal function, representing repeated doses, or some other function of  $t$  providing an initial and substantial boost to the drug level and then very little during the remaining time period before the next dose is taken. We do not consider those cases here, but what is required in the model is the replacement of  $I$  with an appropriate time dependent function.

**Summary of skills developed here:**

- Be able to model a sequence of processes using the compartmental technique.
- Understand how to find numerical solutions, with Maple or Maple, and analytically, in each of the sequence of compartments.
- Sketch graphs of solutions in each compartment over time.
- Establish how changes in parameters impact on these solutions.

## 2.8 Case Study: Dull, dizzy or dead?

This case study has been adapted from Oakley and Ksir (1993).

Alcohol is unusual in that it requires no digestion and can be absorbed extremely rapidly from the stomach into the bloodstream (particularly if the stomach is empty of food or other liquids), and is absorbed even more rapidly from the intestines. The vapour can also be absorbed through the lungs. Thus, unless alcohol is heavily diluted or taken with food, very little metabolism occurs in the GI-tract (gastrointestinal tract) and all the alcohol is absorbed into the bloodstream. Alcohol is distributed freely to all body fluids and the concentration of alcohol in the brain rapidly approaches that in the blood. Most of the alcohol (90–98%) is oxidised through the liver and excreted while the remainder leaves the body through the lungs, urine, saliva and sweat. However, the liver can only metabolise alcohol at a constant rate if the concentrations are not small.

The state of drunkenness (or ‘happy feeling’) experienced is a measure of the blood alcohol level (BAL) or the alcohol concentration in the blood. This concentration is a measure of the total mass of alcohol in grams divided by the total fluid volume in the body. It is measured in grams/100 ml of blood. Thus 100 g/100 ml corresponds to a BAL of 100 (grams/100 ml), and 100 mg/100 ml measures a BAL of 0.1 (grams/100 ml). As is common practice we will not stipulate the units of BAL on each occurrence, but assume that grams/(100 ml blood) is understood.

Australian law prohibits the driving of vehicles (including boats and horse or camel-drawn vehicles) for those with a BAL above 0.05. This then relates to 50 mg/100 ml alcohol in the bloodstream. The restriction is a result of U.S. statistics which indicate that a person with a BAL of 0.15 is 25 times more likely to have a fatal accident than one with no

alcohol. Furthermore, for 41% of Australian men excessive alcohol leads to confrontational behaviour. (For women the figure is 12%).)

Table 2.2: Blood alcohol level (BAL in g/(100 ml blood)) and behavioural effects.

BAL	Behavioural effects
0.05	Lowered alertness, usually good feeling, release of inhibitions, impaired judgement
0.10	Slowed reaction times and impaired motor function, less caution
0.15	Large consistent increases in reaction time
0.20	Marked depression in sensory and motor capability, decidedly intoxicated
0.25	Severe motor disturbance, staggering, sensory perceptions greatly impaired, smashed!
0.30	Stuporous but conscious, no comprehension of what's going on
0.35	Surgical anaesthesia; minimal level causing death
0.40	50 times the minimal level; causing death

The alcohol intake into the GI-tract is 'controlled' by the drinker. The amount of alcohol subsequently absorbed into the bloodstream depends on the concentration of alcohol, other liquids and food in the GI-tract, as well as on the weight and sex of the individual. Alcohol is removed from the bloodstream at a constant rate by the liver. This is independent of the body weight, sex of the individual and concentration of alcohol in the bloodstream and assumes that the liver has not been damaged by large doses of alcohol. (As mentioned above, a small percentage leaves through sweat, saliva, breath and urine. Ignoring this could mean the BAL estimate may be slightly above the true value.)

Table 2.3: Effective alcohol intake during drinking.

Absolute alcohol content	Beverage intake	Number of drinks
14 g	1 oz spirits, or 1 glass wine, or 1 can beer	$n = 1$
28 g	2 oz spirits, or 2 glasses of wine, or 2 cans of beer	$n = 2$
$(n \times 14) g$	$n$ oz spirits, or $n$ glasses of wine, or $n$ cans of beer	$n$

Let  $C_1(t)$  be the concentration of alcohol (effective BAL) in the GI-tract at time  $t$  and

let  $C_2(t)$  be the concentration of alcohol (in BAL) in the bloodstream at time  $t$ . Applying the balance law, the rates of change of alcohol in the GI-tract and the bloodstream can be modelled as

$$\begin{aligned}\frac{dC_1}{dt} &= I - k_1 C_2, \\ \frac{dC_2}{dt} &= k_2 C_1 - \frac{k_3 C_2}{C_2 + M},\end{aligned}\tag{2.25}$$

with constants  $k_1$ ,  $k_2$  and  $M$  positive. Here  $I$  is related to the amount of alcohol consumed per unit of time (here taken as one hour). Since  $C_1$  and  $C_2$  are concentrations measured in units of BAL, then we can show that  $I = i/V_b$  where  $i$  is the ingestion rate of alcohol measured in units of BAL/hour and  $V_b$  is the volume of fluid in the blood, measured in 100 ml (see Question 16 in the exercises).

In the case of drinking on an empty stomach  $k_1 = k_2$ , if drinking occurs together with a meal (or is diluted) then  $k_1 > k_2$ . Note that the amount of alcohol leaving the GI-tract, and the amount entering the bloodstream, is directly proportional to the amount present in the GI-tract.

On the other hand the amount of alcohol metabolised through the liver is represented as a more complicated function, a Michaelis-Menten type function (Michaelis and Menten (1913)). As was mentioned above the amount removed by the liver is constant regardless of the amount of alcohol or its concentration.

This has been modelled with the function  $-k_3 C_2 / (C_2 + M)$  for the following reason. If  $C_2$  is large compared with  $M$  then  $C'_2 \simeq -k_3$  and  $C_2(t)$  is decreasing at the constant rate  $k_3$ . As  $C_2$  decreases and becomes small compared with  $M$ , then  $C'_2 \simeq -(k_3/M)C_2$  and  $C_2(t)$  is an exponentially decaying function ( $C_2 \simeq c_0 e^{-(k_3/M)t}$ ) which ensures that  $C_2(t)$  remains positive. An appropriate value for  $M$  in this case is  $M = 0.005$  in units of BAL.

What follows are model runs for cases where drinking occurred on an empty stomach or with a meal, and where drinking occurred within a short period or continued over several hours. In each case Maple or MATLAB can be used to solve the equations and display the graphs.

**Drinking on an empty stomach:** In this case the alcohol is modelled as being very rapidly absorbed into the bloodstream in the first hour, that is  $k_1 = k_2 = 6$ , and the intent is to model the increasing/decreasing BAL in subsequent hours. In the case where  $n$  initial drinks are consumed and no more alcohol is taken we have  $C_1(0) = c_0$ , where  $c_0$  is the effective BAL from the initial drink(s) consumed, and  $I = 0$  as there is no subsequent drinking in this case. In the bloodstream, the initial amount of alcohol is 0 (that is, there is no alcohol in the bloodstream prior to drinking) and so  $C_2(0) = 0$ . The system above becomes

$$\begin{aligned}\frac{dC_1}{dt} &= -k_1 C_1, & C_1(0) &= c_0 \\ \frac{dC_2}{dt} &= k_2 C_1 - \frac{k_3 C_2}{C_2 + M}, & C_2(0) &= 0.\end{aligned}\tag{2.26}$$

The initial value  $c_0$  is given by  $c_0 = nc_s$  where  $n$  is the number of drinks as listed in Table 2.3 and  $c_s$  is the effective BAL produced by a single standard drink. The value of  $c_s$  depends on the sex and weight of the individual, since they dictate the total amount of body fluid for that person. One drink produces 14 g effective alcohol. The total volume of blood fluids in a woman is approximately  $0.67 \times W$  litres, where  $W$  is her body weight in kg. (For a man the volume of blood fluids is approximately  $0.82 \times W$  litres.) The concentration of alcohol will be (amount of alcohol/total fluids in grams per litre) and this can be expressed in g/100 ml, that is, BAL.

So for a male of 68 kg who has 3 glasses of wine rapidly and then stops drinking,  $c_0 = 3 \times c_s$ . His total body fluids are  $\approx 0.82 \times 68 = 55.76$  litres. Then the concentration of alcohol per drink is given as  $c_s = 14/55.76$  g/litre which converts to an effective BAL of 0.025. Thus  $c_0 = 3c_s = 0.075$ .

Further,  $k_3$  is a measure of the rate at which the liver removes alcohol from the blood, and this value is the same for all persons and is approximately 8g/hr. The associated reduction in BAL depends on the total body fluids of the individual, and for the 68 kg man can be calculated as  $8/(55 \times 10) = 0.014$  g/100 ml. Then  $k_3 = 0.014$  BAL.

For the case of drinking continuously over time we take  $I = (n/T)c_s$  (BAL/hr) and  $c_0 = 0$  in the differential equations (2.25) where  $n$  is the average number of drinks consumed in  $T$  hours. The results are illustrated in Figure 2.12 for the 68 kg male. (The constants are as described above.)

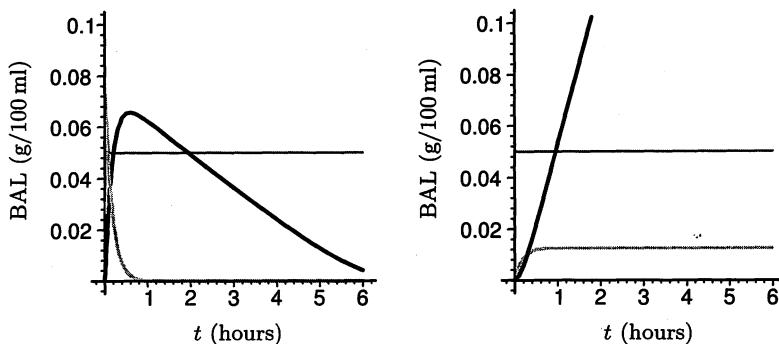


Figure 2.12: The BAL of a 68 kg man drinking on an empty stomach, with  $n = 3$  drinks per hour. The first diagram is for a single drinking bout, and the second for a continuous drinking binge. The black line illustrates the BAL in the bloodstream,  $C_2(t)$ , and the grey line the level in the GI-tract,  $C_1(t)$ . The legal limit BAL 0.05 is also indicated by the horizontal line.

**Drinking with a substantial meal:** The rate at which alcohol is absorbed into the bloodstream from the GI-tract is substantially reduced when alcohol is diluted or taken with a meal. The presence of fats in particular reduces the resulting BAL. Returning to equation system (2.26) above we now have that  $k_1 > k_2$ , that is, the rate at which alcohol leaves the GI-tract is greater than the rate at which alcohol enters the bloodstream. In fact, after a substantial meal the rate of absorption into the bloodstream is approximately halved so that we can replace  $k_2$  with  $k_1/2$ . (This is a very simplistic approximation and the model would be improved by including a more realistic mathematical relationship between food intake and alcohol absorption into the bloodstream.) The graphs of Figure 2.13 illustrate the effect of a meal on the BAL for the 68 kg man in the case of an initial alcohol intake without further drinking, and in the case of continuous drinking.

As for the aftermath of all this? Well the Germans hear the ‘wailing of cats’, the Italians call it ‘out of tune’, the French refer to it as ‘woody mouth’, the Norwegians say there are ‘workmen in my head’, the Swedes have ‘pain in the roots of my hair’ and the English suffer the hangover.

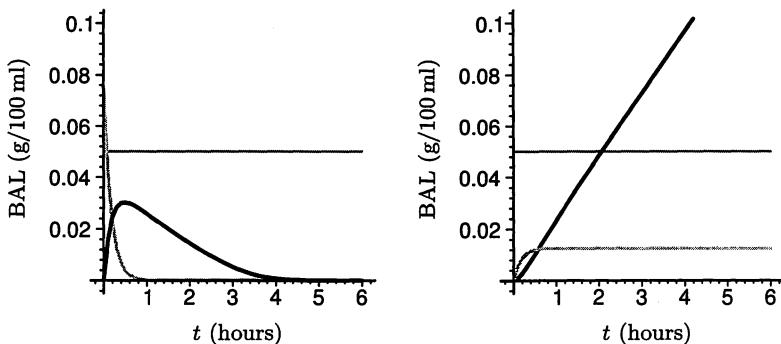


Figure 2.13: The BAL in the bloodstream of a 68 kg man drinking after a meal, with  $n = 3$  drinks per hour. The first diagram is for a single drinking bout, and the second for a continuous drinking binge. The black line illustrates the BAL in the bloodstream,  $C_2(t)$ , and the grey line the level in the GI-tract,  $C_1(t)$ . The legal limit BAL 0.05 is also indicated by the horizontal line.

## 2.9 Cascades of compartments

As exemplified in the previous section(s), linear cascades are models with a series of compartments, as in Figure 2.14. Here each compartment feeds into the next one without any loops. An example was the case of drug assimilation or a series of lakes in Section 2.5.

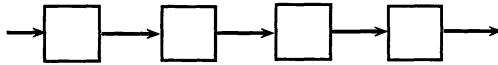


Figure 2.14: Linear cascade of compartments.

In other cases more than one source can feed into one compartment, or a compartment may output into many compartments, as in Figure 2.15. Such an arrangement is called a branching linear cascade.

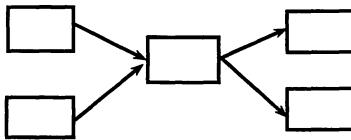


Figure 2.15: Branching cascade of compartments.

Usually in these cases the equations can be solved using the top-down approach which we followed in Section 2.7. That is, solving the first equation and using this solution to solve the second, and so on. Such models are also applicable to the decay of radioactive elements such as Uranium-238 which decays to Lead-206 in a decay cascade involving 16

intermediate elements and isotopes; see Borelli and Coleman (1996):

$$\begin{aligned}x'_1 &= -k_1 x_1 \\x'_2 &= k_1 x_1 - k_2 x_2 \\\vdots \\x'_{17} &= k_{18} x_{15} - k_{19} x_{16} \\x'_{18} &= k_{19} x_{16} + k_{20} x_{17}.\end{aligned}$$

However, situations leading to simultaneous differential equations, which cannot be solved this way, form the basis of Chapter 5.

As with the section on exponential decay, these constants  $k_i$  are expressed in terms of the half-lives of the radioactive elements using the relation  $\ln 2 = \tau_i k_i$  (see equation (2.7) in Section 2.2). This particular problem is difficult to solve using a computer because of the very different time lengths involved. The half-life of Uranium-238 is approximately 4.5 billion years, whilst that for the next element, Thorium-234, is 24 days. This problem of very different time lengths in two parts of the same problem, a *stiff problem*, is discussed in Chapter 4.

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## 2.10 First-order linear DEs

When we examined the solutions to the linear differential equations above more closely there were some interesting features. For the lake problems we had

$$\begin{aligned}\frac{dC}{dt} &= \frac{F}{V} c_{\text{in}} - \frac{F}{V} C, \\C &= c_0 e^{-Ft/V} + c_{\text{in}}(1 - e^{-Ft/V}).\end{aligned}$$

Notice that this solution has two parts: one dependent on the initial value of the system  $c_0$  and the other dependent on the input to the system  $c_{\text{in}}$ . Further, the effect of  $c_0$  decreases, approaching 0 with time while that of  $c_{\text{in}}$  grows with time.

This phenomenon is a general feature of such linear differential equations and there are some elegant general results which follow. (They are included here to provide a better ‘feel’ for expected results and the reader is referred to other texts for proofs and more details if they are required.)

Consider the *normal form* of a first-order linear ordinary differential equation (ODE)

$$y' + p(t)y = q(t) \quad (2.27)$$

(normal form just means that the coefficient of  $y'$  is one) where the coefficient  $p(t)$  and the driving term (or input)  $q(t)$  are continuous over a finite time interval. If there is no input ( $q(t) = 0$ ) the equation is said to be *homogeneous*. If  $q(t) \neq 0$ , then the equation is *inhomogeneous*, that is, it is *driven or forced*.

