

E. coli are found in the gut of animals, and colicin production varies markedly between populations. The process of cell lysis has been studied in detail by Levin (1988); Frank (1994); Gordon and Riley (1999); Kerr et al. (2002); Kirkup and Riley (2004); however, in this case study we investigate a different phenomenon. We examine whether the turnover rate in the gastro-intestinal tract determines which strains of *E. coli* dominate when colicin producing strains interact with colicin sensitive strains. It has been observed that in hosts with fast gut turnover rates, such as carnivores, non-colicin producing strains dominate, while in hosts with slow turnover rates, such as herbivores, colicin producing strains dominate.

To examine the dynamics we consider a gastro-intestinal tract of fixed volume V , and consider the interaction between two strains of *E. coli*; one a colicin producing strain x with density X in the gut, and one a colicin sensitive strain y with density Y . We assume a constant flow rate of food F into and from the gut and the densities with which the strains enter with the flow are X_{in} and Y_{in} . Within the gut we assume exponential growth for each strain with growth rates of β_x and β_y , which is a reasonable assumption during the initial stages of the dynamics. It should be noted that the qualitative results were unchanged when logistic growth was considered (see exercises, Question 19).

We now introduce the process of cell lysis. We assume that cells of strain x lyse at the per-capita rate α_x , with each lysed cell producing 10^6 colicin molecules, and each molecule capable of killing a cell of the opposing strain, destroying itself in the process. A model for this process is

$$\begin{aligned}\frac{dX}{dt} &= \beta_x X + (X_{\text{in}} - X) \frac{F}{V} - \alpha_x X \\ \frac{dY}{dt} &= \beta_y Y + (Y_{\text{in}} - Y) \frac{F}{V} - c_2 XY.\end{aligned}\quad (6.24)$$

Note that the last term of dY/dt , c_2XY is a mortality rate of Y cells due to the rate of contact between the two different strains of cells. From Gordon and Riley (1999), the probability of an encounter of a colicin cell with a sensitive cell is of the order 10^{-11} . We can therefore determine the form of the c_2XY terms and estimate the c_2 parameter. We can calculate the rate of Y cells dying from a colicin molecule produced by all the lysed X cells as

$$\begin{aligned}\left\{ \begin{array}{l} \text{rate of} \\ Y \text{ cells} \\ \text{dying} \end{array} \right\} &= \left\{ \begin{array}{l} \text{rate of} \\ X \text{ cells} \\ \text{lysed} \end{array} \right\} \times \left\{ \begin{array}{l} \text{no. of colicin} \\ \text{molecules produced} \\ \text{per } X \text{ cell} \end{array} \right\} \times \left\{ \begin{array}{l} \text{probability of} \\ \text{contact} \end{array} \right\} \times \left\{ \begin{array}{l} \text{no. of} \\ Y \text{ cells} \end{array} \right\} \\ &\simeq (\alpha_x X) \times 10^6 \times 10^{-11} \times Y \\ &= 10^{-5} \alpha_x X Y.\end{aligned}$$

Since typical cell densities are of the order 10^6 , we rescale both X and Y in the equations (6.24) to be in units of 10^6 cells. This now gives $c_2 \simeq 10\alpha_x$ (i.e. a factor of 10^6 cancels out from all terms in both sides of each equation except for the XY term).

Our aim is to investigate whether the mean residence time $\tau = V/F$ (where turnover rate is $F/V = 1/\tau$) determines which strain dominates. To do so we examine the nullclines, by setting $dX/dt = 0$ and $dY/dt = 0$, and consider any stable equilibrium points in the positive phase plane. Our results are illustrated in Figure 6.13, where the stable node is plotted against F (recalling that F/V is turnover rate that increases with F). We note that the ‘change’ between the dominance of colicin producing cells (X) and non-colicin producing cells (Y), according to this model, occurs for $F \approx 6$. It is evident that for low turnover rates (herbivores), the colicin producing strain dominates, while for high turnover rates (carnivores), the non-colicin producing strain dominates. This is in agreement with

observations. Thus, in spite of the relative simplicity of this model, the results seem to encapsulate the observed phenomena.

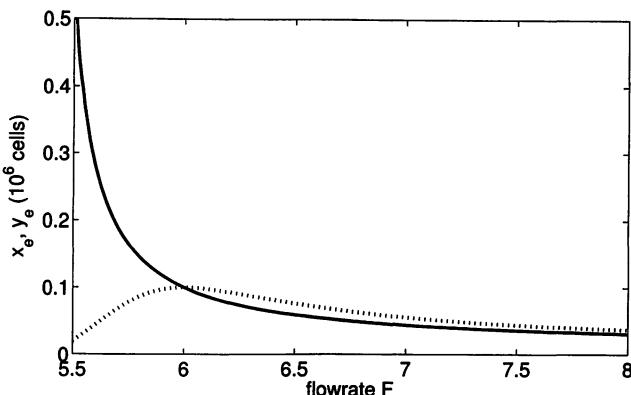


Figure 6.13: The equilibrium values for X (solid line) and Y (dashed line) are plotted for increasing values of F , and hence increasing turnover rate. (Parameter values were $\beta_x = \beta_y = 0.3$, $X_{\text{in}} = Y_{\text{in}} = 0.01 \times 10^6$, $V = 20$ units and $\alpha_x = 0.03$.)

We note that in reality bacteria enter at variable and random rates, not a constant rate as applied here. Barnes et al. (2007) considered this scenario using random values for X_{in} and Y_{in} . They found that the qualitative results were unchanged in that, over hundreds of simulations, colicin producing strains dominated in the majority of cases for low turnover rates, and vice versa.

Interest in such bacteria and their dynamics continues to increase since they have the potential for use as bio-control agents for the management of fungal and bacterial plant pathogens, and also as the active agent in probiotic formulations. Probiotic therapy is a disease prevention strategy used in humans and domestic animals, as well as being a means of enhancing growth in livestock. The ultimate aim is to ensure the presence of ‘good’ bacteria in the gut that knock out bacterial pathogens. However, effective use of bacteria will require a sound understanding of microbial ecology and, from the results presented here, diet has a significant impact.

6.8 Exercises for Chapter 6

6.1. Simple example. Find the only equilibrium point for the system

$$x' = x - 5y, \quad y' = x - y.$$

Then use Maple or MATLAB to numerically plot phase-plane trajectories for this system, showing the trajectories are closed, and enclose this equilibrium point.

6.2. Finding equilibrium points. For the following, find all the equilibrium solutions.

$$(a) \frac{dX}{dt} = 3X - 2XY, \quad \frac{dY}{dt} = XY - Y,$$

$$(b) \frac{dX}{dt} = 2X - XY, \quad \frac{dY}{dt} = Y - XY,$$

$$(c) \frac{dX}{dt} = Y - 2XY, \quad \frac{dY}{dt} = XY - Y^2.$$

6.3. Using the chain rule. For the differential equations

$$\frac{dX}{dt} = -XY, \quad \frac{dY}{dt} = -2Y,$$

use the chain rule to find a relation between Y and X .

6.4. Contagious for life. Consider a disease where all those infected remain contagious for life. A model describing this is given by the differential equations

$$\frac{dS}{dt} = -\beta SI, \quad \frac{dI}{dt} = \beta SI.$$

where β is a positive constant.

- (a) Use the chain rule to find a relation between S and I .
- (b) Obtain and sketch the phase-plane curves. Determine the direction of travel along the trajectories.
- (c) Using this model, is it possible for all the susceptibles to be infected?

6.5. Disease with reinfection. A model for the spread of a disease, where all infectives recover from the disease and become susceptibles again, is given by the pair of differential equations

$$\frac{dS}{dt} = -\beta SI + \gamma I, \quad \frac{dI}{dt} = \beta SI - \gamma I,$$

where β and γ are positive constants, $S(t)$ denotes the number of susceptibles and $I(t)$ denotes the number of infectives at time t .

- (a) Use the chain rule to find a relationship between the number of susceptibles and the number of infectives given the initial number of susceptibles is s_0 and there was initially only one infective.
- (b) Draw a sketch of typical phase-plane trajectories. Deduce the direction of travel along the trajectories providing reasons.
- (c) Using the phase-plane diagram describe how the number of infectives changes with time.

6.6. Predator-prey with density dependent growth of prey. Consider the system

$$\frac{dX}{dt} = \beta_1 X \left(1 - \frac{X}{K}\right) - c_1 XY, \quad \frac{dY}{dt} = c_2 XY - \alpha_2 Y,$$

for the dynamics of a predator-prey model, with density dependent growth of the prey, and all parameters positive constants.

- (a) Find all the equilibrium points. How do they differ from those of the standard Lotka-Volterra system in Section 6.4?
- (b) Use Maple or MATLAB to explore the phase-plane trajectories for different parameter values and initial conditions.

6.7. Predator-prey with DDT. The predator-prey equations with additional deaths by DDT are

$$\frac{dX}{dt} = \beta_1 X - c_1 XY - p_1 X, \quad \frac{dY}{dt} = -\alpha_2 Y + c_2 XY - p_2 Y,$$

where all parameters are positive constants.

- (a) Find all the equilibrium points.
- (b) What effect does the DDT have on the non-zero equilibrium populations compared with the case when there is no DDT? Compare this with Figure 5.7 in Section 5.3, which was for a specific set of parameter values. What general conclusions can you draw?
- (c) Show that the predator fraction of the total average prey population is given by

$$f = \frac{1}{1 + \left(\frac{c_1(c_2+p_2)}{c_2(\beta_1-p_1)} \right)}.$$

What happens to this proportion f as the DDT kill rates, p_1 and p_2 , increase?

6.8. Predator-prey with density dependence and DDT. For the predator-prey model with density dependence for the prey and DDT acting on both species,

$$\frac{dX}{dt} = \beta_1 X \left(1 - \frac{X}{K} \right) - c_1 XY - p_1 X, \quad \frac{dY}{dt} = c_2 XY - \alpha_2 Y - p_2 Y,$$

show that (X_e, Y_e) , where

$$X_e = \frac{\alpha_2 + p_2}{c_2}, \quad Y_e = \frac{\beta_1 \left(1 - \frac{X_e}{K} \right) - p_1}{c_1},$$

is one equilibrium point, and determine if there are any other equilibrium points.

6.9. One prey and two predators. A model of a three species interaction is

$$\frac{dX}{dt} = a_1 X - b_1 XY - c_1 XZ, \quad \frac{dY}{dt} = a_2 XY - b_2 Y, \quad \frac{dZ}{dt} = a_3 XZ - b_3 Z,$$

where a_i , b_i , c_i , for $i = 1, 2, 3$, are all positive constants. Here $X(t)$ is the prey density and $Y(t)$ and $Z(t)$ are the two predator species densities.

- (a) Find all possible equilibrium populations. Is it possible for all three populations to coexist in equilibrium?
- (b) What does this suggest about introducing an additional predator into an ecosystem?

6.10. Competing species without density dependence. For the competing species model developed in Section 5.5, exhibiting exponential growth in the absence of a competitor, find the equilibrium points and trajectory directions in different parts of the (X, Y) -plane. Hence sketch the phase-plane diagram. Show that this diagram is consistent with the numerical results generated in Section 5.5, and illustrated in Figure 5.10.

6.11. Competing species with density dependence. Consider the competition population model with density dependent growth

$$\frac{dX}{dt} = X(\beta_1 - c_1 Y - d_1 X), \quad \frac{dY}{dt} = Y(\beta_2 - c_2 X - d_2 Y).$$

- (a) Find all four equilibrium points for the system.

- (b) Establish all four possible direction vector diagrams for the phase-plane. (This will complete Example 12 in Section 6.5, which considers only Case 3 in detail.)
- (c) From your results above, choose appropriate parameter values to represent each of the four cases, and then using Maple or MATLAB with these parameter values, plot a phase-plane diagram for each case.

6.12. Rabbits and foxes. A population of sterile rabbits $X(t)$ is preyed upon by a population of foxes $Y(t)$. A model for this population interaction is the pair of differential equations

$$\frac{dX}{dt} = -aXY, \quad \frac{dY}{dt} = bXY - cY$$

where a , b and c are positive constants.

- (a) Use the chain rule to obtain a relationship between the density of foxes and the density of rabbits.
- (b) Sketch typical phase-plane trajectories, indicating the direction of movement along the trajectories.
- (c) According to the model, is it possible for the foxes to completely wipe out the rabbit population? Give reasons.

6.13. Microorganisms and toxins. The pair of differential equations

$$\frac{dP}{dt} = rP - \gamma PT, \quad \frac{dT}{dt} = qP,$$

where r , γ and q are positive constants, is a model for a population of microorganisms P , which produces toxins T which kill the microorganisms.

- (a) Given that initially there are no toxins and p_0 microorganisms, obtain an expression relating the population density and the amount of toxins. (Hint: Use the chain rule.)
- (b) Hence, give a sketch of a typical phase-plane trajectory. Using this, describe what happens to the microorganisms over time.

6.14. Fatal disease. The following model is for a fatal disease, where all infectives die from the disease, with death rate α , and where the transmission is assumed to be frequency dependent so the contact rate is constant. The differential equations are

$$\frac{dS}{dt} = -\frac{pc}{N}SI, \quad \frac{dI}{dt} = \frac{pc}{N}SI - \alpha I,$$

where $N = S + I$ is the total population size and c is the (constant) per-capita contact rate and p is the constant probability of a contact resulting in an infection.

- (a) Write the system in terms of the variables N and I (i.e. obtain a differential equation for N) and hence show that

$$\frac{dI}{dN} = \frac{pc}{\alpha N} I + \left(1 - \frac{pc}{\alpha}\right).$$

- (b) Solve the differential equation in (a) to obtain

$$I = N + KN^{pc/\alpha}$$

where K is the arbitrary constant of integration.

- (c) Discuss any qualitative differences between this model and the one studied in Section 6.2. (Hint: Substitute $S = N - I$ for a meaningful comparison, and graph I against S .)

6.15. Battle model with desertion. The following battle model represents two armies where both are exposed to aimed fire, and for one of the armies there is significant loss due to desertion (at a constant rate). The numbers of soldiers, R and B , satisfy the differential equations

$$\frac{dR}{dt} = -a_1 B - c, \quad \frac{dB}{dt} = -a_2 R,$$

where a_1 , a_2 and c are positive constants.

- (a) If the initial number of red soldiers is r_0 and the initial number of blue soldiers is b_0 , use the chain rule to find a relationship between B and R .
- (b) For $a_1 = a_2 = c = 0.01$ give a sketch of typical phase-plane trajectories and deduce the direction of travel along the trajectories.

6.16. Jungle warfare. A simple mathematical model describing a jungle warfare, with one army exposed to random fire and the other to aimed fire, is given by the coupled differential equations

$$\frac{dR}{dt} = -c_1 RB, \quad \frac{dB}{dt} = -a_2 R,$$

where c_1 and a_2 are positive constants.

- (a) Use the chain rule to find a relation between R and B , given initial numbers of soldiers r_0 and b_0 . Hence sketch some typical phase-plane trajectories. Give directions of travel along the trajectories, providing reasons for your choice.
- (b) Given that, initially, both the red and blue armies have 1000 soldiers, and the constants c_1 and a_2 are 10^{-4} and 10^{-1} , respectively, determine how many soldiers are left if the battle is fought so that all the soldiers of one army are killed.
- (c) In this model, one of the armies is hidden whereas the other is visible to their enemy. Which is the hidden army? Give reasons for your answer.

6.17. Battle with long range weapons. In a long range battle, neither army can see the other, but fires into a given area. A simple mathematical model describing this battle is given by the coupled differential equations

$$\frac{dR}{dt} = -c_1 RB, \quad \frac{dB}{dt} = -c_2 RB$$

where c_1 and c_2 are positive constants.

- (a) Use the chain rule to find a relationship between R and B , given the initial numbers of soldiers for the two armies are r_0 and b_0 , respectively.
- (b) Draw a sketch of typical phase-plane trajectories.
- (c) Explain how to estimate the parameter c_1 given that the blue army fires into a region of area A .

6.18. SIR model, estimating the transmission coefficient. Adapted from Brauer and Castillo-Chàvez (2001).

For the standard SIR epidemic model

$$S' = -\beta SI, \quad I' = \beta SI - \gamma I,$$

state, from the notes, the equation for the analytic form of the phase-plane trajectories. If s_f denotes the remaining number of susceptibles when there are no remaining infectives then show that

$$\frac{\beta}{\gamma} = \frac{\ln(s_0/S_f)}{S_0 + i_0 - s_f}$$

where s_0 and i_0 are the initial numbers of susceptibles and infectives, respectively.

- (a) A study at Yale university in 1982 described an influenza epidemic with initial proportions of susceptibles of the student population as 91.1% and final proportion of susceptibles as 51.3%. (Assume, initially, that no one had recovered).
- (b) Given the mean infectious period for influenza γ^{-1} is approximately 3 days, estimate the combination βN , where N is the total population size, and hence estimate R_0 , the basic reproduction number.

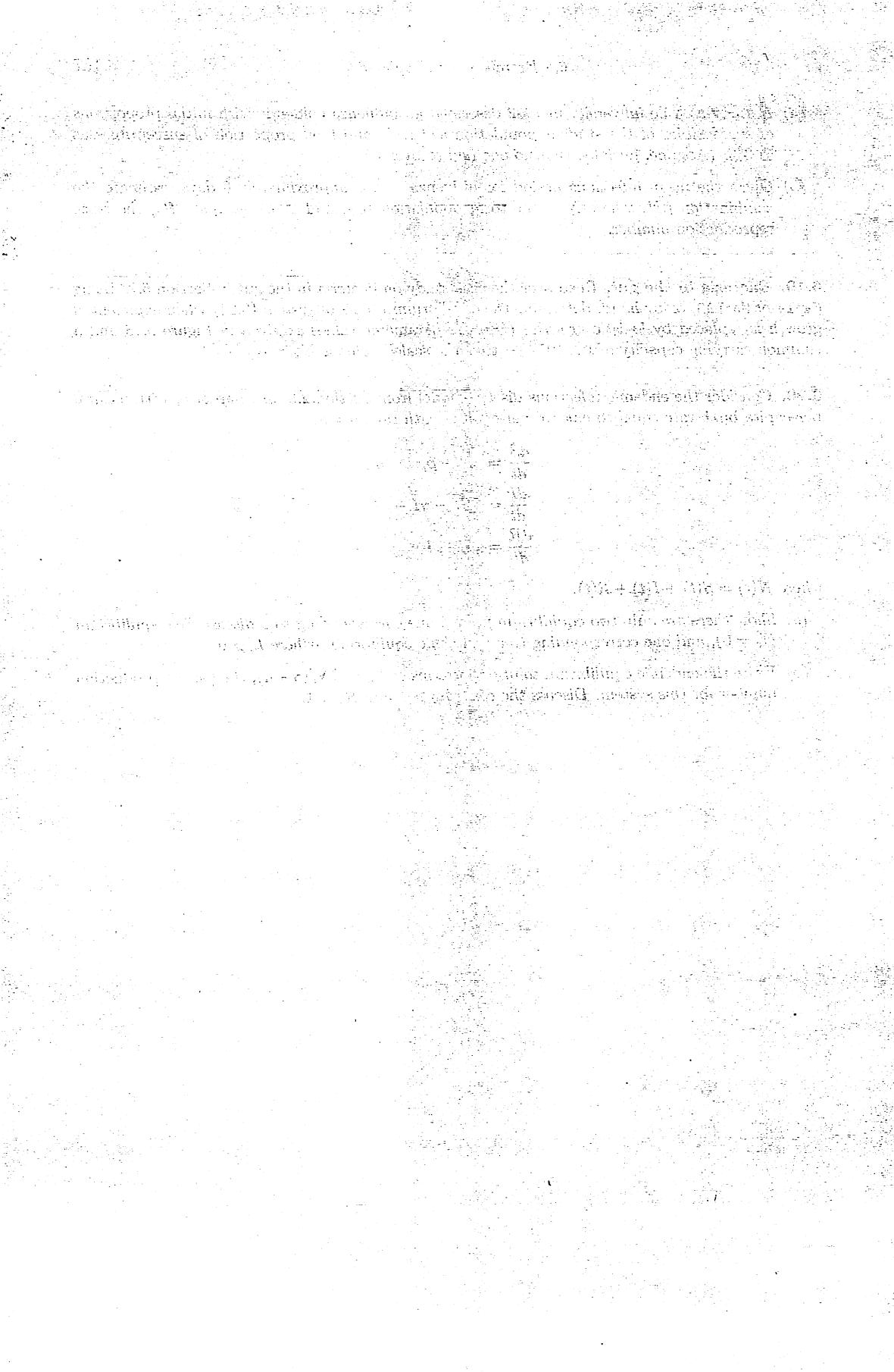
6.19. Bacteria in the gut. Read over the case study on bacteria in the gut in Section 6.7. Using Maple or MATLAB, or by hand, determine the equilibrium points of system (6.24) when exponential growth is replaced by logistic growth. (Use the parameter values as given in Figure 6.13 and a common carrying capacity of 1×10^{-6} — thus the scaled value is $K_x = K_y = 1$.)

6.20. Consider the endemic infectious disease model from Section 2.5, in Chapter 5, with natural per-capita birth rate equal to natural per-capita death rate, $b = a$,

$$\begin{aligned}\frac{dS}{dt} &= aN - \beta SI - aS \\ \frac{dI}{dt} &= \beta SI - \gamma I - aI \\ \frac{dR}{dt} &= \gamma I - aI\end{aligned}$$

where $N(t) = S(t) + I(t) + R(t)$.

- (a) Show there are only two equilibrium points, one corresponding to a disease-free equilibrium ($I_e = 0$), and one corresponding to an endemic equilibrium, where $I_e > 0$.
- (b) Write the endemic equilibrium solution in terms of $R_0 = \beta N / (\gamma + a)$, the basic reproduction number for this system. Discuss the cases $R_0 > 1$ and $R_0 < 1$.



Chapter 7

Linearisation analysis

In the following chapter we develop some powerful theory, which often allows us to predict the dynamics of a system in general terms. It provides the means by which we can establish the phase-plane behaviour of a system and predict the outcome for any possible parameter combination. The theory is developed for both linear and nonlinear systems, and is applied to some of the nonlinear systems studied in Chapters 5 and 6.

7.1 Introduction

From the small sample of examples we have examined in the previous chapters, we have seen that systems of equations can result in many different types of behaviour. Depending on the initial conditions or the chosen parameter values, the outcome may be stable or unstable, cyclic or divergent.

In this chapter we develop some powerful theory which allows us to predict the dynamical behaviour of a system. In the first case, we consider only linear systems of equations. However, since many of the interacting population models we have met are nonlinear (and in fact most natural systems are nonlinear), we then show how this theory for the linear case may be extended to nonlinear systems as well. In the final section we apply the process to the nonlinear models of population interactions, which we developed in Chapters 5 and 6, and shall extend in Chapter 8.

7.2 Linear theory

So far, in our phase-plane analysis of systems of equations, we have encountered a variety of behaviours of trajectories near equilibrium points. For example we saw trajectories approaching some of these points, trajectories being repelled by others, as well as spiralling trajectories and closed loops.

In the following theory we develop techniques which allow us to predict, for each equilibrium point, the behaviour of the trajectories close to that point. From this we can establish a complete picture of the system phase-plane. Initially, we consider the linear case (a pair of coupled linear equations in two unknowns) and then show how this can be extended to the nonlinear case. (Whilst we restrict our analysis to two equations in two unknowns, the theory is applicable to larger systems with many unknowns.)

The general linear system

We start by considering the following general form of a pair of coupled linear equations:

$$\begin{aligned} X' &= a_1X + b_1Y \\ Y' &= a_2X + b_2Y \end{aligned}$$

where differentiation is with respect to time t (i.e. $X' = dX/dt$, $Y' = dY/dt$) and a_1, a_2, b_1 and b_2 are constant.

We denote an equilibrium point (critical point or steady-state) for the system by (x_e, y_e) . Thus $a_1x_e + b_1y_e = 0$ and $a_2x_e + b_2y_e = 0$.

Linear algebra notation

The system above can be written in terms of matrices and vectors in the following way. Let

$$\mathbf{x} = \begin{bmatrix} X \\ Y \end{bmatrix} \quad \text{and} \quad \mathbf{x}' = \begin{bmatrix} X' \\ Y' \end{bmatrix}$$

where \mathbf{x} is a vector. Let

$$\mathbf{A} = \begin{bmatrix} a_1 & b_1 \\ a_2 & b_2 \end{bmatrix}$$

where \mathbf{A} is a matrix. Then the above system of two equations can be written as

$$\mathbf{x}' = \mathbf{Ax}.$$

This means that

$$\begin{bmatrix} X' \\ Y' \end{bmatrix} = \begin{bmatrix} a_1 & b_1 \\ a_2 & b_2 \end{bmatrix} \begin{bmatrix} X \\ Y \end{bmatrix} = \begin{bmatrix} a_1 X + b_1 Y \\ a_2 X + b_2 Y \end{bmatrix} \quad (7.1)$$

using normal matrix multiplication.

