Chapter 1

First-Order Non-Linear Differential Equations

1.1 Introduction

In this chapter we study properties of models that are defined by a single first-order non-linear differential equation. An example of such a model is an equation that defines the population size of a single species. In such models $x(t)$ denotes the size of the population, either the total number of individuals or a population density, at time t, and $\frac{\mathrm{d}x}{\mathrm{d}t}$, or $x'(t)$, the rate of change of population size. We assume that the rate of change of population size depends upon its current value. The population model can then be written in the general form

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x), \qquad x(t=0) = x_0. \tag{1.1}$$

In undergraduate courses we spend a great deal of time learning how to integrate a first-order differential equation. If we can integrate the equation, the solution gives us the population size as a function of time. What happens if we are unable to integrate the equation analytically? Does this mean that we must resort to numerical integration to learn how the population size evolves with time?

The critical issue, from the perspective of population biology, is to identify the long-time behaviour of the population, i.e. does the population become extinct? In section 1.2 we learn how to predict the long-term behaviour of *any* autonomous first-order differential equation without having to integrate the equation. All we need to do is to plot the curve $y = f(x)$.

In section 1.3 we introduce the concept of a steady-state solution for the differential equation (1.1). A steady-state solution of this differential equation is a value of x, call it x^*, which has the property that

$$f(x^*) = 0.$$

The importance of steady-state solutions in predicting the long-term behaviour of equation (1.1) will already be apparent from section 1.2.

It turns out that not all steady-state solutions are equal. In section 1.4 we introduce the distinction between *stable* and *unstable* steady-state solutions. Stable steady-state solutions may be observed in the 'real-world', unstable steady-state solutions never are. Stability can be determined in two-ways. In section 1.4.3 we show how to determine the stability of the steady-state solution, x^*, by plotting the function $y = f(x)$. In section 1.4.4 we show how to determine the stability of a steady-state solution *algebraically* by finding the *eigenvalue*[1] of the *linearised system*. The eigenvalue for a steady-state solution, x^*, of equation (1.1), is given by

$$\lambda(x^*) = f'(x^*).$$

[1]The word *eigenvalue* comes from the German word *eigenwert*, meaning characteristic value.

Many problems of interest contain a parameter, μ, which can be readily changed. Such models are written in the general form

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x, \mu). \tag{1.2}$$

A natural question to ask about equation (1.2) is 'how do the number of its steady-state solutions depend upon the value of the parameter μ'? A second natural question to ask is 'how does the stability of the steady-state solutions depend upon the value of the parameter μ'? Once these questions have been answered a good way to represent this information is to draw a ***steady-state diagram.*** Of particular interest on any steady-state diagram is the presence of ***bifurcation points.*** These are points on the steady-state diagram where the 'number' of steady-state solutions changes. Steady-state diagrams and bifurcation points are the subject of section 1.5.

In section 1.6 we consider a particular first-order non-linear autonomous differential equation, the spruce budworm model. Some of the questions that arise during our investigation of this model act as motivation for chapter 2.

A common idea throughout this chapter is that important information about the solution to the differential equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x)$$

can be obtained by plotting the function

$$y = f(x).$$

Unfortunately, the power of this method is restricted to models that are given by a single first-order differential equation. However, concepts such as steady-state solutions, stability, steady-state diagrams and bifurcation points are important when considering a system of differential equations.

1.2 First-order ODEs: Graphical insights

First-order autonomous differential equations of the general form

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x)$$

are usually impossible to solve analytically although it is a straightforward matter to determine a *numerical* solution. Although numerical solutions can be very informative, they have limitations. We can extract a considerable amount of information about the dynamics of this equation without recourse to either analytical or numerical solutions by using a graphical technique.

To investigate the solution of equation (1.1) graphically use the following procedure

1. Sketch the function $y = f(x)$. This shows how the derivative of the solution depends upon the value of x.
2. Determine the values of x for which
   (a) $\frac{\mathrm{d}x}{\mathrm{d}t} > 0$. For such values of x the function $x(t)$ *increases* as t increases.
   (b) $\frac{\mathrm{d}x}{\mathrm{d}t} < 0$. For such values of x the function $x(t)$ *decreases* as t increases.
   (c) $\frac{\mathrm{d}x}{\mathrm{d}t} = 0$. For such values of x the function $x(t)$ is constant, i.e. it does not depend upon the value of t.
3. Hence identify how the long-time dynamics of the model depends upon the choice of initial condition.

Question 1.1 *Using figure 1.1 determine how the long-term dynamics of the population depend upon the initial condition for the logistic differential equation*

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right), \quad x(t=0) = x_0 \geq 0. \tag{1.3}$$

Assume that the parameters r, the static birth rate, and K, the carrying capacity of the environment, are both positive.

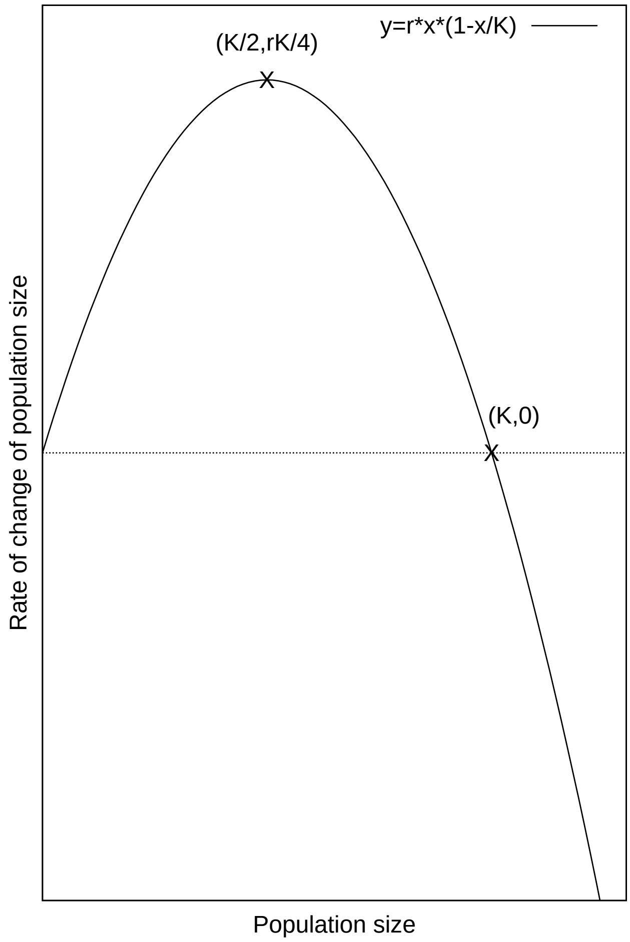


Figure 1.1: Sketch of the function $y = rx\,(1 - x/K)$.

Once we have sketched the function $y = f\,(x)$ we can use the sketch to show how the solution of the differential equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f\,(x)\,, \qquad x\,(0) = x_0,$$

evolves with time. Before doing this, we consider Figure 1.2 which shows the solution of the logistic equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = 0.02x\,(1 - x)$$

for three initial conditions.

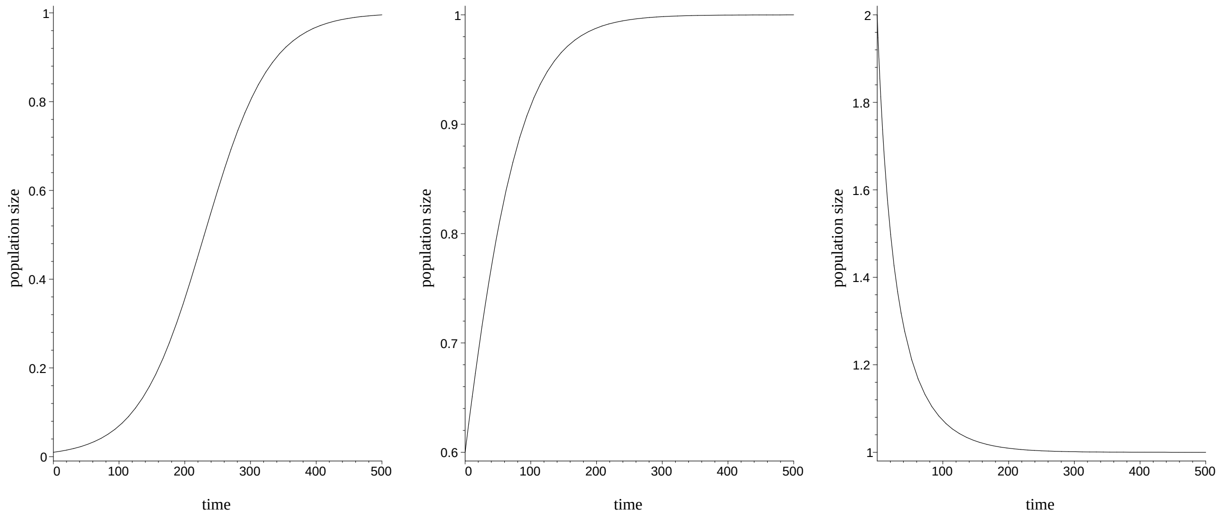
In figures 1.2 (a & b) the solution is an *increasing* function of time with $x\,(t) \to 1$ as $t \to \infty$. We can distinguish between the solution behaviour in these figures by examining how the solution derivative changes with time. In figure 1.2 (a) the derivative is initially small and positive. It increases to a maximum value and then decreases towards zero as time approaches infinity. In figure 1.2 (b) the derivative of the solution is positive and decreases towards zero as time approaches infinity.

In figure 1.2 (c) the solution is a *decreasing* function of time with $x\,(t) \to 1$ as $t \to \infty$.

Question 1.2 *By considering figure 1.1, or otherwise, sketch the dynamic evolution of the logistic differential equation*

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right), \quad x\,(t = 0) = x_0.$$

Consider the cases



(a) $x_0 = 0.01$. (b) $x_0 = 0.6$. (c) $x_0 = 2$.

Figure 1.2: The solution to the logistic differential equation $\frac{dx}{dt} = 0.02x\,(1-x)$ for three initial conditions.

1. $0 < x_0 < \frac{K}{2}$.

2. $\frac{K}{2} \leq x_0 < K$.

3. $K < x_0$.

From your answer to question 1.2, shown in figure 1.3, we that if $0 < x_0 < K$ then the solution is an *increasing* function of time with $x\,(t) \to K$ as $t \to \infty$. (We can distinguish the behaviour exhibited in figure 1.3 (a) from that shown in figure 1.3 (b) by considering how the solution derivative changes as a function of time). From figure 1.3 (c) we see that if $K < x_0$ then the solution is a *decreasing* function of time with $x\,(t) \to K$ as $t \to \infty$. Thus every solution with $x_0 > 0$ tends to K as $t \to \infty$, and we have obtained this information *without* explicitly solving the differential equation.