Such an ODE has infinitely many solutions, each associated with a distinct constant of integration. Given an initial condition for the above equation,  $y(t_0) = y_0$ , the solution will be unique. Further, as we noticed above the solution to the system can be divided into two parts:

- the response to the initial conditions, and

- the response to the forcing term.

We state this in some theorems:

**Theorem 1 (General solution theorem)** Consider the linear ODE (2.27) with  $p(t)$  and  $q(t)$  continuous on some interval containing  $t_0$ . Let

$$P(t) = \int_{t_0}^t p(r) dr, \quad R(t) = \int_{t_0}^t e^{P(s)} q(s) ds$$

on that interval. Then every solution  $y(t)$  of the ODE has the form

$$y(t) = e^{-P(t)} K + e^{-P(t)} R(t), \quad \text{with } K \text{ an arbitrary constant.} \quad (2.28)$$

Conversely, any function  $y(t)$  of the form (2.28) is a solution of the differential equation on the interval.

Note that one important consequence of this theorem is that every solution of the ODE exists at least in the interval in which  $p(t)$  and  $q(t)$  are continuous. Another important consequence is that no two solutions corresponding to different values of  $K$  can ever intersect. Why? Because suppose they did for  $t = T$ , then rearranging  $y_1(T) = y_2(T)$  gives

$$\begin{aligned} 0 &= y_1(T) - y_2(T) \\ &= [e^{-P(T)} K_1 + e^{-P(T)} R(T)] - [e^{-P(T)} K_2 + e^{-P(T)} R(T)] \\ &= e^{-P(T)} (K_1 - K_2) \\ &\neq 0 \quad \text{since } K_1 \neq K_2. \end{aligned}$$

Since  $T$  is arbitrary, no two solutions corresponding to different initial values can intersect.

**Theorem 2 (Solution of initial value problem (IVP))** Let  $p(t)$  and  $q(t)$  be continuous in some interval containing  $t_0$ , and let  $y_0$  be any constant. Then the IVP

$$y' + p(t)y = q(t), \quad y(t_0) = y_0$$

has exactly one solution.

Writing  $P_0(t) = \int_{t_0}^t p(r) dr$ , this solution is given by

$$\underbrace{y(t)}_{\substack{\text{total} \\ \text{response}}} = \underbrace{e^{-P_0(t)} y_0}_{\substack{\text{response to} \\ \text{initial data}}} + \underbrace{e^{-P_0(t)} \int_{t_0}^t e^{P_0(s)} q(s) ds}_{\substack{\text{response to} \\ \text{input}}}$$

There is no need to memorise these theorems as they are just the application of the integrating factor technique.

Rewriting the IVP above as  $y' = f(t, y) = q(t) - p(t)y$ ,  $y(t_0) = y_0$ , we have

**Theorem 3 (Existence theorem)** If  $f$  and the partial derivative  $\partial f / \partial y$  are continuous on a region  $R$  in the  $(t, y)$ -plane, and  $(t_0, y_0)$  is a point in  $R$ , then the IVP above has a unique solution  $y(t)$  on an interval containing  $t_0$ .

***Summary of skills developed here:***

- Identify a linear differential equation for which there exists a unique solution.
- Understand the significance of the two separate parts to the solution.

## 2.11 Equilibrium points and stability

We have seen, in Section 2.5, that the solutions of differential equations can tend to a steady-state, i.e. a constant value, as the time becomes very large. It can be useful to determine the value of the steady-state, when it exists, directly from the differential equation, in analytic form. This can then allow us to determine how a steady-state solution (also called an equilibrium solution) depends on the various parameters in the problem.

***Finding equilibrium solutions***

For a differential equation

$$\frac{dx}{dt} = f(x) \quad (2.29)$$

the equilibrium solutions are the solutions  $x = x_e$  such that  $f(x) = 0$ . The following example demonstrates how to find an equilibrium solution.

**Example 2.9:** Find all equilibrium points for the differential equation for the concentration of pollutant in a lake, from Section 2.5,

$$\frac{dC}{dt} = \frac{F}{V}c_{\text{in}} - \frac{F}{V}C.$$

where  $F$  and  $V$  are positive constants

**Solution:** Setting  $dC/dt = 0$  we obtain

$$\frac{F}{V}(c_{\text{in}} - C) = 0 \quad \Rightarrow \quad C = c_{\text{in}}.$$

***Stability***

An equilibrium solution,  $x_e$ , can only be a steady-state solution if the solution tends towards it as the time increases without bound. This is associated with the equilibrium solution being stable. By stable we mean that any solution close to the equilibrium solution will tend towards the equilibrium solution and by unstable then the solution will not get closer to the equilibrium point.

We can determine this by using Taylor series (see Appendix B.2). We let  $x(t) = x_e + \xi(t)$ , with  $\xi(t) \ll 1$ , where the new variable  $\xi$  represents the small perturbation from the equilibrium solution. For the differential equation (2.29), if we expand the RHS about the equilibrium solution, by letting  $x = x_e + \xi$ , then the differential equation for the variable  $\xi$  is

$$\frac{dx}{dt} = \frac{d(x_e + \xi)}{dt} = f(x) = f(x_e + \xi) \simeq f(x_e) + \xi f'(x_e).$$

Since  $f(x_e) = 0$ , by the definition of an equilibrium point, then the original differential equation is approximated, close to the equilibrium solution, by

$$\frac{d\xi}{dt} \simeq \xi f'(x_e)$$

for small values of  $\xi$ . We can now interpret what happens without actually solving this differential equation. For  $\xi > 0$ , if  $f'(x_e) < 0$  then  $d\xi/dt < 0$ , so  $x(t) = x_e + \xi(t)$  approaches  $x_e$ , the equilibrium point. Similarly, for  $\xi(t) < 0$ , then  $x(t) = x_e + \xi(t)$  increases towards the equilibrium solution. Thus the solution is attracted to the equilibrium solution. By a similar argument, when  $f'(x_e) > 0$  the solution is repelled from the equilibrium solution. Thus we have

equilibrium solution is stable if  $f'(x_e) < 0$

and unstable otherwise.

**Example 2.10:** Determine if the equilibrium solution  $c_e = c_{\text{in}}$  is stable or unstable.

**Solution:** Here

$$f(C) = \frac{F}{V}(c_{\text{in}} - C), \quad C_e = c_{\text{in}}, \quad \Rightarrow f'(c_e) = -\frac{F}{V}.$$

Since  $F$  and  $V$  are positive parameters this means that the equilibrium solution  $C = c_{\text{in}}$  is always stable.

We have introduced the idea of equilibrium solutions and stability. We applied these to a linear differential equation where we already knew the solution, so we did not get any great benefit from this analysis. However, the technique can be applied to nonlinear differential equations, some of which we cannot solve easily. In such cases we often end up with more than one equilibrium solution, some of which may be stable and some unstable. More importantly, the concept of equilibrium solutions and stability can also be applied to systems of differential equations where it can provide valuable information about the nature of solutions. We postpone a discussion of this until Chapter 7.

**Summary of skills developed here:**

- Know the definition for an equilibrium solution and be able to find it for a single differential equation.
- Apply the criteria for stability of an equilibrium solution.

## 2.12 Case Study: Money, money, money makes the world go around

We have not considered any economic theories in this book, but differential equation dynamics and equilibrium solutions have been applied in this field also. In the following case study we introduce a simple model for economic growth and look at some of the basic concepts underlying such models. This particular model is one of production, or units of 'output', based on investment capital and available labour. As an example of this structure, we introduce the Cobb-Douglas model. This case-study is adapted from Solow (1956).

Economic growth is currently seen in Western cultures as the production of a greater economic surplus, which can be used to advance society. As early as 1377, an Arabian economic thinker Ibn Khaldun recognised the concept of economic growth. He noted that, with increase in population, the available labour increases and production thrives, and that excess wealth so generated can be used to support luxuries, distinguishing labour for the necessities of life from surplus labour for serving luxury. However, Gross Domestic Product (GDP) per capita changed little for most of human history prior to the industrial revolution and mass education.

The Neo-classical economic growth model, the type of model we consider here, deals with economic growth considered as increased stocks of capital goods (production or output) that are dependent on available labour and investment capital. Solow and Swan introduced the first attempt at long-term predictions for economic growth in the 1950s (Solow (1956); Swan (1956)). One of the consequent predictions was that economies will attain an equilibrium, in the sense that further capital investment and/or labour will not increase growth. Advances in technology, however, have the potential to alter the equilibrium, as does education and other changes in social structure, and data suggest that the world has, slowly, continued to improve its rate of growth, not settling to a fixed equilibrium.

The model presented here (Solow (1956)) is one of production, i.e., units of output, based on investment or capital and available labour. The *warranted rate of growth* is the terminology used for the profitable rate of investment, that is, the growth of capital, and the *natural rate of growth* is that used for the rate of growth of the available labour force. A further term applied in economics is *constant returns to scale*, which implies that a function  $F$  of two variables  $K$  and  $L$  has the property  $F(aK, aL) = aF(K, L)$ .

We now introduce the model. We define output (or production)  $Y(t)$ , as a function of the two factors of production: the stock of capital,  $K(t)$ , and the available labour force,  $L(t)$ , all being functions of time  $t$ . Suppose the rate of output savings is a fraction  $s$  of the total output so that

$$\frac{dK}{dt} = sY \quad (2.30)$$

at any instant in time, with the production function  $Y = F(K, L)$  and  $F$  is a function with constant returns to scale. We now make an assumption concerning the labour force: we assume Harrod's natural growth rate (constant  $n$ ), in the absence of technological advancement, so that

$$L(t) = L_0 e^{nt}, \quad (2.31)$$

which provides a curve describing labour. The basic equation for capital accumulation over time is then

$$\frac{dK}{dt} = sF(K, L_0 e^{nt}). \quad (2.32)$$

Many alternatives are possible for  $F$ , and thus many solutions to equation (2.32); however, we are interested in the qualitative nature of these solutions and the possible economic consequences. To investigate this aspect, we combine the two variables  $K$  and  $L$ , to reduce the number of variables, and carry out some simple analysis.

Let  $r = K/L$  be the ratio of capital to labour, so that  $K = rL_0 e^{nt}$  and thus

$$\frac{dK}{dt} = L_0 e^{nt} \frac{dr}{dt} + nrL_0 e^{nt}.$$

Combining this equation with equation 2.32, and applying the property of constant returns

to scale,

$$\begin{aligned} \left( \frac{dr}{dt} + nr \right) L_0 e^{nt} &= sF(K, L_0 e^{nt}) \\ \Rightarrow \quad \left( \frac{dr}{dt} + nr \right) L_0 e^{nt} &= sL_0 e^{nt} F\left(\frac{K}{L_0 e^{nt}}, 1\right). \end{aligned}$$

Defining  $f(r) = F(K/L, 1)$  we obtain

$$\frac{dr}{dt} = sf(r) - nr. \quad (2.33)$$

The function  $f$  has a simple interpretation: the total product (output) as capital (per single unit of labour) varies. Equivalently,  $f$  is the output per worker as a function of capital per worker. Thus, the rate of change in the capital-labour ratio,  $r$ , is the difference between the increment of capital and the increment of labour.

This equation has an equilibrium point,  $r_e$ , where the capital is expanding at the same rate as the labour force, that is, where  $dr/dt = 0$ . Figure 2.16 illustrates three distinct scenarios that occur for different practical definitions of the production function  $f$ .

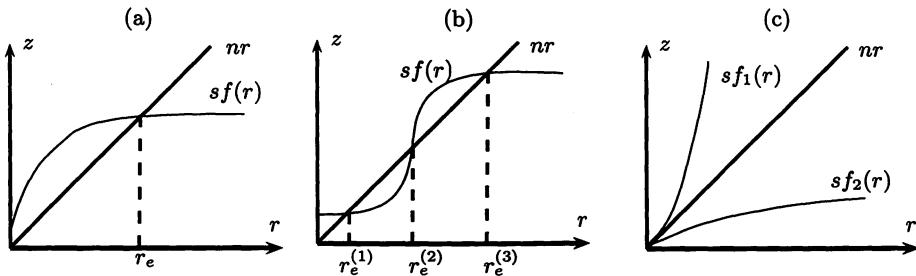


Figure 2.16: Illustration of graphical determination of equilibrium points for the differential equation (2.33). In each graph the terms  $z = nr$  and  $z = sf(r)$  are plotted and the equilibrium points are where these two intersect. In (a) the function  $f$  is such that there is only one equilibrium point. In (b) there are three equilibrium points, denoted by  $r_e^{(1)}$ ,  $r_e^{(2)}$  and  $r_e^{(3)}$ . In (c) there are no equilibrium points for either of  $f_1$  or  $f_2$ .

In Figure 2.16(a),  $r_e$  is stable since for  $sf(r) > nr$ , then  $dr/dt$  is positive and  $r$  increasing, and for  $sf(r) < nr$ ,  $r$  is decreasing. Thus, no matter where one starts with labour and capital, this model predicts that  $r$  approaches  $r_e$ . In Figure 2.16(b), for similar reasons, both  $r_e^{(1)}$  and  $r_e^{(3)}$  are stable, while  $r_e^{(2)}$  is unstable; thus, depending on the initial conditions for  $r(t)$ , the system tracks towards one of the stable points. Note that the figure has been drawn such that production is possible without capital, and hence the curve does not pass through the origin. Figure 2.16(c) illustrates the case where no balanced growth equilibrium exists. For the upper curve,  $sf(r) > nr$ , and  $r(t)$  continues to increase with full employment and capital and income increasing faster than the supply of labour. Alternatively, for the lower case where  $sf(r) < nr$ , the ratio continues to decrease, approaching 0. For this case, on-going full employment leads to decreasing output. Many different curves for  $F(K, L)$  are possible; however, the cases in Figure 2.16 provide a framework through which to interpret them.

One simple example of a production function  $F$  is the Cobb-Douglas model, where  $Y = F(K, L) = K^a L^{1-a}$  with  $a < 1$ . The function  $F$  in this case has the property of constant

returns to scale and thus, in terms of the ratio  $r = K/L$ ,  $Y = sf(r) = sr^a$  and equation (2.33) becomes

$$\frac{dr}{dt} = sr^a - nr. \quad (2.34)$$

Note that  $f$  is a monotonically increasing function of  $r$ . For small  $r$  and with  $a < 1$ , the initial slope of  $sr^a$  is close to vertical, and thus  $sr^a > nr$ . Alternatively, as  $r$  increases, and since  $a < 1$ , the slope of  $sr^a$  decreases with  $sr^a$ , for large values of  $r$ , such that  $sr^a < nr$ . This corresponds to Figure 2.16(a) regardless of the parameter values for  $n$  and  $a$ , and thus implies the existence of a single stable equilibrium point located at  $r_e = (s/n)^{1/(1-a)}$  (from equation (2.34)). We note that this value increases with increased savings,  $s$ , as would be expected.

Further, it is not straightforward to solve equation (2.34) analytically (although straightforward numerically, if the parameter values were known accurately). However, we can establish the dynamics of  $K$  and  $L$  directly. Since

$$\frac{dK}{dt} = sK^a(L_0e^{nt})^{1-a}, \quad (2.35)$$

from equation (2.35), we can integrate to get

$$K(t) = \left[ K_0^{1-a} - \frac{s}{n} L_0^{1-a} + \frac{s}{n} L_0^{1-a} e^{(1-a)nt} \right]^{1/(1-a)}$$

where  $K_0$  and  $L_0$  are the initial values. Thus, according to this model, capital grows as  $(s/n)^{1/(1-a)} L_0 e^{nt}$ , namely at the same rate as labour. We also get an equilibrium value for  $K/Y$ , that is, capital per unit of production. Income, per labour unit is

$$Y = \left( \frac{K}{L} \right)^a L \quad \Rightarrow \quad \frac{Y}{L} = \left( \frac{K}{L} \right)^a = r^a.$$

Clearly, many factors that are not considered in this model have a direct impact on production or output. Technological advances, for example, may reduce the amount of labour and/or capital required for the same output. Work by Romer (1986), Lucas (1988) and Barro (1997) recognise the impact of technology (e.g. innovation) as well as worker productivity (e.g. education) on economic growth predictions. Moreover, recent work indicates a correlation with climate (but perhaps that works both ways?).