What needs to be understood in general is the effect of multiplying a vector by a matrix \mathbf{A} . We look at an example to illustrate this.

Example 7.1: Carry out the multiplication \mathbf{Ax}_1 and \mathbf{Ax}_2 where

$$\mathbf{A} = \begin{bmatrix} 3 & -2 \\ 1 & 0 \end{bmatrix}, \quad \mathbf{x}_1 = \begin{bmatrix} -1 \\ 1 \end{bmatrix}, \quad \mathbf{x}_2 = \begin{bmatrix} 2 \\ 1 \end{bmatrix}.$$

Solution:

$$\mathbf{Ax}_1 = \begin{bmatrix} -3 - 2 \\ -1 \end{bmatrix} = \begin{bmatrix} -5 \\ -1 \end{bmatrix}$$

and

$$\mathbf{Ax}_2 = \begin{bmatrix} 6 - 2 \\ 2 \end{bmatrix} = \begin{bmatrix} 4 \\ 2 \end{bmatrix} = 2 \begin{bmatrix} 2 \\ 1 \end{bmatrix}.$$

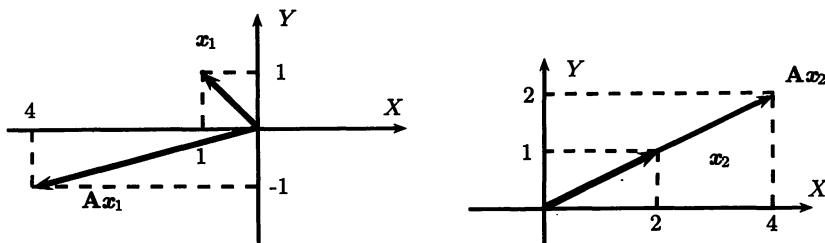


Figure 7.1: The effect of multiplying vectors \mathbf{x}_1 and \mathbf{x}_2 by a matrix \mathbf{A} as defined in Example 1.

These results are illustrated in Figure 7.1. So multiplication by a matrix \mathbf{A} maps a vector onto another vector. In the case of \mathbf{x}_2 we have that

$$\mathbf{Ax}_2 = 2\mathbf{x}_2,$$

so that the effect of multiplying by A is the same as multiplying by a scalar or number (which is 2 in this case). We use this notion of the ‘equivalence’ of multiplication by a matrix and a scalar (number) in the process of finding eigenvalues and eigenvectors: the latter will be the vectors for which there is a nontrivial solution to the equation, and the former will be the associated scalars. These values turn out to be essential in predicting the behaviour of trajectories in the phase-plane associated with the system. For further details of matrix algebra see Appendix B.1.

Outline of method to solve equations

In order to solve a general system of equations, as in (7.1), we can transform the equations onto a different system of axes. In choosing the new axes carefully, the equations transform to simple differential equations of exponential growth or decay, and thus are simple to solve. Finally, these solutions can be transformed back to the original system of axes to provide a solution in the required form.

In order to transform a general pair of differential equations, which may be hard to solve, into a system which is easy to solve, we find and use the eigenvalues and eigenvectors. (These are described fully in Appendix B.1.) Essentially, *eigenvectors* \mathbf{x} are the non-zero solutions of the matrix equation

$$\mathbf{A}\mathbf{x} = \lambda\mathbf{x}$$

where the *eigenvalues* λ are the values for which these non-zero solutions exist.

Rewriting the equation as $\mathbf{A}\mathbf{x} - \lambda\mathbf{x} = 0$ and then expanding using matrix multiplication we get

$$\mathbf{A}\mathbf{x} - \lambda\mathbf{x} = (\mathbf{A} - \lambda\mathbf{I})\mathbf{x} = \begin{bmatrix} a_1 - \lambda & b_1 \\ a_2 & b_2 - \lambda \end{bmatrix} \mathbf{x},$$

where \mathbf{I} is the identity matrix

$$\mathbf{I} = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}.$$

From the theory of linear algebra (see Appendix B.1) it follows that for non-zero solutions of this equation to exist, the determinant of the expression must be zero, and thus we get the *characteristic equation* of matrix \mathbf{A}

$$|\mathbf{A} - \lambda\mathbf{I}| = \lambda^2 - \lambda(a_1 + b_2) + (a_1b_2 - a_2b_1).$$

This equation is central to the theory which is developed here. Note that the coefficient of λ is the sum of the diagonal elements of the matrix \mathbf{A} , namely the *trace* of \mathbf{A} , and also that the last term is the *determinant* of matrix \mathbf{A} . We use these values extensively when applying the theory which we now develop.

We can establish the eigenvalues as the solutions to this characteristic equation. (We could also then solve for the associated pair of eigenvectors from the vector equation, but do not need these values in the applications.) From here the trajectory behaviour can be determined since, as will become apparent, it is dependent entirely on the eigenvalues.

Establishing the trajectory behaviour

We return to the general pair of linear first-order equations

$$\begin{aligned} X' &= a_1X + b_1Y, \\ Y' &= a_2X + b_2Y, \end{aligned}$$

which has an equilibrium point at the origin, $(x_e, y_e) = (0, 0)$. In vector notation then

$$\mathbf{x}' = \mathbf{A}\mathbf{x}.$$

Suppose we have found the eigenvalues, λ_1 and λ_2 , as well as the associated eigenvectors for A , namely

$$\mathbf{u} = \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} \quad \text{and} \quad \mathbf{v} = \begin{bmatrix} v_1 \\ v_2 \end{bmatrix}.$$

We define \mathbf{U} to be the matrix whose columns are the eigenvectors, thus

$$\mathbf{U} = [\mathbf{u} \ \mathbf{v}] = \begin{bmatrix} u_1 & v_1 \\ u_2 & v_2 \end{bmatrix}.$$

From the definition of eigenvectors and eigenvalues we have

$$\mathbf{A}\mathbf{u} = \lambda_1 \mathbf{u} \quad \text{and} \quad \mathbf{A}\mathbf{v} = \lambda_2 \mathbf{v},$$

which implies that

$$\mathbf{A} [\mathbf{u} \ \mathbf{v}] = [\lambda_1 \mathbf{u} \ \lambda_2 \mathbf{v}] = [\mathbf{u} \ \mathbf{v}] \begin{bmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{bmatrix} \quad \text{or} \quad \mathbf{AU} = \mathbf{UD}$$

with

$$\mathbf{D} = \begin{bmatrix} \lambda_1 & 0 \\ 0 & \lambda_2 \end{bmatrix}.$$

Assuming that \mathbf{U} is invertible, we can write

$$\mathbf{U}^{-1} \mathbf{AU} = \mathbf{D}. \quad (7.2)$$

We use this equation below.

First we express \mathbf{x} as a linear combination of the eigenvectors and, assuming this is possible, we have

$$\mathbf{x} = z_1 \mathbf{u} + z_2 \mathbf{v}.$$

Letting

$$\mathbf{z} = \begin{bmatrix} z_1 \\ z_2 \end{bmatrix} \quad \text{then} \quad \mathbf{x} = \mathbf{Uz}.$$

Since X and Y are functions of time, and the eigenvectors are not (since \mathbf{A} is not a function of time), then z_1 and z_2 must also be functions of time. We now establish two expressions for \mathbf{x}' :

$$\mathbf{x} = \mathbf{Uz} \quad \text{so} \quad \mathbf{x}' = \mathbf{Uz}',$$

and also

$$\mathbf{x}' = \mathbf{Ax} \quad \text{so} \quad \mathbf{x}' = \mathbf{AUz}.$$

Equating these two expressions for \mathbf{x}' and then using (7.2) gives

$$\mathbf{Uz}' = \mathbf{AUz},$$

and then

$$\begin{aligned} \mathbf{z}' &= \mathbf{U}^{-1} \mathbf{AUz} \\ &= \mathbf{Dz}. \end{aligned}$$

We are now in a position to solve the differential equations easily. Expanding $\mathbf{z}' = \mathbf{Dz}$

$$\begin{aligned} z'_1 &= \lambda_1 z_1, \\ z'_2 &= \lambda_2 z_2, \end{aligned}$$

we obtain two equations which are easy to solve. They are the equations for exponential growth and decay with which, by now, we are familiar. We have as solutions $z_1 = k_1 e^{\lambda_1 t}$ and $z_2 = k_2 e^{\lambda_2 t}$ where k_1 and k_2 are arbitrary constants.

Using these we can find solutions for X and Y by retracing our steps through this process and carrying the solutions with us. We have

$$\begin{aligned} \mathbf{x} &= k_1 e^{\lambda_1 t} \mathbf{u} + k_2 e^{\lambda_2 t} \mathbf{v} \\ &= e^{\lambda_1 t} \hat{\mathbf{u}} + e^{\lambda_2 t} \hat{\mathbf{v}}, \end{aligned}$$

where $\hat{\mathbf{u}} = k_1 \mathbf{u}$ and $\hat{\mathbf{v}} = k_2 \mathbf{v}$ are two eigenvectors (as any scalar multiple of an eigenvector is again an eigenvector) and so

$$\begin{aligned} X &= e^{\lambda_1 t} \hat{u}_1 + e^{\lambda_2 t} \hat{v}_1, \\ Y &= e^{\lambda_1 t} \hat{u}_2 + e^{\lambda_2 t} \hat{v}_2. \end{aligned}$$

Geometric interpretation

What have we done?

- We start with a set of axes, X and Y .
- We find eigenvectors u and v which give us the directions of a new system of axes z_1 and z_2 along which the effect of multiplying by \mathbf{A} is the same as multiplying by a scalar λ . (It is clear from the diagram that any scalar multiple of the eigenvectors will suffice as an eigenvector.)
- We consider the plane described by the axes z_1 and z_2 and examine the behaviour of the solutions (which are now easy to find) $z_1 = k_1 e^{\lambda_1 t}$ and $z_2 = k_2 e^{\lambda_2 t}$ in this phase-plane. How the trajectories behave depends entirely on λ_1 and λ_2 , the eigenvalues. Suppose they are as illustrated in the left-hand diagram of Figure 7.2.
- Next we return to the (X, Y) phase-plane with the transformation of this solution, which is distorted (stretched or contracted) in some way since we have changed axes again: note that it retains the main features, or dynamics, of the simpler system.

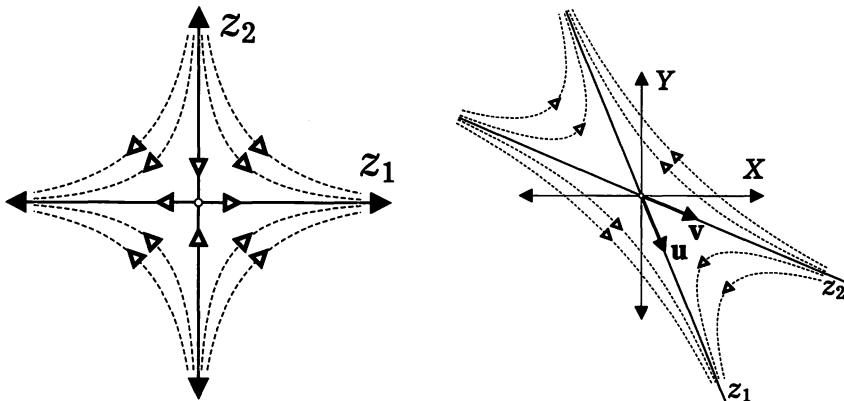


Figure 7.2: Sample saddle solution in the eigenvector phase-plane (left figure) and translated to the original phase-plane (right figure).

Equilibrium point classifications

For the systems described above, we had the origin $(0, 0)$ as the equilibrium (or critical) point. What we have found, using the techniques of eigenvalues and eigenvectors, is the behaviour of the trajectories in the phase-plane close to this point. The behaviour depends on the eigenvalues (λ_1 and λ_2) since the trajectories can be described by $z_1 = k_1 e^{\lambda_1 t}$ and $z_2 = k_2 e^{\lambda_2 t}$. Clearly different values of λ_1 and λ_2 may result in very different behaviours, and thus each case is dealt with separately below.

The following summarises the relationship between the eigenvalues and the forms of the trajectories:

- Case $\lambda_1 < 0$ and $\lambda_2 < 0$ (eigenvalues real and negative): We have

$$\lim_{t \rightarrow \infty} k_1 e^{\lambda_1 t} = 0 \quad \text{and} \quad \lim_{t \rightarrow \infty} k_2 e^{\lambda_2 t} = 0$$

and thus all trajectories approach the equilibrium point at the origin. Such a point is called a *stable node* and is illustrated in Figure 7.3.

- Case $\lambda_1 > 0$ and $\lambda_2 > 0$ (eigenvalues real and positive):

We have both z_1 and z_2 approaching ∞ (diverging) as t increases and thus all trajectories diverge from the equilibrium point. Such a point is called an *unstable node* (see Figure 7.3).

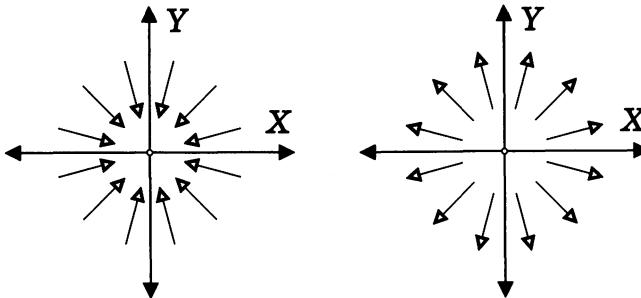


Figure 7.3: Trajectory behaviour close to a stable node (left) and an unstable node (right).

- Case $\lambda_1 > 0$ and $\lambda_2 < 0$ (eigenvalues real and of different sign): We have that $z_1 = k_1 e^{\lambda_1 t}$ and $z_2 = k_1 e^{\lambda_2 t}$, so $z_2 \rightarrow 0$ and $z_1 \rightarrow \infty$ as time increases. The trajectories approach zero along one axis and approach ∞ along the other. Such a point is called a *saddle* or an unstable saddle point and is illustrated in Figure 7.4.

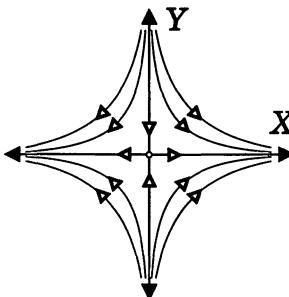


Figure 7.4: Trajectory behaviour close to an unstable saddle point.

- Case $\lambda_1 = \alpha + i\beta$ and $\lambda_2 = \alpha - i\beta$ (complex conjugate eigenvalues with $\alpha \neq 0$ and $\beta \neq 0$): In this case, the solutions can be written in the form $z_1 = e^{\alpha t} \cos \beta t$, $z_2 = e^{\alpha t} \sin \beta t$ and the trajectories spiral around the equilibrium point. If $\alpha < 0$ then they spiral inwards towards the equilibrium point. Such a point is called a *stable focus*. If $\alpha > 0$ then they spiral outwards and away from the equilibrium point. Such a point is called an *unstable focus*. A stable and unstable focus are illustrated in Figure 7.5.
- Case λ_1 and λ_2 purely imaginary. In this case, the solutions can be written in the form $z_1 = \cos \beta t$ and $z_2 = \sin \beta t$ and the trajectories form closed loops enclosing the equilibrium point. Such a point is called a *centre* and the solutions are called periodic. A centre is illustrated in Figure 7.6.

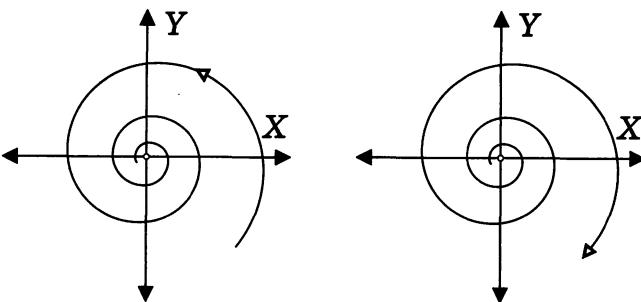


Figure 7.5: Trajectory behaviour close to a stable focus (left) and an unstable focus (right).

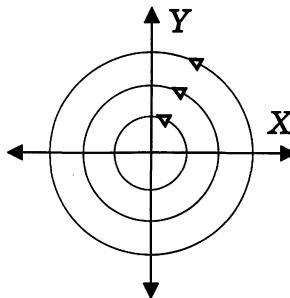


Figure 7.6: Trajectory behaviour close to a centre.

We have already come across examples of most of these types of equilibrium points in Chapter 6, where we considered the behaviour of the trajectories in the phase-plane for some basic population models. The power of the above results is that, having located an equilibrium point, we now have the means to predict its type, once we have found the associated eigenvalues.

Summary

- We start with the characteristic equation

$$\lambda^2 - \lambda(a_1 + b_2) + (a_1b_2 - a_2b_1) = 0$$

and solve for λ . This provides us with the eigenvalues.

- Solving the quadratic characteristic equation gives

$$\lambda_1 = \frac{1}{2}p + \frac{1}{2}\sqrt{\Delta}, \quad \lambda_2 = \frac{1}{2}p - \frac{1}{2}\sqrt{\Delta}$$

where $p = a_1 + b_2$ is the trace of matrix A , $q = a_1b_2 - a_2b_1$ is the determinant of A and $\Delta = p^2 - 4q$ the discriminant of the characteristic equation. The different possible classifications of the equilibrium points are given in Table 7.1.

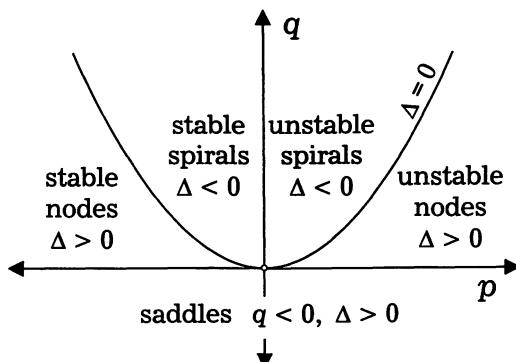
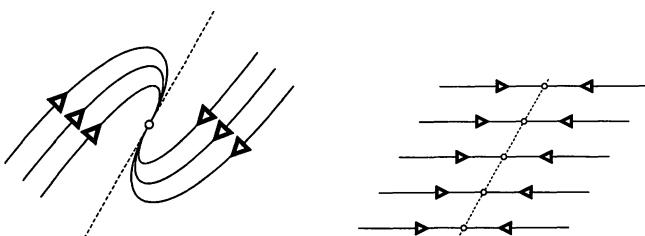
- This can all be displayed in a diagram, Figure 7.7, which illustrates the general classifications.

Discussion

Note, we have not included the cases where $\Delta = 0$ or $q = 0$. When $\Delta = 0$ the roots are equal and the equilibrium point is a stable/unstable inflection node. Such equilibrium points

Table 7.1: Table showing different classifications of equilibrium points.

Δ	p	q	Equilibrium point
$\Delta > 0$	$p < 0$		\Rightarrow stable node
$\Delta > 0$	$p > 0$		\Rightarrow unstable node
		$q < 0$	\Rightarrow saddle point
$\Delta < 0$	$p < 0$		\Rightarrow stable spiral
$\Delta < 0$	$p = 0$		\Rightarrow centre
$\Delta < 0$	$p > 0$		\Rightarrow unstable spiral

Figure 7.7: General classification diagram for equilibrium points using p , q and Δ from the characteristic equation.Figure 7.8: Trajectory behaviour when $\Delta = 0$ (left) and $q = 0$ (right), illustrated for the stable case when $p < 0$.

are called degenerate. When $q = 0$ the system ‘equilibrium point’ consists of a line and the trajectories are parallel. These special cases are illustrated in Figure 7.8.

Stable nodes and spirals are known as attractors, while unstable nodes and spirals are known as repellers. It is important to note that changes in the parameters a_1, a_2, b_1, b_2 can result in very different dynamics. Thus, it is possible to choose the dynamics through controlled variation of the parameters.

We have considered only the case of an equilibrium point at the origin, i.e. $(x_e, y_e) = (0, 0)$, but in general this is not so. Suppose we have a system as before, but with $(x_e, y_e) \neq (0, 0)$,

$$\begin{aligned} X' &= a_1 X + b_1 Y + c_1, \\ Y' &= a_2 X + b_2 Y + c_2. \end{aligned}$$

Let $\xi = X - x_e$ and $\eta = Y - y_e$ (so that $X = x_e$ implies that $\xi = 0$ and $Y = y_e$ implies

that $\eta = 0$). Then

$$\begin{aligned}\xi' &= X' = a_1(\xi + x_e) + b_1(\eta + y_e) + c_1 \\ &= (a_1x_e + b_1y_e + c_1) + a_1\xi + b_1\eta \\ &= a_1\xi + b_1\eta\end{aligned}$$

since $a_1x_e + b_1y_e + c_1 = 0$. Similarly

$$\eta' = Y' = a_2(\xi + x_e) + b_2(\eta + y_e) + c_2 = a_2\xi + b_2\eta.$$

This process is called a change of variable and allows us to transform the original system in X and Y with an equilibrium at (x_e, y_e) , to a system with variables ξ and η which has its equilibrium point at the origin. We can now apply the above theory to this system, which is equivalent to the original system of equations.

Another assumption we made was that we could express \mathbf{x} as a linear combination of the eigenvectors and the new axes z_1 and z_2 . This is a result of the linear algebra presented in Appendix B.1.

Furthermore, we assumed that $\mathbf{U} = [\mathbf{u} \ \mathbf{v}]$ was invertible, that is, there exists a matrix \mathbf{U}^{-1} such that $\mathbf{U}^{-1}\mathbf{U} = \mathbf{I} = \mathbf{U}\mathbf{U}^{-1}$. This follows as a consequence of Theorem 5 in Appendix B.1.

An alternative approach

The above approach requires some understanding of linear algebra theory, and this can be avoided if we make the assumption that the solution is an exponential of the form $ke^{\lambda t}$, with λ possibly imaginary. In this case we need to write the coupled linear system

$$\begin{aligned}X' &= a_1X + b_1Y, \\ Y' &= a_2X + b_2Y,\end{aligned}$$

as a single second-order equation

$$X'' - (a_1 + b_2)X' + (a_1b_2 - a_2b_1)X = 0.$$

(This can be done by differentiating the first equation and then eliminating Y using substitution from the second equation. For further details see Appendix A.5.)

Assuming that there is a solution of the form $X = ke^{\lambda t}$, we can calculate X'' and X' and substitute them into the second-order equation to give

$$k\lambda^2e^{\lambda t} - (a_1 + b_2)k\lambda e^{\lambda t} + (a_1b_2 - a_2b_1)ke^{\lambda t} = 0,$$

and then

$$\lambda^2 - (a_1 + b_2)\lambda + (a_1b_2 - a_2b_1) = 0.$$

Note that this is the characteristic equation once again. The solutions of this equation are the eigenvalues (λ_1 and λ_2) and from here the general solution is a linear combination of $e^{\lambda_1 t}$ and $e^{\lambda_2 t}$, that is

$$X(t) = C_1e^{\lambda_1 t} + C_2e^{\lambda_2 t}.$$

We are now in a position to classify the equilibrium points, as before.

Summary of skills developed here:

- Write a system of equations in vector notation, or convert a vector equation into a system of equations.
- Find the trace and determinant of a matrix.
- Calculate the eigenvalues of a matrix.
- From the eigenvalues of a matrix, and for a given equilibrium point, classify the equilibrium point and sketch the trajectory behaviour in the phase-plane close to this point.

7.3 Applications of linear theory

What we are most interested in is how this theory can be applied to the models we have been studying. However, to start with we apply the linear theory developed above to the example of a simple harmonic oscillator. This consists of a mass attached to a spring, which oscillates back and forth. (For further details see, for example, Fulford et al. (1997).) One example is a regularly vibrating (oscillating) object such as an idealised skateboard in a ramp, equipped with perfect bearings to ensure that no friction damps the motion. Such a skateboard would continue oscillating indefinitely between the edges of the ramp.

Simple harmonic motion

The following example examines an equation for simple harmonic motion.

Example 7.2: Find all equilibrium points associated with the system

$$X' = Y \quad Y' = -\omega^2 X \quad (7.3)$$

and determine their classification(s).

Solution: In matrix form, the system is

$$\mathbf{x}' = \mathbf{A}\mathbf{x} \quad \text{where} \quad \mathbf{A} = \begin{bmatrix} 0 & 1 \\ -\omega^2 & 0 \end{bmatrix}.$$

The only equilibrium point is $(x_e, y_e) = (0, 0)$.