The above conclusions could have been obtained from the explicit solution of equation (1.3). However, we can apply this graphical technique to problems that do *not* have explicit solutions.

In question 1.2 we considered the evolution of the logistic difference equations for initial conditions satisfying $0 < x_0 < K$ and $K < x_0$. We finish our analysis of the logistic difference equation by considering the initial conditions $x_0 = 0$ and $x_0 = K$.

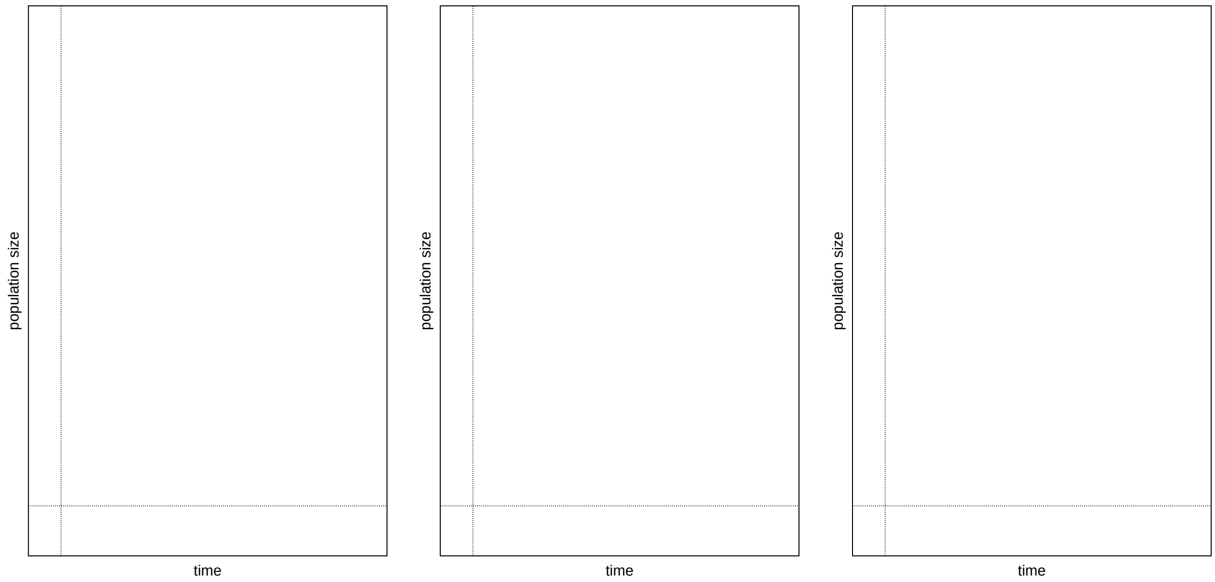
Question 1.3 *Sketch the dynamic evolution of the logistic differential equation*

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right), \quad x\,(t=0) = x_0,$$

for the initial conditions $x_0 = 0$ *and* $x_0 = K$.

1.3 Steady-state solutions

In many mathematical models we expect that as time increases the value of the dependent variable x should approach a constant, or equilibrium, value. For instance, in a population model we expect that the population size becomes constant, i.e. it does not vary from year to year. If the value of the dependent variable becomes



(a) $0 < x_0 < \frac{K}{2}$.

(b) $\frac{K}{2} < x_0 < K$.

(c) $K < x_0$.

Figure 1.3: The dependence of the solution to the logistic differential equation $\frac{\mathrm{d}x}{\mathrm{d}t} = rx\left(1 - \frac{x}{K}\right)$ upon the initial condition x_0.

constant, i.e. it does not depend upon the value of the independent variable t, then we must have

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x) = 0. \tag{1.4}$$

Values of x which satisfy equation (1.4) are known as *steady-states solutions* or *steady-states* or *equilibrium solutions* of the differential equation. The *first-step* in understanding the long-time behaviour of a first-order nonlinear differential equation is to find the steady-states of the function $f(x)$.

Question 1.4

1. *Why do you think steady-state's are called steady-state's?*
   Hint. *Consider the problem*
   $$\frac{dx}{dt} = f(x), \quad x(0) = x^*,$$
   where x^* is a steady-state of the function $f(x)$.
2. *What does a steady-state represent biologically?*

Question 1.5 *Find the steady-state(s) of the logistic differential equation*

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

Comment on the biological interpretation of your answers.

Question 1.6 *The population model*

$$\frac{dx}{dt} = rx\ln\frac{K}{x}, \quad x(0) = x_0 > 0,$$

is known as the Gompertz model [33]. The parameters r and K are positive.

(a) Sketch $\frac{dx}{dt}$ as a function of x. Hence determine how the long-term dynamics of the model depends upon the initial value x_0.

(b) Find the steady-state(s) of the model.

1.4 Stability of steady-state solutions

1.4.1 Introduction

Consider the differential equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x) . \tag{1.5}$$

In the previous section we introduced the concept of a *steady-state solution* of a differential equation. This is value of x such that $f(x) = 0$ and it gives a time independent solution of the differential equation (1.5). Steady-state solutions are of interest in mathematical modelling as they represent static equilibrium.

In this section we introduce the concept of the *stability* of a steady-state solution. It will turn out that not all steady-state solutions are equal, because they can be divided into two types: *stable* and *unstable* solutions. Furthermore, this distinction has important practical consequences.

We start in section 1.4.2 by providing physical motivation for the distinction between stable and unstable steady-state solutions. In section 1.4.3 we combine our newly coined concept of stability with the graphical method of section 1.2 to develop a graphical method to distinguish between stable and unstable steady-state solutions. In section 1.4.4 we derive an algebraic method to determine the stability of a steady-state solution.

Thus by the end of this section we will have two techniques to determine the stability of a steady-state solution: graphically or algebraically.

1.4.2 Physical motivation for the concept of stability

The physical motivation for the concept of stability is given by figure 1.4 which shows the placement of three balls in a landscape. In this figure balls one and three are analogous to steady-states of a differential equation as they are at rest: we have $\frac{\mathrm{d}x}{\mathrm{d}t} = 0$. Ball two does not represent a steady state, since its position and speed are continuously changing: we have $\frac{\mathrm{d}x}{\mathrm{d}t} \neq 0$.

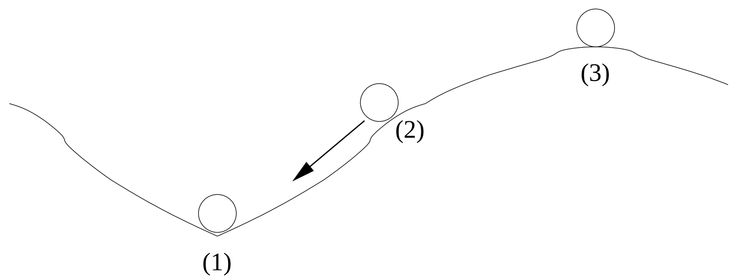


Figure 1.4: Physical motivation for the concept of stability. Ball one and three represent stable and unstable steady-states respectively. Ball two is not in a steady-state. (After Edelstein-Keshet [27])

The concept of stability is related to what happens to either ball one or three if they are moved by a 'small' amount. In fact, the question that we want to answer is this: If either ball is moved by a 'small' amount will it return to its original location?

Suppose that the placement of ball one is changed by moving it by a *small* amount to slightly higher ground, either to the left or the right of its static position. The ball will roll down the slope, eventually returning to its static position. On the other hand, suppose that the placement of ball three is changed by moving it by a *small* amount to slightly lower ground, either to the left or the right of its static position. The ball will roll down the slope. If it was displaced to the left it may finish in position (1). If it is displaced to the right the ball will proceed on some lengthy excursion — the figure does not show us where the ball will finish. But evidently, in either scenario, the ball does not return to its original placement: it can't roll up hill! It is important to recognise that stability is solely concerned with whether the ball will return to its original position if it is displaced by a 'small' amount; it is not concerned with where the ball goes if it does not return to its original location.

Thus although balls one and three are both at steady-state we can draw a distinction between them because they respond to a small change in displacement in very different ways: a *small* change to ball one does not change its long-term position whereas a *small* change to ball three does change its long-term position. This distinction leads to the concept of stable and unstable steady-state solutions. A steady state is termed *stable* if sufficiently near neighbouring states are attracted to it and *unstable* if the converse is true. Thus ball one represents a stable steady-state because if it is moved by a small amount it returns to its original position (the steady-state is 'attracting'). Ball three is an unstable steady-state as it will not return to this position if it is moved by a small amount (the steady-state is 'repelling').

In this discussion it is essential that the ball is only moved by a *small* amount. For if we move ball one sufficiently far to the right, past the location of ball three, then it will *not* return to its original position.

How does the distinction between stable and unstable steady-state solutions relate to the predictions of a mathematical model and to what we observe in the real-world? The crucial point is that it is not possible to observe unstable steady-state solutions in the 'real world'. The reason for this is that in the 'real world' there are always small random flucturations. For example, in a population model we assume that the death-rate is fixed. However, in practice the death-rate may vary slightly from year-to-year; sometimes being a little bit smaller and sometimes a little bit larger. Such flucturations have the effect of slightly moving systems that are at steady-state away from the steady-state solution. And an unstable steady-state is like a ball balanced precariously on a hill: a dependent variable will not return not return to an unstable steady-state if it is disturbed in the slightest.

Thus if we using a mathematical model to make predictions about the future behaviour of a system we can discount the possibility that the dependent variable will evolve to an unstable steady-state solution. Does this mean that unstable steady-state solutions are not of intrinsic interest? Far from it! In fact, unstable steady-state solutions often play a role in determining the dynamics of a model and knowledge about their location often provides insights that are helpful in predicting the behaviour of a model. Furthermore, many models contain a parameter that can be changed. As this parameter is changed the stability of the steady-states may change. (The number of steady-states may also change). The change in stability of a steady-state often has important *practical implications*. For example, a change in stability can indicate that the size of a population is about to crash, possibly becoming extinct, or that a disease will spread through a population. This *qualitative* information about whether change is imminent is potential of *great importance*.

1.4.3 Biological motivation for the concept of stability

In the previous section we introduced the concept of stability . In this section we combine this concept with the graphical techniques of section 1.2 to determine the stability of the steady-state solutions of the following population model

$$\frac{\mathrm{d}x}{\mathrm{d}t} = rx\left(1 - \frac{x}{K}\right)\left(\frac{x}{K_0} - 1\right), \qquad x\,(t=0) = x_0 > 0, \tag{1.6}$$
$$0 < K_0 < K, \qquad r > 0.$$

The steady-state solutions of this model are $x_1 = 0$, $x_2 = K_0$ and $x_3 = K$. Not knowing about stability we might expect that as time increases either $x\,(t) \to 0$ or $x\,(t) \to K_0$ or $x\,(t) \to K$. However, based upon the discussion in section 1.4.2 we anticipate that the system can not evolve to an unstable steady-state solution.