Whatever model is adopted it should be kept in mind that "All theory depends on assumptions that are not quite true", (Solow, 1956, page 65), and economic models are no exception. Debate continues as to what a 'best' model might look like, and is likely to continue indefinitely. However, as Robert Lucas commented on growth theory: "The consequences for human welfare are simply staggering".

## 2.13 Exercises for Chapter 2

**2.1. Atmospheric pressure.** The earth's atmospheric pressure  $p$  is often modelled by assuming that  $dp/dh$  (the rate at which pressure  $p$  changes with altitude  $h$  above sea level) is proportional to  $p$ . Suppose that the pressure at sea level is 1013 millibars and that the pressure at an altitude of 20 km is 50 millibars. Answer the following questions using analytical techniques and then check them with Maple or MATLAB.

- (a) Use an exponential decay model

$$\frac{dp}{dh} = -kp$$

to describe the system, and then by solving the equation find an expression for  $p$  in terms of  $h$ . Determine  $k$  and the constant of integration from the initial conditions.

- (b) What is the atmospheric pressure at an altitude of 50 km?

- (c) At what altitude is the pressure equal to 900 millibars?

**2.2. The Rule of 72.** Continuous compounding for invested money can be described by a simple exponential model,  $M'(t) = 0.01rM(t)$ , where  $M(t)$  is the amount of money at time  $t$  and  $r$  is the percent interest compounding. Business managers commonly apply the Rule of 72, which says that the number of years it takes for a sum of money invested at  $r\%$  interest to double, can be approximated by  $72/r$ . Show that this rule always overestimates the time required for the investment to double.

**2.3. Dating a sea shell.** If an archaeologist uncovers a sea shell which contains 60% of the  $^{14}\text{C}$  of a living shell, how old do you estimate that shell, and thus that site, to be? (You may assume the half-life of  $^{14}\text{C}$  to be 5568 years.)

**2.4. Olduvai Gorge.** (From Borelli and Coleman (1996).) Olduvai Gorge, in Kenya, cuts through volcanic flows, tuff (volcanic ash), and sedimentary deposits. It is the site of bones and artifacts of early hominids, considered by some to be precursors of man. In 1959, Mary and Louis Leakey uncovered a fossil hominid skull and primitive stone tools of obviously great age, older by far than any hominid remains found up to that time. Carbon-14 dating methods being inappropriate for a specimen of that age and nature, dating had to be based on the ages of the underlying and overlying volcanic strata.

The method used was that of potassium-argon decay. The potassium-argon clock is an accumulation clock, in contrast to the  $^{14}\text{C}$  dating method. The potassium-argon method depends on measuring the accumulation of 'daughter' argon atoms, which are decay products of radioactive potassium atoms. Specifically, potassium-40 ( $^{40}\text{K}$ ) decays to argon ( $^{40}\text{Ar}$ ) and to Calcium-40 ( $^{40}\text{Ca}$ ) by the branching cascade illustrated below in Figure 2.17. Potassium decays to calcium by emitting a  $\beta$  particle (i.e. an electron). Some of the potassium atoms, however, decay to argon by capturing an extra-nuclear electron and emitting a  $\gamma$  particle.

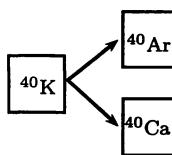


Figure 2.17: Branching cascade diagram for Question 4.

The rate equations for this decay process may be written in terms of  $K(t)$ ,  $A(t)$  and  $C(t)$ , the potassium, argon and calcium in the sample of rock:

$$K' = -(k_1 + k_2)K,$$

$$A' = k_1 K,$$

$$C' = k_2 K,$$

where

$$k_1 = 5.76 \times 10^{-11} \text{ year}^{-1}, \quad k_2 = 4.85 \times 10^{-10} \text{ year}^{-1}.$$

- (a) Solve the system to find  $K(t)$ ,  $A(t)$  and  $C(t)$  in terms of  $k_1$ ,  $k_2$ , and  $k_3 = k_1 + k_2$ , using the initial conditions  $K(0) = k_0$ ,  $A(0) = C(0) = 0$ .
- (b) Using the above result, show that  $K(t) + A(t) + C(t) = k_0$  for all  $t \geq 0$ . Why would this be the case?
- (c) Show that  $K(t) \rightarrow 0$ ,  $A(t) \rightarrow k_1 k_0 / k_3$  and  $C(t) \rightarrow k_2 k_0 / k_3$  as  $t \rightarrow \infty$ .
- (d) The age of the volcanic strata is the current value of the time variable  $t$  because the potassium-argon clock started when the volcanic material was laid down. This age is estimated by measuring the ratio of argon to potassium in a sample. Show that this ratio is

$$\frac{A}{K} = \frac{k_1}{k_3} (e^{k_3 t} - 1).$$

- (e) Now show that the age of the sample in years is

$$\frac{1}{k_3} \ln \left[ \left( \frac{k_3 A}{k_1 K} \right) + 1 \right].$$

- (f) When the actual measurements were made at the University of California at Berkeley, the age of the volcanic material (and thus the age of the bones) was estimated to be 1.75 million years. What was the value of the measured ratio  $A/K$ ?

**2.5. Tracers in the body.** (Adapted from Borelli and Coleman (1996).) In a biochemical laboratory radioactive phosphorus ( $^{32}\text{P}$ ) was used as a tracer. (A tracer, through its radioactive emission, allows the course followed by a substance through a system to be tracked, which otherwise would not be visible.)  $^{32}\text{P}$  decays exponentially with a half-life of 14.5 days and its quantity is measured in curies (Ci). (Although it is not necessary for the calculations, one curie is the quantity of a radioactive isotope undergoing  $3.7 \times 10^{-5}$  disintegrations per second.) After the experiment the biochemists needed to dispose of the contents, but they had to store them until the radioactivity had decreased to the acceptably safe level of  $1 \times 10^{-5}$  Ci. The experiment required 8Ci of  $^{32}\text{P}$ . Using a simple model of exponential decay, establish how long they had to store the contents of the experiment before it could be disposed of safely.

**2.6. Lake Burley Griffin.** Read the case study on Lake Burley Griffin. The average summer flow rate for the water into and out of the lake is  $4 \times 10^6 \text{ m}^3/\text{month}$ .

- (a) Using this summer flow, how long will it take to reduce the pollution level to 5% of its current level? How long would it take for the lake with pollution concentration of  $10^7 \text{ parts/m}^3$ , to drop below the safety threshold? (Assume in both cases that only fresh water enters the lake.)
- (b) Use Maple or MATLAB to replicate the results in the case study, for both constant and seasonal flow and constant and seasonal pollution concentrations entering the lake. Comment on the solutions.

**2.7. North American lake system.** Consider the American system of two lakes: Lake Erie feeding into Lake Ontario. What is of interest is how the pollution concentrations change in the lakes over time. You may assume the volume in each lake to remain constant and that Lake Erie is the only source of pollution for Lake Ontario.

- (a) Write down a differential equation describing the concentration of pollution in each of the two lakes, using the variables  $V$  for volume,  $F$  for flow,  $c(t)$  for concentration at time  $t$  and subscripts 1 for Lake Erie and 2 for Lake Ontario.
- (b) Suppose that only unpolluted water flows into Lake Erie. How does this change the model proposed?

- (c) Solve the system of equations to get expressions for the pollution concentrations,  $c_1(t)$  and  $c_2(t)$ .
- (d) Set  $T_1 = V_1/F_1$  and  $T_2 = V_2/F_2$ , and then  $T_1 = kT_2$  for some constant  $k$  as  $V$  and  $F$  are constants in the model. Substitute this into the equation describing pollution levels in Lake Ontario to eliminate  $T_1$ . Then show that, with the initial conditions  $c_{1,0}$  and  $c_{2,0}$ , the solution to the differential equation for Lake Ontario is

$$c_2(t) = \frac{k}{k-1} c_{1,0} \left( e^{-t/(kT_2)} - e^{-t/T_2} \right) + c_{2,0} e^{t/T_2}.$$

(One way of finding the solution would be to use an integrating factor. See Appendix A.4.)

- (e) Compare the effects of  $c_1(0)$  and  $c_2(0)$  on the solution  $c_2(t)$  over time.

**2.8. Smoke in the bar.** (Adapted from Fulford et al. (1997).) A public bar opens at 6 p.m. and is rapidly filled with clients of whom the majority are smokers. The bar is equipped with ventilators which exchange the smoke-air mixture with fresh air. Cigarette smoke contains 4% carbon monoxide and a prolonged exposure to a concentration of more than 0.012% can be fatal. The bar has a floor area of 20 m by 15 m, and a height of 4 m. It is estimated that smoke enters the room at a constant rate of 0.006 m<sup>3</sup>/min, and that the ventilators remove the mixture of smoke and air at 10 times the rate at which smoke is produced. The problem is to establish a wise time to leave the bar. That is, sometime before the concentration of carbon monoxide reaches the lethal limit.

- (a) Starting from a word equation or a compartmental diagram, formulate the differential equation for the changing concentration of carbon monoxide in the bar over time.
- (b) By solving the equation above, establish at what time the lethal limit will be reached.

**2.9. Detecting art forgeries.** Based on methods used in the case study describing the detection of art forgeries (Section 2.3), comment on the authenticity of the following two paintings using the information provided:

- (a) ‘Washing of Feet’, where the disintegration rate for  $^{210}\text{Po}$  is 8.2 per minute per gram of white lead, and for  $^{226}\text{Ra}$  is 0.26 per minute per gram of white lead.
- (b) ‘Laughing Girl’, where the disintegration rate for  $^{210}\text{Po}$  is 5.2 per minute per gram of white lead and for  $^{226}\text{Ra}$  is 6 per minute per gram of white lead.

**2.10. Cold pills.** In Section 2.7, we developed the model

$$\begin{aligned} \frac{dx}{dt} &= -k_1 x, & x(0) &= x_0, \\ \frac{dy}{dt} &= k_1 x - k_2 y, & y(0) &= 0, \end{aligned}$$

where  $k_1, k_2 > 0$  determine the rate at which a drug, antihistamine or decongestant moves between two compartments in the body, the GI-tract and the bloodstream, when a patient takes a single pill. Here  $x(t)$  is the level of the drug in the GI-tract and  $y(t)$  the level in the bloodstream at time  $t$ .

- (a) Find solution expressions for  $x(t)$  and  $y(t)$  which satisfy this pair of differential equations, when  $k_1 \neq k_2$ . Show that this solution is equivalent to that provided in the text.
- (b) The solution above is invalid at  $k_1 = k_2$ . Why is this and what is the solution in this case?
- (c) For old and sick people the clearance coefficient (that is, the rate at which the drug is removed from the bloodstream) is often much lower than that for young, healthy individuals. How does an increase or decrease in  $k_2$  change the results of the model? Using Maple or MATLAB to generate the time-dependent plots, check your results.

**2.11. Cold pills.** In Section 2.7, we also developed a model to describe the levels of antihistamine and decongestant in a patient taking a course of cold pills:

$$\begin{aligned}\frac{dx}{dt} &= I - k_1x, \quad x(0) = 0, \\ \frac{dy}{dt} &= k_1x - k_2y, \quad y(0) = 0.\end{aligned}$$

Here  $k_1$  and  $k_2$  describe rates at which the drugs move between the two sequential compartments (the GI-tract and the bloodstream) and  $I$  denotes the amount of drug released into the GI-tract in each time step. The levels of the drug in the GI-tract and bloodstream are  $x$  and  $y$  respectively. By solving the equations sequentially show that the solution is

$$x(t) = \frac{I}{k_1} \left(1 - e^{-k_1 t}\right), \quad y(t) = \frac{I}{k_2} \left[1 - \frac{1}{k_2 - k_1} \left(k_2 e^{-k_1 t} - k_1 e^{-k_2 t}\right)\right].$$

**2.12. Antibiotics.** (Adapted from Borelli and Coleman (1996).) Tetracycline is an antibiotic prescribed for a range of problems, from acne to acute infections. A course is taken orally and the drug moves from the GI-tract through the bloodstream, from which it is removed by the kidneys and excreted in the urine.

- (a) Write down word equations which describe the movement of a drug through the body, using three compartments: the GI-tract, the bloodstream and the urinary tract. Note that the urinary tract can be considered as an absorbing compartment, that is, the drug enters but is not removed from the urinary tract.
- (b) From the word equations develop the differential equation system which describes this process, defining all variables and parameters as required.
- (c) The constants of proportionality associated with the rates at which tetracycline (measured in milligrams) diffuses from the GI-tract into the bloodstream, and then is removed, are  $0.72 \text{ hour}^{-1}$  and  $0.15 \text{ hour}^{-1}$ , respectively (Borelli and Coleman (1996)). Suppose, initially, the amount of tetracycline in the GI-tract is 0.0001 milligrams, while there is none in the bloodstream or urinary tract. Use Maple or MATLAB (with symbolic toolbox) to solve this system analytically, and thus establish how the levels of tetracycline change with time in each of the compartments. In the case of a single dose, establish the maximum level reached by the drug in the bloodstream and how long it takes to reach this level with the initial conditions as given above.
- (d) Suppose that, initially, the body is free from the drug and then the patient takes a course of antibiotics: 1 unit per hour. Use Maple or MATLAB to examine the level of tetracycline (expressed as units) in each of the compartments over a 24-hour period. Use the constants as given above.

**2.13. Alcohol consumption.** Use the model from the case study on alcohol consumption (Dull, dizzy or dead, Section 2.8), to establish, for the case of drinking on an empty stomach, the following:

- (a) Use Maple or MATLAB to generate graphs to investigate the effects of alcohol on a woman of 55 kg, over a period of time.
- (b) Compare these results with those for a man of the same weight.
- (c) Assuming the legal limit to be 0.05 BAL (the Australian limit) establish roughly how much alcohol the man and woman above can consume each hour and remain below this limit.
- (d) Repeat (a–c) for the case of drinking together with a meal.

**2.14. Alcohol consumption.** Alcohol is unusual in that it is removed (that is, metabolised through the liver) from the bloodstream by a constant amount each time period, independent of the amount in the bloodstream. This removal can be modelled by a Michaelis-Menten type function  $y' = -k_3y/(y + M)$  where  $y(t)$  is the ‘amount’ (BAL) of alcohol in the bloodstream at time  $t$ ,  $k_3$  is a positive constant and  $M$  a small positive constant.

- (a) If  $y$  is large compared with  $M$  then show that  $y' \approx -k_3$ . Solve for  $y$  in this case.
- (b) Alternatively, as  $y$  decreases and becomes small compared with  $M$ , show that then  $y' \approx -k_3y/M$ . Solve for  $y$  in this case.
- (c) Now sketch the solution function for  $y' = -k_3y/(y + M)$  assuming that, initially,  $y$  is much greater than  $M$ . Indicate clearly how the graph changes in character when  $y$  is small compared with  $M$ , compared with when  $y$  is large compared with  $M$ . Show how the solution behaves as  $t \rightarrow \infty$ .
- (d) When and why would this function be more suitable than simply using  $y' = -k_3$  to model the removal rate?

**2.15. Solving differential equations.** Consider the differential equations

$$t \frac{dx}{dt} = x, \quad x(t_0) = x_0,$$

and

$$y^2 \frac{dx}{dy} + xy = 2y^2 + 1, \quad x(y_0) = x_0.$$

Put each equation into normal form and then use the integrating factor technique to find the solutions. Establish whether these solutions are unique, and which part of each solution is a response to the initial data and which part a response to the input or forcing.