To classify this point we need to examine the characteristic equation

$$\lambda^2 - \lambda \text{trace}(\mathbf{A}) + \det(\mathbf{A}) = 0 \quad \text{whence} \quad \lambda^2 - \lambda \times 0 + \omega^2 = 0.$$

Solving this equation yields imaginary eigenvalues

$$\lambda = \pm i\omega.$$

Now, with the notation as in Section 7.2,

$$p = \text{trace}(\mathbf{A}) = 0,$$

$$\Delta = p^2 - 4q = 0 - 4\omega^2 < 0.$$

This implies that the equilibrium point at $(0, 0)$ is a centre, and all solutions are periodic, as could be expected.

By eliminating the variable Y , the system (7.3) can be written as a single second-order differential equation $X'' = -\omega^2 X$. This is the well-known simple harmonic oscillator, and periodic solutions are exactly what we would expect.

We will now include damping, that is, some friction. In this case our idealised skateboard will eventually come to rest if the skateboarder does no work to keep it going. We consider what the changes will be. The differential equation is

$$X'' = -cX' - \omega^2 X$$

where c is a positive constant. Setting $Y = X'$, this can be written as the system

$$X' = Y, \quad Y' = -cY - \omega^2 X. \quad (7.4)$$

The term $-cY$ describes the damping. In the following example we classify the equilibrium point.

Example 7.3: Find and classify the equilibrium point(s) of the system (7.4).

Solution: The system can be written in matrix form

$$\mathbf{x}' = \mathbf{A}\mathbf{x} \quad \text{where} \quad \mathbf{A} = \begin{bmatrix} 0 & 1 \\ -\omega^2 & -c \end{bmatrix}.$$

We still have $(0, 0)$ as the only equilibrium point.

For its classification we consider the characteristic equation

$$\lambda^2 - \lambda \text{trace}(\mathbf{A}) + \det(\mathbf{A}) = 0 \quad \text{or} \quad \lambda^2 - \lambda(-c) + \omega^2 = 0.$$

Hence

$$\lambda = \frac{-c}{2} \pm \frac{1}{2} \sqrt{c^2 - 4\omega^2}.$$

Again, with the notation of Section 7.2, we have $p = \text{tr } \mathbf{A} = -c < 0$, since $c > 0$, and $\Delta = c^2 - 4\omega^2$. There are three cases to consider:

- If $\Delta > 0$, i.e. $c > 2\omega$ then $(0, 0)$ is a stable node. This case is known as strong damping.
- If $\Delta < 0$, i.e. $c < 2\omega$ then this implies that $(0, 0)$ is a stable focus. This case is known as weak damping.
- If $\Delta = 0$, i.e. $c = 2\omega$ then $(0, 0)$ is a stable inflected node. This case is known as critical damping.

Battle model

In Section 5.7, we introduced a simple model of a battle between two armies using aimed fire against each other. The resulting coupled system of differential equations for the numbers of soldiers of the two armies were the linear Lanchester equations

$$\frac{dR}{dt} = -a_1 B, \quad \frac{dB}{dt} = -a_2 R, \quad (7.5)$$

where the attrition coefficients a_1 and a_2 are positive constants.

Example 7.4: Classify the equilibrium points for the system (7.5).

Solution: The system (7.5) can be written in matrix form

$$\mathbf{x}' = \mathbf{A}\mathbf{x}, \quad \mathbf{A} = \begin{bmatrix} 0 & -a_1 \\ -a_2 & 0 \end{bmatrix},$$

and the only equilibrium point is $(0, 0)$.

The characteristic equation is

$$\lambda^2 - \text{trace}(\mathbf{A}) + \det(\mathbf{A}) = 0 \quad \text{or} \quad \lambda^2 + (-a_1 a_2) = 0.$$

With the notation of Section 7.2,

$$q = \det(\mathbf{A}) < 0$$

which implies the equilibrium point is a saddle point. This is consistent with what we found in Section 6.3.

7.4 Nonlinear theory

In Chapters 5 and 6, we examined coupled systems of nonlinear equations to describe interacting populations. We found equilibrium points and, at times, it was possible to establish the long-term behaviour of the system using graphical techniques such as the phase-plane and time-dependent diagrams. However, it would be extremely useful if we could extend the system of classification of the equilibrium points for linear systems, to nonlinear systems as well.

We can do this by approximating the nonlinear system with a linear system close to the equilibrium point: this process is called *linearisation*. We then examine the dynamics of the linearised system close to an equilibrium point, and use the classifications from linear theory to predict the dynamics in the nonlinear system. It can be shown that in all classification cases (except that of a centre) the predictions of linear theory extend to the nonlinear system. (For proof see, for example, Hurewicz (1990).)

Linearisation

Our first task is to establish a linear approximation to the nonlinear equations. Consider a general system of two nonlinear differential equations

$$\begin{aligned} \frac{dX}{dt} &= F(X, Y), \\ \frac{dY}{dt} &= G(X, Y). \end{aligned}$$

Let (x_e, y_e) be any equilibrium point for this system, not necessarily at $(0, 0)$, and then

$$F(x_e, y_e) = 0 \quad \text{and} \quad G(x_e, y_e) = 0.$$

Consider solutions close to the steady state (equilibrium) solutions

$$X(t) = x_e + \xi(t), \quad Y(t) = y_e + \eta(t)$$

where $\xi(t)$ and $\eta(t)$ are small, and approach zero when X and Y approach the equilibrium point. (ξ and η are called *perturbations* of the steady state.)

We now change the variables in the system from X and Y to ξ and η . Then

$$\begin{aligned}\frac{d(x_e + \xi)}{dt} &= F(x_e + \xi, y_e + \eta), \\ \frac{d(y_e + \eta)}{dt} &= G(x_e + \xi, y_e + \eta),\end{aligned}$$

where ξ and η are functions of t . But we have, since x_e and y_e are constant,

$$\begin{aligned}\frac{dX}{dt} &= \frac{d(x_e + \xi)}{dt} = \frac{d\xi}{dt}, \\ \frac{dY}{dt} &= \frac{d(y_e + \eta)}{dt} = \frac{d\eta}{dt}.\end{aligned}$$

So

$$\begin{aligned}\frac{dX}{dt} &= \frac{d\xi}{dt} = F(x_e + \xi, y_e + \eta), \\ \frac{dY}{dt} &= \frac{d\eta}{dt} = G(x_e + \xi, y_e + \eta).\end{aligned}$$

We now apply the Taylor series expansion in two variables to expand $F(x_e + \xi, y_e + \eta)$ and $G(x_e + \xi, y_e + \eta)$ and then take a linear approximation for each: a *tangent-plane approximation* for the system. (For details of partial derivatives and the Taylor series expansion, refer to Appendix B.2.) Applying the Taylor series expansion in two variables we find

$$\begin{aligned}\xi' &= F(x_e, y_e) + F_\xi(x_e, y_e)\xi + F_\eta(x_e, y_e)\eta \\ &\quad + (\text{terms of higher order}), \\ \eta' &= G(x_e, y_e) + G_\xi(x_e, y_e)\xi + G_\eta(x_e, y_e)\eta \\ &\quad + (\text{terms of higher order}),\end{aligned}$$

where $F_\xi = \partial F / \partial \xi$, $F_\eta = \partial F / \partial \eta$ and likewise for G . Now $F(x_e, y_e) = 0$, since (x_e, y_e) is an equilibrium point, and similarly $G(x_e, y_e) = 0$. Then, taking the linear approximation of each Taylor series expansion (i.e. ignoring all terms of higher order) we are left with the tangent-plane approximation

$$\begin{aligned}\xi' &= F_\xi(x_e, y_e)\xi + F_\eta(x_e, y_e)\eta, \\ \eta' &= G_\xi(x_e, y_e)\xi + G_\eta(x_e, y_e)\eta.\end{aligned}$$

In vector notation the linearised system is

$$\begin{bmatrix} \xi' \\ \eta' \end{bmatrix} = \begin{bmatrix} F_\xi & F_\eta \\ G_\xi & G_\eta \end{bmatrix} \begin{bmatrix} \xi \\ \eta \end{bmatrix}. \quad (7.6)$$

Equilibrium point classification

Recall that we can predict the behaviour (the dynamics) of a linear system $\dot{\mathbf{x}} = A\mathbf{x}$ merely by considering the eigenvalues of A . Further, these eigenvalues are the solutions to the characteristic equation $\lambda^2 - \lambda(\text{trace A}) + |\mathbf{A}| = 0$. Clearly from (7.6)

$$\begin{aligned}\text{trace}(\mathbf{A}) &= F_\xi + G_\eta, \\ |\mathbf{A}| &= \det(A) = F_\xi G_\eta - F_\eta G_\xi,\end{aligned}$$

and λ_1, λ_2 can be found for any equilibrium point.

Recall that ξ and η were not variables of the original equation. However, $X = x_e + \xi$ and $Y = y_e + \eta$ so that

$$\frac{\partial F}{\partial \xi} = \frac{\partial F}{\partial X} \frac{dX}{d\xi} = \frac{\partial F}{\partial X} \frac{d(x_e + \xi)}{d\xi} = \frac{\partial F}{\partial X},$$

and similarly

$$\frac{\partial F}{\partial \eta} = \frac{\partial F}{\partial Y}, \quad \frac{\partial G}{\partial \xi} = \frac{\partial G}{\partial X} \quad \text{and} \quad \frac{\partial G}{\partial \eta} = \frac{\partial G}{\partial Y}.$$

This means that we have

$$\begin{bmatrix} F_\xi & F_\eta \\ G_\xi & G_\eta \end{bmatrix} = \begin{bmatrix} F_X & F_Y \\ G_X & G_Y \end{bmatrix}$$

and in vector notation the linearised system is

$$\begin{bmatrix} \xi' \\ \eta' \end{bmatrix} = \begin{bmatrix} F_\xi & F_\eta \\ G_\xi & G_\eta \end{bmatrix} \begin{bmatrix} \xi \\ \eta \end{bmatrix} \quad \text{or} \quad \begin{bmatrix} X' \\ Y' \end{bmatrix} = \begin{bmatrix} F_X & F_Y \\ G_X & G_Y \end{bmatrix} \begin{bmatrix} X - x_e \\ Y - y_e \end{bmatrix}. \quad (7.7)$$

This is in the form $\dot{\mathbf{x}}' = \mathbf{J}\mathbf{x}'$. Here \mathbf{J} is the matrix of first order partial derivatives which is called the *Jacobian* matrix of the system above. Clearly, from this Jacobian matrix, which follows directly from the original system, the characteristic equation and eigenvalues can be calculated immediately.

Summary

In summary, if we start with a general nonlinear system

$$\begin{aligned} \frac{dX}{dt} &= F(X, Y), \\ \frac{dY}{dt} &= G(X, Y), \end{aligned}$$

with any equilibrium point (x_e, y_e) we can establish the dynamics of the system close to this point in the following way:

- First linearise the system to get

$$\begin{bmatrix} \xi' \\ \eta' \end{bmatrix} = \begin{bmatrix} F_X & F_Y \\ G_X & G_Y \end{bmatrix} \begin{bmatrix} \xi \\ \eta \end{bmatrix}.$$

- Evaluate the Jacobian matrix at the equilibrium point of interest. Each equilibrium point will produce different values of the Jacobian matrix.
- Then apply the linear theory of classification to this system.

It can be proved (see, for example, Hurewicz (1990)) that, with the exception of the prediction of a centre, the classification established for the linearised system can be extended to the nonlinear system. Furthermore, if an equilibrium point is a centre in the linearised system then it is either a focus or a centre in the nonlinear system. In this case, it is necessary to consider the nonlinear terms to establish the exact dynamics. However, such analysis is beyond the scope of this book and we refer the interested reader to, for example, Hurewicz (1990).

Summary of skills developed here:

- Find the Jacobian of a matrix.
- Linearise a system of nonlinear equations and derive the linearised system.
- From the eigenvalues of the Jacobian matrix classify any equilibrium point and sketch the trajectory behaviour in the phase-plane close to this point.

7.5 Applications of nonlinear theory

We now apply this linearisation technique to some of the models of population dynamics we developed in Chapter 5.

Predator-prey model

Recall the model of the predator-prey interaction from Chapter 5,

$$\begin{aligned} X' &= \beta_1 X - c_1 XY, \\ Y' &= -\alpha_2 Y + c_2 XY, \end{aligned} \tag{7.8}$$

for which we found two equilibrium points $(0, 0)$ and $(\alpha_2/c_2, \beta_1/c_1)$ (see Section 6.4).

Example 7.5: Find the linearised system for model (7.8), and hence classify all equilibrium points of the basic predator-prey model.

Solution: From (7.8) we label $F(X, Y) = \beta_1 X - c_1 XY$ and $G(X, Y) = -\alpha_2 Y + c_2 XY$. The Jacobian matrix is

$$J = \begin{bmatrix} F_X & F_Y \\ G_X & G_Y \end{bmatrix} = \begin{bmatrix} \beta_1 - c_1 Y & -c_1 X \\ c_2 Y & -\alpha_2 + c_2 X \end{bmatrix}.$$

There were two equilibrium points for this system, and we consider each in turn.

For the case where the equilibrium point is $(x_e, y_e) = (0, 0)$ we have that

$$J = \begin{bmatrix} \beta_1 & 0 \\ 0 & -\alpha_2 \end{bmatrix}.$$

The trace is then $\beta_1 - \alpha_2$ and the determinant is given by $\det(J) = -\beta_1 \alpha_2$. Using the notation of Section 7.2, the characteristic equation follows as $\lambda^2 - (\beta_1 - \alpha_2)\lambda + (-\beta_1 \alpha_2) = 0$ and we have $q = -\beta_1 \alpha_2 < 0$ which implies that the equilibrium point is a saddle point.

In the second case where the equilibrium point is

$$(x_e, y_e) = \left(\frac{\alpha_2}{c_2}, \frac{\beta_1}{c_1} \right)$$

we have that

$$J = \begin{bmatrix} 0 & -\frac{c_1 \alpha_2}{c_2} \\ \frac{\beta_1 c_2}{c_1} & 0 \end{bmatrix}.$$

The trace of this matrix is 0 and its determinant is given by $\det(J) = \beta_1 \alpha_2$. As above, with the notation of Section 7.2, the characteristic equation in this case is $\lambda^2 - 0\lambda + \beta_1 \alpha_2 = 0$ and we have $p = 0$ and $\Delta < 0$ which implies that this equilibrium point is a centre.

The results from this example are those we might have expected from the numerical solutions obtained earlier using **Maple**. However, the latter critical point is predicted as a centre and, as we have stated, linear theory is not adequate in this case where it is necessary to consider the nonlinear terms to establish the true dynamics. On the other hand, we were able, for this example, to solve for the phase-trajectories exactly in Section 6.6. The solution obtained there shows that the critical point is indeed a centre.

Epidemic model

Recall the basic model for the spread of a disease in a population from Section 5.2. The differential equations were

$$\frac{dS}{dt} = -\beta SI, \quad \frac{dI}{dt} = \beta SI - \gamma I. \quad (7.9)$$

Here $S(t)$ describes the susceptible population and $I(t)$ describes contagious infectives, as functions of time. Parameter β is the disease transmission rate (transmission coefficient) and γ is the removal rate.

Example 7.6: Classify the equilibrium points of the epidemic model (7.9).

Solution: We established in Section 6.2 that (7.9) has an infinite set of equilibrium points, $(S, I) = (s_e, 0)$, where s_e is an arbitrary positive real number.

From (7.9) we label $F(S, I) = -\beta SI$ and $G(S, I) = \beta SI - \gamma I$. The Jacobian matrix is

$$J = \begin{bmatrix} \frac{\partial F}{\partial S} & \frac{\partial F}{\partial I} \\ \frac{\partial G}{\partial S} & \frac{\partial G}{\partial I} \end{bmatrix} = \begin{bmatrix} -\beta I & -\beta S \\ \beta I & \beta S - \gamma \end{bmatrix}.$$

At any given equilibrium point, $(S, I) = (s_e, 0)$, we have the linearised system

$$\begin{bmatrix} S' \\ I' \end{bmatrix} = \begin{bmatrix} 0 & -\beta s_e \\ 0 & \beta s_e - \gamma \end{bmatrix} \begin{bmatrix} S - s_e \\ I - 0 \end{bmatrix}.$$

At these equilibrium points the trace $\text{trace}(J) = \beta s_e - \gamma$ is negative if $s_e < \gamma/\beta$ and positive if $s_e > \gamma/\beta$. This implies stable points for $S < \gamma/\beta$ and unstable points for $S > \gamma/\beta$. With the notation of Section 7.2, we have that $q = \det(J) = -\beta I(\beta S - \gamma) + \beta^2 SI = 0$ at $(S, I) = (s_e, 0)$. This is a case of parallel trajectories as discussed in Section 7.2.

We have a line of stable nodes for $S < \gamma/\beta$ and a line of unstable nodes for $S > \gamma/\beta$. The same is true for the original nonlinear system (7.9).

These results are consistent with the phase-plane analysis of Section 6.2.

Computer algebra analysis

Most symbolic mathematics software packages, such as **Maple**, will have inbuilt routines to find equilibrium solutions, Jacobian matrices, characteristic polynomials and eigenvalues. What follows, in Listing 7.1, is some **Maple** code, which has been used to solve the basic predator-prey example at the beginning of Section 7.5.

Listing 7.1: Maple code: c.pl.predprey.txt

```

> restart:with(linalg):
> eqn1:=beta[1]*X-c[1]*X*Y;
> eqn2:=-alpha[2]*Y+c[2]*X*Y;

#Critical/equilibrium points
> critpts:=solve({eqn1=0,eqn2=0},{X,Y});

# The Jacobian matrix
> sys:=vector([eqn1,eqn2]);
> J:=jacobian(sys,[X,Y]);

# The characteristic equation
> ch:=charpoly(J,lambda);

# Eigenvalues
> ch1:=subs(critpts[1],ch);
> ev1:=solve({ch1},{lambda});
> ch2:=subs(critpts[2],ch);
> ev2:=solve({ch2},{lambda});

# Using the p, q , Delta approach for classification
> p:=trace(J);
> q:=det(J);
> delta:=p^2-4*q;
> critpts[1];
> p1:=subs(critpts[1],p);
> q1:=subs(critpts[1],q);
> delta1:=subs(critpts[1],delta);
> critpts[2];
> p2:=subs(critpts[2],p);
> q2:=subs(critpts[2],q);
> delta2:=subs(critpts[2],delta);

# Calculating the eigenvalues from p, q and Delta
> lambda1a:=p1*1/2 +1/2*sqrt(delta1);
> lambda1b:=p1*1/2 -1/2*sqrt(delta1);
> lambda2a:=p2*1/2 +1/2*sqrt(delta2);
> lambda2b:=p2*1/2 -1/2*sqrt(delta2);

# Calculating the eigenvalues directly from Maple
> eigs:=eigenvals(J);eigs[1];
> eig1a:=subs(critpts[1],eigs[1]);
> eig1b:=subs(critpts[1],eigs[2]);
> eig2a:=subs(critpts[2],eigs[1]);
> eig2b:=subs(critpts[2],eigs[2]);

```

Further Maple commands, such as `simplify(X)` and `factor(X)`, can reduce complex expressions of X to a more manageable form.

Discussion

The above applications give some indication of the power of linearisation theory, and the equilibrium point classification process developed. It should be noted that changes in the parameter values in each case may alter the equilibrium point classification and predict different dynamics. In this way it is not only possible to predict the system dynamics, but also to control the outcome in certain dynamical systems where such control parameters determine changes in the classification. This is an extremely important aspect in the study of dynamical systems.

Summary of skills developed here:

- For a nonlinear system of equations, find all the equilibrium points and establish the trajectory behaviour close to each of them.
- Sketch a picture of the entire phase-plane indicating the direction of the trajectories in any part of the plane.
- Identify how a parameter might be changed to alter the dynamics in the phase-plane.

7.6 Exercises for Chapter 7

7.1. Constructing a phase-plane. Consider the linear system

$$x' = x - y, \quad y' = x + y,$$

where differentiation is with respect to time.

- Find the equilibrium point(s) and establish what type of equilibrium it is (they are).
- Using the above results draw a sketch of how you would expect the phase-plane trajectories to behave. (Note that, along the line $x = y$ (or equivalently $x' = 0$) there is no change in x , and along the line $x = -y$ there is no change in y .)
- Use Maple or MATLAB to draw the phase-plane to confirm your results.

7.2. Defining the trajectories. Consider the system

$$x' = x - 5y, \quad y' = x - y,$$

where differentiation is with respect to time.

- Confirm there is only one equilibrium point which is a centre.
- Confirm that the family of ellipses given by

$$x^2 - 2xy + 5y^2 = K,$$

with K some constant, describes the solution trajectories in the (x, y) -plane. (Hint: One way to do this is to use direct substitution.)

7.3. Linearisation example. Consider the nonlinear system of equations

$$x' = x - y, \quad y' = 1 - xy,$$

where differentiation is with respect to time.

- Find all equilibrium points for the system.
- Linearise the system and establish the classification of each equilibrium point.
- From the above results sketch the trajectory behaviour in the phase-plane. (Note that along $x = y$ we have $x' = 0$ and along $y = 1/x$ we have $y' = 0$.)
- Use Maple or MATLAB (with symbolic toolbox) to check your results.

7.4. Linearisation example. Given the system of equations

$$x' = 3 + q(x - y), \quad y' = 4 - xy,$$

where differentiation is with respect to time.

- (a) Assume $q = 1$. Give the linearised system of equations.
- (b) Assume $q = 1$. Find all equilibrium points for the system and classify each point. Hence sketch the phase-plane.
- (c) Consider q to be a variable parameter. Prove that one equilibrium point will always be a saddle point. Give full reasons for your answer. (Hint: Show graphically, or otherwise, that for each such equilibrium point (x_e, y_e) , the x and y coordinates will have the same sign.)

7.5. Linearisation of competition model. Consider a competing species model, species X competing with species Y , including logistic growth for both species

$$X' = \beta_1 X - d_1 X^2 - c_1 XY, \quad Y' = \beta_2 Y - d_2 Y^2 - c_2 XY.$$

Suppose that the parameter values are $\beta_1 = 3$, $\beta_2 = 2.5$, $d_1 = 2.8$, $d_2 = 2$, $c_1 = 2$ and $c_2 = 1$. The equilibrium values are

$$(0, 0), \quad \left(0, \frac{\beta_2}{d_2}\right), \quad \left(\frac{\beta_1}{d_1}, 0\right), \quad \left(\frac{c_1\beta_2 - d_2\beta_1}{c_1c_2 - d_1d_2}, \frac{c_2\beta_1 - d_1\beta_2}{c_1c_2 - d_1d_2}\right)$$

and the phase-plane indicates that, with time, the populations will settle to coexistence of both species.

- (a) Linearise the system, giving the general form of the linearised equations and substituting in the parameter values as given.
- (b) Use the linearised system to classify each equilibrium point. Sketch the phase-plane and illustrate the trajectory behaviour close to each equilibrium point from your classifications. Verify that these classifications agree with coexistence of the species.
- (c) How, by varying the interaction parameters, could you change the phase-plane predictions to ensure that X will always die out?

7.6. Comparison of nonlinear and linearised systems. In order to compare the nonlinear system with the linearised system we can draw them both on the same system of axes and compare them directly.

- (a) For the predator-prey model

$$X' = X(\beta_1 - c_1 Y), \quad Y' = Y(-\alpha_2 + c_2 X),$$

taking $\beta_1 = 1.3$, $c_1 = 0.01$, $\alpha_2 = 1$ and $c_2 = 0.01$, and considering the trajectories close to the non-zero equilibrium, draw on the same system of axes the time-dependent plots for the nonlinear and the linearised systems. (Use Maple or MATLAB to solve the systems numerically).

- (b) Also compare the trajectories in the phase-plane of the nonlinear and the linearised systems. (Hint: Set up the equations for the linearised system, and then write them in terms of the X and Y coordinate system of the given nonlinear equations. For example $X = x_e + \xi$, or $\xi = X - x_e$, where x_e is the equilibrium value. Then solve both systems of equations using Maple or MATLAB and display the results in the same diagram.)

7.7. Linearisation of an epidemic model. Consider the following model for the spread of a disease, with susceptibles constantly renewed by births at a constant overall birth rate of μ .

$$S' = -\beta SI + \mu, \quad I' = \beta SI - \gamma I.$$

- (a) Show that the only equilibrium point is $(r/b, \mu/r)$.
- (b) Linearise the system and determine the behaviour of the trajectories near the equilibrium point.
- (c) Discuss, briefly, the implications for the time-dependent behaviour of both $S(t)$ and $I(t)$.

7.8. Linearisation of jungle warfare model. A model for a battle between red soldiers and blue soldiers, where one army uses random fire and the other uses aimed fire, is

$$R' = -a_1 RB, \quad B' = -a_2 R.$$

Linearise the system about the only equilibrium point, and hence determine the behaviour of trajectories near that point.