In the previous section we determined the stability of balls one and three by considering what happens if the ball is moved by a 'small' amount away from its steady-state location: if it returns to its steady-state location (ball one) it is stable; otherwise (ball three) it is unstable.

We can determine the stability of the steady-state solutions $x_1 = 0$, $x_2 = K_0$ and $x_3 = K$ in a similar manner. We imagine that the system has been moved away from a steady-state solution by a small amount and then determine if it will return to the steady-state solution (stable) or go somewhere else (unstable).

The difference between the problem in section 1.4.2 and our current problem is that in the former we used the 'geography of the landscape', figure 1.4, to determine 'stability' whereas for equation 1.6 we determine stability using the graph of the derivative, figure 1.5.

Question 1.7 *Using figure 1.5 determine the stability of the three steady-state solutions* x_1, x_2 *&* x_3.

Hint 1. Suppose that the system is at rest in steady-state x_2 and that is then a small displacement in position. Will the system return to steady-state x_2? Repeat for steady-states x_3 and x_1.

Hint 2. For the case of steady-state x_1 we are only in displacements that result in a *positive* initial value. (Why?)

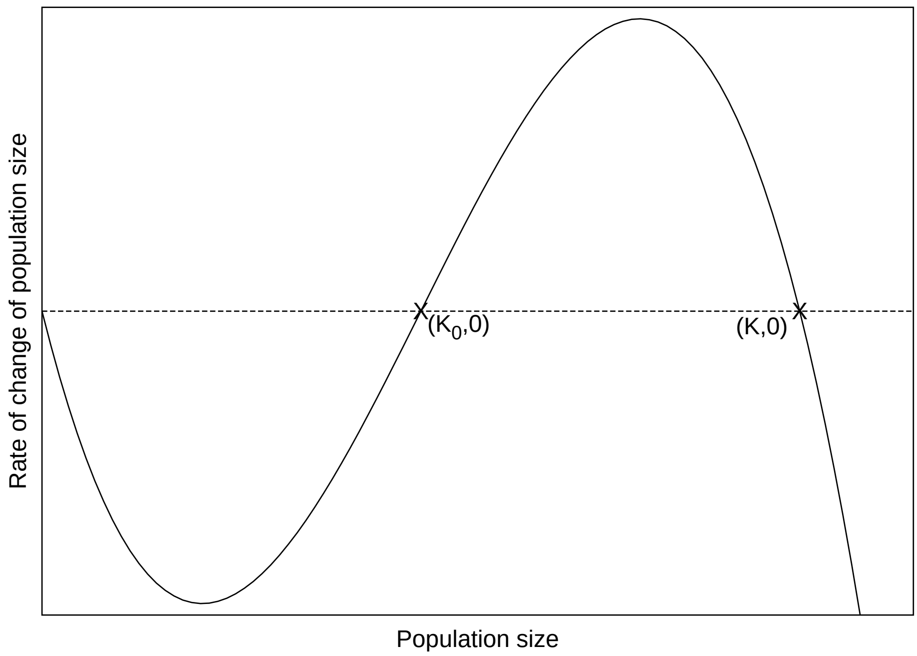


Figure 1.5: Sketch of the function $y = rx\left(1 - \frac{x}{K}\right)\left(\frac{x}{K_0} - 1\right)$, $0 < K_0 < K$, $r > 0$.

To determine graphically the stability of a steady-state solution x^* of the differential equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x)$$

use the following algorithm.

1. Plot the function
$$y = f(x).$$
2. Examine the sign of $y = f(x)$ on either side of the steady-state solution $x = x^*$.
   (a) If $y > 0$ then the solution is an *increasing* function of time. Draw an arrow from left-to-right.
   (b) If $y < 0$ then the solution is a *decreasing* function of time. Draw an arrow from right-to-left.
3. The stability is now determined by the direction of the arrows on either side of the steady-state solution

(a) If both arrows point towards the steady-state solution (x^*) then it is *stable.* (This means that the function $y = (x)$ is positive to the left of the steady-state and negative to the right of the steady-state.)

The steady-state solution is stable because if we move the system away from the steady-state by a small amount then the signs of the derivative show that the solution $x(t)$ will return to the steady-state solution x^*.

(b) If both arrows point away from the steady-state solution (x^*) then it is *unstable.* (This means that the function $y = (x)$ is negative to the left of the steady-state and negative to the right of the steady-state.)

The steady-state solution is unstable because if we move the system away from the steady-state by a small amount then the signs of the derivative show that the solution $x(t)$ will *not* return to the steady-state solution x^*.

(c) If one arrow points towards the steady-state solution and one arrow points away from the steady-state solution then the steady-state solution is said to be *semi-stable.* For practical purposes we consider such a steady-state solution to be unstable. This case is discussed in section 1.4.5.

In answering question 1.7 you should have found that the steady-states $x_1 = 0$ and $x_3 = K$ are stable whilst the steady-state $x_2 = K_0$ is unstable. Thus we know that a population can not evolve to the steady-state $x_2 = K_0$. Is the unstable steady-state solution $x_2 = K_0$ of interest? Yes! Very much so! We know that the steady-state $x_3 = K$ is stable, so that if the population changes by a small amount the system will evolve back to the value $x_3 = K$. However, from figure 1.5 we see that if the population is reduced too much then the system will evolve not to the stable steady-state $x_3 = K$ but to the stable steady-state $x_1 = 0$. The biological interpretation of this is that if the population size is reduced too low, perhaps by over-hunting or through the spread of a disease through the population, then the species will become extinct even if cease hunting or stop the spread of the disease.

How low is 'too low'? The threshold value is given by the unstable steady-state $x_2 = K_0$. Thus, in this model, knowledge about the unstable steady-state is crucial in determining the long-term dynamics of the model.

1.4.4 Determining the stability of steady-state solutions: Linear stability analysis

The concept of stability, and the related ideas of stable and unstable steady state solutions, was introduced in section 1.4.2. We can distinguish between stable and unstable steady-state solutions by considering what happens if a system initially at a steady-state solution is perturbed by a small amount: does the system return to the steady-state solution (stable) or does it go somewhere else (unstable)?

In section 1.4.3 we showed how the stability of a steady-state solution (x^*) of the differential equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x)$$

can be determined *graphically* by drawing the function

$$y = f(x).$$

In this section we show how to determine the stability of the steady-state solution (x^*) *algebraically* by carefully examining what happens to a system when it is *near* x^*.

Suppose that we have already found a steady-state solution x^* of the differential equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x).$$

We now proceed to explore its stability by asking the following key question: given an initial condition $x(0)$ *close* to x^*, will the solution of the differential equation, i.e. the values $x(t)$, tend toward or away from the steady state x^*? To answer this question we write

$$\xi(t) = x(t) - x^*, \qquad |\xi(t)| \ll 1,$$

where $\xi(t)$ is the distance between the dependent variable at time t, $x(t)$, and the steady-state solution, x^*. If $\xi(t) > 0$ then $x(t) > x^*$ and conversely if $\xi(t) < 0$ then $x(t) < x^*$.

Using equation (1.5) we derive a differential equation for $\xi(t)$ that is valid provided that the distance between the dependent variable at time t and the steady-state solution is small ($|\xi(t)| \ll 1$).

$$\begin{aligned}
\xi &= x(t) - x^* \\
\frac{\mathrm{d}\xi}{\mathrm{d}t} &= \frac{\mathrm{d}}{\mathrm{d}t}\left[x(t) - x^*\right] \\
&= \frac{\mathrm{d}x}{\mathrm{d}t} && \text{(why?)} \\
&= f(x) && \text{(why?)} \\
&= f(x^* + \xi) && \text{(why?)} \\
&= f(x^*) + f'(x^*)\,\xi + O\left(\xi^2\right); \quad |\xi| \ll 1. && \text{(why?)} \\
&= \xi f'(x^*) && \text{(why?)} \\
&= \lambda\xi, \\
\text{where} \quad \lambda &= f'(x^*).
\end{aligned}$$

(In deriving this equation we made a Taylor series expansion of a function of one variable. If you've forgotten how to do this read appendix B.2).

We have obtained a *linear* differential equation for the distance between the solution of our differential equation, $x(t)$, and the steady-state x^*. (This is where *linear stability analysis* gets its name. We have reduced a non-linear problem to a linear-problem). In this equation the parameter λ is known as the *eigenvalue* of the steady-state x^*. The solution of the differential equation

$$\frac{\mathrm{d}\xi}{\mathrm{d}t} = \lambda\xi$$

is

$$\xi(t) = \xi(0)\exp\left[f'(x^*)\,t\right],$$
$$\Rightarrow \lim_{t\to\infty}\xi(t) = \begin{cases} 0 \\ \infty \end{cases} \text{if} \begin{cases} \lambda < 0 \\ \lambda > 0. \end{cases}$$

Recall that the stability of a steady-state solution is determined by the answer to the following question: given an initial condition $x(0)$ *close* to x^*, will the solution of the differential equation, i.e. the values $x(t)$, tend toward (stable) or away (unstable) from the steady state x^*?

We see that:

> The stability of the steady-state solution x^* is determined by the value of $f'(x^*)$.

Definition 1.1 (Stable and unstable steady-state) *A steady-state x^* is*

stable	*if*	$f'(x^*) < 0$	(1.7)
unstable	*if*	$f'(x^*) > 0$	(1.8)

Note that if $\lambda = f'(x^*) = 0$ then $\xi(t) = \xi(0)$. Under these circumstances we can not determine the stability of the steady-state solution using linear stability analysis. The reason for this was that in deriving the eigenvalue equation we assumed that the size of the first term in the Taylor series expansion was larger than the size of the second term, i.e.

$$|f'(x^*)\,\xi| \gg \left|\frac{1}{2!}f''(x^*)\,{\xi^*}^2\right|.$$

This assumption is not true when $f'(x^*) = 0$, unless $f''(x^*) \neq 0$.

How do we determine the stability of a steady-state solution when $\lambda = 0$? This is discussed in section 1.4.5.

In the discussion of section 1.4.2 we noted that the transition from a stable to unstable steady-state, or vice-versa, is often of great interest. Suppose that x^* is a stable steady-state solution of the differential equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x).$$

Stability can change in only one way: the eigenvalue ($\lambda = f'(x^*)$) must either increase or decrease through the value $\lambda = 0$.