**2.16. Formulating DEs for alcohol case study.** Read over the case study in Section 2.8. Consider two compartments, one for the GI tract and one for the blood. Let  $C_1(t)$  be the concentration of alcohol in the GI tract and  $C_2(t)$  be the concentration in the blood, with both concentrations measured in BAL (gper100 ml). Also let  $F_1$  be the flow rate of fluid from the GI tract and let  $F_2$  be the flow rate of fluid from the blood to the tissues. Finally, we let  $i_0$  be the rate of ingestion of alcohol (in g/hr). Use conservation of mass of alcohol to deduce the equations in the form

$$\begin{aligned} \frac{dC_1}{dt} &= I - k_1 C_1, \\ \frac{dC_2}{dt} &= k_2 C_2 - k_4 C_2 \end{aligned}$$

and determine  $I$ ,  $k_1$ ,  $k_2$  and  $k_3$  all in terms of  $i_0$ ,  $F_1$ ,  $F_2$  and  $V_g$ , the volume of the fluid in the GI tract,  $V_b$  the volume of fluid in the blood, and  $\alpha$ , where  $\alpha$  is the proportion of the alcohol leaving the GI tract goes into the bloodstream.

Note: in the case study we let the rate constant  $k_4$  depend on the blood alcohol concentration

$$k_4 = \frac{k_3}{M + C_2},$$

where  $k_3$  and  $M$  are positive constants,  $k_3$  with the same units as  $k_1$  and  $k_2$ , namely hours<sup>-1</sup> and  $M$  with the same units as  $C_2$ , namely BAL.

**2.17. Economic growth.** Read over the case study on a model of economic growth in Section 2.12. In this model the Cobb-Douglas function was used to model production. An alternative model is the Harrod-Domar model of fixed proportions,  $Y = \min \{K/a, L/b\}$  is the minimum of the two values, with  $a$  units of capital and  $b$  units of labour required to produce a unit of output. The expression for  $Y$  describes the ‘bottlenecks’ for the system, that is, whether it is limitations in capital or labour that determine the outcome for production.

(a) For the case  $r/a < 1/b$  show that

$$\frac{dr}{dt} = \left( \frac{s}{a} - n \right) r$$

and solve this to obtain

$$r(t) = r_0 e^{(s-na)t}.$$

(b) Consider the case when  $n > s/a$  and  $r_0 > a/b$ . Give an interpretation when  $r_0 = a/b$ .

**2.18. Return to scale property.** Show that the Cobb-Douglas function, from Section 2.12,

$$Y = F(K, L) = K^\alpha L^{1-\alpha}$$

has the return to scale property.

**2.19. Stability of equilibrium solution.** Consider Figure 2.16(b), in Section 2.12. Establish the stability of each of the equilibrium points,  $r_e^{(1)}$ ,  $r_e^{(2)}$  and  $r_e^{(3)}$ , from the underlying equation.

# **Chapter 3**

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## **Models of single populations**

In this chapter, we develop models describing the growth and decline of single populations with continuous breeding programs. Initially we model exponential growth. A more realistic model would include the effects on population growth of limited resources, and thus we extend our model to take account of density dependent growth (logistic growth), which describes the population size as stabilising after an initial exponential growth spurt. We examine the effects of harvesting the population and see that there is a critical harvesting rate, above which extinction ensues. Furthermore, we consider single populations with discrete breeding seasons and examine how the concept of ‘chaos’ can arise in population dynamics. Finally, we briefly introduce the notion of time delayed models through a case study.

### 3.1 Exponential growth

We begin by developing a very simple mathematical model which describes the growth of a population. This leads to exponential growth.

#### *Background*

In many cases mathematical modelling is applied to understand population growth dynamics for animal and human populations. For example, modelling the way fish populations grow, and accounting for the effect of fishing is essential to the fishing industry, as we cannot afford to deplete this resource. Another use of modelling is to understand the manner in which human populations grow: in the world, in individual countries, in towns and in organisations.

The population of the world was estimated in 1990 to be approximately 5.3 billion individuals. Estimates from census data show that this has grown from approximately 1.6 billion at the turn of the century. What will the population be in 5 years' time or even one hundred years time? By developing simple mathematical models we attempt to predict this, based upon certain assumptions about birth rates and death rates.

One important factor in modelling populations is whether the population grows continuously with time or in discrete jumps. Many animal populations grow in discrete times, due to having well-defined breeding seasons, whereas human populations grow continuously in time. Some insect populations also have non-overlapping generations, where the adults all die directly after giving birth. Even if a population grows in discrete time jumps it may still be reasonable to use a continuous time model provided the time interval between jumps is small compared with the overall time in which we are interested.

Another important factor in deciding on how to model population growth is the size of the population. Small populations are subject to random fluctuations in that we cannot predict with certainty when a parent will give birth, or what the size of an animal litter will be. For small populations it makes sense to talk about the probability of giving birth in a certain time interval, and the mean population at a given time. When the population is large, however, random fluctuations between individuals are small compared with the whole population size and so we can model this without the need for probability functions.

For an entire population it would only be appropriate for  $X(t)$ , a measure of the population size, to be an integer, but for large populations it is usual to work with a value of  $X(t)$  which is continuous in  $t$  and round off to the integer value at the end. Of course for population densities, that is, number per unit of area, using fractional numbers poses no problem.

#### *General compartmental model*

We can consider this problem as a compartmental model with the compartment being the 'world', 'town', 'organisation', 'ocean', etc.

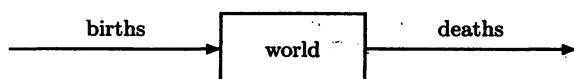


Figure 3.1: Input-output compartmental diagram for a population.

This compartmental sketch leads to a word equation describing a changing population,

$$\left\{ \begin{array}{l} \text{rate of} \\ \text{change of} \\ \text{population size} \end{array} \right\} = \left\{ \begin{array}{l} \text{rate} \\ \text{of} \\ \text{births} \end{array} \right\} - \left\{ \begin{array}{l} \text{rate} \\ \text{of} \\ \text{deaths} \end{array} \right\}. \quad (3.1)$$

We now develop equations by making some assumptions and then, under these conditions, describe the birth and death processes in symbols.

### **Model assumptions**

When dealing with large populations we can ignore random fluctuations between individuals and treat each individual as being identical. Thus we assume that each individual in the population has an equal chance of giving birth and we also assume that each individual has an equal chance of dying within a given time interval. It thus makes sense to talk about a *per-capita birth rate*  $\beta$  per unit time, per member of the population, and a *per-capita death rate*  $\alpha$ .

The per-capita birth rate for the world has been estimated at  $\beta = 0.027$  per year per individual and the per-capita death rate is  $\alpha = 0.010$  per year per individual (1990 estimate, Microsoft (1995)). This is not homogeneous over all countries in the world. For Australia SBS (1998) between 1990 and 1995 the per-capita birth rate was  $\beta = 0.014$  per year per individual and the per-capita death rate was  $\alpha = 0.007$  per year per individual. The population of Australia in 1993 was approximately 17.8 million people, with a population density of 2.1 persons per km<sup>2</sup>. Note that some other countries have much higher per-capita birth and death rates, which is consistent with the higher world per-capita birth and death rates compared with those for Australia.

We make the following assumptions and then build the model on them.

- We assume that the populations are sufficiently large so that we can ignore random differences between individuals.
- We assume that births and deaths are continuous in time.
- We assume that per-capita birth and death rates are constant in time.
- In the model development, we ignore immigration and emigration, which can be included later.

### **Formulating the differential equation**

Let us consider a population whose initial value is  $x_0$ , with constant per-capita birth rate given as  $\beta$ , and constant per-capita death rate given as  $\alpha$ . Our aim is to find the population size at any time  $t$ . The first step is to determine an equation for the population. We assume that the population can only change due to births or deaths, neglecting here any immigration or emigration. Also, we assume that this change in population at any time is proportional to the size of the population at that time. The appropriate word equation was given in (3.1).

Since the per-capita birth rate  $\beta$  is assumed constant, the overall birth rate at any time is the per-capita birth rate multiplied by the current population size. Similarly, the overall death rate is the per-capita death rate multiplied by the population size. Thus we write

$$\left\{ \begin{array}{l} \text{rate} \\ \text{of} \\ \text{births} \end{array} \right\} = \beta X(t), \quad \left\{ \begin{array}{l} \text{rate} \\ \text{of} \\ \text{deaths} \end{array} \right\} = \alpha X(t). \quad (3.2)$$

Substituting (3.2) into (3.1) we obtain

$$\frac{dX}{dt} = \beta X - \alpha X. \quad (3.3)$$

(Note that  $X(t)$  can be written as just  $X$ , since it is clear that  $X$  is evaluated at  $t$ .)

We have obtained a differential equation for the population size  $X(t)$ . We need one initial condition to ensure a unique solution since this is a first-order, linear differential equation. For the population of the world, if we define the initial time to be 1990 then we have  $X(0) = x_0 = 5.3$  billion people.

### **Solving the differential equation**

We now solve the differential equation (3.3) for continuous population growth. Let  $r = \beta - \alpha$  and then

$$\frac{dX}{dt} = rX.$$

We call  $r$  the *growth rate* or the *reproduction rate* for the population. When  $r > 0$  this is a model describing exponential growth and when  $r < 0$  the process is exponential decay. (Note the similarities here with Section 2.2 on exponential decay.)

This differential equation can be solved using the separation of variables technique covered in Appendix A.3. (The Appendices provide a summary of techniques for solving differential equations.) The general solution is

$$X = Ae^{rt}$$

and applying the initial condition  $X(0) = x_0$  to obtain the value of the arbitrary constant  $A$ , the solution to the differential equation is

$$X(t) = x_0 e^{rt}. \quad (3.4)$$

Clearly this describes exponential growth or decay depending on the sign of  $r$ .

### **Interpretation of parameters**

Returning to the formulation of the differential equation we can provide an approximate interpretation of the per-capita death rate  $\alpha$ . From the rate of deaths we can approximate the number of deaths by multiplying the rate of deaths by the length of the time interval. This approximation would be better if the time interval were short. Thus we can write

$$\left\{ \begin{array}{c} \text{number} \\ \text{of deaths} \\ \text{in time interval } \Delta t \end{array} \right\} \simeq \alpha X(t) \Delta t.$$

Let us now suppose that  $x_0$  people will die in time  $t_1$ , that is,  $t_1$  is the *average life expectancy*. Then, let  $X(t) = x_0$  and  $\Delta t = t_1$  so that (from above) we have

$$x_0 \simeq \alpha x_0 t_1.$$

Hence we obtain

$$\alpha \simeq \frac{1}{t_1}$$

giving an estimate for  $\alpha$  as the reciprocal of the average life expectancy.

For human populations, in developed countries, typically the per-capita death rate is quoted as  $\alpha \simeq 0.007$  (year $^{-1}$ , or 7 deaths per 1,000 persons per year (see, for example, SBS (1998)). This approximates an average life expectancy of  $1/\alpha = 1/0.007 = 140$  years. This value is too high for humans, but nevertheless is of the correct order of magnitude compared with the measured average life expectancy of humans which is 70–80 years. The reason for the discrepancy is due to the fact that the real age distribution does not approximately

follow an exponential distribution; instead the population tends to fall off rapidly at older ages. An exponential distribution is the natural distribution for compartment models (see exercises). For many animal populations, with shorter lifespans and greater probability of dying at younger ages, the reciprocal of the per-capita death rate is usually a more accurate approximation to the average life expectancy.

Using the model we can predict the time taken for the population size to double. Note the similarity between this concept of doubling time and the half-life of radioactive substances discussed in Chapter 2.

**Example 3.1:** Find an expression for the time for the population to double in size.

**Solution:** We solve

$$X(t+T) = 2X(t)$$

where  $T$  is the time taken to double the current size. So, using the solution (3.4),

$$\frac{X(t+T)}{X(t)} = 2 = \frac{x_0 e^{r(t+T)}}{x_0 e^{rt}}$$

whence  $T = \frac{\ln 2}{r}$ .

So the time taken for a population to double in size is  $T = \ln 2/r$ .

### Model validation

Let us now see what this model predicts for known values of the parameters. Taking the 1990 world population values  $r = 0.017$  and  $x_0 = 5.3$  billion, we apply equation (3.4) to predict the population in 1995 as  $X(5) = 5.77$  billion. In 10 years we have  $X(10) = 6.28$  billion and in 100 years  $X(100) = 29.01$  billion. Thus, in just 100 years, this predicts that the world population will have increased by 2500%!

We should also compare our predictions with population sizes at previous times for which data is available. Looking back to 1960 the world's population was 3.005 billion and in 1900 it was 1.608 billion. Our model predicts in 1960,  $X(-30) = 3.18$  billion, which is not too far out and in 1900,  $X(-90) = 1.15$  billion. The predictions appear to get worse the further back we go. One possible contributing factor towards this discrepancy is that the per-capita birth and death rates have changed gradually due to improvements in technology and changing attitudes. (In 1970, the reproduction rate was somewhat higher, at  $r = 2.0$ .)

Another way to test the model is to measure the population of some very simple organism which breeds fast and is sufficiently small, for example, a yeast culture. A comparison with data from an experiment growing a yeast culture is given in Renshaw (1991), and the results illustrated in the diagram of Figure 3.2. Note that the model appears to be in good agreement in the earlier stages of the growth, but for later times the population levels out rather than continuing to grow exponentially.

The cause of this is that the per-capita death rate increases due to crowding and competition for limited resources, and thus the overall population size growth rate decreases. In certain animal populations the per-capita birth rate (number of births per unit of time) decreases when the death rate increases. For example, rabbits reabsorb their embryos when their population density is high. However, in the model we develop to describe this observed growth pattern in Section 3.2, we consider only a change in the per-capita death rate dependent on the population density.

There are several other ways in which this basic population model could be extended. It is easy to incorporate immigration and emigration, which is appropriate for models of populations in specific countries, rather than the world. This is done by adding terms to

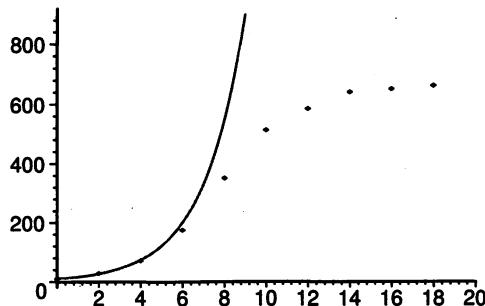


Figure 3.2: Illustration of the difference between the trend of experimental data for a yeast culture, and the continuous growth model predictions, over a period of hours ( $t$ ).  $X(t)$  is a measure of the yeast population size. (Adapted from Renshaw (1991).)

the word equation for the change in population, and making assumptions about the rates of immigration and emigration. A similar concept is the inclusion of the harvesting of a population which we cover in Section 3.3. Some other important extensions (which are not addressed in this book) include discrete growth for animals with distinct breeding seasons, stochastic (random) growth and age dependent growth.

**Summary of skills developed here:**

- Formulate differential equations for single populations, including immigration, emigration or harvesting.
- Obtain exact solutions by solving the differential equations.
- For simple solutions, draw general sketches.

## 3.2 Density dependent growth

Realistically, populations cannot continue growing exponentially over time due to limited resources and/or competition for these with other species. If populations are observed over long periods they often appear to reach a limit, or to *stabilise*. We modify the exponential growth model of the previous section to account for competition or limited resources and to include the stabilising effect observed in populations.

### Background

As a population grows, individuals eventually will compete for the limited resources available. In principle this competition means that a given environment can support only a limited number of individuals. This number is called the *carrying capacity* for the population and is usually denoted by the symbol  $K$  in biological literature. Technically, we define it as the population size (or density) for which the per-capita birth rate is equal to the per-capita death rate, excluding external factors such as harvesting or interaction with another population. We need to extend the model to include an additional death rate due to the resource limitations, and thus curb the exponential growth and allow the population to stabilise.