7.9. Bacteria in the gut. This question refers to the case study in section Section 6.7. Derive expressions for the equilibrium point(s) for the system of differential equations (6.24). Determine the type and stability of all points and establish, approximately, when the points change stability and classification as the turnover rate increases. (Use the parameter values as given in Figure 6.13.)

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2034-2035 2035-2036 2036-2037 2037-2038 2038-2039

2039-2040 2040-2041 2041-2042 2042-2043 2043-2044

2044-2045 2045-2046 2046-2047 2047-2048 2048-2049

2049-2050 2050-2051 2051-2052 2052-2053 2053-2054

Chapter 8

Some extended population models

In this chapter, we present a variety of case studies based on research papers or articles. Each study significantly extends one or more of the simple models we have developed in Chapter 5 and applies the techniques of analysis developed in Chapter 6 and particularly Chapter 7. It serves to illustrate the relevance of the theory presented in this text and its current use in practice.

8.1 Introduction

There are many interesting problems requiring the use of population models, and we present a sample of them here with the aim of illustrating the versatility, diversity and applicability of these models to current issues.

In previous chapters, we developed the simplest type of population models. Each of those may be extended or combined with others to reflect the particular features of the population under study. As we see in the case studies which follow, the models examined so far form the basis on which the further models proposed are built. The concept of the balance law and the compartmental structure are integral in each case.

The references from which the following case studies are adapted are provided, and all figures presented have been generated using **Maple**. (The code has not been included here, although all figures can be generated from code integrated into the text of earlier chapters.) Code building and model exploration are encouraged in the exercises.

8.2 Case Study: Competition, predation and diversity

In Section 5.5, we developed simple models for predator-prey interactions and for competing species. For the latter we found that the model predicted, in most cases, the survival of one species and the extinction of all others. We noted that this was a limitation of the model, as in many instances observations in nature confirm the stability and coexistence of a number of competing species. One notion which would explain coexistence as well as diversity is that of cooperation, as opposed to competition. In the infertile country of the arid regions of Australia, this is one hypothesis for the substantial diversity and coexistence of species relying on the same resources for survival.

In the following case study we examine a different hypothesis. A combination of the basic competition model together with the predator-prey model provides a mathematical argument for the stability and coexistence of competing species within an ecosystem. The case study supports the earlier comment in Section 5.1, that systems operating in isolation may be unstable, but when incorporated into more complex systems they typically display stability.

Note here the use of the word stability. A stable system in this sense is a system in which species coexist, whereas if one species suffers extinction, the system is referred to as unstable. This use appears in practice, but does not satisfy the strict definition we have met previously in the text. The following is adapted from Cramer and May (1972).

Observations have confirmed that whilst simple systems (for example, a single trophic level) are likely to be unstable in isolation, more complex systems comprising a collection of interacting trophic levels are often extremely stable.

Parrish and Saila (1970) attempted to validate this idea with some computer experiments. They proposed that while a two species competition model might be unstable, the introduction of a predator could allow the system to stabilise, thus permitting all three species to coexist.

For the two species of prey, N_1 and N_2 , and a predator N_3 , the model they constructed was a simple competition model between N_1 and N_2 (both populations following a logistic

growth pattern) with a predator N_3 included, whose birth rate was dependent on both N_1 and N_2 , namely

$$\begin{aligned} N'_1 &= N_1(\epsilon_1 - \alpha_{11}N_1 - \alpha_{12}N_2 - \alpha_{13}N_3) \\ N'_2 &= N_2(\epsilon_2 - \alpha_{21}N_1 - \alpha_{22}N_2 - \alpha_{23}N_3) \\ N'_3 &= N_3(-\epsilon_3 + \alpha_{31}N_1 + \alpha_{32}N_2). \end{aligned} \quad (8.1)$$

In the absence of the predator ($N_3 = 0$) we have a simple competition model which predicts the extinction of all but one species in most cases: that is, $\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21} \leq 0$. Now starting with parameter values which ensure instability for the competition model, the predator is included. The new system can be stable, even when we do not have equal predation (that is, $\alpha_{13} = \alpha_{23}$ and $\alpha_{31} = \alpha_{32}$).

Figure 8.1 illustrates the case of the unstable competition model without predation. In this case N_1 dies out and $N_2 \rightarrow 3.5 \times 10^5$. Figure 8.2 corresponds to the case where a predator is included and predation of each of the species is the same, that is, $\alpha_{13} = \alpha_{23}$. In this case all populations approach fixed positive population sizes with $N_1 \rightarrow 11.66 \times 10^3$, $N_2 \rightarrow 8.34 \times 10^3$ and $N_3 \rightarrow 11.3$. Finally, Figure 8.3 illustrates the case of a stable system where all three populations coexist, but without the condition of equal predation. The results are that $N_1 \rightarrow 69.4 \times 10^3$, $N_2 \rightarrow 16.7 \times 10^3$ and $N_3 \rightarrow 11.1$.

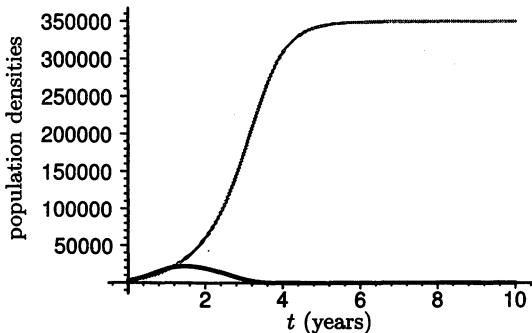


Figure 8.1: Unstable competition model without predation, with N_1 (black) and N_2 (grey). Parameter values: $\alpha_{11} = 9 \times 10^{-5}$, $\alpha_{12} = 3 \times 10^{-5}$, $\alpha_{13} = 0$, $\alpha_{21} = 3 \times 10^{-5}$, $\alpha_{22} = 0.6 \times 10^{-5}$, $\alpha_{23} = 0$, $\epsilon_1 = 3$ and $\epsilon_2 = 2.1$. The initial populations are $N_1(0) = N_2(0) = 3 \times 10^3$.

The example serves to illustrate that while a single two species population model may be unstable, the introduction of a further species (in this case a predator of both other species) may result in a stable system with the persistence and coexistence of all species. This provides an argument for the existence of a rich diversity of species, some of which may rely on the same resources, as is apparent in any natural ecosystem.

8.3 Extended predator-prey model

In this section we improve on the predator-prey model by incorporating further biological observations. The new model also exhibits oscillatory behaviour, which means that in the phase-plane we have a limit cycle or periodic solution.

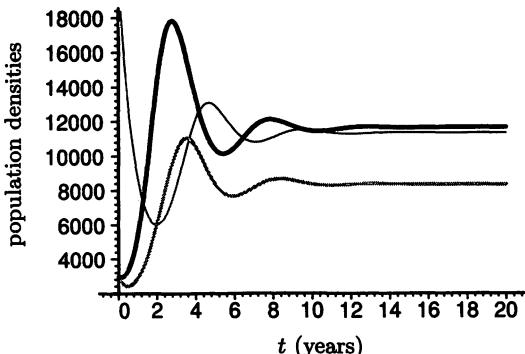


Figure 8.2: Unstable competition model with predation and N_1 (black), N_2 (grey) and N_3 (fine black). Parameter values are as in Figure 8.1 but with $\alpha_{13} = 0.15$, $\alpha_{23} = 0.15$, $\alpha_{31} = \alpha_{32} = 0.6 \times 10^{-4}$ and $\epsilon_3 = 1.2$. The initial populations are $N_1(0) = N_2(0) = 3 \times 10^3$ and $N_3(0) = 20$. In the displayed results N_3 has been multiplied by 10^3 .

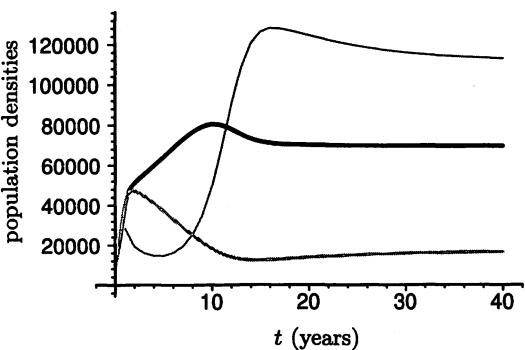


Figure 8.3: Unstable competition model with predation and N_1 (black), N_2 (grey) and N_3 (fine black). Parameter values: $\alpha_{11} = 0.9 \times 3.22 \times 10^{-5}$, $\alpha_{12} = 3.22 \times 10^{-5}$, $\alpha_{13} = 0.06$, $\alpha_{21} = 3.22 \times 10^{-5}$, $\alpha_{22} = 3.22 \times 10^{-5}$, $\alpha_{23} = 0.04$, $\alpha_{31} = 3 \times 10^{-5}$, $\alpha_{32} = 10^{-5}$, $\epsilon_1 = 3.22$, $\epsilon_2 = 3.22$ and $\epsilon_3 = 2.25$. The initial populations are $N_1(0) = N_2(0) = 10^4$ and $N_3(0) = 10$. In the displayed results N_3 has been multiplied by 10^4 .

Review of previous models

In Section 5.3, we developed a predator-prey model which predicted oscillations in the population densities, and we saw, in Section 6.6, how this led to closed curves, or a set of periodic solutions, in the phase-plane.

We then improved the model to include logistic growth and noted that the oscillations died out and the populations stabilised to some fixed equilibrium point. In the phase-plane this translated to an inwardly moving spiral approaching this equilibrium point. The differential equations for this model were

$$\frac{dX}{dt} = r_1 X \left(1 - \frac{X}{K}\right) - c_1 X Y, \quad \frac{dY}{dt} = c_2 X Y - \alpha_2 Y. \quad (8.2)$$

Here $X(t)$ is the prey density and $Y(t)$ is the predator density. The constant K is the prey carrying capacity, r_1 is the prey per-capita intrinsic growth rate (the per-capita growth rate for small populations), α_2 is the predator per-capita death rate and c_1 and c_2 are positive constants which may be interpreted in terms of the predator searching rate (see Section 5.3).

However, oscillating predator-prey pairs have been observed in nature, and this ‘improved’ model does not predict periodic solutions. This is a fundamental flaw, and we now suggest possible extensions which make the model more realistic.

Extending the model

The basic problem with the Lotka-Volterra predator-prey model is that the assumptions made regarding prey deaths and predator births and deaths are not sufficiently realistic. In practice, field ecologists studying predator populations measure two quantities: the *functional response*, $F(X)$, and the *numerical response* $N(X, Y)$. The functional response is the rate at which a single predator kills prey, as a function of the prey population. The numerical response is the per-capita growth rate of the predators, which may be dependent on both prey and predator populations.

A general model for a predator-prey system, based upon functional and numerical response functions, and with X and Y the population densities, is

$$\frac{dX}{dt} = r_1 X \left(1 - \frac{X}{K} \right) - F(X)Y, \quad \frac{dY}{dt} = N(X, Y)Y. \quad (8.3)$$

In equations (8.2) the functional response is $F(X) = c_1 X$. This states that a single predator continues to increase its rate of killing prey as the prey density increases. In practice, it is observed that this function levels off to a constant amount as X increases, representing the maximum that a single predator will want to eat (in a given time). Another way of thinking about this is that if the prey are plentiful, the predator will not have to spend much time hunting for them, but will spend more time waiting until they need to hunt again. The following example uses the idea of a handling time to formulate a suitable functional response function.

Example 8.1: Assuming that a single predator takes a time t_h to handle each prey find a suitable functional response.

Solution: We modify the argument given in Section 5.3 for the interpretation of one of the parameters in terms of a searching rate c_1 . Let T denote the time left available to the predator for searching (hunting prey). Consider a time interval Δt .

The number of prey eaten is determined from the searching rate c_1 multiplied by the prey density $X(t)$

$$\left\{ \begin{array}{l} \text{no. prey eaten} \\ \text{in time } \Delta t \\ \text{by one predator} \end{array} \right\} = c_1 T X(t). \quad (8.4)$$

The rate of prey (number per unit time) eaten by a single predator is then $c_1 T X(t)/\Delta t$. Now

$$\Delta t = T + t_h \times \left\{ \begin{array}{l} \text{no. prey eaten} \\ \text{in time } \Delta t \\ \text{by one predator} \end{array} \right\} = T(1 + t_h c_1 X(t)). \quad (8.5)$$

The functional response $F(X)$ is the rate of prey eaten by a single predator, which is given by dividing equation (8.4) by Δt . Using (8.5) we obtain

$$F(X) = \frac{c_1 X}{1 + t_h c_1 X}. \quad (8.6)$$

As $X \rightarrow 0$, we see that $F(X) \rightarrow 0$. For large prey densities, or as $X \rightarrow \infty$, then $F(X) \rightarrow t_h^{-1}$. This value is the maximum possible removal rate of prey: the functional response is *saturated* at this value. For large X , the prey are very easy for a predator to find, so this maximum rate is the reciprocal of the handling time t_h , for a single predator.

This function also arises in the theory of reaction kinetics in chemistry, see Murray (1990), where it is known as the Michaelis-Menten function.

This particular form of the functional response $F(X)$ is called a Holling type II response function and is commonly used for invertebrate predators; see May (1981). Some examples of fitting the Holling type II model to field data are given in Hassell (1978, 1976) and Gotelli (1995), together with data for handling times and searching rates. For vertebrate predators a Holling type III response is often used: this is obtained by setting the searching rate $c_1 = a'$ in (8.6) proportional to prey density. This could be thought of as reflecting the higher intelligence of vertebrates whose searching rates improve with higher prey density, since they learn how to track the prey.

For the numerical response, $N(X, Y)$, we assume a logistic growth function for the predator population, $r_2(1 - Y/K_2)$ but with the predator carrying capacity assumed to be proportional to the prey density, $K_2 = c_3X$. Hence

$$N(X, Y) = r_2 \left(1 - \frac{Y}{c_3 X} \right), \quad (8.7)$$

where r_2 and c_3 are positive constants. Note that as X increases, the deaths due to over-crowding decrease, but an increase in Y implies an overall increase in the deaths proportional to Y^2 .

Our model becomes

$$\frac{dX}{dt} = r_1 X \left(1 - \frac{X}{K} \right) - \frac{c_1 X Y}{1 + t_h c_1 X}, \quad \frac{dY}{dt} = r_2 Y \left(1 - \frac{Y}{c_3 X} \right). \quad (8.8)$$

This model is sometimes called the Holling-Tanner predator-prey model.

Scaling the equations

Before using Maple or MATLAB to examine the time-dependent graphs and phase-plane we apply a technique often adopted in practice to simplify the analysis. We scale the equations. This process may offer several advantages.

After scaling, the parameters are in dimensionless form and provide a measure of the relative strengths of the interacting or competing effects within the model. This may provide important information towards improving the design of experimental processes, in turn creating a more applicable model. Also as a result of scaling, the mathematics may be simplified, or the number of parameters reduced. However, this is not necessarily true in all cases.

We can scale the above system of equations by defining new dimensionless variables x , y and τ , by

$$x = \frac{X}{K}, \quad y = \frac{Y}{c_3 K}, \quad \tau = r_2 t.$$

Then, using the chain rule, it can be shown that (see Exercises, Question 3) the system becomes

$$\frac{dx}{d\tau} = \lambda_1 x(1 - x) - \frac{\lambda_2 x y}{(\lambda_3 + x)}, \quad \frac{dy}{d\tau} = y \left(1 - \frac{y}{x} \right), \quad (8.9)$$

with dimensionless parameters

$$\lambda_1 = \frac{r_1}{r_2}, \quad \lambda_2 = \frac{c_3}{t_h r_2}, \quad \lambda_3 = \frac{1}{t_h c_1 K}.$$

Interpretation of the parameters

The newly defined parameters can be interpreted in the following way. Since r_1 is the maximum specific growth rate of the prey with no predators and r_2 is the specific growth rate of predators with infinite prey density, then λ_1 is the ratio of the specific growth rates under ideal conditions.

The quantity λ_2 measures the predators' maximum prey removal rate t_h^{-1} relative to its ideal specific growth rate r_2 . Parameter c_3 is already dimensionless as $c_3 X = K$.

Since t_h is the handling time per prey then the combination $t_h K$ represents a time scale (per unit area) for the total time to handle the maximum possible prey density (given by the carrying capacity K in the absence of predation). Since c_1 is the searching rate (area per unit time) then c_1^{-1} is a time scale for searching a unit area. Hence the parameter λ_3 represents a ratio of time scales (searching time to handling time). For large λ_3 the handling time is insignificant, but for small values of λ_3 the predators ability to remove prey is more likely to rise to its saturation value of λ_2 .

Numerical solution for scaled model

We use Maple to solve the system numerically with parameter values of $\lambda_1 = 5$, $\lambda_2 = 10$ and $\lambda_3 = 0.015$. Consider the phase-plane diagram as illustrated in Figure 8.4. Note that for all the initial conditions chosen from the illustrated domain, the solution is a single periodic solution.

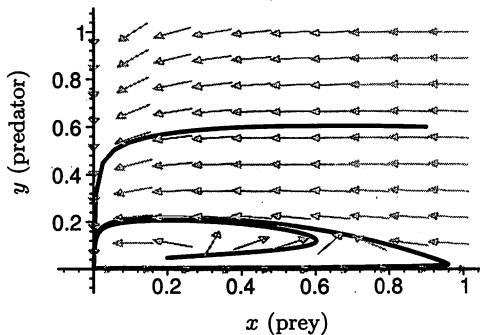


Figure 8.4: Phase-plane diagram for the scaled system (8.9) with $\lambda_1 = 5$, $\lambda_2 = 10$ and $\lambda_3 = 0.015$.

For different parameter values, $\lambda_1 = 5$, $\lambda_2 = 1$ and $\lambda_3 = 0.6$, the equilibrium solution is a stable node similar to Figure 8.5,. Trajectories with initial values close to the equilibrium are attracted to the equilibrium.

Discussion

Notice that this new system can give rise to a single periodic solution for certain parameters (Figure 8.4). In this case, the periodic cycle is always the same, regardless of the initial conditions chosen. This is very different from the infinite series of closed curves, each associated with a different set of initial values, which we obtained from our basic predator-prey model in Section 6.4.

The system also predicts populations stabilising to fixed densities for other parameter combinations (Figure 8.5). It would be useful to establish a diagram of the parameter values which lead to periodic solutions and those which do not. This is left as an exercise for the interested reader; however, such a diagram, establishing the parameter regimes which

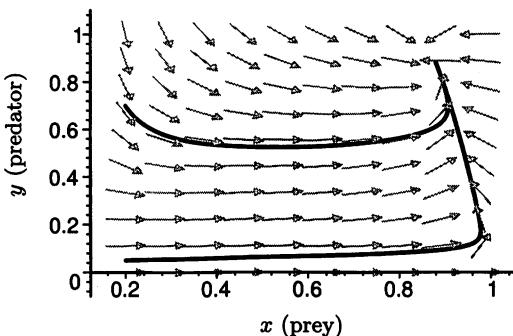


Figure 8.5: Phase-plane diagram for the scaled system (8.9) with $\lambda_1 = 5$, $\lambda_2 = 1$ and $\lambda_3 = 0.6$.

result in different dynamics, is an important part of the system analysis process.

8.4 Case Study: Lemming mass suicides?

Dramatic fluctuations have been observed in the populations of several rodents. In the case of lemmings, several myths have evolved to account for these fluctuations, such as lemmings hurling themselves off cliffs in mass suicides. In the following case study, a simple model of rate equations is presented to describe these dramatic cycles. The model proposed is a further extension of the basic predator-prey model and makes use of the concept of modelling a single population in two parts, each part having different behavioural characteristics. This is similar to the notion we made use of when modelling the spread of a disease in a population by dividing the population into two subpopulations of infectives and susceptibles. Adapted from Dekker (1975).

Legend has it that lemmings periodically ‘migrate’ into the sea in an act of mass suicide. Early Scandinavians believed that lemmings fell from heaven in stormy weather! More recently it has been proposed by natural historians that epidemic disease, or possibly predation, intermittently wipe out large numbers of the lemming population. Each of the above attempts to explain the drastic fluctuations in the populations of lemmings, true also for certain other small rodents or voles, which have been observed.

It appears from collected data that the population cycles have a period of three to four years. Further, there appear to be no external forces causing these fluctuations, suggesting the existence of some internal control mechanism. To support this idea, the observations indicate changes in the population characteristics during a cycle, in terms of (amongst others) sex and age.

Following the work of Myers and Krebs (1974), populations can be divided into two main genotypes: one with a high reproduction rate and intolerant of high population density living conditions, and the other with a low reproduction rate and well adapted to crowded living conditions. The former population, which deals with overcrowding by migrating (not necessarily jumping off a cliff into the ocean, as was once believed for lemmings), are called the Emigrants and their density will be denoted by n_1 , while the latter population, which are known as the tolerants, and their density is denoted as n_2 . The mathematical model

proposed to describe these interacting populations is given as

$$\begin{aligned}\frac{dn_1}{dt} &= n_1 [a_1 - (b_1 - c_1)n_2 - c_1(n_1 + n_2)], \\ \frac{dn_2}{dt} &= n_2 [-a_2 + b_2n_1],\end{aligned}\tag{8.10}$$

where a_1 , a_2 , b_1 , b_2 and c_1 are parameters which will be described below.

First, consider the growth of the emigrants in the absence of the tolerants. In that case the emigrants follow a logistic growth pattern and, since emigration depends on the total population density, the term which curbs the infinite exponential growth is $-n_1^2 c_1$. The individuals which migrate are those with a high reproductive potential, largely the young, lactating females.

On the other hand the tolerants, in the absence of emigrants, will die off exponentially. They have an average age far greater than that of the emigrant population, but a far lower reproductive potential. The tolerants interact with the emigrants in both a social and sexual manner, which leads to an improved birth rate for the tolerants.

Thus the parameter b_2 can be split into parts: b_2^0 governing the sexual creation of individuals, and b_2^1 governing the possible creation of a tolerant from an emigrant through a social encounter. The latter process allows a flow of individuals from the emigrant to the tolerant population. Similarly, the parameter $(b_1 - c_1)$ describing the reduction in emigrant population consists of three parts: a social contribution where individuals flow to the tolerants, a sexual contribution where individuals are created, and a dispersive contribution where individuals leave the population (largely young females and usually when the total density of the populations is large).

A further consideration is that of seasonal fluctuations in the reproductive rates, a_1 and a_2 , which reflect the observed maximum rate in late summer and minimum in late winter. Assuming a simple sinusoidal rate, the time dependent parameters are taken to be

$$a_1(t) = a_1^0 + a_1^1 \sin\left(\frac{\pi}{6}t\right), \quad a_2(t) = a_2^0 - a_2^1 \sin\left(\frac{\pi}{6}t\right).\tag{8.11}$$

The following figures (Figures 8.6 and 8.7) are constructed applying the above model and estimating the parameters from data collected by Krebs et al. (1973) and Myers and Krebs (1974) for the rodent voles *Microtus pennsylvanicus* (or meadow mouse).

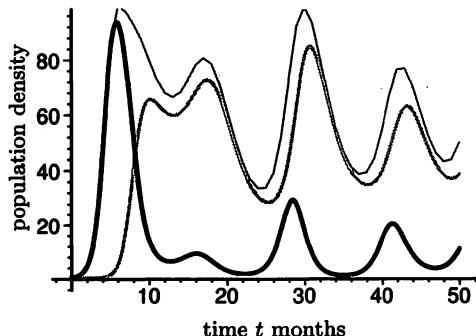


Figure 8.6: Population cycles for the meadow mouse. Parameters $a_1^0 = 1$, $a_1^1 = 0.35$, $b_1 = 1.75 \times 10^{-2}$, $c_1 = 1 \times 10^{-2}$, $a_2^0 = 0.140$, $a_2^1 = 0.075$ and $b_2 = 1.5 \times 10^{-2}$ with initial populations of $n_1 = 0.5$ and $n_2 = 0.5$. Emigrants n_1 (black), tolerants n_2 (grey) and total population (fine black).

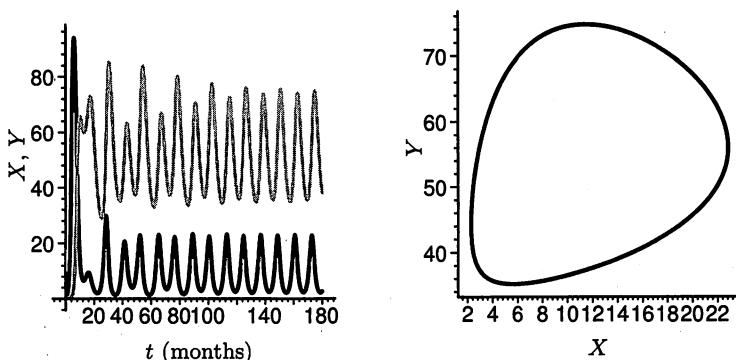


Figure 8.7: The time-dependent (first graph) and phase-plane (second graph) plots for the population cycles of the meadow mouse. Parameters as for Figure 8.6, but the model is run over a longer time period. (n_1 represented with black, and n_2 with grey in the first graph.)