Question 1.8 *Why does $\lambda < 0$ mean that the steady-state solution x^* is stable?*

Question 1.9 *Is the distinction between a stable steady-state solution and an unstable steady-state solution of practical importance?*

Question 1.10 *If you start near a stable steady-state how quickly do you approach it?*

Example 1.1 (Stability of the steady-states in the logistic equation) *The logistic differential equation is given by*

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right), \qquad r > 0, \qquad K > 0. \tag{1.9}$$

Thus

$$f(x) = rx\left(1 - \frac{x}{K}\right)$$

and

$$\frac{df(x)}{dx} = r\left(1 - \frac{2x}{K}\right).$$

The steady-states of the logistic equation are given by

$$\begin{aligned} f(x) &= 0, \\ \Rightarrow rx\left(1 - \frac{x}{K}\right) &= 0, \\ \Rightarrow x_1^* &= 0 \quad \textit{or} \quad x_2^* = K. \end{aligned}$$

The steady-states and their corresponding eigenvalues λ are

$$x_1^* = 0, \qquad \lambda = f'(x_1^*) = r, \tag{1.10}$$

$$x_2^* = K, \qquad \lambda = f'(x_2^*) = -r. \tag{1.11}$$

Both of these steady-states are biologically meaningful, that is non-negative. The trivial steady-state solution ($x_1^* = 0$) is unstable whereas the non-trivial steady-state solution ($x_2^* = K$) is stable. □

Example 1.2 (Stability of the steady-state in the Gompertz model) *The Gompertz model is given by*

$$\frac{dx}{dt} = rx \ln \frac{K}{x}, \qquad r > 0, \qquad K > 0.$$

Thus

$$f(x) = rx \ln \frac{K}{x}$$

and

$$\frac{df(x)}{dx} = r\ln\frac{K}{x} - r$$

The steady-state of the Gompertz model is give by

$$\begin{aligned} f(x) &= 0, \\ \Rightarrow rx\ln\frac{K}{x} &= 0, \\ \Rightarrow x^* &= K. \end{aligned}$$

The corresponding eigenvalue is given by

$$\lambda = f'(x^*) = -r.$$

Thus the steady-state solution x^* is stable. □

Question 1.11 *Explain why the trivial solution ($x^* = 0$) is not a steady-state solution of the Gompertz model.*

The following observation is useful in some stability calculations and one that many students don't make...

Question 1.12 *Let x^* be a solution of the equation $f(x) = 0$. Consider the differential equation*

$$\frac{dx}{dt} = f(x)\,g(x).$$

Show that the eigenvalue of the steady-state solution x^* is given by

$$\lambda = g(x)\,f'(x).$$

Question 1.13 *Let x^* be a solution of the equation $f(x) = 0$. Consider the differential equation*

$$\frac{dx}{dt} = f(x)\,g(x)\,h(x)$$

Find an expression for the eigenvalue associated with the steady-state solution x^*, simplifying as far as possible.

1.4.5 What happens when the eigenvalue is equal to zero?

The linear stability analysis introduced in section 1.4.4 reveals that a steady-state solution is stable (unstable) if the eigenvalue is less than (greater than) zero: the stability is undetermined if the eigenvalue is equal to zero.

The reason for this is that in deriving the eigenvalue equation we assumed that

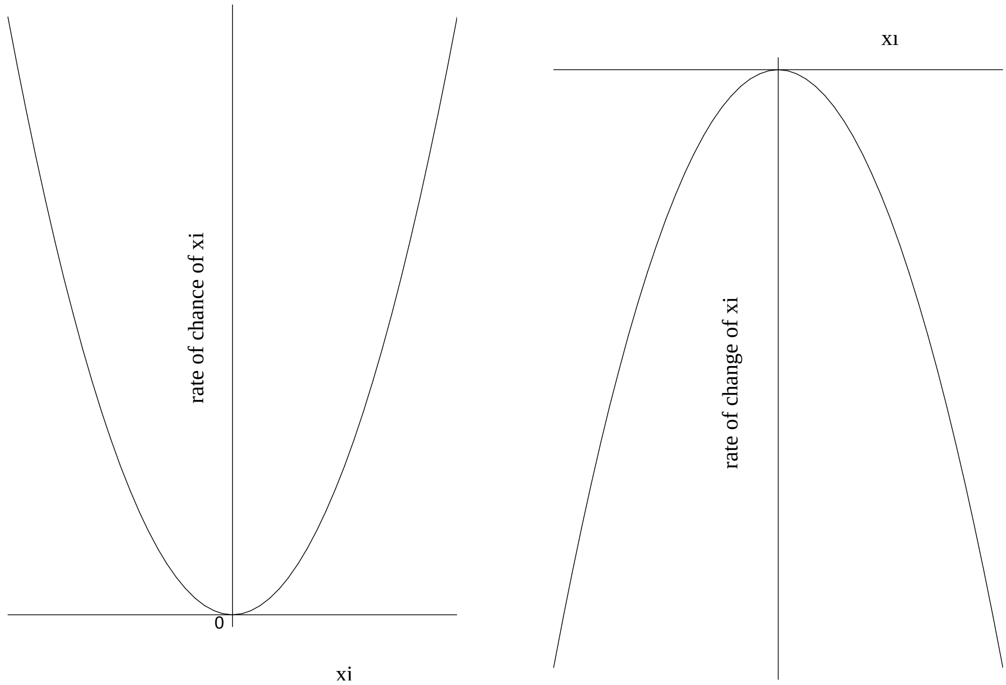
$$|f'(x^*)\,\xi| \gg \left|\frac{1}{2}f''(x^*)\right|\xi^2$$

which is not true if

$$f'(x^*) = 0.$$

When this happens we need to re-derive the eigenvalue equation by including higher-order terms. Assuming that $f''(x^*) \neq 0$ the eigenvalue equation becomes

$$\frac{\mathrm{d}\xi}{\mathrm{d}t} = a\xi^2. \tag{1.12}$$



(a) The case $a > 0$ (b) The case $a < 0$

Figure 1.6: Sketch of the function $y = a\xi^2$ for $a > 0$ and $a < 0$

(The derivation of this equation is question 1 in section 1.10.2).

We analyse this equation using the graphical technique from section 1.2. Figure 1.6 shows the necessary plots. Is the steady-state solution $\xi = 0$ stable or unstable?

Consider the case $a > 0$. We see from figure 1.6 (a) that if the initial displacement is to the right of the steady-state solution, i.e. $\xi(0) > 0$, then the derivative is positive and the solution of the differential equation moves away from the steady-state solution. This is *unstable behaviour*.

On the other hand we see that if the initial displacement is to the left of the steady-state solution, i.e. $\xi(0) < 0$, then the derivative is positive and the solution of the differential equation approaches the steady-state solution. This is *stable behaviour*.

Thus the stability of the system depends upon the direction of the initial displacement. Such steady-state solutions are said to be *semi-stable*. For practical purposes we can consider such an equilibrium to be unstable. The reason for this is that the displacements are random and there is no reason to suppose that they will always be to the left of the steady-state solution. We only need one displacement to the right of the steady-state solution and the solution will move away from the steady-state solution.

Question 1.14 *Using figure 1.6 (b) determine the stability of the steady-state solution $\xi = 0$ when $a < 0$.*

What happens if $a = 0$? Then we need to include the next term in the Taylor series expansion. It turns out that in this case the steady-state solution is either stable or non-stable. (This is question 2 in section 1.10.2).

Finally, in mathematical modelling it is usually not of interest to know whether a steady-state solution with eigenvalue equal to zero is stable, unstable or semi-stable. The reason for this is that it is very unlikely that any real system will have an eigenvalue that is equal to zero.

Question 1.15 *Justify in loose terms the statement that it's very unlikely that a first-order differential equation, arising as a mathematical model, will have an eigenvalue that is equal to zero.*

1.5 Steady-state diagrams and bifurcation points

1.5.1 What are steady-state diagrams and bifurcation points?

Many problems of practical interest contain a parameter (μ) that can be varied. When considering such problems we write the first-order autonomous differential equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f\left(x\right),$$

in the form

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f\left(x, \mu\right). \tag{1.13}$$

When the differential equation is written in the form 1.13 we say that the parameter μ is the 'bifurcation parameter'. The steady-state solution(s) of (1.13) are found by solving the equation

$$f\left(x, \mu\right) = 0.$$

Usually the value of the steady-state solutions of differential equation (1.13) will depend upon the value of the bifurcation parameter (μ). Furthermore, the stability of these steady-state solutions may change as the control parameter is changed. This information is usefully expressed in a steady-state, or response, diagram.

Definition 1.2 (Steady-state diagram) *The graph of x versus μ is called a steady-state diagram or a response curve. This shows how the steady-state solutions of equation* (1.13)*, x, and their stability depend upon the bifurcation parameter μ.*

(In many books and research articles what I have called a 'steady-state diagram' is called a 'bifurcation diagram'. In these notes a 'bifurcation diagram' is something very different. The phrase 'bifurcation diagram' is defined in section 2.5, definition 2.1).

In a steady-state diagram stable steady-states are indicated by a solid line whilst unstable steady-states are indicated by a dotted line. Figures 1.7–1.9 are examples of steady-state diagrams.

Question 1.16 *Examine each of the steady-state diagrams: figures 1.7–1.9. Identify how the number of steady-state solutions and their stability varies as the parameter μ is varied.*

Of particular interest on steady-state diagrams are *bifurcation points*[2]. Loosely speaking, a bifurcation point is a point $(\mu, x) = (\mu_0, x_0)$ on a steady-state diagram where two solution branches with distinct tangents intersect. At such a point the number of steady-state solutions to the differential equation changes.

Definition 1.3 (Bifurcation point) *The point (μ_0, x_0) is called a bifurcation point if the number of steady-state solutions of equation* (1.13) *in the neighbourhood of the point (μ_0, x_0) is not constant for any arbitrary small change of μ.*

Each of figures 1.7–1.9 contains one bifurcation point.

Question 1.17

1. *Identify the bifurcation point in each of figures 1.7–1.9*
2. *Check how the definition 1.3 'works' for each bifurcation point.*

[2]The meanings of the word bifurcate are: 1. To divide into two branches or parts. 2. To branch or separate into two parts. 3. Divided into two branches or parts; forked. Bifurcate comes from the past participle of Medieval Latin bifurcare, "to divide," from Latin bifurcus, "two-pronged," from bi- + furca, "fork." Source: `dictionary.com`

1.5.2 Examples of steady-state diagrams and bifurcation points

In this section we analyse three differential equations. The steady-state diagram for each equation contains a different type of bifurcation point.