### Formulating the differential equation

The population is described by the same word equation as before,

$$\left\{ \begin{array}{l} \text{rate of} \\ \text{change in} \\ \text{population} \end{array} \right\} = \left\{ \begin{array}{l} \text{rate} \\ \text{of} \\ \text{births} \end{array} \right\} - \left\{ \begin{array}{l} \text{rate} \\ \text{of} \\ \text{deaths} \end{array} \right\} \quad (3.5)$$

and, as in the previous section, we assume a constant per-capita birth rate of  $\beta$ . Thus

$$\left\{ \begin{array}{l} \text{rate} \\ \text{of} \\ \text{births} \end{array} \right\} = \beta X(t).$$

Instead of assuming a constant per-capita death rate, we allow the per-capita death rate to increase as the population increases, as can be observed in some populations. We can model this behaviour by assuming a linear dependence of the per-capita death rate on the population size,

$$\left\{ \begin{array}{l} \text{per-capita} \\ \text{death} \\ \text{rate} \end{array} \right\} = \alpha + \gamma X(t)$$

where  $\alpha$  (positive) is the per-capita death rate due to natural attrition, and  $\gamma$  (positive) is the per-capita dependence of deaths on the population size. Note that as  $X \rightarrow 0$  the per-capita death rate tends to  $\alpha$ , while for increasing population size the per-capita death rate increases. This linear form is the simplest for a population dependent per-capita death rate which increases with increasing population size. The overall death rate is thus given by multiplying the per-capita death rate by the population size, so that

$$\left\{ \begin{array}{l} \text{rate} \\ \text{of} \\ \text{deaths} \end{array} \right\} = \alpha X(t) + \gamma X^2(t). \quad (3.6)$$

The word equation (3.5) then translates to

$$\frac{dX}{dt} = \beta X - \alpha X - \gamma X^2.$$

Writing  $r = \beta - \alpha$ , which is the reproduction rate, we obtain the model for density dependent growth

$$\boxed{\frac{dX}{dt} = rX - \gamma X^2.} \quad (3.7)$$

An alternative formulation of this equation comes from splitting the death rate into a normal death rate and an extra death rate due to members of the population competing with each other for limited resources. Thus we can write

$$\left\{ \begin{array}{l} \text{rate of} \\ \text{change in} \\ \text{population} \end{array} \right\} = \left\{ \begin{array}{l} \text{rate} \\ \text{of} \\ \text{births} \end{array} \right\} - \left\{ \begin{array}{l} \text{normal} \\ \text{rate of} \\ \text{deaths} \end{array} \right\} - \left\{ \begin{array}{l} \text{rate of} \\ \text{deaths by} \\ \text{crowding} \end{array} \right\}.$$

For the birth rate and normal death rate we assume constant per-capita rates  $\beta$  and  $\alpha$  respectively.

For the extra deaths by crowding we assume that the per-capita death rate increases with population size. If we assume that it is proportional to the population size and thus

given by  $\gamma X$  (where  $\gamma$  is a positive constant), then the extra overall death rate is the extra per-capita death rate multiplied by the current population size. Thus we have

$$\left\{ \begin{array}{l} \text{extra rate} \\ \text{of deaths} \\ \text{by crowding} \end{array} \right\} = \gamma X^2$$

with  $\gamma$  a positive constant. The result is again (3.7).

Without actually solving the differential equation, we can infer how the solution would behave. The population has an initial value,  $x_0$ . The derivative  $dX/dt$  is always positive for  $X < K$  and thus the population is increasing. The rate of growth increases initially and then slows down as the population approaches the carrying capacity  $K$ . The sketch is illustrated in Figure 3.3.

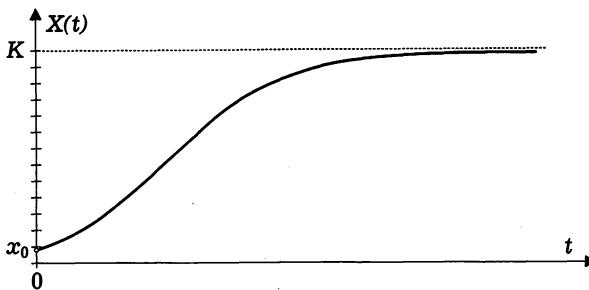


Figure 3.3: Sketch of the general solution to the continuous logistic equation, provided  $x_0 < K$ .

### The logistic equation

With  $K = r/\gamma$  the differential equation (3.7) becomes

$$\frac{dX}{dt} = rX - \frac{r}{K}X^2$$

which can be written as

$$\frac{dX}{dt} = rX \left( 1 - \frac{X}{K} \right). \quad (3.8)$$

This model leads to a nonlinear differential equation. It is the *logistic equation* and is also referred to as the limited growth model or the density dependent model. We consider only  $r > 0$  and  $K > 0$  to ensure positive population values.

### Interpretation of the parameters

Recall the differential equation for unrestricted population growth (see Section 3.1)

$$\frac{dX}{dt} = rX.$$

We can write down a general differential equation for population growth as

$$\frac{dX}{dt} = R(X)X$$

where  $R(X)$  represents a population dependent per-capita growth rate. It is interesting to interpret the logistic equation in terms of this population dependent per-capita growth rate, and thus from (3.8) we identify  $R(X)$  as

$$R(X) = r \left(1 - \frac{X}{K}\right).$$

Note that  $R(X)$ , a linear function of  $X$ , tends to zero as the population approaches its carrying capacity  $K$ , while as the population size tends to zero  $R(X)$  approaches  $r$ . This form corresponds to a straight line, which passes through the points  $R = 0$  when  $X = K$  and  $R = r$  when  $X = 0$  as illustrated in Figure 3.4. If  $R < 0$  then we have that  $X > K$  and the population ( $X$ ) is decreasing as it approaches the carrying capacity.

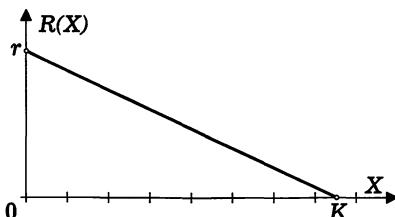


Figure 3.4: The simplest assumption for a population dependent per-capita growth rate is a straight line.

### **Equilibrium solutions and stability**

If we observe the levelling of a population over time, this implies that the rate of change of the population approaches 0, that is,  $X' \rightarrow 0$ . Any value of  $X$  which gives a zero rate of change is called an *equilibrium point* or *equilibrium solution*.

Equilibrium solutions are constant solutions where, here, the rate of increase (births) exactly balances the rate of decrease (deaths). Equilibrium solutions satisfy

$$\left( \frac{dX}{dt} = 0; \Rightarrow rX \left(1 - \frac{X}{K}\right) = 0. \right) \quad (3.9)$$

There are two possible equilibrium solutions,  $X_e = 0$  and  $X_e = K$ , that satisfy equation (3.9). We are interested in which of these are stable. For stable solutions this means that if we start near the equilibrium solution then we are attracted towards it. The condition for local stability is  $f'(X_e) < 0$ , where  $f$  is the RHS of the differential equation (see Section 2.11). Here  $f(X) = rX(1 - X/K)$  and so

$$f'(X) = r - \frac{2rX}{K}$$

so  $f'(0) = r > 0$  and  $f'(K) = -r < 0$ , for all positive values of  $r$ . So the equilibrium solution  $X = 0$  is always unstable and the equilibrium solution  $X = K$  is always stable. We can further show that, even if we are not close to the equilibrium solutions, these stability conclusions still hold here.

Returning to the differential equation in factored form,

$$\frac{dX}{dt} = rX(1 - X/K)$$

we see that if  $X < K$  then the rate of change of  $X$  is always positive. This implies the population is increasing with time and will approach  $X = K$ . Similarly, if  $X > K$  then  $dX/dt < 0$  which implies that the population is always decreasing towards  $X = K$ . When the population *always* approaches the equilibrium population we say the equilibrium is *globally stable*. Conversely, if it is repelled from the equilibrium, we say the equilibrium is *unstable*. (Note that for  $0 < X < K$ ,  $dX/dt > 0$  and thus the equilibrium point at  $X = 0$  is globally unstable.)

Thus the model predicts that all populations approach the equilibrium value  $K$  which we have already defined as the carrying capacity for the population. The stable equilibrium point and carrying capacity coincide in this case.

### Solving the logistic equation

We can solve the logistic equation in two ways. First, using **Maple** to obtain a numerical solution, and second, analytically using the separation of variables technique.

**Maple** is a symbolic language which means that it can use analytic methods (where possible) to solve such equations. Often analytic solutions cannot be found and numerical schemes are required. (We have a closer look at some of these numerical methods in Chapter 4.) We can use **Maple** to solve the equation and draw the family of graphs in Figure 3.5 with the following commands (see Listing 3.1)

Listing 3.1: Maple code: c\_cp.logistic.txt

---

```
> restart:with(plots):
> r:=1;K:=1000;
> de1:=diff(x(t),t)=r*x(t)*(1-x(t)/K);
> soln:=x0->dsolve({de1,x(0)=x0},x(t),numeric):
> plot1:=x0->(odeplot(soln(x0),[t,x(t)],0..8)):
> list1:=seq(plot1(i*50),i=1..24):
> line1:=plot([[0,K],[8,K]],colour=gray):
> plot11:=display(list1,line1,view=[0..8,0..1200]):
> display(plot11);
```

---

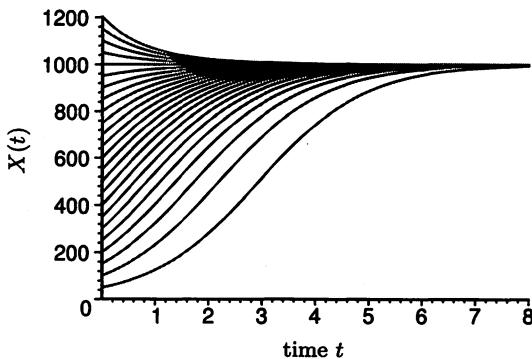


Figure 3.5: Logistic growth model with  $r = 1$  and  $K = 1000$ , and for a number of different initial conditions.

### Analytic solution

The next example illustrates how to obtain the analytic solution. (For details on partial fractions and separable techniques see the Appendices.)

---

**Example 3.2:** Solve the logistic differential equation (3.8) given the initial condition  $X(0) = x_0$ .

**Solution:** The logistic equation is not linear, but it is separable,

$$\frac{dX}{dt} = rX \left(1 - \frac{X}{K}\right) = \frac{rX(K-X)}{K} \quad (3.10)$$

which is in the form  $X' = F(X)G(t)$  where  $G(t) = 1$ . Separating the variables

$$\frac{K}{X(K-X)} \frac{dX}{dt} = r$$

assuming that  $X \neq 0$  and  $X \neq K$ . Integrating gives

$$\int \frac{K}{X(K-X)} dX = \int r dt.$$

For the integral on the left hand side (LHS) we need to use partial fractions (see Appendix B.5) and thus

$$\frac{K}{X(K-X)} = \frac{a}{X} + \frac{b}{K-X} = \frac{a(K-X) + bX}{X(K-X)}.$$

Solving for the constants  $a$  and  $b$  gives

$$\begin{aligned} aK &= K, \\ (-a+b)X &= 0, \end{aligned}$$

which implies that  $a = b = 1$ , and then

$$\frac{K}{X(K-X)} = \frac{1}{X} + \frac{1}{K-X}.$$

Now

$$\int \frac{K}{X(K-X)} dX = \int \frac{1}{X} dX + \int \frac{1}{K-X} dX = \int r dt$$

and we can integrate to get

$$\begin{aligned} \ln|X| - \ln|K-X| &= rt + c \quad (c \text{ an arbitrary constant}), \\ \left| \frac{X}{K-X} \right| &= c_1 e^{rt} \end{aligned}$$

where  $c_1 = e^c$ . Assuming  $0 < X < K$  then

$$X = c_1 e^{rt}(K-X). \quad (3.11)$$

Using the initial condition  $X(0) = x_0$  we deduce that  $c_1 = x_0/(K-x_0)$  and then solving (3.11) for  $X$  we obtain

$$X = \frac{K}{1+me^{-rt}} \quad \text{where } m = \frac{K}{x_0} - 1. \quad (3.12)$$

Alternatively, in the case where  $0 < K < X$ , then

$$X = c_1 e^{rt}(X-K).$$

With the initial condition  $X(0) = x_0$  we have that  $x_0 = c_1(x_0 - K)$  and hence  $c_1 = x_0/(x_0 - K)$ . The solution is as in (3.12).

---

It is also possible to use Maple to find the analytic solution. The commands are given in Listing 3.2.

Listing 3.2: Maple code: c\_cp.logistic.analytic.txt

---

```
> restart;
> de := diff(X(t),t) = r*X(t)*(1-X(t)/K);
> dsolve( {de, X(0)=x0}, X(t));
```

---

### Solutions over time

As usual we are interested in the long-term behaviour of the population as predicted by our model. The following example shows how to sketch the graph and draw conclusions about the long-term behaviour forecast by this model.

---

**Example 3.3:** Using the differential equation and considering the second derivative, sketch the graph of the solution.

**Solution:** Since  $r > 0$ , as  $t$  increases we have  $\lim_{t \rightarrow \infty} X(t) = K$  which is the carrying capacity of the population. If  $0 < x_0 < K$  then  $X(t)$  is strictly increasing (a monotonically increasing function). If  $x_0 > K$ , then  $X(t)$  is strictly decreasing (a monotonically decreasing function). What happens if  $x_0 = K$ ?

Considering the second derivative,

$$X'' = rX' - \frac{2XrX'}{K} = X'r \left(1 - \frac{2X}{K}\right) = rX \left(1 - \frac{X}{K}\right) r \left(1 - \frac{2X}{K}\right)$$

which changes sign at  $X = 0$ ,  $K/2$ , and  $K$ . These are inflection points of the curve, that is, where the curve changes from concave to convex or vice versa. This, together with the limit above and nature of the slope, provides the information required to sketch the graph which was illustrated earlier in Figure 3.3 and generated with Maple in Figure 3.5.

---

With the logistic model developed above we have incorporated an instantaneous reaction to the environment. That is, increased pressure on the resources produces an immediate response from the system in terms of, for example, more deaths. This is often not realistic in that the response usually takes effect after some time delay, or time lag. Vegetation needs time to recover and changed environmental conditions, which may lead to increased birth rates, will take time to appear in the numbers of an adult population. This leads us to a model which includes a time delay resulting from a multitude of sources such as maturation times, food supply, resources, or crowding: each a measurable quantity. If the time lag is small compared with the natural response time ( $1/r$ ) then there is a tendency to overcompensate which may produce oscillatory behaviour. This is exemplified in Section 3.6 and Section 3.7.

**Summary of skills developed here:**

- Understand how to modify the differential equation to account for a change in reproduction rate due to crowding.
- Be able to find the equilibrium populations for a given differential equation.
- Determine if the population approaches or is repelled from the equilibrium.

### 3.3 Limited growth with harvesting

The effect of harvesting a population on a regular or constant basis is extremely important to many industries. One example is the fishing industry. Will a high harvesting rate destroy the population? Will a low harvesting rate destroy the viability of the industry?

#### D Formulating the equation

Including a constant harvesting rate in our logistic model gives

$$\left\{ \begin{array}{l} \text{rate of} \\ \text{change in} \\ \text{population} \end{array} \right\} = \left\{ \begin{array}{l} \text{rate} \\ \text{of} \\ \text{births} \end{array} \right\} - \left\{ \begin{array}{l} \text{normal} \\ \text{rate of} \\ \text{deaths} \end{array} \right\} \\ - \left\{ \begin{array}{l} \text{rate of} \\ \text{deaths by} \\ \text{crowding} \end{array} \right\} - \left\{ \begin{array}{l} \text{rate of} \\ \text{deaths by} \\ \text{harvesting} \end{array} \right\}. \quad (3.13)$$

Assuming the harvesting rate to be constant, equation (3.13) translates to the differential equation

$$\frac{dX}{dt} = rX \left( 1 - \frac{X}{K} \right) - h. \quad (3.14)$$

Here  $h$  is included as the constant rate of harvesting (total number caught per unit time, or deaths due to harvesting per unit time) and it is independent of the population size and thus could be interpreted as a quota.