For the figures, a monthly time step was taken and the parameter values are listed in the associated captions. From Figure 8.6 (following Dekker (1975)) it should be noted that the total population constitution of the two genotypes is very different in different phases of the first 48-month (four year) cycle. Furthermore, for the total rodent population the dramatic fluctuations are observed in the initial four year period. While the model is simple, easy to analyse, and provides a close resemblance to the observations in terms of the initial main cycles, it is not robust over long time periods.

If the time-dependent graph is considered over long periods (more than 20 years) then the population settles to a simple 1-year oscillation. This is illustrated in the time-dependent plot and phase-plane of Figure 8.7, and is not included or discussed in Dekker (1975).

However, if disease or predation (or some other mechanism) forced a reduction in the population of the emigrants in particular, then this model would predict dramatic fluctuations over the following decade. Thus the model requires further refinement, which might include different sex groups and an age distribution, as well as a better representation of the rodent dispersion with respect to distance and location, namely their spatial distribution. Furthermore, some statistics on the likelihood of interspecies and between-species interactions, such as predation, would provide an enhancement.

8.5 Case Study: Prickly-pear meets its moth

In Chapter 5, we studied a predator-prey model describing a case where the introduction of an insect species to a region to eradicate a previously introduced pest was unsuccessful. Many such introductions have been and are currently being carried out, with many disasters and unforeseen ramifications for the environment, as we saw in Section 5.4 with the introduction of the Nile Perch to Lake Victoria. However, there have also been success stories and the following case study examines one spectacular success.

The model proposed in this case study is a plant-herbivore system, which is similar to the predator-prey model. It includes extensions of the basic form, and the inclusion of a Michaelis-Menten type function. Adapted from a discussion in May (1981) and a description in Rolls (1969).

In 1864 Captain Phillip, on his way to Australia with the First Fleet, stopped off in Brazil to collect the cochineal insect and their host plant the prickly-pear (*Opuntia inermis* and *Opuntia stricta*). He was to introduce them to Australia to ensure a plentiful supply of red dye (from the cochineal insects) for his soldiers' coats. The insects did not fare well and several more introductions were tried but failed. However the cacti, which were also planted as hedges for additional stock feed as well as garden plants, adapted well: far too well in fact. They ran wild. Extensive, dense stands of the cacti spread into the farmland of northern New South Wales and southern Queensland, averaging about 500 plants per acre (or 1250 plants per hectare). They walled in homesteads with growth of impenetrable density, and destroyed the viability of thousands of square kilometres of farmland.

Attempts were made to eradicate the cacti by spraying them with arsenic pentoxide and sulphuric acid from horseback. Whilst this destroyed the cacti it came into contact with, it was a drop in the ocean and, furthermore, it destroyed the mens' clothing, their boots and saddles and finally their horses, which lost their hair and developed sores which would not heal.

In 1925 a moth *Cactoblastis cactorum* was introduced from Argentina to combat the cactus growth. Its larvae bore through the plant, their breeding being restricted solely to the cacti. They were bred up in Brisbane, from where some 3000 million eggs were distributed to farmers. Within only two years they had virtually wiped out the cacti.

The eggs of the moth are not laid at random, but in clumps of egg-sticks on the plants with each egg-stick comprising about 80 eggs. Thus some plants were hit with large numbers of the moths while others escaped completely. Since about 1.5 sticks of eggs produce sufficient larvae to destroy a plant, many plants received many more larvae than were required to destroy them.

A mathematical predator-prey type model is proposed (May, 1981) to describe this plant-herbivore system. With V the plant mass (in plants per acre) and H the herbivore (moth) population size (in egg-sticks), the model is

$$\begin{aligned}\frac{dV}{dt} &= r_1 V \left(1 - \frac{V}{K}\right) - c_1 H \left(\frac{V}{V+D}\right) \\ \frac{dH}{dt} &= r_2 H \left(1 - \frac{JH}{V}\right).\end{aligned}\tag{8.12}$$

Here K is the maximum biomass, r_1 is the intrinsic rate of increase in the cacti biomass, c_1 is the per-capita maximum rate of food intake by the moths, D is a grazing efficiency term at low plant density, J is the proportionality constant associated with the biomass required to sustain a moth at equilibrium, and r_2 is the per-capita rate of increase of the moth population.

Values for these parameters have been estimated from data collected by Dodd (1940) and Monro (1967), and the older unit of measurement, the acre, is retained to make use of the whole numbers from this collected data. (The conversion is 1 ha = 2.471 acres.) Since the root stock of the cacti can increase to 250 tons per acre in 2 years, r_1 is close to 2.7; however, this is only based on vegetative growth, and if we consider sexual reproduction r_1 is estimated to be 2, at maximum. The carrying capacity K is taken to be 5000 plants per acre. Laboratory experiments were used to get an estimate for r_2 in which 2750 eggs increased to 100 605 eggs in the following cycle, providing an estimate of 3.6. This compares with field data where 5 000 larvae could multiply to 10 000 000 in two years, suggesting a larger r_2 of 3.8 a year. Both figures may underestimate the rate and so r_2 was taken as 4.

From the work of Monro (1967) J was estimated as 2.23 in units of cactus plants per egg-stick. The parameters c_1 and D were more difficult to estimate. The former should be large, reflecting the damage to the plants by the feeding larvae, while the latter should

be small to reflect the efficiency with which the female moths choose plants on which to lay eggs. Following the near total destruction of the cacti in a period of only two years, the model should predict this crash and then settle to a stable 11 plants per acre, as was observed. For this result $c_1 = 6.2$ and $D = 4$.

Figure 8.8 plots the results of applying the proposed model with the parameter values as above.

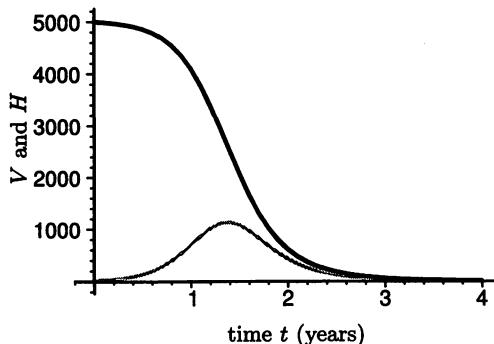


Figure 8.8: The crash of the prickly-pear cactus in just two years. The plants per acre V (black) and the moth population H in egg-sticks per acre (grey).

Clearly the destruction after two years is apparent, albeit with caution we should accept the model as it does not incorporate many of the features of the system under study.

Today, the cacti can still be found in certain small regions of southern Queensland, but they are well under control and no longer pose a threat to the environment. As a token of their gratitude to the moths, affected communities constructed memorial halls, still in current use, in honour of *Cactoblastis*.

8.6 Case Study: Geese defy mathematical convention

So far we have followed the convention that more available food or prey means more animals or predators: the result of the top-down approach of control theory. However, observations do not always support this theory, and the following case study provides an argument and model for a slightly different approach. The model presented below is based on the predator-prey model, in this case a plant-herbivore system, with a Michaelis-Menten type function to allow for an increase in predator (herbivore) numbers to a maximum, and then a reduction as the amount of prey (grass) is increased. The case study is adapted from a model considered by van de Koppel et al. (1996).

Classical exploitation theory has led us to believe that where more grazing is available, more herbivores will be found inflicting more pressure on the standing crop and thus keeping the crop height low; a top-down control in productive environments. This approach is a hotly debated topic, although still widely accepted. van de Koppel et al. (1996) contest the standard plant-herbivore models, arguing that herbivores do not ‘control’ the plant growth entirely.

Their models, supported by empirical evidence, include the possible coexistence of dense vegetation and low herbivore grazing pressure, all in the absence of any predator.

Field data was collected from a salt marsh on the Island of Schiermonnikoog in The Netherlands. It provided an ideal location as the island supports all types of vegetation (sparse, intermediate, and dense) as well as a collection of herbivores (rabbits, hares and two species of geese). Also, there are no predators for these herbivores, other than the occasional raptor or human.

The observation of the maximal grazing pressure by rabbits, hares and geese at the intermediate level of the crop can be explained by several hypotheses. For example, in the denser regions, lack of light may impact on the stem development of the plants, robbing the leaves of the plant protein content and making them less attractive to the herbivores. Alternatively, because of the greater density, the herbivores in these regions may be under greater potential danger from the few predators on the island, and so may avoid them. Another theory is that the herbivores may have greater difficulty penetrating the thicker growth to forage. Whatever the reason, reduced foraging efficiency is observed in the dense regions of vegetation, and typically plant-herbivore models have not incorporated this aspect.

Let P and H be the plant and herbivore densities, respectively, with P measuring the plant mass per unit of area (g/m^2), and H the number of herbivores in the unit of area (number/m^2) calculated from the number of droppings found. The standard form of a plant-herbivore model is

$$\frac{dP}{dt} = G(P) - F(P)H, \quad \frac{dH}{dt} = N(P)H,$$

where $G(P)$ is the plant growth function dependent on density, $F(P)$ is the per-capita consumption rate of a herbivore (the functional response), and $N(P)$ is the per-capita growth rate of herbivores (numerical response). Time t is measured in years. Typically $F(P)$ and $N(P)$ are monotonically increasing functions with increasing P . The proposed models now incorporate the reduced foraging efficiency.

Consider first the case of reduced digestion efficiency. This model assumes that the herbivore digestion is hampered by the change in stem structure of plants in regions of vegetation with greater density. To include this reduced foraging due to reduced digestion efficiency, the per-capita growth rate was taken to decline at high plant density. Let P_1^* and P_2^* be the two densities of vegetation for which herbivore growth is zero, so that below P_1^* there is too little vegetation to support a herbivore population, while above P_2^* there is too much vegetation for the herbivores to thrive and their density decreases.

The model proposed is

$$\begin{aligned} \frac{dP}{dt} &= rP \left(1 - \frac{P}{K}\right) - c_{\max} \left(\frac{P}{a+P}\right) H, \\ \frac{dH}{dt} &= \left(e_{\max} \left(\frac{P}{a+P}\right) e^{-bP} - d\right) H, \end{aligned} \tag{8.13}$$

where clearly the growth rate for P is modelled as logistic. Parameter d is the herbivore mortality rate. The herbivore per-capita growth rate (numerical response),

$$N(P) = \left(e_{\max} \left(\frac{P}{a+P}\right) e^{-bP} - d\right),$$

and the saturating per-capita vegetation mortality rate (functional response),

$$F(P) = c_{\max} \left(\frac{P}{a+P}\right),$$

are illustrated in Figure 8.9 with parameter values $a = 10$, $b = 0.65$, $e_{\max} = 0.4$ and $d = 0.1$.

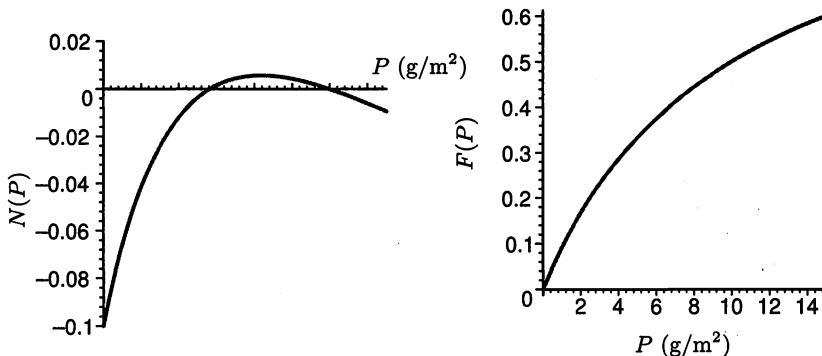


Figure 8.9: For model (8.13) the first figure illustrates the numerical response function (herbivore growth rate) and the second figure the functional response (herbivore consumption rate).

Note that the functional response is approximately $c_{\max}P/a$ when $a \gg P$, and is approximately c_{\max} when $a \ll P$. Here it has been assumed that the consumption rate of the herbivore is an increasing function of plant density but the negative effect of the plant density, when it increases beyond some upper bound, is translated to growth in the herbivores via the factor e^{-bP} .

What is of interest is how this plant-herbivore system may behave with time. Does it settle to a situation of coexistence, or, are there conditions under which the herbivore population dies out? To establish this the phase-plane diagram is examined.

Applying the above model, Figure 8.10 represents a typical phase-plane diagram with $K = 18$, $r = 1$, $c_{\max} = 1$, $a = 10$, $b = 0.065$, $e_{\max} = 0.4$ and $d = 0.1$.

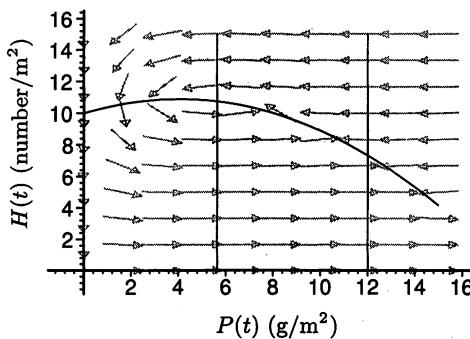


Figure 8.10: Phase-plane diagram with $K = 18$, including the H and P nullclines and the equilibrium points at their intersection.

The nullclines are included and it is clear from the figure (see enlargements in Figure 8.11) that there are three equilibrium points away from the origin in this case, two stable and one unstable. In only one case is there the possibility of long-term coexistence.

Now, considering K (the measure of the plant carrying capacity) as a variable parameter $0 < K < 25$ with all other parameters as before ($r = 1$, $c_{\max} = 1$, $a = 10$, $b = 0.065$,

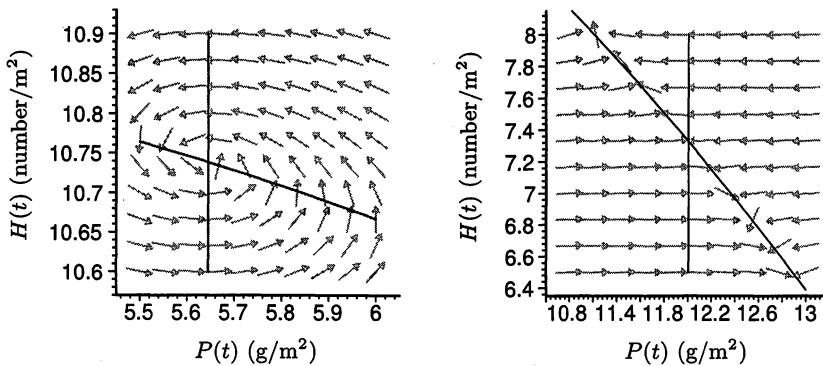


Figure 8.11: The phase-plane of Figure 8.10, magnified about two of the equilibrium points.

$e_{\max} = 0.4$ and $d = 0.1$) several phase-planes are examined to see how this situation may change with changing maximum density of the plant crop. These are illustrated in Figure 8.12.

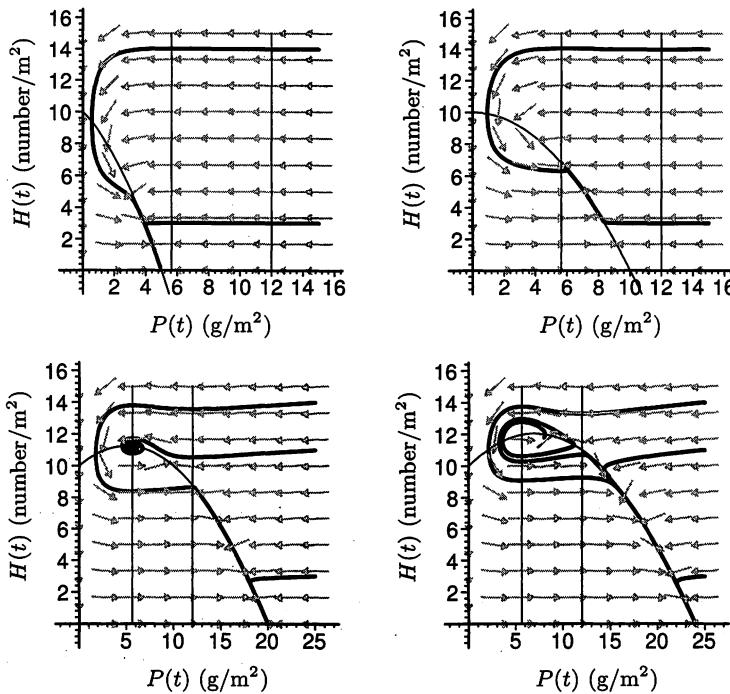


Figure 8.12: Phase-plane diagrams for varying K . From left to right in the first row, $K = 5$ and $K = 10$. In the second row, $K = 20$ and $K = 24$.

From Figure 8.12 it is clear that there is no herbivore population if $K < 5$ or $K > 25$. For $K = 10$ coexistence ensues from any initial densities. The more interesting situation occurs for $10 < K < 24$, where coexistence ensues from only a select number of initial conditions and the herbivores approach extinction otherwise, even with large initial densities.

A second scenario to consider is that of reduced consumption rate. In this case, the model can be further modified to include the increasing crop accompanied by a reduction in consumption rate. This is due to the possible situation where herbivores keep out of the regions of greater density for fear of predators. A further exponential is introduced into the term describing plant consumption as follows:

$$\begin{aligned}\frac{dP}{dt} &= rP \left(1 - \frac{P}{K}\right) - c_{\max} \left(\frac{P}{a+P}\right) e^{-bP} H, \\ \frac{dH}{dt} &= \left(e_{\max} \left(\frac{P}{a+P}\right) e^{-bP} - d\right) H.\end{aligned}\tag{8.14}$$

This reduction in the consumption rate results in a feedback between plant growth of greater density and reduced grazing pressure, greater than in the earlier case of reduced digestion efficiency in system (8.13).

We can summarise the results from the models as follows. For K below P_1^* there is insufficient vegetation to sustain a herbivore population. For K between P_1^* and P_2^* the herbivores control the plant growth at a constant level (as is predicted in traditional plant-herbivore models where increases in plant mass result in increases of the herbivore population). For values of K above P_2^* there are two possible states in which the system can exist. In one there is intermediate plant density as well as herbivores, while in the other only dense vegetation exists. For certain initial conditions the system will tend to the coexistence stable state, while for others it will tend to the extinction of the herbivores. As K increases still further, the only possible stable state becomes that of herbivore extinction and dense vegetation: the vegetation 'escapes' herbivore 'control'.

One consequence of this perspective is that nutrient enrichment, such as fertiliser, is capable of triggering extra growth which may spark a relief from some herbivore control. Furthermore, there is the possibility of permanently destroying a plant-herbivore system; this may have its uses when certain herbivores are considered as pests and not desired as part of the equilibrium.

8.7 Case Study: Possums threaten New Zealand cows

In Chapters 5 and 6, we examined the spread of an influenza in a school; however, we did not consider any strategies to combat the spread. In the following case study we examine a simple disease model which describes the spread of bovine tuberculosis in possums, and the impact of three different strategies to reduce the spread. Note that, unlike epidemics in human communities, we are not concerned about the survival of the New Zealand possum population, in fact if it were wiped out that would be a bonus! This model is adapted from two articles: Wake and Roberts (1995) and Roberts (1992).

Sometime between 1830 and 1860 the brushtailed possum (*Trichosurus vulpecula*) was introduced into New Zealand from its native Australia. It is a cat-sized marsupial with large appealing eyes, a pink nose and a very warm fluffy brown coat. Back in the 1800s it was prized for this coat and thus it was introduced to New Zealand when the fur trade was booming. It thrived in its new environment, without predators of any sort, and while the fur trade died out the possum numbers grew to plague proportions. Its estimated population by 1995 was 70 million with only a few possum-free regions remaining.

Not only does this introduced species have an impact on the native vegetation, where it creates a conservation problem of huge dimensions (by eating approximately 4000 football fields of native forest each day!), it also threatens bird species by robbing their nests of eggs, and as a final straw it harbours and spreads bovine tuberculosis (*Mycobacterium bovis*). This threatens the primary industry of New Zealand, livestock, posing an enormous and extremely costly problem for New Zealand agriculture.

In New Zealand possums are thought to be the main source for bovine tuberculosis in cattle. While the actual mechanisms of transmission from possums to cattle are still being debated, one possibility is that they leave secretions containing the bovine tuberculosis bacteria on the pastures where cattle feed. This is a serious problem for the dairy industry where the disease may be passed through the milk and, without adequate pasteurisation, on to the human population. All animals are tested on a regular basis and any meat or milk from diseased animals cannot be sold. Animals testing positive are slaughtered and whole dairies suspended until they are clear of infection. The economic impact is enormous.

In order to curb the spread of the disease in cattle, it is necessary to examine the dynamics of its spread in the possum population, as well as the resulting changes in these dynamics when various strategies are implemented to reduce the threat. With such large numbers of animals, any feasible plan of action is costly and thus requires extremely careful consideration. We will consider a very simple model for the disease dynamics, and then include some strategies to reduce its spread: culling, sterilisation and vaccination. We are interested in examining the impact of these strategies on the population dynamics.

Consider the possum population to have density $N(t)$ per hectare. We will divide this into two mutually exclusive groups: those with the disease, the contagious infectives $I(t)$, and those who are without disease, the susceptibles $S(t)$. Then $N(t) = S(t) + I(t)$ at any time and subsequently $N' = S' + I'$.

We will assume a simple natural birth rate of b and a natural death rate of a . We will adopt α_d to describe the death rate attributable to the disease and β to describe the infection transmission rate. These parameters are annual estimates and thus we will adopt a yearly time scale for the model. Furthermore, since the population of possums in New Zealand is so large and successful, we will assume that $b - a > 0$.

Then, a system of differential equations describing the dynamics is

$$\begin{aligned} \frac{dS}{dt} &= b(S + I) - aS - \beta SI, \\ \frac{dI}{dt} &= \beta SI - (\alpha_d + a)I. \end{aligned} \tag{8.15}$$

(Note that the symbols used here are different from those used by Roberts (1992), but are consistent with those used for disease models in this text.) It is easy to establish that there are at most two equilibrium points, the first at $(S, I) = (0, 0)$ and the other at

$$(S, I) = \left(\frac{\alpha_d + a}{\beta}, \frac{(b - a)(\alpha_d + a)}{\beta(\alpha_d + a - b)} \right).$$

We are interested in how the populations behave over time, and so we will employ linearisation analysis and examine the system dynamics through the phase-plane. From above, the non-zero equilibrium point becomes very large when α_d is close to, or approaches, $(b - a)$. If this is a stable point, it is very bad news if we are hoping to eradicate the pest. We would like to alter this with the implementation of some strategy, but first we examine the dynamics of the system (8.15). Some of the details are given in Question 8 in the exercises.

For the $(0, 0)$ equilibrium point we can calculate eigenvalues $\lambda_1 = (b - a)$ and $\lambda_2 = -(\alpha_d + a)$, and we can establish that this point is always an unstable saddle point. For the

other equilibrium point the algebra is not quite as simple; however, the real parts of the eigenvalues determine the stability and they can be established from the sign of the trace of J :

$$\text{trace}(J) = \frac{-b(b-a)}{\alpha_d - (b-a)}.$$

Clearly this value is negative when $\alpha_d > b - a$ and then the equilibrium is stable. Alternatively, when $\alpha_d < b - a$ the point is unstable, but in that case the positive populations I and S increase without bound as can be deduced from the gradient of the trajectories in the phase-plane. (It is worth noting here that the measured values of these parameters pertaining to the New Zealand possums, as given by Roberts (1992), have $\alpha_d > b - a$.) Whether this point is a node or a focus can also be established from the Jacobian matrix, and by examining the discriminant of the characteristic polynomial. It can be shown that the equilibrium point is a focus if certain conditions are satisfied by the parameters; otherwise it is a node.

So linear theory predicts that the equilibrium point at the origin is always unstable and a saddle point under our assumption that $b > a$. The non-zero equilibrium point is an unstable node (if $\alpha_d < b - a$) with the trajectories approaching infinity, or a stable node/focus (if $\alpha_d > b - a$) with the trajectories converging to this point. Adopting estimates for the parameter values in Roberts (1992) which relate to the possum population in New Zealand, we have taken $b = 0.305$, $a = 0.105$, $\alpha_d = 3$ and $\beta = 0.7$. These have been incorporated into the time-dependent graphs and phase-plane diagram of Figure 8.13:

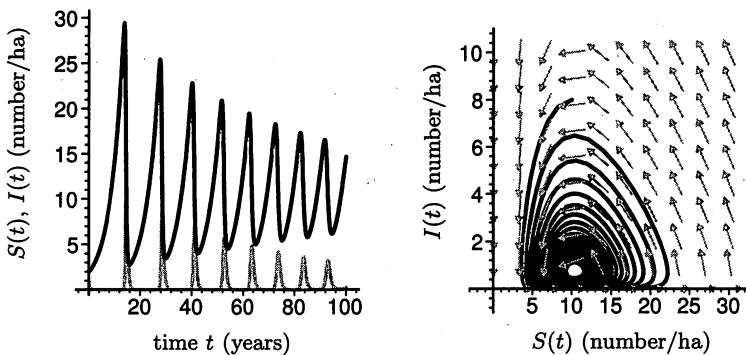


Figure 8.13: The time-dependent plot, S (black line) and I (grey line), and the phase-plane diagram for the NZ possum populations.