1.5.2.1 The limit-point bifurcation

Consider the differential equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = \mu - x^2. \tag{1.14}$$

The set of steady-state solutions is given by

$$x = \sqrt{\mu}, \qquad \mu \geq 0.$$

There are *no* steady-state solutions when $\mu < 0$, one steady-state solution when $\mu = 0$ and two steady-state solutions when $\mu > 0$. Thus the number of steady-state solutions changes at the point $(\mu, x^*) = (0, 0)$. Thus this point is a *bifurcation point.*

Question 1.18 *Show that the steady-state $x = +\sqrt{\mu}$ is stable ($\mu > 0$) whilst the steady-state $x = -\sqrt{\mu}$ is unstable ($\mu > 0$).*

The steady-state diagram for equation (1.14) is shown in figure 1.7. Note that at the point $(\mu, x^*) = (0, 0)$, which we have already identified as a bifurcation point, two solution branches with distinct tangents intersect.

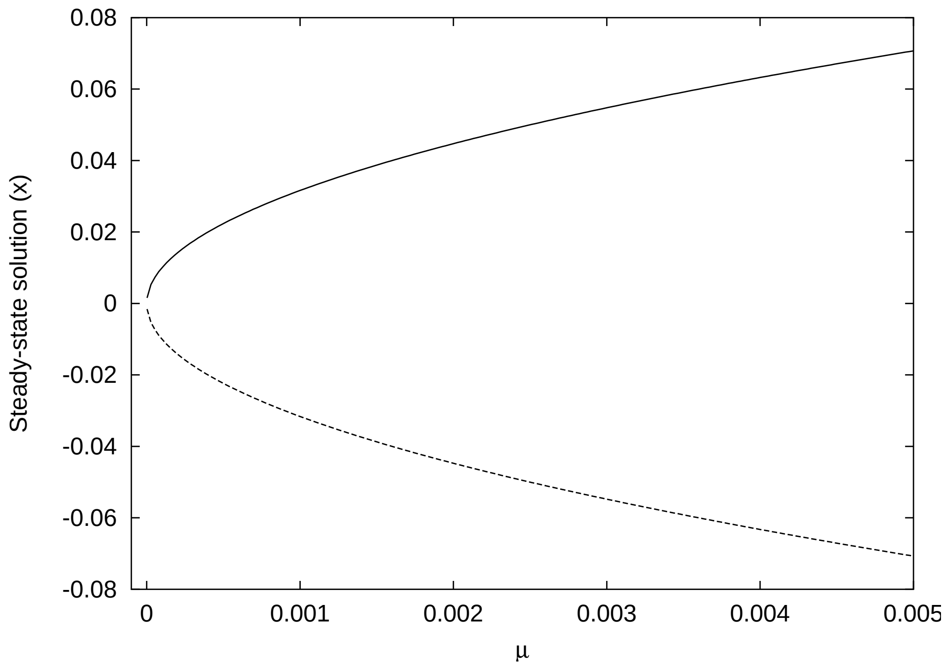


Figure 1.7: Steady-state diagram for the differential equation $\frac{\mathrm{d}x}{\mathrm{d}t} = \mu - x^2$: a solid line indicates a stable solution whilst a dotted line indicates an unstable solution.

The particular type of bifurcation occurring in figure 1.7 (i.e., where on one side of a parameter value there are *no* steady-state solutions in the neighbourhood of the bifurcation point and on the other side there are *two* steady-state solutions in the neighbourhood of the bifurcation point) is known as a *saddle-node bifurcation* or a *limit-point bifurcation.*

1.5.2.2 The transcritical bifurcation

Consider the differential equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = \mu x - x^2. \tag{1.15}$$

The set of steady-state solutions is given by

$$x_1 = 0, \tag{1.16}$$
$$x_2 = \mu. \tag{1.17}$$

There are *two* steady-state solutions for $\mu \neq 0$ and one steady-state solution when $\mu = 0$. Thus the number of steady-state solutions changes at the point $(\mu, x^*) = (0, 0)$. Thus this point is a *bifurcation point.*

Question 1.19

1. *Show that the steady-state branch $x_1 = 0$ is stable for $\mu < 0$ and unstable for $\mu > 0$.*

2. *Show that the steady-state branch $x_2 = \mu$ is unstable for $\mu < 0$ and stable for $\mu > 0$.*

The steady-state diagram for equation (1.15) is shown in figure 1.8. Note that at the point $(\mu, x^*) = (0, 0)$, which we have already identified as a bifurcation point, two solution branches with distinct tangents intersect.

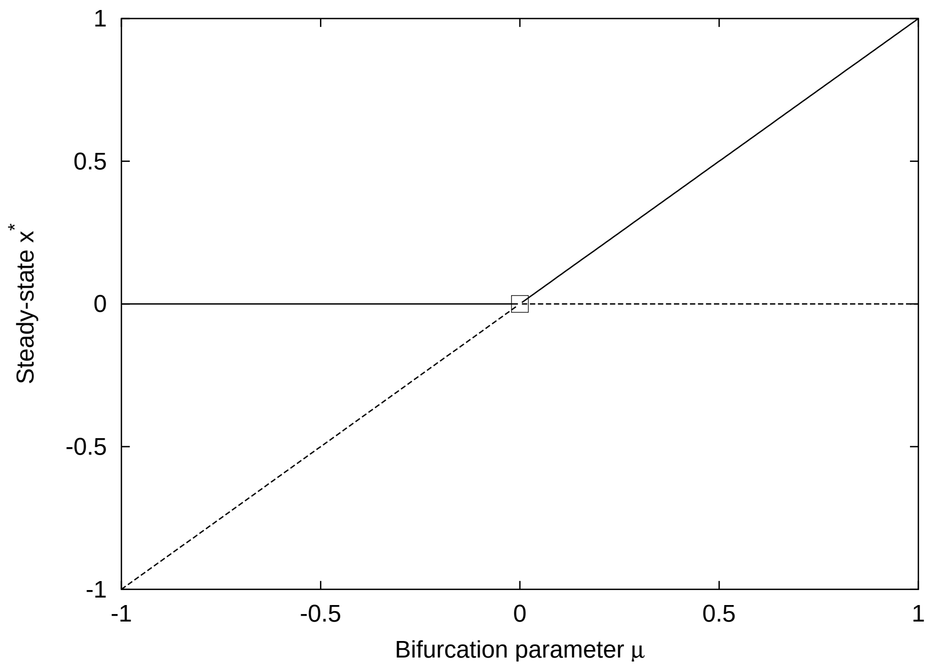


Figure 1.8: Steady-state diagram for the differential equation $\frac{\mathrm{d}x}{\mathrm{d}t} = \mu x - x^2$: a solid line indicates a stable solution whilst a dotted line indicates an unstable solution. The open box indicates a branch point.

The particular type of bifurcation occurring in figure 1.7 (i.e., where on either side of a parameter value there are *two* steady-state solutions in the neighbourhood of the bifurcation point but at the bifurcation point there is only one steady-state solution) is known as a *transcritical bifurcation.* This bifurcation frequently occurs in mathematical epidemiology.

In figure 1.8 a box has been drawn around the bifurcation point to indicate that it is a ‘branch point’. The reasons for this are discussed in section 1.5.2.4.

1.5.2.3 The pitchfork bifurcation

Consider the differential equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = \mu x - x^3. \tag{1.18}$$

The set of steady-state solutions is given by

$$\begin{aligned} x_1 &= 0, \\ x_\pm &= \sqrt{\mu}, \qquad \mu \geq 0. \end{aligned}$$

There is *one* steady-state solution when $\mu \leq 0$ and three steady-state solutions when $\mu > 0$. The number of steady-state solutions to the differential equation changes at the point $(\mu, x^*) = (0, 0)$. Thus this point is a *bifurcation point.*

Question 1.20

1. *Show that the steady-state* $x_1 = 0$ *is stable for* $\mu < 0$ *and unstable for* $\mu > 0$.
2. *Show that the steady-state* $x_\pm = \sqrt{\mu}$ *is stable for* $\mu > 0$.

The steady-state diagram for equation (1.18) is shown in figure 1.9. Note that at the point $(x^*, \mu) = (0, 0)$, which we have already identified as a bifurcation point, two solution branches with distinct tangents intersect.

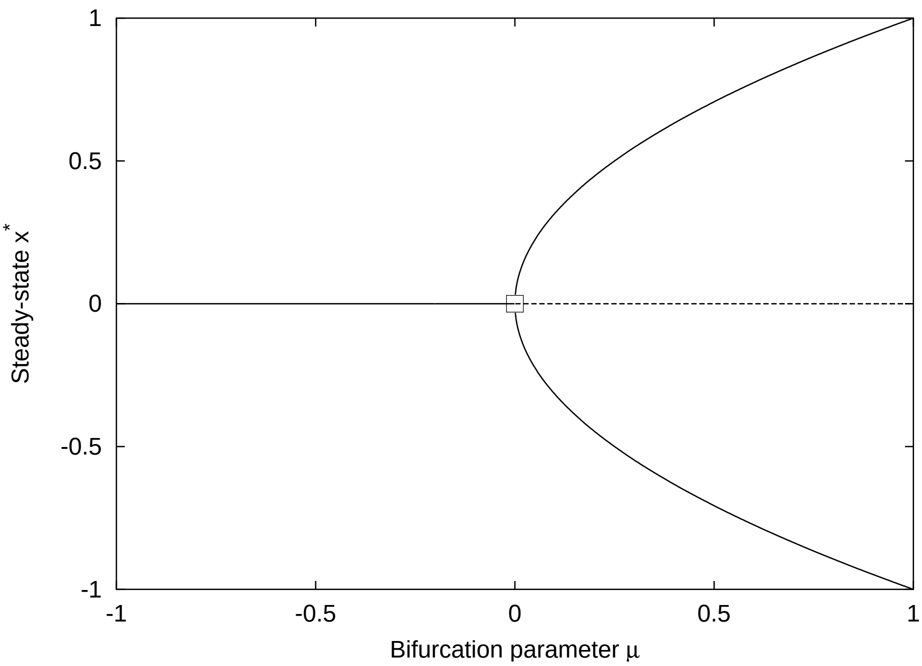


Figure 1.9: Steady-state diagram for the differential equation $\frac{\mathrm{d}x}{\mathrm{d}t} = \mu x - x^3$: a solid line indicates a stable solution whilst a dotted line indicates an unstable solution. The open box indicates a branch point.

The particular type of bifurcation occurring in figure 1.9 (i.e., where on one side of a parameter value there is *one* steady-state solution in the neighbourhood of the bifurcation point and on the other side there are *three* steady-state solutions in the neighbourhood of the bifurcation point) is known as a *pitchfork bifurcation.*

In figure 1.9 a box has been drawn around the bifurcation point to indicate that it is a ‘branch point’. The reasons for this are discussed in section 1.5.2.4.

1.5.2.4 (*) Why bother with 'branch points'?