#### C Solving the differential equation

We can infer much useful information about the solution from the differential equation, as we see below and in the exercises, or we can obtain an explicit solution for specific parameter values which we do first, using Maple.

The code associated with Figure 3.5 was adapted to produce the figures below (Figure 3.6 and Figure 3.7), taking a reproduction rate of  $r = 1$ , a carrying capacity of  $K = 1000$  and harvesting rates of  $h = 100$  and  $h = 500$ .

The following example illustrates how to gain information about the dynamics of the model from the differential equation for certain numerical values of the parameters. (The purely theoretical case, which covers all possible parameter values, is examined in the Exercises, Question 5.)

First, we can write (3.14) in the factored form

$$\frac{dX}{dt} = -\frac{r}{K} \left( X^2 - KX + \frac{Kh}{r} \right)$$

with  $r$ ,  $K$  and  $h$  positive constants.

---

**Example 3.4:** Let  $r = 1$ ,  $K = 10$ ,  $h = 9/10$  and  $X(0) = x_0$ . Use the differential equation to investigate the behaviour of the solution and compare this with the Maple solution.

**Solution:** The differential equation becomes

$$\frac{dX}{dt} = -\frac{1}{10}(X^2 - 10X + 9) = -\frac{1}{10}(X - 1)(X - 9).$$

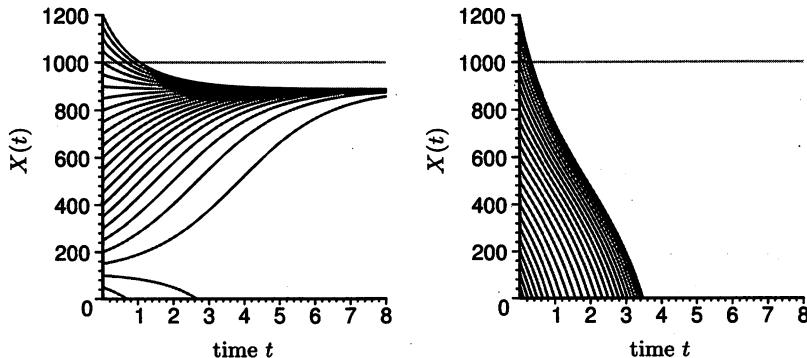


Figure 3.6: Logistic growth including harvesting with  $h = 100$  in the first diagram and with  $h = 500$  in the second. The grey line is the carrying capacity  $K$ . (The parameter values are  $K = 1000$  and  $r = 1$ .)

We have the following cases to consider when sketching a graph. If  $x_0 < 1$  then  $X' < 0$  and the population declines. If  $1 < x_0 < 9$  then  $X' > 0$  and the population increases. If  $x_0 > 9$  then  $X' < 0$  and the population declines. If  $x_0 = 1$  or  $x_0 = 9$  then the population does not change ( $X' = 0$ ). The Maple solution is illustrated in Figure 3.7 and clearly satisfies these predictions.

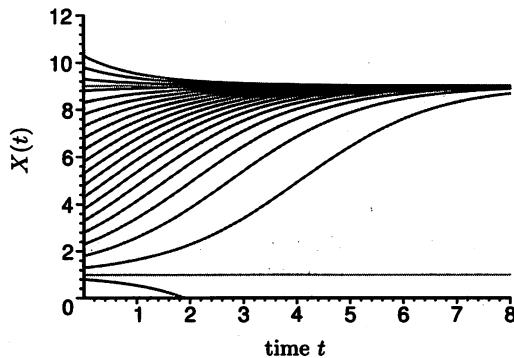


Figure 3.7: The logistic equation with harvesting (3.14) with  $r = 1$ ,  $K = 10$  and  $h = 9/10$ . The grey lines are at  $x = 9$  and  $x = 1$  across which there is a change in the sign of  $X'$ .

Using partial fractions we can solve the differential equation for  $X$  explicitly, as shown in the following example.

**Example 3.5:** Solve the differential equation.

**Solution:** Separating the variables gives

$$\int \frac{1}{(X-1)(X-9)} dX = - \int \frac{1}{10} dt$$

and using partial fractions,

$$\frac{1}{8} \int \left( \frac{1}{X-9} - \frac{1}{X-1} \right) dX = -\frac{1}{10} \int dt.$$

Carrying out the integration gives

$$\ln \left| \frac{X-9}{X-1} \right|^{1/8} = -\frac{1}{10}t + c$$

where  $c$  is some arbitrary constant. Then rearranging with constant  $b = e^{8c}$

$$\left| \frac{X-9}{X-1} \right| = be^{-4t/5}.$$

Now substituting for the initial condition

$$b = \left| \frac{x_0 - 9}{x_0 - 1} \right|$$

and the explicit solution is

$$X(t) = \frac{9 - be^{-4t/5}}{1 - be^{-4t/5}}.$$

From this solution (illustrated in Figure 3.7) we can conclude that the harvesting rate causes the population to stabilise to a value less than the carrying capacity. In the case of harvesting, or some other disaster, causing the population to decrease below a critical level, the threshold level (which in this example is 1), our model predicts that the population will become extinct.

This concept of a threshold level is critical to many industries and thus harvesting rates should be set with extreme caution as the following case studies indicate.

**Summary of skills developed here:**

- Be able to model a population following exponential growth or logistic growth and include harvesting.
- Understand the concept of a threshold harvesting level.
- Sketch graphs of the changes in a population over time and ratify them with Maple generated solutions.
- Modify the model developed to include immigration and/or emigration, or include the impact of a toxin which kills a percentage of the population.

### 3.4 Case Study: Anchovy wipe-out

In the following case study we cite a case in which a population was fished annually. Although measures were taken to ensure that overfishing did not occur, so that there would always be sufficient stock for recovery, a natural event combined with the fishing resulted in the total destruction of the industry associated with that species. The case study is adapted from correspondence with Hearn (1998), and the book, May (1981). A discrete model of the system can be found in Caulkins et al. (1985).

Some decades ago anchovies were a very cheap fish dominating the supermarket shelves: little guys in little tins and very salty. They were a major source of high protein food for people as well as animals. It was noted that the world price of anchovies showed a correlation with the *El Niño* cycle, that is, *El Niño* events increased prices due to shortages in the resource. Ironically it was to be a combination of *El Niño* and fishing practices which destroyed the industry.

In the decades after World War II and the introduction of the nylon fishing nets the anchovy fishery expanded exponentially to become, by the 1960s, the largest fishery in the world and a major part of the Peruvian economy. The anchovies inhabited a narrow strip on the west coast of Peru, where nutrients are available in abundance from strong upwelling in the Pacific Ocean. The upwelling brings nutrients to the surface (into the photic zone) and starts a food chain in that it allows plants to grow on which fish may then feed. Off the coast of Peru, the upwelling is caused by the trade winds, and during the *El Niño* events these weaken, hence reducing the fishery. Most of the world's major fisheries are in regions of coastal upwelling and this region is particularly remarkable in that it accounts for 22% of the worlds' production of fish. Furthermore, the anchovies themselves were within a food chain and in turn provided 80–95% of the diet of guano birds. (Each bird consuming approximately 35 500 fish a year, or close to 100 per day!) Needless to say the population of these birds was extremely sensitive to that of the anchovies.

Over the years the anchovy catch had increased steadily from an annual 2 million tons in 1959 to 12.3 million tons in 1970. A small *El Niño* event in 1965, together with heavy fishing, was sufficient to wipe out the guano birds, and thus the associated guano industry collapsed. Fishery 'experts' advised the Peruvian government, now concerned about overfishing, that a maximum sustainable yield was about 10 million tons annually. This was immediately adopted as the quota. No regulation was placed on the number of boats involved or the number of fish taken per boat: it was a free-for-all and the anchovies declined alarmingly. Still no action was taken to conserve the resource. In 1971, with hugely expanded fishing and processing, the quota was reached in just 3 months and the fishery had to be closed for the remainder of the year. The catch fell dramatically to 4.5 million tons and then along came a particularly severe *El Niño*. The anchovy population slumped still further and has never recovered. The little anchovies have gone.

To be fair, this was before we understood much about *El Niño* but the case emphasises the concept of population thresholds for the sustainability of both industry and environment. With discrete breeding seasons the population lends itself to discrete modelling, and one such model which includes the effect of *El Niño* as well as predators such as the guano birds and the efficiency of fishermen with a variety of net types can be found in Caulkins et al. (1985). Unfortunately it is with hindsight that we see that the adoption of the recommendations from these improved models may have changed anchovy history. Still, one is left wondering as fishing in the region continues, with authorities too afraid of retribution to improve restrictions.

### 3.5 Case Study: How can $2 \times 10^6$ birds mean rare?

Perhaps it is not always easy to judge just what level of harvesting is safe; however, the following case study emphasises the importance of biological research into understanding the species' behaviour, before such levels can be set legitimately. The following is adapted from Quammen (1997).

When it comes to the extinction of species, there is no magic number below which a population ends with extinction. In fact rarity may not mean extinction, just as abundance may not imply survival.

For example, the passenger pigeon, *Ectopistes migratorius*, was probably once the least rare bird on earth. Inhabiting the eastern half of North America the rookeries covered as much as 500 square kilometres and the birds literally darkened the sky when they took off. Around 1810 a flock was seen in Kentucky taking three days to pass overhead! Biologically this species was a huge success. Then, within the very short space of 36 years, its population went from roughly 3 billion to zero. It was people who reduced its number to a few million, enough to tip the balance, and extinction ensued. The decline happened suddenly during the 1880s and the unbelievably numerous pigeons simply ceased to exist.

The massacre/harvest peaked after the civil war. However, during the last years of the pigeons' existence, their population decline was too steep to attribute to hunting alone. Habitat destruction would have been a further cause for population decline, but even so this was not enough to cause the crash. The explanation proposed by biologist T.R. Halliday in 1980 was in terms of a critical colony size. He argued the benefits to the population of crowding, as protection from predators, cooperative food source location, the maintenance of mating and nesting rhythms, and hence also its breeding rate. He suggested that a remnant population of a couple of million occurring in small flocks would be inadequate to sustain the population. That is, abundance was essential to the species and human interference had pushed the numbers below its particular threshold. Although two or so million sounds like abundance, for *Ectopistes migratorius* this was rare.

At the opposite extreme we have the Kestrels of Mauritius, *Falco punctatus*. In that case the population declined slowly. Originally the population would have been roughly 700–800 birds but by the 1950s it had decreased to well below 50 and by 1971 only 4 surviving birds were known to exist. With reduced and fragmented habitat, DDT, introduced exotic predators and plants, human hunters and then a cyclone, the population appeared doomed. It was the most rare bird in the world. Carl Jones, a Welshman and a 'bird person', arrived in 1979 having been sent by the International Council for Bird Preservation (which later withheld funding). He incubated eggs he collected from precarious ledges (replacing them with dummy eggs), used artificial insemination to improve the breeding rates and successfully reared birds in captivity. Furthermore he supplemented the feed of those in the wild. Single handed, and learning on the run, he eventually turned the population decline around.

By 1988 the population had climbed to 80 and although, due to the fragmentation of habitat and exotic predators and plants, the numbers will never reach their original estimates, the population today is relatively healthy.

---

### 3.6 Discrete population growth and chaos

Many animal populations have distinct breeding seasons. It is often more appropriate to model such population growth using difference equations rather than differential equations. In this section we see how discrete growth models with crowding can predict oscillatory or chaotic growth in populations.

### Background

Some observations of the growth of two beetle populations are shown in Figure 3.8. There appears to be quite a large variation in the type of growth. In the first example the effect of overcrowding appears to be levelling out the population. However the population fluctuations in the second example are more complex. The challenge is to find a single model that is capable of predicting both types of population growth in Figure 3.8.

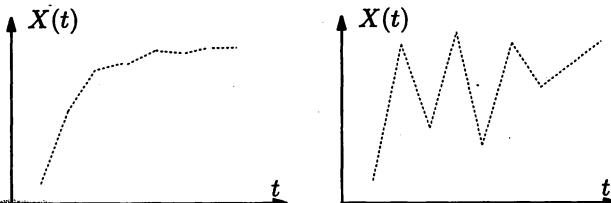


Figure 3.8. Schematic diagrams of some experimental data for growth of two different populations of beetle, where  $X(t)$  is the number of beetles over a number of generations  $t$ . From May (1981).

### Formulating a difference equation

In discrete growth we assume that the population does not change except at discrete intervals, corresponding to breeding seasons. Instead of thinking about the rate of change of the population at an arbitrary time, we consider the time interval as the time from one breeding season to the next. Let us choose to measure time in units of this period. Furthermore, we assume here that the population changes occur from births or deaths alone.

We assume that the deaths are due to normal causes and also to crowding effects. Over a single breeding interval we thus write,

$$\left\{ \begin{array}{l} \text{change in} \\ \text{population} \\ \text{size} \end{array} \right\} = \left\{ \begin{array}{l} \text{no. of} \\ \text{births} \end{array} \right\} - \left\{ \begin{array}{l} \text{no. of} \\ \text{deaths} \end{array} \right\}. \quad (3.15)$$

Let us define  $X_n$  to be the population size in the  $n$ -th breeding interval. Here  $n$  is an integer, representing time, but taking only discrete values. Consequently,  $X_{n+1}$  is the population in the next breeding interval.

Assuming a constant per-capita birth rate  $\beta$  as before, the overall birth rate is  $\beta X_n$ . Since the birth rate is constant over the current breeding interval, the number of births for that interval is obtained by multiplying the birth rate by the length of the time interval (which is 1). Thus, for a single breeding interval

$$\left\{ \begin{array}{l} \text{no. of} \\ \text{births} \end{array} \right\} = \beta X_n. \quad (3.16)$$

For the per-capita death rate we use  $\alpha + \gamma X_n$  where the extra term represents an increased per-capita death rate due to competition for limited resources. The number of deaths is obtained by multiplying by the current population size by the time interval. Thus for a single breeding interval

$$\left\{ \begin{array}{l} \text{no. of} \\ \text{deaths} \end{array} \right\} = \alpha X_n + \gamma X_n^2. \quad (3.17)$$

From one breeding interval to the next the change in population is  $X_{n+1} - X_n$ . Substituting (3.16) and (3.17) into the word equation (3.15) we obtain

$$X_{n+1} - X_n = \beta X_n - \alpha X_n - \gamma X_n^2, \quad i = 0, 1, 2, 3, \dots \quad (3.18)$$

This type of equation is known as a difference equation. It gives the population at one time in terms of the population at the previous time.

Suppose we write  $r = \beta - \alpha$  and  $\gamma = r/K$ , as before, then (3.18) becomes

$$X_{n+1} = X_n + rX_n \left(1 - \frac{X_n}{K}\right), \quad n = 0, 1, 2, 3, \dots \quad (3.19)$$

This equation is sometimes called the *discrete logistic equation*<sup>1</sup>. Here  $K$  is the carrying capacity and  $r$  is the per-capita reproduction rate.

### Solving the equation

We solve (3.19) iteratively, using a computer or calculator, but we first need to choose values for  $r$ ,  $K$  and  $x_0$ . One way of gaining an understanding of the population growth is to slowly vary one of the parameters  $r$ ,  $K$  and  $x_0$ , observing any changes in the behaviour, or dynamics of the population. In this case we examine the effect on the population growth of varying only  $r$ , the intrinsic reproduction rate. We fix the carrying capacity  $K$  at 1000 and the initial population  $x_0$  at 100. Using Maple we can generate the time-dependent values and plot them. A variety of growth patterns emerge as we increase the per-capita growth rate  $r$ : from logistic growth through oscillatory growth to chaotic growth. These are described below together with the diagrams generated using the code in Listing 3.3. Similar MATLAB code is given in Listing 3.4.