Over time, the populations oscillate with decreasing amplitudes and approach a stable population with densities $S = 10.35$ and $I = 0.74$ per hectare, thus predicting a total population of ≈ 11 animals per hectare. This is in agreement with NZ possum population estimates from Roberts (1992).

An important use of mathematical models is to examine how effective certain control strategies can be to help minimise (or in some cases maximise) the impact of a disease. Such strategies may include culling, where the rate of spread of the disease through the population may be slowed by reducing the rate of contact between individuals. Another strategy is to use some form of vaccination (delivered through food supplies). The use of mathematical modelling is to help determine which is the more effective strategy under different circumstances.

We now include in the model a constant per-capita rate of culling per hectare, κ . The system of equations becomes

$$\begin{aligned}\frac{dS}{dt} &= b(S + I) - (a + \kappa)S - \beta SI, \\ \frac{dI}{dt} &= \beta SI - (\alpha_d + a + \kappa)I.\end{aligned}\tag{8.16}$$

This is equivalent to increasing the value of parameter a so that we can use the results from above to predict the dynamics. However, note that now we may have the situation where $b < a + \kappa$ so we need to include this in our interpretations. At this point it is informative to examine a graph of the nullclines to understand how the equilibrium points vary with parameter a . This is illustrated in Figure 8.14.

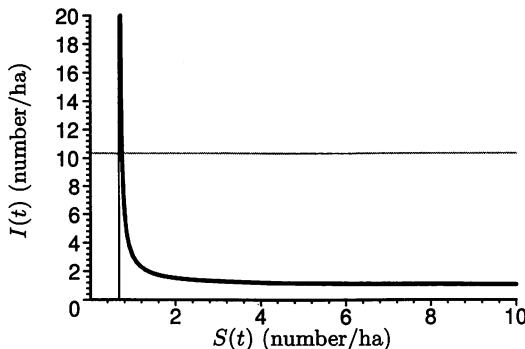


Figure 8.14: Graph of the nullclines (S -nullcline in black, I -nullcline in grey) to establish the impact of varying a . The vertical asymptote is at $(b - a)/\beta$ (fine black).

As a increases, so the hyperbole (with its asymptote at $(b - a)/\beta$) shifts to the left and the I -nullcline at $(a - \alpha_d)/\beta$ increases. This means that at equilibrium the number of susceptibles decreases while the number of infectives increases. However, what is more relevant for the dynamics is that the stability of both equilibrium points changes when $b = a + \kappa$ and we have extinction as the stable equilibrium. For the particular parameter combination given above we have extinction for a cull rate $\kappa > 20\%$.

Using Maple or MATLAB to plot the phase-plane with the parameters as before, but with $\kappa = 0.33$ included, we see that the dynamics match our theoretical predictions. The origin is now a stable equilibrium and the possum population rapidly approaches extinction as illustrated in Figure 8.15.

Instead of culling, we can consider the effect of sterilising a proportion of the population r_s . As a crude approximation, this can be considered to reduce the possum birth rate b to $b - r_s$. (See Roberts (1992) for an alternative model which involves introducing further dependent variables.) This case is similar to that of the culling strategy and the details are omitted.

The more interesting case (from a mathematical perspective) is the inclusion of a vaccination program. We will assume that a proportion of susceptible animals are vaccinated (vS), as obviously there is no gain in vaccinating infected possums. We will also assume that the vaccine will be permanent for that possum, so that once vaccinated, it cannot be infected during its life. (This is not necessarily true, with some vaccines requiring booster shots. In this case it is somewhat hypothetical to include vaccines as they are not currently

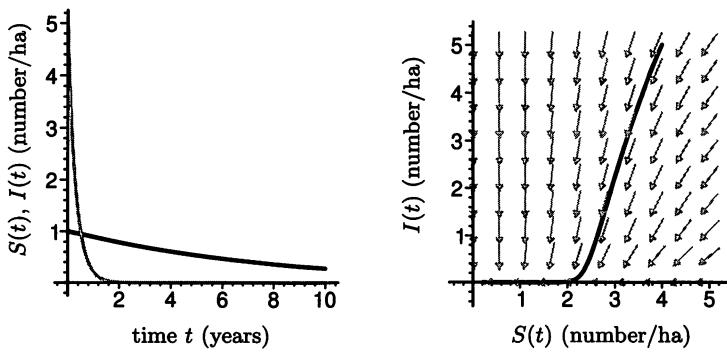


Figure 8.15: The time-dependent plot, S (black line) and I (grey line) and phase-plane diagram for the NZ possum populations with $\kappa = 0.33$.

available; however, we can still gain an understanding of the impact of such a strategy if implementation were possible.)

We introduce a new dependent variable Z to represent the population of vaccinated animals thus rendering three mutually exclusive groups: S the susceptibles, I the infectives and Z the vaccinated. The new model is

$$\begin{aligned} \frac{dS}{dt} &= b(S + I + Z) - aS - \beta SI - \nu S, \\ \frac{dI}{dt} &= \beta SI - (\alpha_d + a)I, \\ \frac{dZ}{dt} &= \nu S - aZ. \end{aligned} \quad (8.17)$$

We do not intend to carry out any further algebraic analysis on this system here. However, we aim to establish, through the use of Maple or MATLAB, some idea of how this vaccination program has affected the dynamics. Figure 8.16 illustrates the time-dependent graphs of the three populations, S , I and Z .

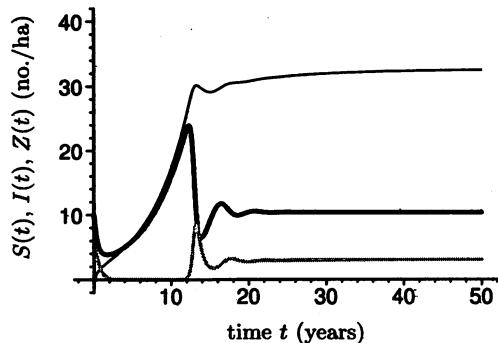


Figure 8.16: The possum population, S (black), I (grey) and Z (fine black), over time with the inclusion of a vaccination program with $\gamma = 0.33$. The initial condition is $(S(0), I(0), Z(0)) = (10, 5, 0)$.

After a few initial oscillations the population settles to the equilibrium value of approximately 48 possums per hectare. Thus there is a substantial increase in the total population,

as one might expect. Furthermore, the non-zero equilibrium point given (approximately) as $(S, I, Z) = (10.35, 3.06, 32.53)$ (from Maple) is stable for the parameter combination of interest, and thus the infected population is in fact larger than that where there is no implemented strategy. Not a very attractive scenario. This shift is due to the initial response to fewer deaths from disease. The scenario is not very attractive from a conservation perspective either, with the destruction of native vegetation increasing substantially.

In Figure 8.17 we have presented a comparison of the three strategies on the possum infective population (I) over time, with the initial number of animals in each case given by the non-zero equilibrium of model (8.15).

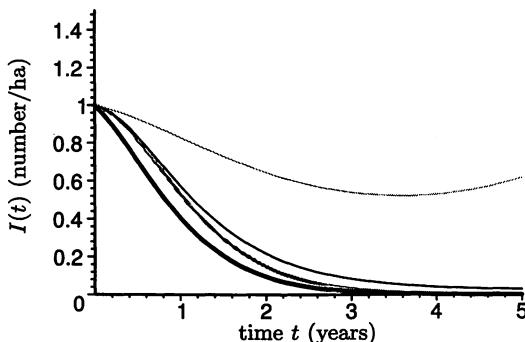


Figure 8.17: The infective possum population over time under a culling strategy (black), under a sterilisation program (grey), vaccinating a percentage of the population (fine black), and the infective population without any applied strategy (fine grey)

Clearly culling appears the most successful strategy in the short term. This conclusion is consistent with the results of more complex models examined by Roberts (1996), which include a density dependent contact rate.

We note that there are still some aspects of the possum and disease dynamics which are not included in these models, and which may have substantial impact. For example, the spatial distribution and movement of possums (see Louie et al. (1993) for an associated model), the rate at which cattle are infected, or the characteristics of a particular vaccine or sterilisation agent. Furthermore, the direct and indirect costs associated with the strategies were not considered, such as the costs in hard dollar terms, or the environmental impact of vaccination which does not reduce the population size. However, we do gain an understanding of the impact on a population of a variety of disease eradication strategies. For this particular case of New Zealand possums, we have some preliminary estimates for the size that these programs would need to be in order to hope for their success. From here, we would need to consider in greater detail the most cost effective strategy for New Zealand.

For more complex models see, for example, Roberts (1992), Roberts (1996) and Fulford et al. (2002). In particular, Roberts (1996) includes a contact rate function to model the change in disease transmission as the population size changes. To model the spatial nature of the spread of Tb Fulford et al. (2002) develop a meta-population model, where the disease spreads on each habitat patch and is carried from patch to patch by maturing juvenile possums migrating to a new patch.

8.8 Exercises for Chapter 8

8.1. Species diversity. With reference to the case study, Competition, predation and diversity, of Section 8.2:

- Using Maple or MATLAB, generate the time-dependent graphs presented in the case study with the parameter values provided in the text.
- Show that for the simple competition model (when $N_3 = 0$) the condition $\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21} \leq 0$ predicts extinction for all but one species in most cases.
- Find the equilibrium points for the system.

8.2. Scaling. Scaling can be used to simplify the mathematical analysis of a model by reducing the number of parameters, and writing the equation in a dimensionless form. Consider the logistic equation

$$\frac{dX}{dt} = rX \left(1 - \frac{X}{K}\right), \quad X(0) = x_0.$$

Since X and K are in the same units, we choose a new dimensionless variable Y as a measure of X in terms of the carrying capacity K , such that $X/K = Y$.

- Show that, with this change of variable, the above logistic equation becomes $dY/dt = r(1 - Y)Y$, with $Y(0) = y_0 = x_0/K$.
- Furthermore, the independent variable can be scaled in units of $1/r$, using $t = s/r$. Recall, the chain rule gives

$$\frac{dY}{ds} = \frac{dY}{dt} \frac{dt}{ds}.$$

Show, by using the chain rule, that with this scaling the logistic equation becomes

$$\frac{dY}{ds} = (1 - Y)Y, \quad Y(0) = \lambda, \quad \lambda = \frac{x_0}{K}.$$

Thus the model is reduced to a dimensionless form with only one parameter, λ .

8.3. Scaling the extended predator-prey model. Consider the extended predator-prey model, the Holling-Tanner model developed in Section 8.3,

$$\frac{dX}{dt} = r_1 X \left(1 - \frac{X}{K}\right) - \frac{c_1 X Y}{1 + t_h c_1 X}, \quad \frac{dY}{dt} = r_2 Y \left(1 - \frac{Y}{c_3 X}\right).$$

To simplify the analysis the equations can be scaled as follows: Define dependent and independent variables x , y and τ by

$$x = \frac{X}{K}, \quad y = \frac{Y}{c_3 K}, \quad \tau = r_2 t.$$

The chain rule can be used to change both the dependent and independent variables in the equations since we have that

$$\frac{dx}{dt} = \frac{dX}{dt} \frac{1}{K}, \quad \frac{dx}{d\tau} = \frac{dx}{dt} \frac{dt}{d\tau}.$$

In order to find the derivative $dx/d\tau$, use the chain rule as above to get expressions for X' in terms of x and dx/dt . Then substitute these expressions into the original equation for X' . In this way, all terms involving X , X' and Y can be replaced with terms in x , x' and y . Similarly, the equation for $dy/d\tau$ can be obtained. Show that

$$\frac{dx}{d\tau} = \lambda_1 x (1 - x) - \frac{\lambda_2 x y}{(\lambda_3 + x)}, \quad \frac{dy}{d\tau} = y \left(1 - \frac{y}{x}\right),$$

with

$$\lambda_1 = \frac{r_1}{r_2}, \quad \lambda_2 = \frac{c_3}{t_h r_2}, \quad \lambda_3 = \frac{1}{t_h c_1 K}.$$

8.4. Extended predator-prey model. Consider the scaled equations for the Holling-Tanner predator-prey model derived in the previous question,

$$\frac{dx}{d\tau} = \lambda_1 x(1-x) - \frac{\lambda_2 xy}{(\lambda_3 + x)}, \quad \frac{dy}{d\tau} = y \left(1 - \frac{y}{x}\right),$$

where λ_1 , λ_2 and λ_3 are dimensionless positive numbers, defined in the previous question.

- (a) Use Maple or MATLAB to draw the phase-plane for the scaled system of Question 3 above, with parameter values $\lambda_1 = 5$, $\lambda_2 = 10$ and $\lambda_3 = 0.015$. Show that, for a variety of initial conditions, the system settles to a single periodic solution over time as illustrated in Figure 8.4.
- (b) By decreasing the ratio of searching time to handling time, estimate roughly for what value of λ_3 this periodic solution collapses to a stable/unstable node/focus. What changes, if any, do you observe in the nature of the periodic solution as the parameter is decreased? What does this mean for the time-dependent graphs of the populations?
- (c) Repeat this process for a variety of λ_2 values between 1 and 10. Then, using these results, plot the points (λ_3, λ_2) , where the change in dynamics takes place, in the (λ_3, λ_2) -plane. Joining the points together provides the definition of a rough boundary in the parameter plane, which divides periodic behaviour from where all trajectories approach a stable point.

8.5. Lemmings. Consider the case study on Lemming mass suicides of Section 8.4.

- (a) The model presented claims to support a four yearly cycle. Using Maple or MATLAB generate the time-dependent plots over both short and long time periods, as well as a phase-plane. Do your results support the claim of the authors? Provide clear reasons for your answers.
- (b) Find the equilibrium values for the system in the case with constant parameter values (not time dependent parameters).
- (c) Linearise the system and classify these equilibrium points. Comment on whether your results support the claim made in (a) above.

8.6. Prickly-pears. Consider the plant-herbivore model presented as a case study on the spread of the prickly-pear in Australia, and its annihilation by an introduced moth *Cactoblastis* (see Section 8.5).

- (a) What growth processes (exponential or logistic) are adopted for the plant biomass and the moths in this model? What are the numerical response and the functional response terms for this system?
- (b) The interaction term appearing in the rate equation for the plant biomass is given as

$$-c_1 H \left(\frac{V}{V+D} \right).$$

Explain clearly why you think a function of this nature has been used, in terms of its changing contribution when the number of plants increases, or decreases, significantly.

- (c) In the case study, the claim is made that the system settles to a fixed and stable number of 11 plants per acre over a period of time. Using Maple or MATLAB show that this is indeed the case for the suggested model with the parameter values given.

8.7. Rabbits, hares and geese. The case study of Section 8.6, Geese defy mathematical convention, presents improved plant-herbivore models appropriate to systems which do not exhibit the top-down control approach.

- (a) Explain the suggested meaning of all parameters used in the models.
- (b) Sketch graphs of the numerical response and the functional response terms for the general case, in each of the two models. When do the two functional response terms differ significantly and when are they similar? Explain how these differences and similarities reflect the different intentions of the two proposed models in the case study.
- (c) Consider the reduced digestion efficiency model with parameter values as in the text, $K = 10$, $r = 1$, $c_{\max} = 1$, $a = 10$, $b = 0.065$, $e_{\max} = 0.04$ and $d = 0.1$. The case study claims that the model can be used to predict when and how, by changing a parameter, the herbivore could move towards extinction. Thus there is the possibility of eradicating a pest by encouraging plant growth beyond a threshold. It is also possible to control the vegetation by increasing herbivore numbers.

Use Maple or MATLAB to generate the phase-plane, together with direction trajectories and system nullclines. Show, considering the phase-plane, how increasing or decreasing the herbivore carrying capacity can force a change in the dynamics so that the two thresholds discussed above can be crossed. Make rough estimates of the values of K for which this change occurs.

- (d) Using the second model proposed, the reduced consumption rate model, with the same parameter values as above, do the threshold values estimated in (b) change? Give reasons for your answer and find the new thresholds if they are different.
- (e) Identify a value of K for which there is a periodic solution in each of the models proposed, and choose appropriate initial conditions to illustrate them in a phase-plane, using Maple or MATLAB.

8.8. Bovine tuberculosis. A model for the bovine tuberculosis epidemic in NZ possums is presented in the case study, Possums threaten New Zealand cows, of Section 8.7:

$$\begin{aligned}\frac{dS}{dt} &= b(S + I) - aS - \beta SI, \\ \frac{dI}{dt} &= \beta SI - (\alpha_d + a)I.\end{aligned}$$

- (a) Show that the only two equilibrium points are at the origin and

$$(S, I) = \left(\frac{\alpha_d + a}{\beta}, \frac{(b - a)(\alpha_d + a)}{\beta(\alpha_d + a - b)} \right).$$

- (b) Construct the Jacobian matrix (J). Show that

$$\text{trace}(J) = \frac{-b(b - a)}{\alpha_d + a - b},$$

and that the equilibrium point is a focus if

$$\frac{4(\alpha_d + a)(\alpha_d + a - b)}{b^2(b - a)} > 1,$$

and alternatively that it is a node.

- (c) Establish the nullclines for the system and sketch a graph to indicate how these nullclines, and thus the equilibrium points, shift when culling is included in the model.
- (d) Alternatively, if a sterilisation program is introduced how are the nullclines, and thus the equilibrium points, changed? Estimate the minimum number of sterilisations which ensures that the model predicts the possible extinction of possums.

8.9. Bovine tuberculosis and a vaccination program. Consider the equations for the possum bovine tuberculosis epidemic from Section 8.7, Possums threaten New Zealand cows, with vaccination included,

$$\begin{aligned}\frac{dS}{dt} &= b(S + I + Z) - aS - \beta SI - \nu S, \\ \frac{dI}{dt} &= \beta SI - (a_d + a)I, \\ \frac{dZ}{dt} &= \nu S - aZ.\end{aligned}$$

- (a) Draw a compartment diagram for this model.
- (b) Show that there are only two equilibrium points: one at the origin and find an expression for the non-zero equilibrium point.
- (c) Construct the associated Jacobian matrix at the non-zero equilibrium point (For known parameter values the trace and determinant can be calculated easily, but for general parameter values the algebra can get complicated and may yield little information.)
- (d) Using MATLAB or Maple, on the same system of axes, and using the parameter values in Section 8.7, draw time-dependent plots for the infective population, comparing the three models (culling, sterilisation, vaccination) with the number of infectives in the population without any applied strategy.

8.10. Density dependent contact rate. As discussed at the end of Section 5.2, a better model for the spread of a disease in a population where the population density changes with time, is one which incorporates a density dependent contact rate function. One basic model, proposed for the spread of TB in possums, (Roberts (1996)) is

$$\begin{aligned}\frac{dS}{dt} &= b(S + I) - aS - \frac{pc(N)}{N}SI, \\ \frac{dI}{dt} &= \frac{pc(N)}{N}SI - (\alpha_d + a)I,\end{aligned}\tag{8.18}$$

where $N = S + I$ and where the contact rate function is

$$c(N) = \frac{c_m N}{K(1 - \epsilon) + \epsilon N}.$$

Here c_m is the maximum per-capita contact rate, p the probability a single contact produces an infection, and ϵ is a parameter describing the degree of social mixing within the population, with $0 \leq \epsilon \leq 1$. For $\epsilon = 1$ then the transmission coefficient $\beta = pc(N)/N = pc_m$ is constant. For $\epsilon = 1$ then β is proportional to the population density.

Using Maple or MATLAB modify the basic model (8.18), and investigate whether culling, or a vaccination program, is the better control strategy for this disease. (Ignore the ecological impact!) Use the parameter values from Section 8.7 and let $p\lambda_m = 5$, $\epsilon = 0.5$, $K = 10$.

de la secció d'informació i comunicació de l'Institut d'Estudis Catalans, que ha estat el seu impulsor i coordinador. La secció d'informació i comunicació del IECA es va crear el 1995 amb la finalitat d'impulsar la divulgació del coneixement i la cultura catalana i d'apropiar-se dels nous mitjans de comunicació. La secció d'informació i comunicació del IECA és una entitat de caràcter interdisciplinari que té com a objectiu principal la difusió dels resultats dels projectes de recerca i els treballs d'investigació que es realitzen en el seu entorn. La secció d'informació i comunicació del IECA està dirigida per un consell de direcció compost per un director, un secretari i un consell d'administració.

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Chapter 9

Formulating basic heat models

This chapter is concerned with modelling processes which involve heat conduction. We concentrate on formulating differential equations for the heat and temperature of systems, and emphasise the difference between them. In the absence of heat conduction we use the input-output principle, or the balance law introduced in Chapter 2, to determine the heat content of the object we are modelling. When conduction is involved, we also apply this input-output of heat energy, but to an arbitrary thin section. The analytic solutions for these models are derived in the subsequent Chapters 10 and 11.

9.1 Introduction

We begin by introducing some problems which involve heating and cooling. It is of great importance to understand whether or not heat conduction is an important factor in any particular application, and to this end we consider a variety of problems, some of which require the consideration of heat conduction and others which do not.

Cooling of a cup of coffee

Suppose we have a hot cup of coffee sitting on a bench top, too hot to drink. If the coffee is at a temperature of 60°C , how long will it take to cool down to 40°C ? To begin to answer this, we introduce some basic physical concepts. In particular, we look at the distinction between temperature and heat, the two most important physical quantities in this problem.

First, consider *temperature*: this represents how hot the coffee is. If we can assume the temperature of the coffee is uniform throughout (we call this homogeneous) then the temperature will be a function of time alone. Temperature is measured in degrees Celsius $^{\circ}\text{C}$, or in Kelvin K, where the temperature in $^{\circ}\text{C}$ is 273 less than the temperature in K, approximately. That is, $^{\circ}\text{C} + 273 = \text{K}$.

Second, consider the quantity *heat*. The temperature of the coffee drops because heat energy is transferred to the surrounding air. This is due to the fact that the surrounding air is at a lower temperature, and heat is always transferred from a region of high temperature to a region of lower temperature. Since heat is a form of energy it is measured in Joules, in units of the SI system.

Thus to answer the question about the cup of coffee we need to formulate a suitable equation for the temperature. But to do this we need to determine what is happening to the heat. So we construct a compartmental diagram for the heat input and output for the cup of coffee (see Figure 9.1).

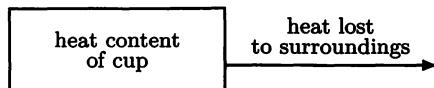


Figure 9.1: Input-output compartment diagram for the heat content in a cup of coffee.

Equations which relate heat energy to temperature are derived in Section 9.2, using the concept of *specific heat*. We assume the temperature to be homogeneous throughout the compartment, and thus a function of time alone. We also need an equation which describes the rate of heat transfer to the surroundings. This too is introduced in Section 9.2 as is *Newton's law of cooling*.

A similar problem which we consider is that of determining the time taken for the body of water in a hot water tank to heat to a specified temperature. We again assume the temperature to be homogeneous, and thus a function of time. In this application we also need to account for the heat supplied to the system by the heating element.

Other heat conduction applications

Consider the problem of finding the rate at which heat can be transferred through a wall. This is important for determining the insulating properties of the wall, which are useful energy efficiency considerations.

The temperature on the outside of the wall will be different from that on the inside, which

suggests we should also think of the temperature as a function of distance. There will be a temperature gradient in the wall and heat will flow in the direction of hot to cold (from the inside to the outside of a wall in winter) as a result of heat conduction.

We also consider heat conduction through a hot water pipe insulating jacket. This is an interesting problem because we get counter-intuitive results. We see that, under certain circumstances, insulating a hot water pipe is less efficient (since more heat escapes) than not insulating it at all! Also, we consider the conduction effect of heat fins which are used to conduct heat away from a source, such as in computers or on a motorbike.

9.2 Some basic physical laws

Before formulating equations for the problems mentioned above, we need to understand some basic physical concepts of heat transport, as well as the distinction and relationship between heat and temperature.

Heat and temperature

The result of applying heat, or heat energy, to an object is to raise its temperature. Similarly, as an object cools, its temperature drops as it loses heat to the surroundings. The greater the mass of the object, the more heat is required to raise its temperature, while if the temperature of a mass drops, then more heat energy is lost from a larger than a lesser mass, for an equivalent drop in temperature.