The steady-state diagrams shown in figures 1.8 & 1.9 both contain a single bifurcation point. In each figure a box has been drawn around the bifurcation point and in each caption the bifurcation point is described as being a "branch point". The identification of the bifurcation point as a branch point means that your eyes are not deceiving you: what looks like a bifurcation point is a bifurcation point.

You may be wondering: "why bother?" After all, loosely speaking, a bifurcation point is where two solution branches with distinct tangents intersect and in both figure 1.8 and figure 1.9 there are two solution branches intersecting with distinct tangents.

For a single equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x, \mu)$$

it is *always* the case that when two solution branches with distinct tangents intersect at a point (μ_0, x_0) on a steady-state diagram that this point is a bifurcation point. (I still haven't answered the "why bother?" retort!) However, this statement is *not* true if you have a system of n differential equations

$$\frac{\mathrm{d}\mathbf{x}}{\mathrm{d}t} = f(\mathbf{x}, \mu), \quad \mathbf{x} \in \mathbb{R}^n.$$

When we have two, or more equations, it is possible for two solution branches, that don't intersect, to *appear* to intersect on the steady-state diagram. The reason for this 'non-intersection' property is that if we have n equations then the steady-state diagram is a figure with $n+1$ dimensions. It's not easy to draw a figure in $n+1$ dimensions when $n > 1$. To obtain a steady-state diagram that we can understand the steady-state diagram has to be projected from $n+1$ dimensions to two dimensions (sometimes three). It is the projection of a figure from $n+1$ dimensions to two (or three) dimensions that creates the *appearance* of branches intersecting. Thus on our steady-state diagrams we need to be able to distinguish 'real' bifurcation points, that really do intersect in $n+1$ dimensions, from 'mirage' bifurcation points, which don't intersect in $n+1$ dimensions. We do this by drawing a box around 'real' bifurcation points and identifying them as 'branch points'. We return to this point when discussing steady-state diagrams for a system of two differential equations in chapter 3.4.1.

For the case of a scalar equation 'mirage' bifurcation points can not occur. However, it makes sense to label bifurcation points on steady-state diagrams arising from a single differential equation in the same way as those on a steady-state diagram arising from a system of differential equations.

1.5.2.5 Discussion

In section 1.5.2 we have investigated three models of the form

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x, \mu)$$

and drew the corresponding steady-state diagrams. The three functions that we considered were

$$\begin{aligned} f(x, \mu) &= \mu - x^2, \\ f(x, \mu) &= \mu x - x^2, \\ f(x, \mu) &= \mu x - x^3. \end{aligned}$$

Each steady-state diagram contained a different type of bifurcation point. It may be thought that if we continue to change the function $f(x, \mu)$ that we will generate new types of bifurcation points. In fact, the three types of bifurcations that we have seen (the limit-point bifurcation, the transcritical bifurcation and the pitchfork bifurcation) are the only types of bifurcations that can occur in systems of the form[3]

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x, \mu). \tag{1.19}$$

At the end of section 1.4 we noted that we are not usually interested in the stability of a steady-state solution when its eigenvalue is equal to zero. However...

[3]To be 'technical', they are the only *generic* types of bifurcation that can occur in systems of the form (1.19).

Question 1.21 *Determine the stability of the steady-state solution at each of the bifurcation points for the systems defined by equations* (1.14), (1.15) *&* (1.18)

Suppose that we are given the equation

$$\mathcal{G}(x, \mu) = 0.$$

Is it possible to find the bifurcation points on the steady-state diagram without finding the steady-state diagram? We will learn how to do this in in chapter 2.4. In the meantime we can classify the bifurcation points by constructing the steady-state diagram and that examining what happens to the number of solutions *near* to the bifurcation point.

1.6 The spruce budworm model

In section 1.5.2 we determined the steady-state diagram for three problems of the form

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x, \mu).$$

In such problems the steady-state solutions, and their stability, is a function of the control parameter, or primary bifurcation parameter, μ.

Many problems have more than one control parameter. Typically, there will be a parameter of primary interest, μ, and one, or more, parameters of secondary interest, α, β... The parameters of secondary interest are called the secondary bifurcation parameters. A problem with one secondary parameter can be written in the form

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x, \mu, \alpha).$$

For a given value of the secondary parameter, α, the steady-state solutions, and their stability, only depends upon the primary bifurcation parameter and we can represent this information in a steady-state diagram. As we change the value for the secondary parameter we may find that the steady-state diagram changes in a 'fundamental' manner. In this section we will not attempt to define what it means for two steady-state diagrams to be considered 'fundamentally different'; this is the topic of chapter 2.

We illustrate the 'fundamental' change in a steady-state diagram as a secondary bifurcation parameter is changed by considering a model for the spruce budworm [44]. The spruce budworm is a major problem in Canada where it can, with ferocious efficiency, defoliate the balsam fir. The population density of the spruce budworm can be modelled by the differential equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = rx\left(1 - \frac{x}{q}\right) - \frac{x^2}{1+x^2}. \tag{1.20}$$

In equation (1.20) the parameter r ($r > 0$) is proportional to the birth rate of the budworm and the parameter q ($q > 0$) is proportional to the density of foliage available on the trees. The term $-\frac{x^2}{1+x^2}$ models predation by birds. The quantitative form of this function is biologically important. When x is small ($0 < x \ll 1$) predation is small, because the birds tend to seek food elsewhere. When x is large ($x \gg 1$) predation reaches a constant value ($\frac{x^2}{1+x^2} \approx 1$) because, although the birds spend all their time eating the budworm, there are only a finite number of birds.

Question 1.22

1. *Show that the steady-state(s) of the spruce budworm differential equation* (1.20) *are given by* $x_1 = 0$ *and the solutions of the algebraic equation*

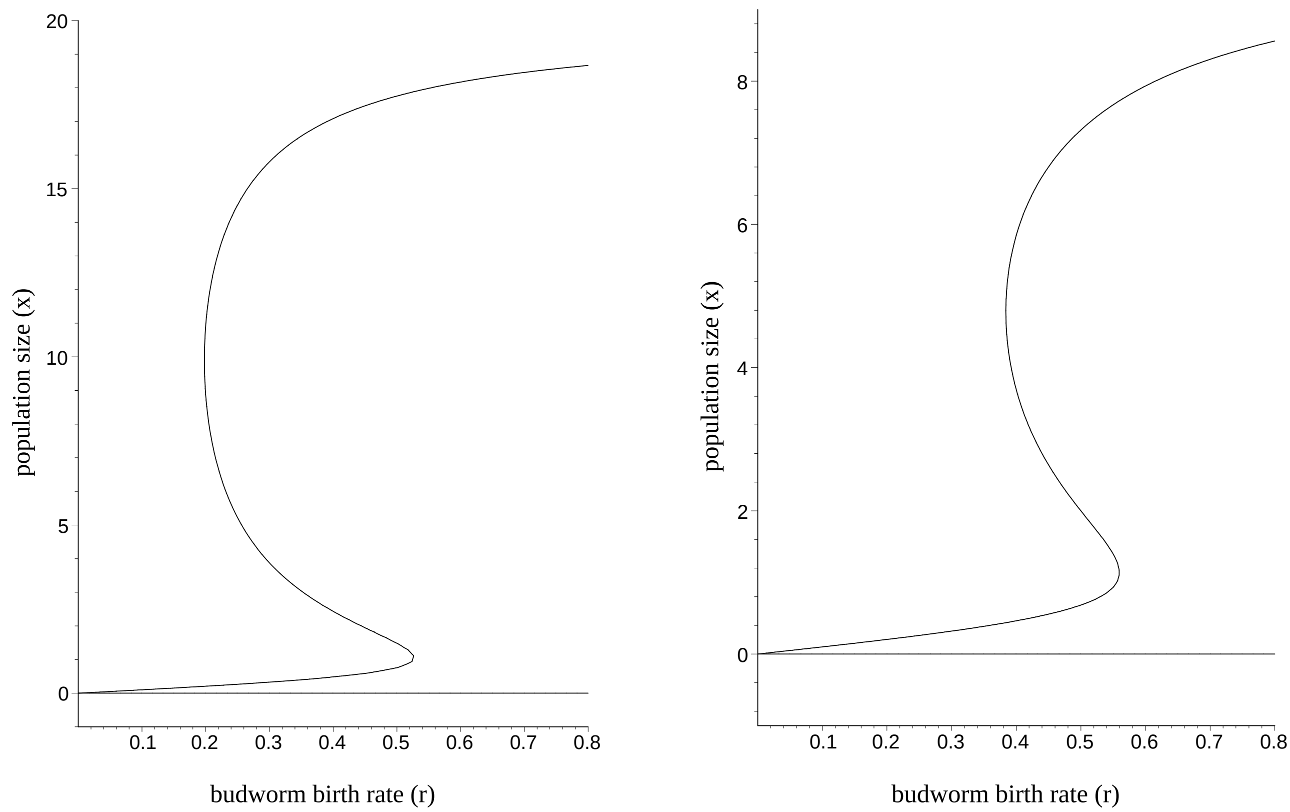
$$\mathcal{G} = r\left(1+x^2\right)\left(1 - \frac{x}{q}\right) - x = 0.$$

2. (a) Explain why the function $\mathcal{G}$ has either one or three positive solutions.

(b) Sketch the function $\mathcal{G}$ for the cases when it has either one or three positive solutions.

3. Determine the stability of the trivial solution $x_1 = 0$.

Figure 1.10 shows steady-state diagrams for the spruce budworm model, equation (1.20), stability not indicated, for the parameter values $q = 20$ and $q = 10$. These diagrams are obtained by combining the steady-state diagram corresponding to the equation $\mathcal{G} = 0$ with that of the trivial solution $x_1 = 0$. Although the 'fine details' of figure 1.10 (a) differ from those of figure 1.10 (b) the figures are 'essentially' the same. By 'fine details' I mean that for a particular value of the primary bifurcation parameter, r, the numerical values of the corresponding steady-state solutions are different. Indeed for a particular value of r the number of steady-state solutions in figure 1.10 (a) may differ from those of figure 1.10 (b).



(a) $q = 20$

(b) $q = 10$

Figure 1.10: Steady-state diagrams for the spruce budworm model, equation (1.20). Stability not shown.

The steady-state diagrams shown in figure 1.10 may be considered to be identical in terms of the shape of the solution branches. As the value of r increases there are regions with two, four and two steady-state solutions. At the interfaces between these regions there are values of r with three steady-state solutions. Both diagrams contain two limit-points; the value of r at which these limit points occur is the interface between regions containing two and four steady-state solutions. We conclude that the 'basic shape' of these diagrams are identical.

Figure 1.11 is a steady-state diagram for equation (1.20) for the parameter value $q = 3$. This diagram differs in a 'fundamental' way from those shown in figure 1.10: there are no regions of multiplicity (multiple steady-states) and there are no bifurcation points.