Listing 3.3: Maple code: c\_cp.logistic.discrete.txt

```
> restart:with(plots):
> X[0]:=100;r:=0.2;K:=1000;
> for n from 0 to 50 do
>   X[n+1]:=X[n]+r*X[n]*(1-X[n]/K):
> end:
> points:=[seq([n,X[n]],n=0..50)]:
> plot1:=plot(points,style=point,symbol=circle):
> plot2:=plot(points,style=line,colour=red):
> display(plot1,plot2);
```

Listing 3.4: MATLAB code: c\_cp.logistic.discrete.m

```
N = 50; %number of iterations
r = 0.2; K = 1000; x0 = 100;
X = zeros(N+1,1); t = zeros(N+1,1);
X(1) = x0; t(1) = 0; %initial values
for n=1:N %loop over interations
    t(n+1) = n; %set time values
    X(n+1) = X(n) + r*X(n)*(1-X(n)/K);
end
plot(t, X, '.');
axis([0, N, 0, K*1.4]);
```

<sup>1</sup>Another version of this equation  $X_{n+1} = rX_n(1 - X_n/K)$  is also called the discrete logistic equation. This form arises for populations with non-overlapping generations — where all the adults die after they have given birth.

### Logistic growth

Figure 3.9 illustrates the population growth for the small value of  $r$ ,  $r = 0.2$ . Note that the growth is very similar to that for the continuous case, with the population growing exponentially at first and then levelling out as the reproduction rate declines due to crowding effects. We see that the population appears to approach its carrying capacity  $K = 1000$ .

As we increase the reproduction rate from  $r = 0.2$  to  $r = 0.8$  we observe that the population curve is initially much steeper and then levels off more quickly. This is illustrated in Figure 3.9.

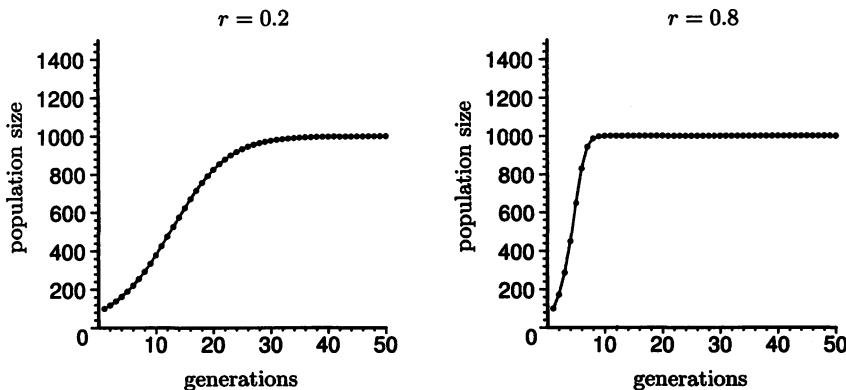


Figure 3.9: Computer generated solutions for the discrete logistic equation with  $K = 1000$ ,  $x_0 = 100$ . Values of  $r$  used were  $r = 0.2$  and  $r = 0.8$ . The growth follows logistic curves.

### Oscillatory growth

When the intrinsic reproduction rate is increased further so that  $r > 1$  it becomes possible for the population to increase above the carrying capacity, but in the next iteration it then falls below  $K$ . A *damped* oscillation results, where the oscillations become smaller with time, as seen in Figure 3.10. As  $r$  increases the amplitude of these damped oscillations increases.

Once the population is above the carrying capacity  $K$  the reproduction rate  $r(X_n)$  now is negative (corresponding to the death rate being higher than the birth rate). Thus in the next breeding season the population drops below the carrying capacity. In the continuous model the reproduction rate changed instantaneously; with the discrete model, however, there is a delay of one breeding season before the reproduction rate can adjust to the change in population. This is why it is possible for the population to jump above the carrying capacity in the discrete model, which is not the case in the continuous model.

As we increase  $r$  further (see Figure 3.10), for  $r = 2.2$  the population is again oscillating about the carrying capacity, but the amplitude of the oscillations appears to be constant. We call this oscillation a 2-cycle since the population size is repeated every second breeding cycle once the initial transients have died out. As  $r$  increases further, the amplitude of the oscillation increases. It is possible to prove, using the difference equation (3.19), that stable 2-cycles persist if  $2 \leq r < 2.4$ . This illustrates an increasingly common approach in mathematics, where computer experiments suggest results which are then proved using analysis. Somewhere between  $r = 2.4$  and  $r = 2.5$  the 2-cycles become unstable.

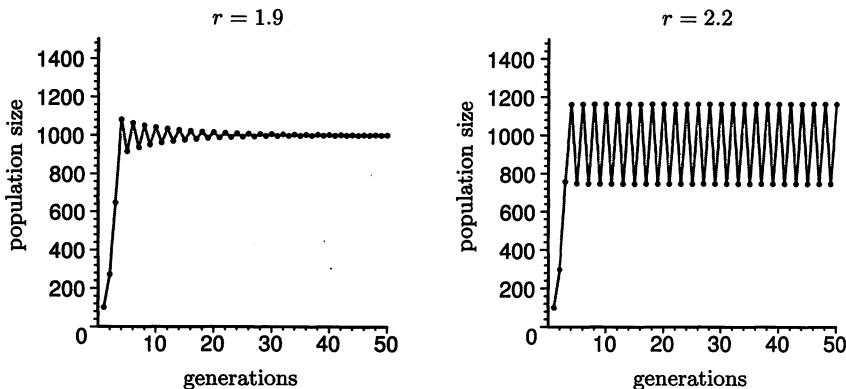


Figure 3.10: Computer generated solutions of the discrete logistic equation with  $K = 1000$ ,  $x_0 = 100$  and with  $r = 1.9$  and  $r = 2.2$ . The graph for  $r = 1.9$  shows a damped oscillation. The graph for  $r = 2.2$  exhibits a 2-cycle.

### *Period doubling and chaotic growth*

Again, the trend here is for the amplitude of the 2-cycles to increase but they do not increase indefinitely. We can see from Figure 3.11 that the 2-cycle has become a 4-cycle by  $r = 2.5$ , where the values repeat themselves every 4 breeding cycles. As  $r$  increases further this becomes an 8-cycle and then a 16-cycle and so on.

When we try  $r \geq 2.6$  some entirely new behaviour is observed. The population does not grow in ordered cycles but seems to change randomly in each breeding period. We call this type of growth chaotic, and it is illustrated in Figure 3.11 for  $r = 2.7$ .

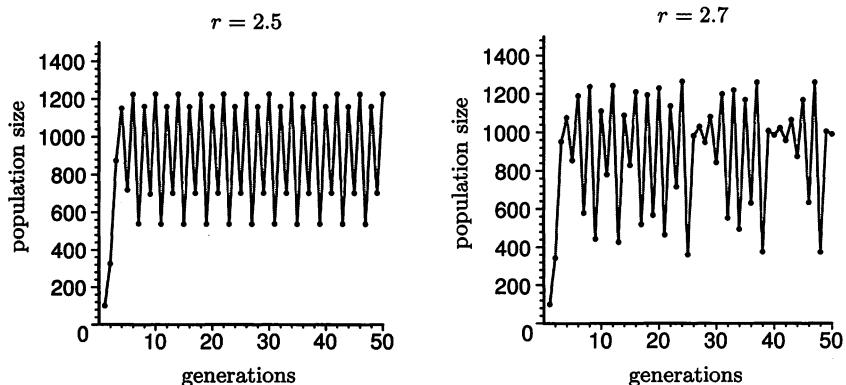


Figure 3.11: Computer generated solutions of the discrete logistic equation with  $K = 1000$ ,  $x_0 = 100$  and  $r = 2.5$  and  $r = 2.7$ . For  $r = 2.5$  we get a 4-cycle. For  $r = 2.7$  we get chaotic growth where there is seemingly a random pattern to the growth.

Another feature of chaotic growth is that it is very sensitive to a change in the initial population. This feature of chaotic growth is illustrated in Figure 3.12 with two initial population sizes of 100 and 101.

Although the difference between the populations is only 1 initially, after some time they become very different. Both populations are increasing and decreasing in a random-like

pattern but there are significant differences in the graphs.

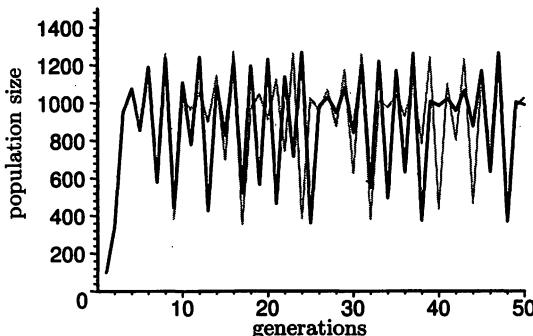


Figure 3.12: Sensitivity to initial conditions. Computer generated solutions of the discrete logistic equation for  $r = 2.7$  and  $K = 1000$ , and for two different initial populations:  $x_0 = 100$  (black line) and  $x_0 = 101$  (grey line). As time increases the solutions move further apart.

If we try to plot a similar graph, using initial conditions  $x_0 = 100$  and  $x_0 = 101$  for any value of  $r$  which gave non-chaotic growth ( $r < 2.6$ ), the graphs of the two populations become indistinguishable after only a few breeding seasons; see exercises, Question 10.

The discovery that simple population models like this can give rise to chaotic growth had an extremely profound effect. Previously, when presented with records of population growth which seemed to have the population growing in a random manner, it was thought that this was due to some external factor such as climate, environment, etc. Now, however, it is known that the random-like behaviour may be a natural feature of the way that the population grows, that is, a nonlinear response to a time delay in compensating the reproduction rate to account for crowding. (It should be noted here that  $r = \beta - \alpha$  and thus that large values of  $r$  are only valid for certain populations.)

### Bifurcation diagram

To summarise the different types of growth as the parameter  $r$  varies, it is useful to plot the possible equilibrium solutions against  $r$ . This is done in Figure 3.13 below. As  $r$  increases, we see that there is a single equilibrium population which increases gradually. At  $r = 2$  the solution curve splits into two and we have two solutions. This is called a *bifurcation* and hence the diagram is called a bifurcation diagram. As  $r$  continues to increase the solution undergoes further bifurcations, corresponding to 4-cycles, 8-cycles and so on. Each bifurcation occurs for a relatively smaller increase in  $r$ . The Maple code used to produce the bifurcation diagram is given in Listing 3.5. Similar MATLAB code is given in Listing 3.6.

Listing 3.5: Maple code: c\_cp.logistic.birf.txt

---

```
> restart:with(plots):
> n:=125: nrep:=32: K:=1000:
> r := array(1..n):
> X := array(1..n):
> y:=array(1..nrep):
> ini := 0.1*K:
> inir := 1.5: endr := 3:
> for i from 1 to n do
>   r[i] := evalf(inir + i*(endr-inir)/n):
>   for j from 1 to n-1 do
>     X[i] := ini:
```

```

> X[j+1] := evalf(X[j]+r[i]*X[j]*(1-X[j]/K));
> end;
> for k from 1 to nrep do
>   y[k] := X[n-nrep+k];
> end;
> pp := [[r[i],y[jj]] $jj=1..nrep];
> bif[i] := plot(pp, x=inir..endr, y=0..1.5*K, style=point);
> col[i] := display([seq(bif[j],j=1..i)]);
> end;
> plot1:=display(col[n]):display(plot1);

```

Listing 3.6: MATLAB code: c\_cp\_logistic.birf.m

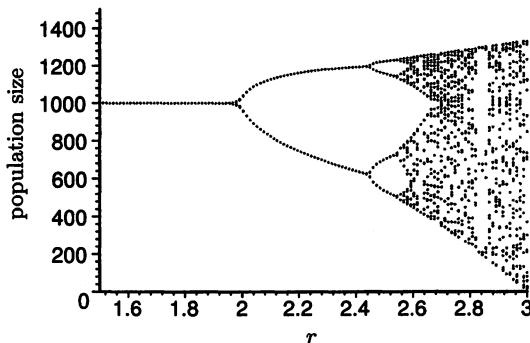
```

Nt = 1000; Nr = 125; Nlast = 20;
K = 1000; x0 = 100;
rv = linspace(1.5,3,Nr); % vector of r values
Xb = zeros(Nr,Nlast); rb = zeros(Nr, Nlast)

for k = 1:Nr; %loop over r values
  r = rv(k);
  X = zeros(Nt,1); t = zeros(Nt,1);
  X(1) = x0; t(1) = 0;
  for n=1:Nt % loop over iterations
    t(n+1) = n;
    X(n+1) = X(n) + r*X(n)*(1-X(n)/K);
  end
  Xb(k,:) = X(end-Nlast+1: end);
  rb(k,:) = r*ones(1,Nlast);
end

plot(rb, Xb, 'r.');
axis([rb(1), rb(end), 0, K*1.4]);

```

Figure 3.13: Bifurcation diagram for the discrete logistic model. This is a plot of the solutions, after a period of time, as the parameter  $r$  increases. They are the equilibrium solutions.

The continual bifurcation behaviour eventually results in chaos. It might be useful to think of chaos as an infinite number of bifurcations. As the parameter  $r$  increases further some unexpected things happen. We appear to get small regions, or windows, of regular behaviour within the chaos. This includes the appearance of 3-cycles.

Even a simple equation, such as the logistic equation, exhibits a rich variety of behaviour. This is a relatively recent area of research, and for the interested reader there is an excellent series of articles in New Scientist which provide a good introduction to the subject, in

particular Vivaldi (1989) and Stewart (1989). For an example of chaos in real populations the articles Costantino et al. (1995) and Costantino et al. (1997) describe experiments on flour beetle populations, where manipulating the adult mortality rate can cause the population to exhibit cycles or become chaotic. They used three difference equations to describe the larvae, pupae and adult populations.

### ***Limitations of the model***

When  $r > 3$  it is possible for the population to become negative. We would interpret this as the population becoming extinct. Of course this may not happen in practice as the stronger members of the population might survive into the next breeding season. Thus this model has a serious weakness if  $r > 3$ ; however, it is useful in demonstrating how extremely complex patterns of growth can evolve from simple assumptions.

A more robust model, which does not have negative populations for any values of  $r$ , is the model

$$X_{n+1} = X_n e^{a(1-X_n/K)}, \quad \text{where} \quad a = \ln(r+1).$$

This model is derived from simple probabilistic arguments<sup>2</sup> and exhibits similar behaviour to the logistic model, with damped oscillations, 2-cycles, 4-cycles and chaotic growth behaviour (although for different values of  $r$ ). It is superior to the logistic model for discrete growth since it incorporates a constant probability of death for each individual. This model is discussed in May (1981).

#### ***Summary of skills developed here:***

- Explore a difference equation model on a computer and describe the range of phenomena.
- Understand the different modelling approaches of discrete and continuous growth.
- Be able to discuss the properties of chaotic growth.

### **3.7 Time-delayed regulation**

We discuss, briefly, how to introduce a time lag response into the logistic model of population growth.

#### ***Background***

With the logistic model developed in Section 3.2, we incorporated an instantaneous reaction to the environment. That is, increased pressure on the resources produces an *immediate response* from the system (in terms of, for example, more deaths).

Often this is not realistic in that the response usually takes effect after some time delay, or time lag. Vegetation needs time to recover and changed environmental conditions which may lead to increased birth rates will take time to show up in the numbers of an adult population. This leads us to a model which includes a time delay which could result from

<sup>2</sup>The model assumes interactions between two different individuals are randomly distributed (as a Poisson distribution) with a rate of contact proportional to  $(1 - X_n/K)$ .

a multitude of measurable sources (maturation times, food supply, resources, crowding, etc.). If the time lag is small compared with the natural response time ( $1/r$ ) then there is a tendency to overcompensate, which may produce oscillatory behaviour. This is what we observe in the following case study (Section 3.8).