When formulating a mathematical model for a problem involving heating or cooling, we need to take account of the amount of heat flowing into or out of a system. While it makes little sense to talk about a 'flow' of temperature, it is a change in temperature which we observe. Thus we need to be able to relate heat and temperature, and this can be done using the specific heat of a substance.

We assume the change in heat is directly proportional to the change in temperature and also the mass of the object. Thus we write

$$\left\{ \frac{\text{rate of change of heat content}}{\text{mass}} \right\} = c \times \left\{ \frac{\text{rate of change of temperature}}{\text{temperature}} \right\} \quad (9.1)$$

where c is a positive constant of proportionality, known as the specific heat of the material. The definition of specific heat is the amount of heat required to raise the temperature of 1 kg of a substance at a given temperature, by 1 °C. In symbols, if we define Q as the rate of change of heat with time (measured in Watts), m as the mass of the material being heated or cooled (measured in kilograms), and U as the temperature¹, then

$$Q = cm \frac{dU}{dt}$$

We have assumed c to be independent of the mass of the object and the temperature, but we know that metals absorb heat more easily than water. Thus a greater amount of heat is needed to raise the temperature of 1 kg of water by one degree than is needed to raise the

¹ U (not T) is used for temperature so that it is not confused with time t .

temperature of 1 kg of metal by one degree. This implies that metals have a smaller specific heat than water. In Table 9.1, the specific heats of some common materials are given.

Table 9.1: Table of specific heats for some common substances. Units are standard SI units, i.e. $\text{J kg}^{-1} \text{ }^{\circ}\text{C}^{-1}$.

Substance	c	Substance	c
Aluminium	896	Asbestos	841
Copper	383	Brick	840
Stainless steel	461	Glass	800
Wood	2 385	Butter	2 300
Concrete	878	Lamb	3 430
Water (at 20 °C)	4 187	Potatoes	3 520

The specific heat, c , is not actually constant over a large temperature range; however, if the temperature range is not too large use of (9.1), with constant specific heat c , provides reasonable predictions.

Newton's law of cooling

A mechanism for heat to be lost from an object is that of exchanging heat energy with its surroundings. This takes place from the surface of the object, and thus we would expect the rate of heat loss to increase with the exposed surface area of the object, and be directly proportional to this area. Further, if the difference in temperature between the surface of the object and the surroundings increases, then we would expect heat to be lost faster.

We therefore make the assumption that the rate of heat flow is directly proportional to the temperature difference between the surface and its immediate surroundings. Further, the existence of slowly moving air across the cooling object (a slight breeze) is assumed. Under these conditions we have Newton's law of cooling, which works equally well with heating problems. Newton's law of cooling states

$$\left\{ \begin{array}{l} \text{rate heat} \\ \text{exchanged with} \\ \text{surroundings} \end{array} \right\} = \pm hS\Delta U \quad (9.2)$$

where ΔU is the temperature difference, S is the surface area from which heat is lost/gained (in units of m^2), and h is a positive constant of proportionality. The constant h is called the *convective heat transfer coefficient*, or the *Newton cooling coefficient*. The units for h are Watts/ $\text{m}^2/\text{ }^{\circ}\text{C}$.

The correct sign for the temperature difference is determined in any specific problem by the direction of heat transfer, and whether the surface is gaining or losing heat. If S is the surface area of an object and if the temperature U of the object is greater than the temperature u_s of the surroundings, then we would write

$$\left\{ \begin{array}{l} \text{rate heat} \\ \text{exchanged with} \\ \text{surroundings} \end{array} \right\} = hS(U - u_s) = hS\Delta U.$$

When the temperature of the surroundings is greater than the temperature of the object ($u_s > U$), then heat is exchanged in the opposite direction and so

$$\left\{ \begin{array}{l} \text{rate heat} \\ \text{exchanged with} \\ \text{surroundings} \end{array} \right\} = hS(u_s - U) = -hS\Delta U.$$

Returning to the cup of coffee

Applying the above expressions, we can now link the rate of change of heat in (9.1) directly to the rate of change of temperature, as in the following example.

Example 9.1: Formulate a differential equation for the temperature of a cup of coffee over time.

Solution: To describe the conservation of heat energy we have, from the heat energy input-output compartment diagram of Figure 9.1 in Section 9.1, that

$$\left\{ \begin{array}{l} \text{rate of} \\ \text{change of} \\ \text{heat content} \end{array} \right\} = \left\{ \begin{array}{l} \text{rate heat} \\ \text{lost to} \\ \text{surroundings} \end{array} \right\}.$$

Using (9.2) and (9.1) we thus obtain the differential equation

$$cm \frac{dU}{dt} = -hS(U - u_s). \quad (9.3)$$

Note that a negative sign is chosen for the term on the RHS. The cup of coffee is cooling, and $(dU/dt) < 0$, and then since $\Delta U = U(t) - u_s$ is always positive we need to include a negative sign for consistency.

Once again we have an example of an equation describing exponential growth or decay, depending on whether the object is warm or cold compared with its environment. The heat loss from the hot cup of coffee left to stand follows an exponential decay process and, as we see in Section 10.1, it stabilises at the temperature of the surroundings u_s as expected.

We have assumed h to be a constant; however, this is a limitation of the model as the rate of heat lost from a surface will be affected by the air flow near it. This is sometimes called a *wind-chill* effect. Table 9.2 illustrates this by showing how the coefficient h increases with the velocity of the air-flow passing over a metal plate, and indicates that the effect is nontrivial.

Table 9.2: The value of the convective heat transfer coefficient h from a plate of length 0.5 m over which an airflow, given in metres per second (m/s), passes.

	h
Plate in still air	4.5
Air-flow at 2 m/s over plate	12
Air-flow at 35 m/s over plate	75

Summary of equations

To express a change of heat in terms of a change of temperature, we use the specific heat equation

$$\left\{ \begin{array}{l} \text{rate of} \\ \text{change of} \\ \text{heat content} \end{array} \right\} = cm \frac{dU}{dt}$$

where U is the temperature, m the mass of an object and c its specific heat. Newton's law of cooling is given by

$$\left\{ \begin{array}{l} \text{rate heat} \\ \text{exchanged with} \\ \text{surroundings} \end{array} \right\} = \pm hS\Delta U$$

where S is the surface area, ΔU the temperature difference and h a positive constant, namely the convective heat transfer coefficient or the Newton cooling coefficient.

Summary of skills developed here:

- Distinguish between heat and temperature.
- Relate heat to temperature using the specific heat of a substance.
- Formulate a differential equation for the temperature of an object that is either heating or cooling.

9.3 Model for a hot water heater

We derive a differential equation for the temperature of water being heated by an electric heating element. The problem applies principles similar to those in the example above, except that in this case heat is added to the system via the heating element. We write down a heat balance equation over a small time interval, and then let the time interval tend to zero to derive the differential equation. This process leads to a differential equation for the temperature as a function of time.

Problem description

Some domestic examples of water heaters include hot water systems, urns and kettles. Our problem specifically refers to an electrically heated hot water system, which is the standard for an average home. It usually contains 250 litres of water and is cylindrical with dimensions of height 1.444 m and diameter 0.564 m. Initially we assume the water to be at a temperature of 15 °C. The heating element when switched on supplies heat at a constant rate (per hour) of 3.6 kW. (The other commonly used elements supply 4.8 kW per hour.) In Figure 9.2 a schematic diagram illustrates the heat input and output for the system. We wish to determine how long it would take to heat the water to 60 °C.

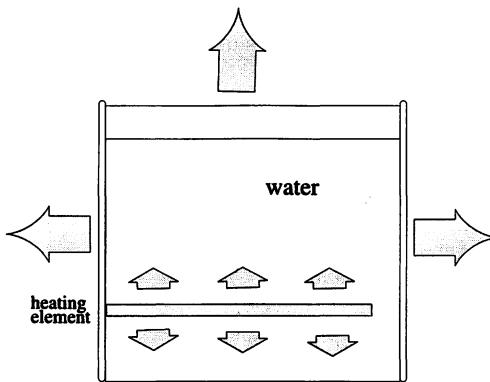


Figure 9.2: Schematic diagram of a hot water heater.

In order to study this problem we introduce some notation. We let $U(t)$ denote the temperature of the water at time t . We denote by u_0 the initial temperature of the water,

u_f as the final temperature, m as the mass of water in the heater and q as the rate of heat energy supplied. S in m^2 will denote the surface area from which heat may escape, which in the case of the hot water heater is the surface of the tank.

Other symbols will be introduced as required. Note that by assigning symbols to these quantities we increase the usefulness of our model, since we can later substitute various values for these symbols. We can thus use the model to explore the effect and sensitivity of change in these different physical quantities.

Model assumptions

We examine what simplifying assumptions can be made about the problem, and build the model using these.

- First, let us assume that the water in the tank is well stirred so that the temperature remains homogeneous throughout. Without this assumption the problem would be far more complex, since temperature would then be a function of both time and position and we would also have to take account of heat transfer (by conduction and convection) between different points in the tank. By assuming that the water is well stirred, we only have to consider the temperature of the water as a function of time.
- We also assume that heat is lost from the surfaces of the tank according to Newton's law of cooling.
- Finally, we assume that thermal constants, such as the specific heat and the Newton cooling coefficient, remain constant in our applications.

General compartmental model

We start formulating the model by writing down a word equation to describe the balance of heat energy in terms of rates of heat input and output. We must account for the heat produced by the heating element, and the heat lost from the surface of the water heater to the surroundings.

Example 9.2: Give a suitable word equation describing the rate of change of heat.

Solution: We start by drawing an input-output diagram for the heat content of the system by applying the balance law. This is shown in Figure 9.3.

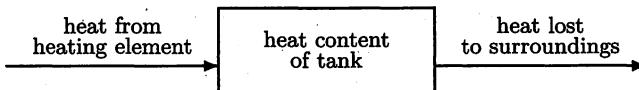


Figure 9.3: Input-output compartment diagram for the heat content in the domestic hot water system.

A heat balance for the system is described by the word equation

$$\left\{ \begin{array}{l} \text{rate of} \\ \text{change} \end{array} \right\}_{\text{of heat}} = \left\{ \begin{array}{l} \text{rate heat} \\ \text{produced by} \\ \text{heating element} \end{array} \right\} - \left\{ \begin{array}{l} \text{rate heat} \\ \text{lost to} \\ \text{surroundings} \end{array} \right\}. \quad (9.4)$$

Formulating the differential equation

As the temperature of the system rises, the net heat produced goes into raising the temperature of the system. To obtain a mathematical expression for the heat used to change

the temperature, we use the fundamental equation relating heat to temperature through the specific heat from the first section of this chapter:

$$\left\{ \begin{array}{l} \text{rate of} \\ \text{change of} \\ \text{heat content} \end{array} \right\} = cm \frac{dU}{dt}$$

where c is the specific heat of the water, m is the mass of the water and $U(t)$ denotes its temperature at time t .

Example 9.3: Find expressions for the other terms in the word equation (9.4) and hence formulate a differential equation for the temperature.

Solution: It is assumed that the heating element produces heat at a constant rate per unit time, which we denote by q . Thus

$$\left\{ \begin{array}{l} \text{rate heat} \\ \text{produced by} \\ \text{heating element} \end{array} \right\} = q. \quad (9.5)$$

For the rate of heat lost to the surroundings we use Newton's law of cooling, which states

$$\left\{ \begin{array}{l} \text{rate heat} \\ \text{lost to} \\ \text{surroundings} \end{array} \right\} = hS \left\{ \begin{array}{l} \text{temperature} \\ \text{difference} \end{array} \right\} = hS(U(t) - u_s), \quad (9.6)$$

where S is the surface area of the heater and h is the Newton cooling coefficient. The temperature difference is the difference between the current water temperature $U(t)$ and the (constant) temperature of the surroundings u_s .

Now that we have suitable expressions for each of the quantities in equation (9.4) we can obtain a differential equation for the temperature. Substituting equations (9.5) and (9.6) into equation (9.4) we obtain the differential equation

$$cm \frac{dU}{dt} = q - hS(U(t) - u_s) \quad (9.7)$$

which describes the temperature variation of the water with time.

Numerical solution

Given an initial condition and suitable values for all the parameters, we can solve this differential equation numerically using Maple or MATLAB. (We also see how to obtain an analytic solution and make use of it in Section 10.2.)

For a typical set of parameters we consider the standard 250 litre tank, of height 1.444 m and diameter 0.564 m. We take $m = 250$ kg, $c = 4200 \text{ W kg}^{-1} \text{ s}^{-1}$, $h = 12 \text{ W m}^{-2} \text{ }^\circ\text{C}^{-1}$, $S = 3.06 \text{ m}^2$, $q = 3600 \text{ W}$ and $u_s = 15^\circ\text{C}$ (all in SI units). The plot of temperature against time is given in Figure 9.4. The Maple code is given in Listing 9.1 and the MATLAB code is given in Listing 9.2.

Listing 9.1: Maple code: c_he_waterheater.txt

```
> restart: with(plots): with(DEtools):
> m:=250: c:=4200: h:=12: S:=3.06: q:=3600: us:=15:

> de1:= c*m*diff(U(t),t) = q - h*S*(U(t) - us);
> init1 := U(0)=15;
> tmin := t/60;
> plot1:=DEplot(de1, [U], t =0..500*60,[[init1]]);
> display(plot1);
```

Listing 9.2: MATLAB code: c.he.waterheater.m

```

function c_he_waterheater
global m c h S q us;
m=250; c=4200; h=12; S=3.06; q=3600; us=15;
u0 = 15;
tend = 500*60;
[tsol, Usol] = ode45(@rhs, [0 tend], u0);
plot(tsol/60, Usol);

function Udot = rhs(t, U)
global m c h S q us;
Udot = q/c/m - h*S/c/m*(U - us);

```

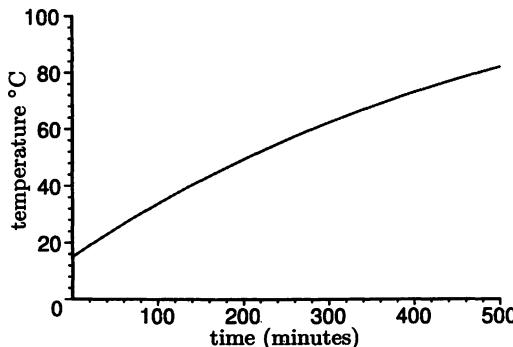


Figure 9.4: Plot of temperature against time (in minutes) using $m = 250 \text{ kg}$, $c = 4200 \text{ W kg}^{-1} \text{s}^{-1}$, $h = 12 \text{ W m}^{-2} \text{C}^{-1}$, $S = 3.06 \text{ m}^2$, $q = 3600 \text{ W}$ and $u_s = 15^\circ\text{C}$. Note that the model no longer applies after the temperature reaches boiling point since it fails to account for the latent heat needed to boil the water.

In Figure 9.5 we repeat the solution with the heat input reduced considerably to only 500 W , and see that the temperature eventually approaches a constant value of approximately 30°C . This constant value is an equilibrium solution to the differential equation. We investigate this further in Section 10.2.

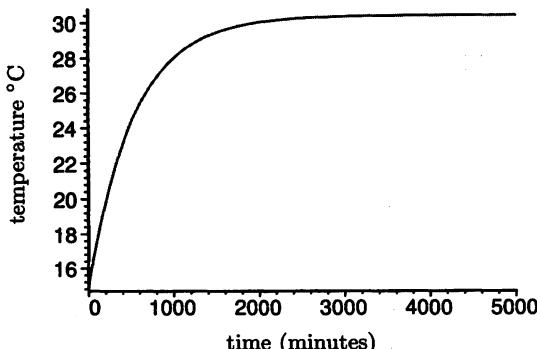


Figure 9.5: Plot of temperature against time (in minutes) using $m = 250$, $c = 4200$, $h = 12$, $S = 3.06$, $q = 500$ and $u_s = 15$ (all in SI units). The temperature approaches an equilibrium value.

9.4 Heat conduction and Fourier's law

Before starting to solve any specific problems, we first lay some groundwork in the basic physics of heat conduction. We define *heat flux* to describe the flow of heat, and introduce *Fourier's law* which relates the heat flux to the temperature.

Heat and temperature

In a given heating problem the temperature starts from some initial state and then, as a body is cooled or heated, the temperature changes. If the temperature is not the same at every point throughout the body then heat will also be conducted through the body from regions of high temperature to regions of lower temperature.

Eventually, the temperature will tend to some equilibrium state where there may still be a flow of heat through the body by conduction, but the temperature at any point within the body will not change with time. When the temperature is in this equilibrium state, none of the heat is used to increase the temperature, nor is any of the heat released to decrease the temperature. We can thus say, for *thermal equilibrium*,

$$\left\{ \begin{array}{l} \text{rate of} \\ \text{change of} \\ \text{heat content} \end{array} \right\} = 0. \quad (9.8)$$

Heat conduction and heat flux

Heat conduction can occur in a solid, liquid or gas, and involves the transfer of heat energy by the vibration of molecules. In this book we are concerned with heat *conduction*; however, there are other heat transport mechanisms such as *convection*, the transfer of heat in a liquid or gas by the fluid flow, and *radiation* which involves heat transfer by electro-magnetic waves.

Observation demonstrates that the rate at which heat is conducted through a body is directly proportional to the cross-sectional area through which the heat flows. It is thus reasonable to talk about a rate of heat flow per unit area through a cross-section. This quantity is called the heat flux. We formally define *heat flux* $J(x)$ by

$$J(x) = \left\{ \begin{array}{l} \text{rate of} \\ \text{flow of heat} \\ \text{per unit time} \\ \text{per unit area} \end{array} \right\} \quad (9.9)$$

Heat flux is measured in SI units as Watts per square metre, where Watts are Joules per second.

Fourier's law of heat conduction

Common observation indicates that some substances conduct heat better than others. Heat flows more easily through certain metals than through substances such as brick and stone.

Fourier did some controlled experiments where he measured the heat conducted through thin plates of different materials. In his experiments he held the temperature constant, but at different values on either side of the plate. He noticed that the heat flux increased with the temperature difference, and decreased as the thickness of the plates increased. He thus came to the conclusion that the heat flux (rate of heat flow per unit area per unit time) is proportional to the temperature gradient, which is the gradient of the temperature expressed as a function of distance through the plate.

We can express this result mathematically. If $J(x)$ denotes the heat flux at x , and $U(x)$ the temperature at x , then *Fourier's law* states

$$J(x) = -k \frac{dU(x)}{dx}. \quad (9.10)$$

The positive constant k is called the *conductivity*, which will be different for different materials.

The minus sign is necessary to ensure a positive rate for the conduction of heat. This means that when the temperature is decreasing (i.e. when the temperature gradient is negative) the heat flows in the positive direction. When the temperature is increasing (i.e. when the temperature gradient is positive) the heat flows in the negative direction. This reflects the fact that heat flows from regions of higher to regions of cooler temperatures, and not the other way around.

Table 9.3 gives values of the conductivity k for some different materials. Note that generally metals have higher conductivities than other materials, which means that heat flows more easily through them.

Indeed, it is sometimes desirable to use materials with low conductivities such as rock wool or polystyrene to provide good insulation, while at other times high conductivity is desired as in heating elements.

Table 9.3: Table of heat conductivities for some common materials (standard SI units).

Substance	k	Substance	k
Copper	386	Brick	0.38–0.52
Aluminium	204	Asbestos	0.113
Iron	73	Concrete	0.128
Stainless steel	14	Glass	0.81
Water (at 0 °C)	0.57	Wood	0.15
Lamb (at 5 °C)	0.42	Rock wool	0.04
Butter (at 5 °C)	0.20	Polystyrene	0.157

Over large temperature ranges the conductivity of a material k is not strictly constant. However, the assumption of constant conductivity over temperature ranges that do not vary dramatically still enables us to make sufficiently accurate predictions.

Summary of key ideas

The important equations of heat transport are summarised as follows: For thermal equilibrium

$$\left\{ \begin{array}{l} \text{rate of} \\ \text{change of} \\ \text{heat} \end{array} \right\} = 0.$$

Fourier's law of heat conduction, where J is the heat flux and k the conductivity, is given by

$$J(x) = -k \frac{dU(x)}{dx}.$$

Summary of skills developed here:

- Understand the physical meaning of thermal equilibrium, and relate it to a zero time-derivative for temperature.
- Describe the flow of heat in terms of heat flux.
- Understand the assumptions for, and application of, Fourier's law.

9.5 Heat conduction through a wall

We now formulate a differential equation for the simplest heat conduction problem. This involves the conduction of heat through a slab of some material in just one direction. We develop a differential equation for the equilibrium temperature reached as time increases.

Problem description

Imagine we have a plate with width L of some material. One side is hot and the other relatively cold, so that heat flows through the material in the x -direction towards the cooler side. A typical application is the wall of a building where the inside and outside are at different temperatures, as in Figure 9.6.

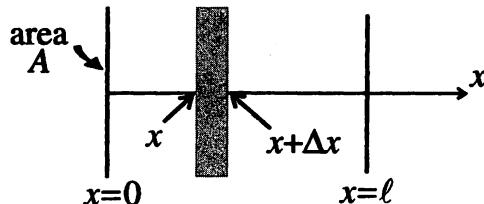


Figure 9.6: Coordinate system for the problem. We focus on the rate of heat going into and coming out of an imaginary section between the surfaces x and $x + \Delta x$.

General compartmental model

Our aim is to formulate a differential equation for the equilibrium temperature inside the material at any point x . We do this by first writing down a word equation describing the rate of heat input to and output from a small section of the material, assuming no heat is used to heat up the material. We then let the thickness of the section tend to zero.

We consider a thin section, or slice, of the material from x to $x + \Delta x$ as shown in Figure 9.6 as our compartment. This is a modified version of the approach we have taken before. The surface area of the face of this slice is A . We must account for all the inputs and outputs of heat for this section, which contribute to the rate of change of heat. We do this in the following example.

Example 9.4: Obtain an input-output word equation for the arbitrary section of width Δx .

Solution:

The only heat input is due to conduction into the section at x , and the only heat output is due to the heat conducted out of the section at $x + \Delta x$. The input-output diagram in Figure 9.7 illustrates this.

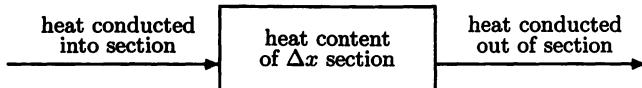


Figure 9.7: Input-output compartmental diagram describing the heat inputs and outputs to the arbitrary section of thickness Δx .

Hence, we have the word-equation

$$\left\{ \begin{array}{l} \text{rate of} \\ \text{change of} \\ \text{heat in section} \end{array} \right\} = \left\{ \begin{array}{l} \text{rate heat} \\ \text{conducted} \\ \text{in at } x \end{array} \right\} - \left\{ \begin{array}{l} \text{rate heat} \\ \text{conducted} \\ \text{out at } x + \Delta x \end{array} \right\}. \quad (9.11)$$

Formulating the differential equation

First we introduce some notation. We let $U(x)$ denote the equilibrium temperature at the point x and let $J(x)$ be the flux of heat at x . Recall that this is the rate of flow of heat, per unit area per unit time, through the material at the point x .

The rate of heat entering the section is obtained by multiplying the heat flux $J(x)$ by the cross-sectional area (surface area of face of the section) A . Thus

$$\left\{ \begin{array}{l} \text{rate heat} \\ \text{conducted} \\ \text{in at } x \end{array} \right\} = J(x)A. \quad (9.12)$$

The rate of heat leaving the section is denoted by $J(x + \Delta x)$. Hence the rate of heat leaving the section, obtained by multiplying the flux by the area A , is

$$\left\{ \begin{array}{l} \text{rate heat} \\ \text{conducted} \\ \text{out at } x + \Delta x \end{array} \right\} = J(x + \Delta x)A. \quad (9.13)$$

For equilibrium temperatures the LHS of the heat balance word equation (9.11) is zero. Substituting (9.12) and (9.13) back into (9.11), with the LHS set to zero, gives

$$J(x)A - J(x + \Delta x)A = 0. \quad (9.14)$$

We are going to let $\Delta x \rightarrow 0$, but first we divide (9.14) by Δx . This leads to an expression involving the derivative with respect to x .

Example 9.5: Obtain a differential equation for the temperature by taking the limit as $\Delta x \rightarrow 0$ in (9.14) and then applying Fourier's law, $J = -k dU/dx$.