You may think that the lack of limit points in this figure is a consequence of the r range that I have chosen. Perhaps if the range were extended the figure would look similar to those exhibited in figure 1.10? You are invited to investigate this. But no matter how far you extend the r range you will not find regions of multiplicity and you will not find bifurcation points.

Question 1.23 *In plotting figure 1.10 how did I know that all the 'interesting action' is revealed by allowing the birth-rate parameter and the population size to vary over the ranges* $0 \leq r \leq 0.8$ *and* $0 \leq x \leq 20$ *respectively?*

The answer to question 1.23 will be answered in chapter 2.

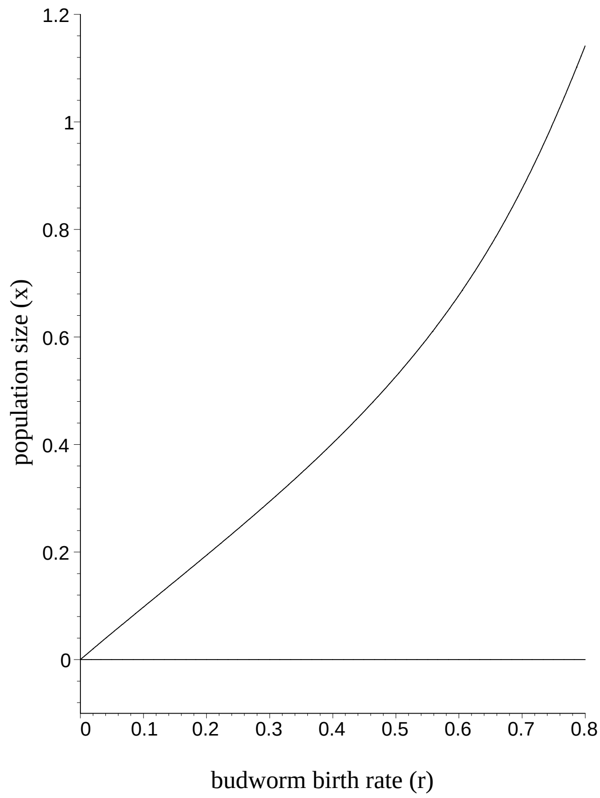


Figure 1.11: Steady-state diagram for the spruce budworm mode, equation (1.20). Stability not shown. Parameter value: $q = 3$.

Question 1.24

1. *In figure 1.10 the number of steady-state solutions changes in a two-four-two pattern as the value of* r *increases. In figure 1.11 the number of steady-state solutions is independent of the value of* r *and is two.*

   By considering the function $\mathcal{G}$ *defined by*

   $$\mathcal{G} = r\left(1 + x^2\right)\left(1 - \frac{x}{q}\right) - x = 0,$$

   explain why these observations are plausible.

2. *By generating steady-state diagrams for different values of* q *find a critical value of* q, q_{cr}, *(to one decimal place) at which the features of the steady-state diagram changes from the type shown in figure 1.10 to that shown in figure 1.11.*

3. *Try to explain how the steady-state diagram changes during the transition from one type to the other.*

1.7 Conclusions

A powerful tool to investigate the solution to the differential equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x)$$

is to plot the function

$$y = f(x).$$

This plot will:

- show you if the dependent variable (x), is an increasing or decreasing function of the independent variable (t) and how this behaviour depends upon the choice of initial condition;
- show you how the derivative of the solution changes with time;
- enable you to find the steady-state solutions of the equation;
- enable you to state the stability of the steady-state solutions(s).

The steady-state solutions of the differential equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x)$$

can be found either graphically, by plotting the function

$$y = f(x),$$

or algebraically, by solving the equation

$$f(x) = 0.$$

Not all steady-state solutions are equal and it is important to distinguish between stable steady-state solutions, which may be observed experimentally, and unstable solution, which may not be observed experimentally. The stability of a steady-state solutions, x^*, may be determined either graphically, by plotting the function

$$y = f(x),$$

or algebraically by determining the sign of the eigenvalue (λ), where

$$\lambda = f'(x^*).$$

In exceptional circumstances a steady-state solution will be semi-stable. For practical purposes these can be considered to be unstable.

In models of the form

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x, \mu)$$

the steady-state solutions (x^*), and their stability, are a function of the primary bifurcation parameter (μ). A good way to show this relationship is to draw a steady-state diagram and to identify the nature of any bifurcation points that it contains. If the steady-state diagram contains either a transcritical bifurcation or a pitchfork bifurcation an open box is drawn around the bifurcation point to indicate that it is a 'branch point' and not a mirage.

In section 1.6 we looked at a mathematical model that contained two parameters

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x, \mu, \alpha).$$

We saw that different values of the secondary bifurcation parameter (α) might produce different 'types' of steady-state diagrams. The first 'type' of steady-state diagram, seen in figure 1.10, had two limit points and contained regions in which the multiplicity of the solutions changed (two-four-two pattern). The second 'type' of steady-state diagram, seen in figure 1.11, had no limit points and there were always two steady-state solutions.

There are several questions to ponder about these observations. Firstly, is it possible to find the critical value of the secondary bifurcation parameter at which one 'type' changes to another 'type' without resorting to numerical trial-and-error (as you are asked to do in question 1.24)? Secondly, is it possible to define what is meant by steady-state diagrams differing in a 'fundamental' way? Thirdly, we have shown that the spruce budworm model has at least two different types of steady-state diagram — are there more? These questions are answered in chapter 2.

We finish our summary of the content of this chapter with the following observation.

> The study of steady-state solutions, their stability and their bifurcations is the process through which the properties of non-linear differential equations are elucidated in a systematic manner.

1.7.1 Historical comments

One instance of the scientific importance of stability is the mathematical investigation of the rings of the planet Saturn by James Clerk Maxwell[4]. He showed that whilst either a solid ring or a fluid ring were mathematically possible, both were unstable. Maxwell showed that there are *stable* solutions of the equations of motion when the rings are comprised of numerous small particles and therefore concluded that the rings must be composed of many small separate bodies.[5] This theory was confirmed by the Voyager flybys of the 1980s[6].

1.7.2 Further reading

For more about the qualitative analysis of the behaviour of a single ordinary differential equation see [21, Chapter 1.4].

For more information about the spruce budworm model see [51, Chapter 1.2].

1.8 Maple commands

1.8.1 Plotting commands

A common theme in this chapter is that properties of the differential equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x)$$

are readily found by plotting the function

$$y = f(x)$$

This can be done using the maple `plot` command. For example, consider the model

$$\frac{\mathrm{d}x}{\mathrm{d}t} = 2x\left(1 - \frac{x}{2}\right).$$

The required maple code is

[4] Scottish theoretical physicist and mathematician (1831–1879). His contributions to science are considered by many to be of the same magnitude of those of Newton and Einstein.

[5] In 1855 'The Motions of Saturn's Rings' was selected as the topic for the Adams Prize at Cambridge in 1857. The winner, and sole entrant, was James Maxwell. The Adams Prize is still awarded, every two years, for a substantial scholarly essay on an announced theme. [24, page 183, foonote 370].

[6] This account is taken from [37, page 191] and the wikipedia entry on Maxwell.

```
f := 2*x*(1-x/2);
plot(f,x=0..4);
```

In section 1.6 we showed that the steady-states of the spruce budworm model, equation (1.20) are given by $x_1 = 0$ and the solutions of the algebraic equation

$$\mathcal{G} = r\left(1+x^2\right)\left(1-\frac{x}{q}\right) - x = 0.$$

A steady-state diagram, ignoring the trivial solution $x_1 = 0$, not indicating stability, can be obtained using the maple `implicitplot` command as follows.

```
with(plots):
eqn := r*(1+x**2)*(1-x/q)-x;
q   := 20;
implicitplot(eqn,r=0..1,x=0..20,grid=[60,60],colour=black);
```

The `grid` option is used to improve the quality of the steady-state diagram. (Replace `grid=[60,60]` with `grid=[25,25]` and compare figures).

The steady-state diagrams shown in figure 1.10 are obtained by combining two plots into one as follows.

```
with(plots):
G := r*(1+x**2)*(1-x/q)-x;
q := 20;
p1 := implicitplot(G,r=0..0.8,x=-1..20,grid=[120,120],colour=BLACK,thickness=2,axes=FRAMED):
p2 := plot(0,r=0..0.8,x=-1..20,thickness=2,colour=BLACK,labels=["",""],axes=FRAMED):
display({p1,p2},labels=["budworm birth rate (r)","population size (x)"],\
       labeldirections=[horizontal,vertical],labelfont=[TIMES,ROMAN,18]);
```

Note the use of the colon at the end of the definition of `p1` and `p2`. You should try this command sequence by replacing the colon with a semi-colon. You will then see why it is better to use the colon!

1.8.2 Numerical integration of a differential equation

This is not a book on the numerical integration of ordinary differential equations. There are many ways to integrate a differential equation, each has their own advantages and disadvantages. The following code integrates the first-order differential equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = rx\left(1-\frac{x}{q}\right) - \frac{x^2}{1+x^2}$$

for a variety of initial conditions.

```
# budworm.maple  Maple program to solve a first-order
# 17.09.03       ordinary differential equation.
#
# NOTE. This is NOT the maple code that one would use to
# investigate a research problem, but it's good enough for the
# present purpose.
with(DEtools):

step := 0.1:  # this number controls how accurate the numerical
              # solution is.
tstart := 0:  # the initial value of time.
tend   := 30: # the final value of time.
```

```
ic1 := [0,0.1];          # one initial condition in the form (t0, x(t0));
                         # two initial conditions both in the form (t0, x(t0));
ic2 := [0,0.1],[0,1.0];
                         # four initial conditions
ic3 := [0,0.1],[0,1.0],[0,12.0],[0,20.0];

r   := 0.3;    # budworm 'birth-rate'.
q   := 20.0;   # 'foilage density'.

# define the differential equation.  Note that we have to TELL maple
# that x is a function of time by writing x(t)
de1 := diff(x(t),t) = r*x(t)*(1-x(t)/q) -x(t)**2/(1+x(t)**2);

# calculate a solution trajectory from an initial condition.
DEplot(de1,x(t),t=tstart..tend,[ic1],stepsize=step,arrows=NONE, \
       linecolor=BLACK);

# compare solution trajectories from TWO initial conditions.
DEplot(de1,x(t),t=tstart..tend,[ic2],stepsize=step,arrows=NONE, \
       linecolor=BLACK);

# compare solution trajectories from FOUR initial conditions.
DEplot(de1,x(t),t=tstart..tend,[ic3],stepsize=step,arrows=NONE, \
       linecolor=BLACK);
```

1.9 Revision of key ideas

The following questions are about the key ideas in this chapter.