### **Logistic equation with time lag**

From Section 3.2, the logistic equation for population growth was

$$\frac{dX}{dt} = rX(t) \left(1 - \frac{X(t)}{K}\right),$$

where  $X(t)$  is the population size,  $r$  the intrinsic reproduction rate and  $K$  the carrying capacity for the environment. The term  $r(1 - X(t)/K)$  represents the density dependent reproduction rate. This states that the reproduction rate decreases with population size owing to increased deaths from overcrowding. If we now suppose that this is applied at the earlier time  $t - T$ , where  $T$  represents the time delay between increased deaths and the resulting decrease in population reproduction, then we obtain

$$\frac{dX}{dt} = rX(t) \left(1 - \frac{X(t-T)}{K}\right). \quad (3.20)$$

This type of equation is known as a *differential-difference* equation and also known as a differential-delay equation. While some linear equations of this type can yield analytic solutions, equation (3.20) is non-linear and we must use numerical techniques. These techniques are similar to the techniques for solving ordinary differential equations (see Chapter 4) but also take account of the fact that the term  $X(t - \tau)$  is evaluated at an earlier time.

MATLAB has a built-in routine for dealing with differential-delay equations, `dde23`, similar to `ode45` for solving ordinary differential equations. In addition to specifying the RHS of the differential equation we also need to specify the lag time  $\tau$  and separately any terms that are lagged (i.e. evaluated at an earlier time). Some MATLAB code for solving (3.20) is given in Listing 3.7. The graph of the solution is given in Figure 3.14. The effect of the time delay has been to induce some oscillations in the population. Again, like with the discrete logistic equation, it occurs because the regulating effect is delayed, meaning that the population can grow larger than the carrying capacity, but when the regulating effect can respond to this larger population it causes a larger death rate, consequently allowing oscillations. For smaller values of the intrinsic growth rate  $r$  and the time delay  $\tau$  the population growth is more like the typical logistic growth, as in Figure 3.5.

Listing 3.7: MATLAB code: `c_cp_logistic.dde.m`

```
function c_cp_logistic dde
global r K tau;
r=2.0; K=100;
tau=1.0; % delay amount
tend = 30; %end time
X0 = 50; %initial value

sol = dde23(@rhs, tau, X0, [0 tend]);
plot(sol.x, sol.y);
```

```
function Xdot = rhs(t, X, Xlag)
global r K;
Xdot = r*X*(1-Xlag/K);
```

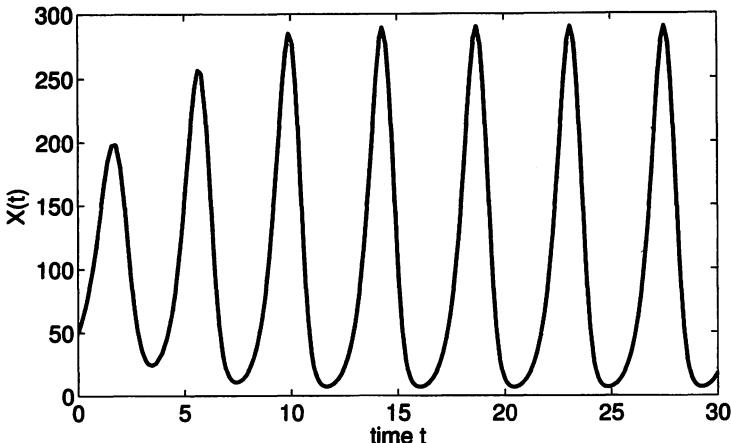


Figure 3.14: Solution of the delayed logistic equation with initial population  $X(0) = 50$ , and with parameter values  $r = 2.0$ ,  $K = 500$ .

We cannot use **Maple** directly to solve equation (3.20); however, we can approximate it by writing

$$\frac{dX}{dt} \simeq \frac{X(t + \Delta t) - X(t)}{\Delta t}.$$

Let  $\tau$  be defined as  $T$  measured as an integer multiple of  $\Delta t$ ,  $T = \tau\Delta t$ . Defining our time scale so that  $\Delta t = 1$  and writing  $X(t) = X_n$  and  $X(t + \Delta t) = X_{n+1}$ , the differential-difference equation (3.20) becomes the difference equation

Discrete 
$$X_{n+1} = X_n + rX_n \left(1 - \frac{X_{n-\tau}}{K}\right). \quad (3.21)$$

This can be iterated from an initial condition using **Maple** by adapting the code provided in Section 3.6.

We do not examine the model further here, but the interested reader will find details in May (1981). What follows is a case study adopting one such model.

### 3.8 Case Study: Australian blowflies

We now present an example of a time-delayed model, and, although we do not examine it in any depth, it serves to illustrate how the inclusion of a time lag produces oscillatory behaviour. These model results closely replicate Nicholson's data, which recorded the size of Australian blowfly populations. The following is adapted from May (1981).

Blowflies reproduce by laying their eggs in carcasses and meat or in the open wounds or sores of live animals. In the latter case the maggots hatch, and after eating the rotten flesh burrow into the animal, literally eating it alive. The open wound becomes worse, attracting more flies and so the process can snowball within a single day. Over the years, blowflies have caused a particular problem in the Australian sheep industry where farms may comprise many thousands of hectares, and the fly population is huge.

In the early part of this century A.J. Nicholson conducted single-species experiments on this Australian sheep-blowfly population (*Lucilia cuprina*). His results are well approximated by the model described by a differential-difference equation, which can itself be approximated by the difference equation

$$X_{n+1} = X_n + rX_n \left( 1 - \frac{X_{n-\tau}}{K} \right).$$

Here  $X$  is the fly population size,  $r$  its reproduction rate and  $K$  its carrying capacity. This formulation assumes the time for a newly laid egg to mature into a blowfly is  $\tau$  days and further assumes that the density dependence occurs when the eggs are laid rather than the current time.

Using Maple or MATLAB this can be solved iteratively with the following relevant parameter values  $r = 0.212 \text{ days}^{-1}$ ,  $K = 2.8 \times 10^3$  flies and  $\tau = 9$  days. Different to the delay equation in Section 2.9, here we do not assume the population is constant for  $t < 0$  but instead simulate the population from  $t = \tau$  and use historical data to calculate  $X(t - \tau)$  for  $t \leq \tau$ .

The match between the data collected and the time-delayed model predictions can be seen in Figure 3.15 where the model output is imposed on Nicholson's data (obtained from May (1981)). The model performs well in spite of being somewhat simplistic in not including accurate details of reproduction, age classes or other details associated with the flies.

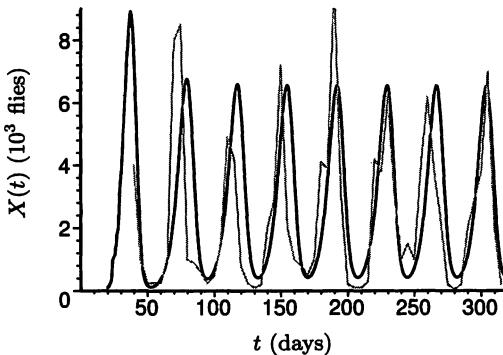


Figure 3.15: A plot of Nicholson's measurements (grey) with the model output (black). The model parameter values used are  $r = 0.212 \text{ days}^{-1}$ ,  $K = 2.8 \times 10^3$  flies and  $\tau = 9$  days. Here time steps of  $1/2$  days have been used.

### 3.9 Exercises for Chapter 3

**3.1. Farming fish.** In a fish farm, fish are harvested at a constant rate of 2100 fish per week. The per-capita death rate for the fish is 0.2 fish per day per fish, and the per-capita birth rate is 0.7 fish per day per fish.

- (a) Write down a word equation describing the rate of change of the fish population. Hence obtain a differential equation for the number of fish. (Define any symbols you introduce.)

- (b) If the fish population at a given time is 240 000, give an estimate of the number of fish born in one week.
- (c) Determine if there are any values for which the fish population is in equilibrium. (That is, look for values of the fish population for which there is no change over time.)

**3.2. Modelling the spread of technology.** Models for the spread of technology are very similar to the logistic model for population growth. Let  $N(t)$  be the number of ranchers who have adopted an improved pasture technology in Uruguay. Then  $N(t)$  satisfies the differential equation

$$\frac{dN}{dt} = aN \left(1 - \frac{N}{N^*}\right)$$

where  $N^*$  is the total population of ranchers. It is assumed that the rate of adoption is proportional to both the number who have adopted the technology and the fraction of the population of ranchers who have not adopted the technology.

- (a) Which terms correspond to the fraction of the population who have not yet adopted the improved pasture technology?
- (b) According to Banks (1994),  $N^* = 17015$ ,  $a = 0.490$  and  $N_0 = 141$ . Determine how long it takes for the improved pasture technology to spread to 80% of the population.

Note: This same model can be used to describe the spread of a rumour within an organisation or population.

**3.3. Density dependent births.** Many animal populations have decreasing per-capita birth rates when the population density increases, as well as increasing per-capita death rates. Suppose the density dependent per-capita birth rate  $B(X)$  and density dependent death rate  $A(X)$  is given by

$$B(X) = \beta - (\beta - \alpha)\delta \frac{X}{K}, \quad A(X) = \alpha + (\beta - \alpha)(1 - \delta) \frac{X}{K}$$

where  $K$  is the population carrying capacity,  $\beta$  is the intrinsic per-capita birth rate,  $\alpha$  is the intrinsic per-capita death rate and  $\delta$ , where  $0 \leq \delta \leq 1$ , is a parameter describing the extent that density dependence is expressed in births or deaths.

Show that this still gives rise to the standard logistic differential equation

$$\frac{dX}{dt} = rX \left(1 - \frac{X}{K}\right).$$

**3.4. Mouse population model.** A population, initially consisting of 1000 mice, has a per-capita birth rate of 8 mice per month (per mouse) and a per-capita death rate of 2 mice per month (per mouse). Also, 20 mouse traps are set each week and they are always filled.

Write down a word equation describing the rate of change in the number of mice and hence write down a differential equation for the population.

**3.5. Harvesting model.** Consider the harvesting model from Section 3.3,

$$\frac{dX}{dt} = rX \left(1 - \frac{X}{K}\right) - h.$$

- (a) Show there can be two non-zero equilibrium populations, with the larger value given by

$$X_e = \frac{K}{2} \left(1 + \sqrt{1 - \frac{4h}{rK}}\right).$$

For the parameter values used in Figure 3.7, calculate the value of this equilibrium population.

- (b) If the harvesting rate  $h$  is greater than some critical value  $h_c$ , the non-zero equilibrium values do not exist and the population tends to extinction. What is this critical value  $h_c$ ?
- (c) If the harvesting rate is  $h < h_c$ , the population may still become extinct if the initial population  $x_0$  is below some critical level, perhaps due to an ecological disaster. Show that this critical initial value is

$$x_c = \frac{K}{2} \left( 1 - \sqrt{1 - \frac{4h}{rK}} \right).$$

(Hint: Consider where  $X' < 0$ .)

**3.6. Fishing with quotas.** In view of the potentially disastrous effects of overfishing causing a population to become extinct, some governments impose quotas which vary depending on estimates of the population at the current time. One harvesting model that takes this into account is

$$\frac{dX}{dt} = rX \left( 1 - \frac{X}{K} \right) - h_0 X.$$

- (a) Show that the only non-zero equilibrium population is

$$X_e = K \left( 1 - \frac{h}{r} \right).$$

- (b) At what critical harvesting rate can extinction occur?

Although extinction can occur with this model, as the harvesting parameter  $h$  increases towards the critical value the equilibrium population tends to zero. This contrasts with the constant harvesting model in Section 3.3 and Question 5, where a sudden population crash (from a large population to extinction) can occur as the harvesting rate increases beyond a critical value.

**3.7. Predicting population size.** In a population the initial population is  $x_0 = 100$ . Suppose a population can be modelled using the differential equation

$$\frac{dX}{dt} = 0.2X - 0.001X^2,$$

with an initial population size of  $x_0 = 100$  and a time step of 1 month. Find the predicted population after two months. (Use either an analytical solution, or a numerical solution from Maple or MATLAB.)

**3.8. Plant biomass.** Let the dry weight of some plant (that is, its biomass) at time  $t$  be denoted by  $x(t)$ . And suppose this plant feeds off a fixed amount of some single substrate, or a nutrient medium, for which the amount remaining at time  $t$  is denoted by  $S(t)$ . Assume that the growth rate of the plant is proportional to its dry weight as well as to the amount of nutrient available, and that no material is lost in the conversion of  $S$  into  $x$ .

- (a) Starting with a word equation, model the rate of plant growth  $dx/dt$  with an initial plant biomass of  $x_0$  and with  $x_f$  the amount of plant material associated with  $S = 0$ . (Use the fact that  $S$  can be written as a function of  $x$  and  $x_f$ :  $S(t) = x_f - x(t)$ .)
- (b) Solve the equation using analytical techniques or numerically with Maple or MATLAB. (Separable techniques together with partial fractions are one way to solve the equation.)
- (c) Using this model why can the plant biomass of  $x_f$  never be attained? (In spite of this, and the fact that plants do reach a maximum biomass with finite time, this model does give a reasonable prediction of annual plant growth.)

**3.9. Modelling the population of a country.** Consider the population of a country. Assume constant per-capita birth and death rates, and that the population follows an exponential growth (or decay) process. Assume there to be significant immigration and emigration of people into and out of the country.

- Assuming the overall immigration and emigration rates are constant, formulate a single differential equation to describe the population size over time.
- Suppose instead that all immigration and emigration occurs with a neighbouring country, such that the net movement from one country to the other is proportional to the population difference between the two countries and such that people move to the country with the larger population. Formulate a coupled system of equations as a model for this situation.

In both (a) and (b) start with appropriate word equations and ensure all variables are defined. Give clear explanations of how the differential equations are obtained from the word equations.

**3.10. Sensitivity to initial conditions.** Referring to the results generated in Figure 3.12 for two separate initial conditions,  $x_0 = 100$  and  $x_0 = 101$ , generate the results with these initial conditions for  $r < 2.7$ ,  $r = 2.5$  and  $r = 1.9$ . What do you notice about the distance between the two graphs at each time step? (The relevant code is given in Section 3.6.)

**3.11. Investigating parameter change.** Using Maple or MATLAB examine the effect of increasing the parameter  $r$  on the solution to the equation

$$X_{n+1} = X_n e^{a(1-X_n/K)}, \quad \text{where } a = \ln(r+1).$$

Establish (roughly) for what values of  $r$  the system undergoes its first two bifurcations. (Code can be adapted from that in Section 3.6.)

**3.12. Modelling insect populations with a difference equation.** Many insect populations breed only at specific times of the year and all the adults die after breeding. These may be best modelled by a difference equation, such as

$$X_{n+1} = r(X_n - 0.001X_n^2).$$

Using Maple or MATLAB investigate what happens as the parameter  $r$  (the growth rate) is varied from  $r = 0$  to  $r = 3$ . Sketch all the different types of growth patterns observed, together with the corresponding value of  $r$ .

**3.13. Chemostat.** A chemostat is used by microbiologists and ecologists to model aquatic environments, or waste treatment plants. It consists of a tank filled with a mixture of some medium and nutrients, which microorganisms require to grow and multiply. A fresh nutrient-medium mixture is pumped into the tank at a constant rate  $F$  and the tank mixture is pumped from the tank at the same rate. In this way the volume of liquid in the tank remains constant. Let  $S(t)$  denote the concentration of the nutrient in the tank at time  $t$ , and assume the mixture in the tank is well stirred. Let  $x(t)$  denote the concentration of the microorganism in the tank at time  $t$ .

- Draw a compartmental diagram for the system.
- In the absence of the organism, suggest a model for the rate of change of  $S(t)$ .
- If the microorganisms' per-capita uptake of the nutrient is dependent on the amount of nutrient present and is given by  $p(S)$ , and the per-capita reproduction rate of the microorganism is directly proportional to  $p(S)$ , extend the model equation above to include the effect of the organism. (The per-capita uptake function measures the rate at which the organism is able to absorb the nutrient when the nutrient's concentration level is  $S$ .)
- Now develop an equation describing the rate of change of the concentration of the live organism ( $x'$ ) in the tank to derive the second equation for the system.