Solution: We divide (9.14) by Δx and rearrange to obtain

$$\frac{J(x + \Delta x) - J(x)}{\Delta x} = 0. \quad (9.15)$$

From the definition of the derivative² of J with respect to x , equation (9.15) becomes

$$\frac{dJ}{dx} = 0. \quad (9.16)$$

Since the heat flux through the material is due to conduction only we can apply Fourier's law to express the differential equation in terms of temperature. Substituting this into equation (9.16) gives

$$\frac{d}{dx} \left(-k \frac{dU}{dx} \right) = 0. \quad (9.17)$$

Since we assume the conductivity k to be a constant, (9.17) reduces to

$$\frac{d^2U}{dx^2} = 0. \quad (9.18)$$

This is a second-order differential equation for the equilibrium temperature $U(x)$. It is a trivial example of a differential equation but serves to illustrate how such equations arise. More complicated differential equations can occur when we include volumetric heat sources, as is the case when heat is produced by an electric current or chemical reaction.

Numerical solution

Using Maple we can obtain a numerical solution, where we specify both the temperature and heat flux at $x = 0$ (see Figure 9.8). The Maple code to produce this is given in Listing 9.3. Equivalent MATLAB code is given in Listing 9.4, where the second-order differential equation has been written as a system of two first-order differential equations using $J = -kdU/dx$.

Listing 9.3: Maple code: c_he_wall.txt

```
> restart: with(plots): with(DEtools):
> k := 1.0:
> de1 := diff(U(x),x$2) = 0;
> init1 := U(0)=10, D(U)(0)=-1/k;
> plot1 := DEplot(de1, U, x=0..1, [[init1]]):
> display(plot1);
```

Listing 9.4: Maple code: c_he_wall.m

```
function c_he_wall
global k
k = 1;
u0 = 10; %temp at x=0
J0 = 1; %flux at x=0
y0 = [u0; J0]; %set initial condition vector
xend = 1;
[xsol, ysol] = ode45(@rhs, [0 xend], y0);
Usol = ysol(:,1);
plot(xsol, Usol);

function ydot = rhs(x, y)
global k
```

²From first principles the derivative of $J(x)$ with respect to x is

$$\frac{dJ}{dx} = \lim_{\Delta x \rightarrow 0} \frac{J(x + \Delta x) - J(x)}{\Delta x}.$$

```

U = y(1); J = y(2);
Udot = -k*J;
Jdot = 0;
ydot = [Udot; Jdot];

```

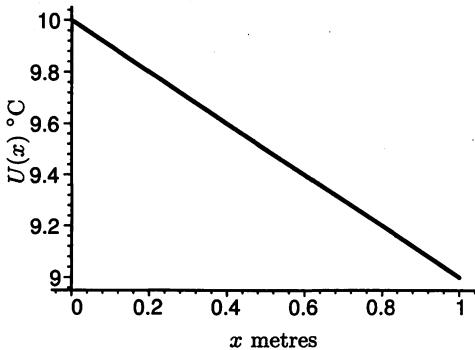


Figure 9.8: Numerical solution with $k = 1 \text{ W m}^{-1} \text{ }^{\circ}\text{C}^{-1}$, $U(0) = 10 \text{ }^{\circ}\text{C}$ and $J(0) = 1 \text{ W/m}^2$.

However, more usually we would know either temperature or heat flux at both $x = 0$ and $x = l$. This changes the problem into a *boundary value problem* instead of an IVP. We consider such problems in greater detail later, and discuss methods for solving them in Chapter 11.

When the temperature is not at equilibrium, the temperatures are dependent on time as well as position. Furthermore, account must be taken of the amount of heat ‘used up’ in raising the temperature. This is examined in detail in Chapter 12 where we consider a problem similar to the present one, but derive a partial differential equation with two independent variables, x and t .

Modelling approach summary

The procedure adopted to derive models for heat conduction depends on a set of physical principles and is slightly different from what we have done before. A summary of the basic procedures for formulating differential equations describing heat transport problems is:

- Consider all inputs and outputs of heat from a thin section of width Δx .
- Develop a word equation for the rate of change of heat.
- Divide by Δx and then take the limit as $\Delta x \rightarrow 0$ to derive a differential equation.
- Using Fourier’s law, substitute to express heat flux J in terms of temperature U .

Summary of skills developed here:

- Be able to reproduce the derivations of the equilibrium temperature equation.
- Reproduce the derivation of the second-order differential equation.
- Modify the word equation if there is an internal heat source, such as an electric current, providing heat at a given rate.

9.6 Radial heat conduction

Radial heat flow occurs in problems involving cylinders and spheres where the temperatures are the same at any given distance from the centre of the cylinder or sphere. We now formulate a differential equation for the equilibrium temperature in a cylinder. The procedure is similar to that used in the previous two sections but we must take account of the fact that the area through which heat is conducted now changes with the radial distance from the centre of the cylinder or sphere.

Fourier's law for radial heat conduction

Radial heat flow occurs in cylinders and spheres. In radial heat flow we need to account for the heat spreading out as it is transferred into or out of a cylindrical or spherical shell.

If r denotes the radial distance of a point from the centre of a cylinder or sphere then we denote the heat flux at r by $J(r)$. The overall rate of flow of heat is

$$\left\{ \begin{array}{l} \text{rate of} \\ \text{flow of} \\ \text{heat} \end{array} \right\} = J(r)A(r)$$

where $A(r)$ denotes the area through which the heat flows. For a cylindrical surface of radius r and length l , $A(r) = 2\pi rl$, while for a spherical surface of radius r , $A(r) = 4\pi r^2$.

For radial heat conduction Fourier's law takes the form

$$J(r) = -k \frac{dU(r)}{dr} \quad (9.19)$$

where $J(r)$ is the heat flux at r , $U(r)$ is the temperature at r and k is the conductivity. Thus Fourier's law states that the heat flux is directly proportional to the temperature gradient.

Model assumptions and approach

Let us consider a cylindrical object, which is hottest on the inside and coolest on the outer surface (see Figure 9.9). Define the outer radius of the cylinder at b and the inner radius at a , and then as a approaches zero the cylinder becomes solid, while for a close to b the cylinder models a hollow pipe. Take the length of the cylinder as ℓ , and let r denote the radial distance from its centreline.

We now make some assumptions on which to build the mathematical model.

- We assume that heat flows in the radial direction only; the temperature inside the cylinder will then depend on r and the time t only.
- If we also assume thermal equilibrium, then the equilibrium temperature will be a function of the radial distance r alone.

General compartmental model

Let us consider an imaginary small annular shell, inside the cylinder, from r to $r + \Delta r$. This is shown in Figure 9.9 and is the compartment. Then, applying the balance law, we consider any heat inputs into and outputs from this shell. Assuming no heat is generated inside the shell, heat input is through conduction only, as is the heat output, and thus we have the compartmental diagram, Figure 9.10.

From this we can formulate a word equation.

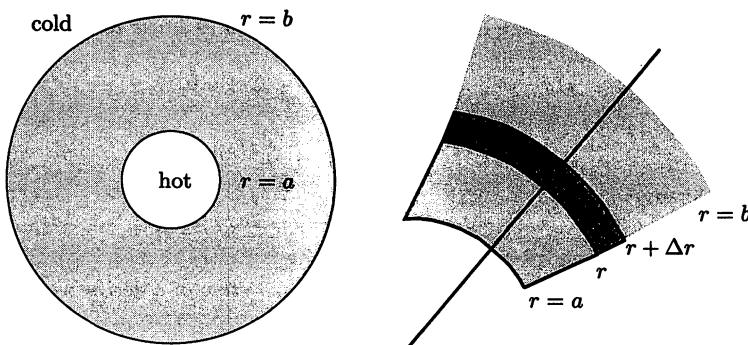


Figure 9.9: Radial heat flow in a cylinder. The first diagram illustrates the cross-section of a cylinder. Heat flows from the centre of the cylinder to the outside in all directions. The second diagram is of an arbitrary cylindrical shell, inside the cylindrical region, from r to $r + \Delta r$.

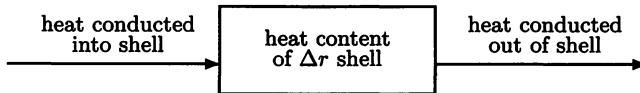


Figure 9.10: Input-output compartment diagram describing all the heat inputs and outputs for the arbitrary cylindrical shell.

Example 9.6: Obtain a suitable word equation for a thin annular shell inside which no heat is generated.

Solution:

Heat enters the shell at r and leaves at $r + \Delta r$ through the process of conduction. For this problem there is no heat generated internally in the shell. A word equation describing this balance of heat entering and leaving the cylindrical shell is thus

$$\left\{ \begin{array}{l} \text{rate of} \\ \text{change of} \\ \text{heat in shell} \end{array} \right\} = \left\{ \begin{array}{l} \text{rate heat} \\ \text{conducted} \\ \text{in at } r \end{array} \right\} - \left\{ \begin{array}{l} \text{rate heat} \\ \text{conducted} \\ \text{out at } r + \Delta r \end{array} \right\}. \quad (9.20)$$

Formulating the differential equation

We let $U(r)$ denote the equilibrium temperature at a distance r from the centreline. We also let $J(r)$ be the heat flux at a distance r from the origin.

Example 9.7: Obtain a differential equation for the equilibrium temperature inside the annular shell.

Solution: The heat entering the cylindrical shell flows through an area $A(r) = 2\pi r l$. Similarly, the heat leaving the annular section flows through an area $A(r + \Delta r) = 2\pi(r + \Delta r)l$. In terms of the heat flux $J(r)$ we have

$$\begin{aligned} \left\{ \begin{array}{l} \text{rate heat} \\ \text{conducted} \\ \text{in at } r \end{array} \right\} &= J(r)A(r), \\ \left\{ \begin{array}{l} \text{rate heat} \\ \text{conducted} \\ \text{out at } r + \Delta r \end{array} \right\} &= J(r + \Delta r)A(r + \Delta r). \end{aligned} \quad (9.21)$$

For equilibrium temperatures the LHS of the word equation (9.20) is zero. Substituting (9.21) back into (9.20) gives

$$J(r)A(r) - J(r + \Delta r)A(r + \Delta r) = 0.$$

We can write this as

$$-[J(r + \Delta r)A(r + \Delta r) - J(r)A(r)] = 0. \quad (9.22)$$

Dividing by Δr gives

$$-\left[\frac{J(r + \Delta r)A(r + \Delta r) - J(r)A(r)}{\Delta r}\right] = 0 \quad (9.23)$$

and then taking the limit as $\Delta r \rightarrow 0$ we have, from the definition of a derivative³,

$$-\frac{d}{dr}[J(r)A(r)] = 0. \quad (9.24)$$

Thus, regardless of the radius, this equation implies that the combination of the heat flux multiplied by the area is the same at any point inside the cylinder.

Substituting for the area $A(r) = 2\pi rl$ and using Fourier's law, ($J = -k dU/dr$) we obtain the second-order differential equation

$$-\frac{d}{dr}\left(-2k\pi lr\frac{dU}{dr}\right) = 0. \quad (9.25)$$

Since $2k\pi l$ is a constant, for the equilibrium temperature $U(r)$ this simplifies to

$$\frac{d}{dr}\left(r\frac{dU}{dr}\right) = 0. \quad (9.26)$$

Summary of skills developed here:

- Derive a differential equation for the equilibrium temperatures in spherical heat flow.
- Derive the equilibrium temperatures for radial (cylindrical or spherical) heat flow with an internal generation of heat.

9.7 Heat fins

We extend the approach adopted above to develop a mathematical model for a heat fin, which is a cooling device. Such a model describes the heat distribution along the fin, which will change with distance from the heat source.

³Let $f(r) = J(r)A(r)$. Note that the derivative of f with respect to r is

$$\frac{df}{dr} = \lim_{\Delta r \rightarrow 0} \frac{f(r + \Delta r) - f(r)}{\Delta r} = \lim_{\Delta r \rightarrow 0} \frac{J(r + \Delta r)A(r + \Delta r) - J(r)A(r)}{\Delta r}.$$

Background

Heat fins are used to enhance the dissipation of heat from machinery in which damage may be caused if heat is allowed to build up. Thus they are found on many types of machinery such as in motorcycle engines, refrigerators and computers. These fins work by increasing the surface area through which heat can be lost, and often have fans attached to them to force air across the fins, thus reducing the temperature more efficiently. There are many different forms which these fins can take, and some types are illustrated in Figure 9.11.

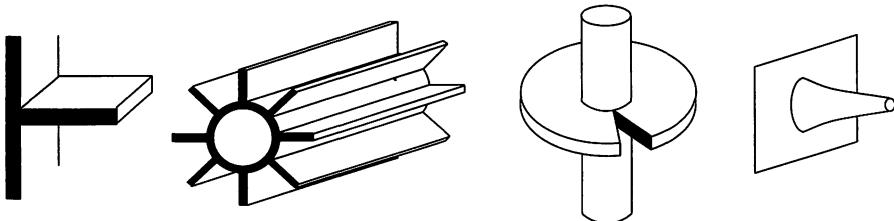


Figure 9.11: Some different types of heat fins.

A typical problem is to calculate the temperature distribution along a heat fin. From this, the rate of heat dissipation can be calculated, and the cooling efficiency for the heat fin determined. But first we need to formulate a differential equation for the changing temperature along the heat fin.

Model assumptions and approach

As our mathematical model we consider a rectangular heat fin of length ℓ , width w and thickness b (see Figure 9.12).

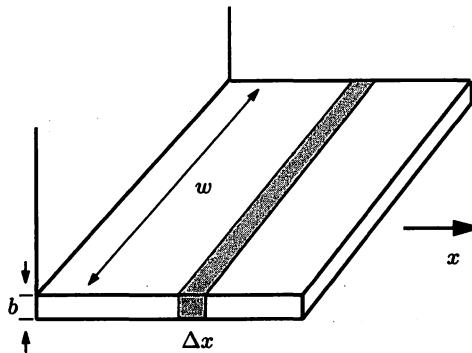


Figure 9.12: Schematic diagram for mathematical model.

We make some assumptions and build our mathematical model on these.

- We assume the thickness of the heat fin b to be small compared with its length ℓ .
- We assume that heat is lost from the surfaces of the heat fin to the surroundings (at temperature u_s) according to Newton's law of cooling.

- Because most of the heat loss occurs from the faces of the fin, both top and bottom, in our initial model we neglect the heat lost from the sides. Improving the model by including heat lost from the sides is not difficult and is explored in the exercises.
- A further assumption is to neglect the temperature variation over the cross-section of the fin. This assumption is reasonable provided the heat fin is thin (that is, $b \ll \ell$). In doing this, we can effectively assume the equilibrium temperature to be a function of x alone.

General compartmental model

Let us consider a small section of the heat fin from x to $x + \Delta x$, as shown in Figure 9.12. We first consider all the heat inputs into and outputs from this section, and later we let Δx tend to zero to establish the differential equation.

Example 9.8: Determine an input-output word equation for an arbitrary section of the heat fin.

Solution: The thin section of the heat fin is shown in Figure 9.12 and we use the balance law to establish the inputs and outputs in Figure 9.13. Heat is conducted into the section at x and out from the section at $x + \Delta x$. We should also account for the heat lost from the top and bottom surfaces to the surroundings and for this we use Newton's law of cooling. Thus there is a single means by which heat enters the section and two mechanisms by which it leaves. (Recall that we have neglected any heat loss from the sides.)

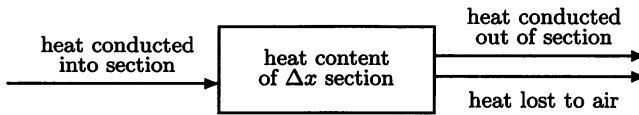


Figure 9.13: Input-output diagram for an arbitrary thin section of the heat fin.

The basic heat balance equation, for the section, is then

$$\left\{ \begin{array}{l} \text{rate of} \\ \text{change of} \\ \text{heat in section} \end{array} \right\} = \left\{ \begin{array}{l} \text{rate heat} \\ \text{conducted} \\ \text{in at } x \end{array} \right\} - \left\{ \begin{array}{l} \text{rate heat} \\ \text{conducted} \\ \text{out at } x + \Delta x \end{array} \right\} - \left\{ \begin{array}{l} \text{rate heat} \\ \text{lost to} \\ \text{surroundings} \end{array} \right\}. \quad (9.27)$$

For the equilibrium temperature the rate of change of heat is zero and so

$$\left\{ \begin{array}{l} \text{rate heat} \\ \text{conducted} \\ \text{in at } x \end{array} \right\} - \left\{ \begin{array}{l} \text{rate heat} \\ \text{conducted} \\ \text{out at } x + \Delta x \end{array} \right\} - \left\{ \begin{array}{l} \text{rate of heat} \\ \text{lost to} \\ \text{surroundings} \end{array} \right\} = 0. \quad (9.28)$$

Formulating the differential equation

The next step is to assign appropriate symbols to each of the terms in the word equation (9.28). We express the heat conduction quantities in terms of the heat flux J and later use Fourier's law of heat conduction to express these in terms of temperature. Once again we develop the model with symbols, so that we can examine the effect of changing some of these physical quantities, easily.

Example 9.9: Express each of the quantities of (9.28) in terms of the heat flux J or the temperature U .

Solution: The area through which heat is being conducted is bw . In terms of the heat flux $J(x)$,

$$\left\{ \begin{array}{l} \text{rate heat} \\ \text{conducted} \\ \text{in at } x \end{array} \right\} = J(x)bw, \quad \left\{ \begin{array}{l} \text{rate heat} \\ \text{conducted} \\ \text{out at } x + \Delta x \end{array} \right\} = J(x + \Delta x)bw. \quad (9.29)$$

We use Newton's law of cooling for the heat loss from the surface of the section in the time interval. Recall that Newton's law of cooling states that the rate of heat loss is proportional to the surface area and the temperature difference between the object and its surroundings. The surface area of the section through which heat is lost to the surroundings is $2w\Delta x$. This corresponds to the top and bottom faces only, as we are neglecting heat lost from the sides.

To calculate the approximate heat loss by Newton's law of cooling we could use the temperature at x to give $hS(U(x) - u_s)$. (Recall that S is the surface area, u_s is the temperature of the surroundings and h is the Newton cooling coefficient.) But this would give a slight overestimate of the temperature since $U(x)$ decreases with x . Similarly, if we used the temperature at $x + \Delta x$ we would obtain a slight underestimate. The true value would use the temperature somewhere in between, say at x^* , where $x < x^* < x + \Delta x$. Thus we write

$$\left\{ \begin{array}{l} \text{rate heat} \\ \text{lost to} \\ \text{surroundings} \end{array} \right\} = 2hw\Delta x [U(x^*) - u_s]. \quad (9.30)$$

(Although we do not know the exact value of x^* , it does not matter as eventually we let Δx tend to zero and then $x^* \rightarrow x$.)

We now substitute the individual terms (9.29) and (9.30) into the heat balance equation (9.28) to obtain

$$J(x)bw - J(x + \Delta x)bw - 2hw\Delta x [U(x + \lambda\Delta x) - u_s] = 0, \quad (9.31)$$

where $x^* = x + \lambda\Delta x$ and $0 \leq \lambda \leq 1$.

Taking the limit as $\Delta x \rightarrow 0$ to get the derivative, and then applying Fourier's law to give the equation in terms of temperature, we establish the differential equation required.

Example 9.10: Let $\Delta x \rightarrow 0$ in equation (9.31) and obtain a differential equation for the temperature.

Solution: Dividing (9.31) by $bw\Delta x$ we are left with

$$-\left(\frac{J(x + \Delta x) - J(x)}{\Delta x}\right) - \frac{2h}{b} (U(x + \lambda\Delta x) - u_s) = 0. \quad (9.32)$$

Then, taking the limit as $\Delta x \rightarrow 0$ and applying the definition of the derivative⁴,

$$-\frac{dJ}{dx} - \frac{2h}{b} (U(x) - u_s) = 0. \quad (9.33)$$

From (9.33), substituting for J and applying Fourier's law ($J(x) = -k dU/dx$), we find

$$k \frac{d^2U}{dx^2} - \frac{2h}{b} (U(x) - u_s) = 0. \quad (9.34)$$

⁴By first principles, the derivative of $J(x)$ with respect to x is

$$\frac{dJ}{dx} = \lim_{\Delta x \rightarrow 0} \frac{J(x + \Delta x) - J(x)}{\Delta x}.$$

This equation can be written in the compact form

$$\frac{d^2U}{dx^2} = \beta(U - u_s) \quad \text{where } \beta = \frac{2h}{kb} \quad (9.35)$$

establishing a second-order differential equation describing the heat flux in terms of temperature.

Extensions and further problems

Heat fins come in many shapes and sizes. The derivation of the differential equation for heat fins with different cross-sections, such as circular, is almost identical to the above. In fact we end up with the same equation (9.35) but with a different value for β .

Obtaining a differential equation for when the cross-section varies with distance from the origin is more difficult but still follows the same procedure. Together with the previous section which deals with radial heat conduction, you have the required theory to deal with such problems.

Other possible extensions include the incorporation of a heat production term. Another case is that where the temperature of the surroundings may be higher than the temperature of the fin, so that the fin gains heat rather than loses it.

Summary of skills developed here:

- Derive the differential equation for a solid cylindrical heat fin (using ideas from this section and Section 9.6).
- Formulate differential equations for heat fins of rectangular, or other, cross-sections in the case of an equilibrium temperature.
- Formulate a differential equation for one-dimensional heat flow with a non-constant internal heat source.



9.8 Exercises for Chapter 9

9.1. Simple heat calculations. The following questions require the use of appropriate equations from Chapter 9.

- (a) If the heat flux through a wall is 30 (in SI units), how much heat is lost in 1 hour?
- (b) How much heat does it take to heat a copper sphere of radius 1 cm from 5 °C to 25 °C?
- (c) If the outside of a wall of a house loses heat to the surrounding at a rate of 20 W, and the temperature of the surroundings is 5 °C, what is the outside temperature of the wall? You may assume Newton's law of cooling.

9.2. Including an internal heat source. Heat flows inside a slab of material from left to right. Inside the material, an electric current generates heat at a constant rate Q_0 Watts m $^{-3}$.

- (a) Write down a suitable word equation for the rate of change of heat in a section x to $x + \Delta x$ of the slab, where x is in the direction of heat flow.
- (b) Hence deduce that the equilibrium temperature satisfies the differential equation of the form

$$\frac{d^2U}{dx^2} + \beta = 0,$$

where β is a constant you must determine.

9.3. Formulating model extensions. Consider the formulation of the ordinary differential equation in Section 9.5 for the equilibrium temperature.

- (a) Suppose, instead, heat flows in the opposite direction. Does the differential equation (9.18) remain the same? Justify your answer.
- (b) Suppose, instead, the conductivity is not a constant but depends on temperature. Does the differential equation (9.18) remain the same? Justify your answer.

9.4. Model formulation with circular cross-section. A heat fin has circular cross-section of radius a . The heat fin loses heat to the surrounding air, which is at temperature u_a . Starting from a suitable word equation, show that the equilibrium temperature satisfies the differential equation of the form

$$\frac{d^2U}{dx^2} - \alpha U = -\beta,$$

where α and β are constants you must determine.

9.5. Nuclear radiation. In a shielding wall for a nuclear reactor, gamma-ray radiation causes the wall to heat up internally at a given rate $q(x)$ per unit time per unit volume, within the wall. Formulate the differential equation for the equilibrium temperature.

9.6. Including an internal heat source. Heat flows radially in a solid cylinder of length ℓ and radius a . Heat is also generated internally by an electric current at a constant rate Q_0 Watts per unit volume. The temperature on the inside is maintained at temperature u_a and heat is lost from the outer surface to the surroundings at temperature u_s , according to Newton's law of cooling.

- (a) Write down a word equation for the change in heat, for a cylindrical shell r to $r + \Delta r$ and over a time interval t to $t + \Delta t$.
- (b) What is the volume of the shell in (a)? Hence give an expression for the rate of heat generated by the electric current.
- (c) Obtain a differential equation for the equilibrium temperature. (Hint: not all of the information in the question need be used.)

9.7. Equilibrium temperature inside a sphere. Heat flows radially, by conduction, through a spherical shell of radius a . Formulate the differential equation for the equilibrium temperature inside the sphere.

9.8. Cylindrical heat fin. In the thin cylindrical heat fin (shown in Figure 9.14) of thickness ℓ , inner radius a and outer radius b , heat flows radially. Also, heat is lost from the surface of the fin to the atmosphere, at temperature u_s , according to Newton's law of cooling.

Deduce the differential equation for the equilibrium temperature assuming the temperature variation over the cross-section of the heat fin is negligible.

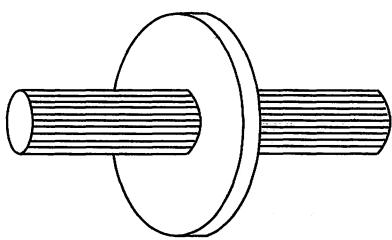


Figure 9.14: A cylindrical heat fin (see Question 8).