1. What information about the solutions of the differential equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x)$$

   can be found by plotting the function

$$y = f(x)?$$

2. Consider the differential equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x).$$

   What does it mean for the point x^* to be a steady-state of this differential equation?

3. Consider the population model

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x).$$

   Explain why it is important to find the steady-states of the function $f(x)$.

4. Suppose that x^* is a steady-state solution of the differential equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x).$$

   (a) What does it mean for the steady-state to be stable?

   (b) What does it mean for the steady-state to be unstable?

(c) What does it mean for the steady-state to be semi-stable?

5. Suppose that x^* is a steady-state solution of the differential equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x).$$

Explain how the stability of the steady-state solution x^* can be determined graphically and algebraically.

6. What is the importance of finding the stability of a steady-state?

7. Suppose that x^* is a steady-state solution of the equation

$$\frac{\mathrm{d}x^*}{\mathrm{d}t} = f(x).$$

Derive the eigenvalue equation

$$\frac{\mathrm{d}\xi}{\mathrm{d}t} = \lambda\xi$$

and state its interpretation in terms of stability.

8. Suppose that x^* is a steady-state solution of the differential equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x)$$

with eigenvalue $\lambda < 0$. Why does this mean that the steady-state solution is stable?

9. Explain what you understand by the word '*bifurcation*'.

10. Suppose that x^* is a steady-state solution of the differential equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x, \mu)$$

Define what is meant by the phrases: *limit-point bifurcation*, *transcritical bifurcation* & *pitchfork bifurcation.*

11. Consider the differential equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x, \mu).$$

What information does a *steady-state diagram* contain?

12. Suppose that the point $(x, \mu) = (x_0, \mu_0)$ is a *bifurcation point* on a steady-state diagram. What does this mean?

13. Consider the differential equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = f(x)$$

where the function $f(x)$ is defined by

$$f(x) = 0.3\exp[x] - x.$$

Write maple code to:

(a) plot the function $f(x)$ over the range $0 \leq x \leq 2$;

(b) find the numerical value of the two steady-state solutions;

(c) find the eigenvalue of each of the two steady-state solutions.

1.10 Questions on first-order non-linear differential equations

1.10.1 Graphical techniques

1. Consider the population model (Smith 1963)
$$\frac{\mathrm{d}x}{\mathrm{d}t} = \frac{r\,(K-x)}{K+ax}x, \quad x\,(0) = x_0 \geq 0.$$
(The parameters a, r,& K are strictly positive.).
   (a) Sketch $\frac{\mathrm{d}x}{\mathrm{d}t}$ as a function of x. Hence determine how the long-term dynamics of the model depends upon the initial value x_0.
   (b) Sketch the solution $x\,(t)$. How does the qualitative form of your sketch depend upon the initial value x_0?
   (c) Determine the stability of the steady-state solutions of this model.
2. For which initial values $y\,(0)$ does the solution $y\,(t)$ of the differential equation
$$y' = y\left(e^{-y} - 2y\right)$$
approach zero as $t \to \infty$? (Note that is *not* a population model so that $y\,(0)$ may be negative). [21, page 25, exercise 7]
3. The Semenov model for the self-heating of a combustible material can be written in the form
$$\frac{\mathrm{d}\theta}{\mathrm{d}\tau} = \psi \exp\,[\theta] - \theta,$$
where θ is essentially the temperature difference between the combustible material and its surroundings, τ is scaled time and ψ is known as the Semenov number. Assume that $\psi = 0.3$.
   (a) By plotting $\frac{\mathrm{d}\theta}{\mathrm{d}\tau}$ as a function of θ show graphically that the model has two steady-state solutions, θ_1 and θ_2 with $0 < \theta_1 < \theta_2$.
   (b) Using your graph determine the stability of the steady-state solutions θ_1 and θ_2.
   (c) Using maple find the values of θ_1 and θ_2 to three decimal places.
   (d) Using maple find the eigenvalue, to two decimal places, of the steady-state solution θ_1 and the steady-state solution θ_2.

1.10.2 Stability

1. Suppose that x^* is a steady-state solution of the differential equation
$$\frac{\mathrm{d}x}{\mathrm{d}t} = f\,(x)$$
such that $f'\,(x^*) = 0$. Show that a stability analysis leads to the equation
$$\frac{\mathrm{d}\xi}{\mathrm{d}t} = \frac{1}{2!}f''\,(x^*)\,\xi^2.$$
2. Suppose that x^* is a steady-state solution of the differential equation
$$\frac{\mathrm{d}x}{\mathrm{d}t} = f\,(x)$$
such that $f'\,(x^*) = f''\,(x^*) = 0$.
By carrying out a suitable Taylor series expansion of the function $f\,(x)$ determine the stability of the steady-state solution.
3. Suppose that the steady-state solutions of a differential equation are found by solving the equation $G\,(x) = 0$. Is it possible to determine the stability of the steady-state solutions from the information provided?

1.10.3 Steady-state diagrams

1. For each of the following differential equations [35, problem 1 on page 273]

   (a) Find the steady-state solutions.

   (b) Determine the stability of the steady-state solutions as a function of the primary bifurcation parameter μ.

   (c) Draw a steady-state diagram.

   (d) For what value of the parameter μ does a bifurcation occur? What kind of bifurcation is it?

$$x' = 2\mu + x^2,$$
$$x' = x\left(\mu - 2x + x^2\right),$$
$$x' = x\left(\mu + x - x^2\right)\left(1 - \mu + x^2\right).$$

2. Obtain the steady-state diagrams for the following equations and identify any bifurcation points that they contain. For the purpose of this question you do not need to discuss the stability of the solutions.

   (a) $\dfrac{\mathrm{d}x}{\mathrm{d}t} = \lambda x - x^4$

   (b) $\dfrac{\mathrm{d}x}{\mathrm{d}t} = \lambda x^2 - x^4$

   (c) $\dfrac{\mathrm{d}x}{\mathrm{d}t} = \lambda^2 - x^4$

   (d) $\dfrac{\mathrm{d}x}{\mathrm{d}t} = \lambda^2 x - x^4$

1.10.4 Longer questions

This questions are more 'exam-like' in nature.

1. Consider the population model

$$x' = f(x), \quad x(t=0) = x_0$$
$$f(x) = -rx\left(1 - \frac{x}{K_1}\right)\left(1 - \frac{x}{K_2}\right),$$

   subject to constant yield harvesting

$$x' = f(x) - h, \quad x(t=0) = x_0. \tag{1.21}$$

   where $0 < K_1 < K_2$, $r > 0$ and $h \geq 0$.

   (a) Consider the case when there is no harvesting, i.e. $h = 0$.

      (i) Find the steady-state solutions of equation (1.21) and determine their stability.

      (ii) Identify how the long-term behaviour of the model depends upon the choice of the initial condition (x_0).

   (b) Consider the case when there is harvesting, i.e. $h > 0$.

      (i) Sketch the graph $y = f(x)$. By considering how the graph of $y = f(x) - h$ changes as h is increased from 0 identify the maximum sustainable value of the harvesting parameter, h_{cr}, on your sketch. Identify on your sketch the value of x, $\hat{x}$, that corresponds to the maximum sustainable value of the harvesting parameter.

      (ii) Determine an analytic expression for $\hat{x}$ in terms of r, K_1 and K_2.

      (iii) Suppose that, in a particular fishery, $r = 1\,\mathrm{year}^{-1}$ and that $K_1 = 10^3$ and $K_2 = 10^4$, measured in kilograms. Determine the maximum sustainable yearly harvest (h_{cr}).

(iv) Suppose that, in a particular fishery, $r = 1\,\text{year}^{-1}$ and that $h = 4 \times 10^3$, $K_1 = 10^3$ and $K_2 = 10^4$, measured in kilograms. The current population size is estimated to be 1.5×10^3 (kilograms).
- Describe the long-term behaviour of the population.
- Given the estimated population size what is the maximum sustainable harvest yield?

2. The spruce budworm model is given by

$$\frac{\mathrm{d}x}{\mathrm{d}t} = rx\left(1 - \frac{x}{q}\right) - \frac{x^2}{1 + x^2},$$

with $r > 0$ and $q > 0$.

(a) Show that the steady-state(s) of the spruce budworm model are given by $x_1 = 0$ and the solutions of the algebraic equation

$$\mathcal{G} = r\left(1 + x^2\right)\left(1 - \frac{x}{q}\right) - x = 0.$$

(b) Determine the stability of the trivial solution $x_1 = 0$.

(c) Suppose that the value of q is such that the steady-state diagram of the function $\mathcal{G}$ is given by figure 1.8 of the lecture notes.

(i) Show that when the function $\mathcal{G}$ has a single steady-state it is stable.

(ii) Show that when the function $\mathcal{G}$ has three steady-states the lower and upper solutions are stable and the middle-solution is unstable.

(iii) Hence sketch the full steady-state diagram when $q = 20$, indicating stability. Don't forget to include the solution $x_1 = 0$.

Hint Graphical techniques make the stability analysis easy!

(d) Suppose that the value of q is such that the steady-state diagram for the function $\mathcal{G}$ is given by figure 1.9 of the lecture notes.

(i) Show the the unique steady-state solution of the the function $\mathcal{G}$ is stable.

(ii) Hence sketch the *full* steady-state diagram when $q = 3$, indicating stability.

(e) By generating steady-state diagrams for different values of q find a critical value of q, q_{cr}, (to one decimal place) at which the features of the steady-state diagram changes from the type shown in figure 1.8 of the notes to that shown in figure 1.9.

To illustrate the reasoning for you answer provide steady-state diagrams when $q = q_{\text{cr}} + 0.1$, $q = q_{\text{cr}}$ and $q = q_{\text{cr}} - 0.1$ and any other supplementary material you consider appropriate.

(f) Try to explain how the steady-state diagram changes during the transition from one type to the other.

1.11 Things to do

This is a list of things that I'd like to add to the notes at a latter date.

1. Add a historical comment regarding the notation $\frac{\mathrm{d}x}{\mathrm{d}t}$, x' and $\dot{x}$. C. Montelle. "A Symbolic History of the Derivative", in MAA's *Mathematical Time Capsules* ed. A. Shell-Gellasch and R. Jardine (Forthcoming June 2009).
2. Add historical information on the logistic equation and on the Gompertz model.
3. Track down the reference for the population model (Smith, 1963).
4. Mention that the concept of branch point has more to it than distinguishing between real and mirage bifurcation points.
5. When you classify a bifurcation point you only look locally. Thus on question 2 from assignment 1 (2009) the bifurcation point is a limit point NOT a pitchfork.

6. Worked solutions to some questions.
7. Track down a reference for the Semenov model.

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