

11 First-Order Non-Linear Differential Equations

1.1 Introduction

- We study first-order non-linear differential equations.
- *Motivation:* We primarily consider population models for a single species.

- $x(t)$ denotes the size of the population at time t
- $\frac{dx}{dt}$, 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

$$\frac{dx}{dt} = f(x). \quad (11.1)$$

Note.

1. Equation (11.1) is autonomous.
2. Instead of representing ‘popⁿ size’ $x(t)$ can represent ‘popⁿ density’.

The critical issue from the perspective of population biology is to identify the long-time behaviour of the population, e.g. does the population become extinct?

Question 1.1

1. *For some species it would be appropriate to replace equation (11.1) by a non-autonomous equation. Why?*
2. *We have assumed that the rate of change of population depends upon its current size. Any comments on this?*

1.2 Aim^s

After working through this chapter you should be able to

1. Explain the defects of the linear population model.
2. Use the graph of the function

$$y = f(x)$$

to predict the long-time behaviour of the DE

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

3. Explain what *steady-state* solutions are and know how to find them.

4. Appreciate the importance of finding the steady-state solutions of the differential equation

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

as the first step towards understanding the dynamics of the population model.

5. To derive the *logistic differential equation* and find its steady-state solutions.

1.3 A linear model for population growth

11.3.1 Derivation of Model

To motivate the use of a *non-linear* model for a population we first consider the *linear* model that we derived in chapter 8.4.1.

$$\frac{dx}{dt} = \beta x - \alpha x,$$

where β is the per-capita _____ and α is the per-capita _____.

11.3.2 Assumptions of the Model

10.3.2.1 Birth-rate We have assumed that:

1. The per-capita birth-rate (β) is constant.
2. The birth-rate (βx) is a linear function of the current population size (x).
3. Obviously $\beta \geq 0$.

10.3.2.2 Death-rate We have assumed that:

1. The per-capita death rate (α) is constant.
2. The death-rate (αx) is a linear function of the current population size (x).
3. Obviously $\alpha \geq 0$.

10.3.2.3 Other processes

Question 1.2 *Are there any other significant factors that we could add to our model?*

11.3.3 Solution of the linear model

The *linear population model* is

$$\begin{aligned} \frac{dx}{dt} &= \beta x - \alpha x, & x(t=0) &= x_0, \\ &\equiv (\beta - \alpha)x, & x(t=0) &= x_0, \\ &\equiv \gamma x, & x(t=0) &= x_0, \end{aligned} \quad (11.2)$$

where $\gamma = \beta - \alpha$.

Equation (11.2) accurately describes the population growth for only short times, when the population is small (dilute).

The solution of equation (11.2) is,

$$x(t) = \frac{x_0 e^{\gamma t}}{1 - \frac{\gamma x_0 t}{e^{\gamma t}}} \quad (11.3)$$

Question 1.3 *How does the solution to equation (11.2) depend upon the value of γ ?*

$$\gamma < 0 \quad \lim_{t \rightarrow \infty} x(t) = _.$$

$$\gamma = 0 \quad x(t) = _$$

$$\gamma > 0 \quad \lim_{t \rightarrow \infty} x(t) = _.$$

Question 1.4 *Is the constant population $x(t) = x_0$, corresponding to the $\gamma = 0$, a solution that is likely to occur in the real world?*

1.4 The failure of the linear model: Nonlinear models

In the previous section we assumed that the *per-capita growth rate* is constant.

Thus the *total* growth rate was proportional to the population size. A better assumption is that the growth rate decreases as the population size increases. This leads to the study of differential equations of the form

$$\begin{aligned}\frac{dx}{dt} &= x\gamma(x), \\ &= f(x),\end{aligned}$$

in which $\gamma(x)$ represents the effective per-capita birth-rate.

The simplest form of the per capita growth rate which is a decreasing function of population size is $\beta(x) = \beta_0 - ax$. This leads to the *logistic* differential equation

$$\begin{aligned}\frac{dx}{dt} &= (\beta_0 - ax)x - \alpha x, \\ &= (\beta_0 - \alpha)x - ax^2 \\ &= (\beta_0 - \alpha)x \left(1 - \frac{a}{\beta_0 - \alpha}x\right),\end{aligned}$$

where we have assumed that $\alpha \neq \beta_0$. This equation is usually written as

$$\frac{dx}{dt} = \underline{rx \left(1 - \frac{x}{K}\right)}, \quad (11.4)$$

with parameters $r = \beta_0 - \alpha$ and $K = \frac{\beta_0 - \alpha}{a}$. It is assumed that these are both greater than zero.

The solution of equation (11.4) is

$$x(t) = \frac{Kx_0}{x_0 + (K - x_0)e^{-rt}}. \quad (11.5)$$

where x_0 is the population size at time $t = 0$.

Question 1.5 Using equation (11.5) determine the population size $x(t)$ in the limit as $t \rightarrow \infty$.

The parameters r and K may now be given biological meaning.

The value K is called the carrying capacity of the popⁿ because it represents the popⁿ size that available resources can continue to support.

The value r is called the intrinsic growth rate because it represents the per capita growth rate achieved if the popⁿ size were small enough to ensure negligible resource limitations.

That is to say, when $x \ll K$ we have

$$\frac{dx}{dt} \approx \text{_____},$$

and the population undergoes exponential growth.

Although simple, the behaviour predicted by the logistic differential equation is in agreement with the observed behaviour of many populations and, for this reason, the logistic model is often used as a means of describing population dynamics.

Question 1.6 *What is the biological significance of assuming that $r > 0$.*

1.5 First-order ODEs: Graphical insights

First-order autonomous differential equations of the general form

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

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 population dynamics without recourse to either analytical or numerical solutions by using a graphical technique.

Of course, we are only interested in non-negative populations.

The use of a graphical technique to gain an insight into the solution of equation (11.1) is similar to the use of cobwebbing, introduced in chapter 4.5, to investigate the dynamics of the difference equation

$$x_{n+1} = f(x_n).$$

To investigate the solution of equation (11.1) 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) $\frac{dx}{dt} > 0$.

(b) $\frac{dx}{dt} < 0$.

(c) $\frac{dx}{dt} = 0$.

3. Hence identify how the long-time dynamics of the model depends upon the choice of initial condition.

Question 1.7 Using figure 11.1 determine how the long-term dynamics of the population depend upon the initial condition for the logistic differential equation

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

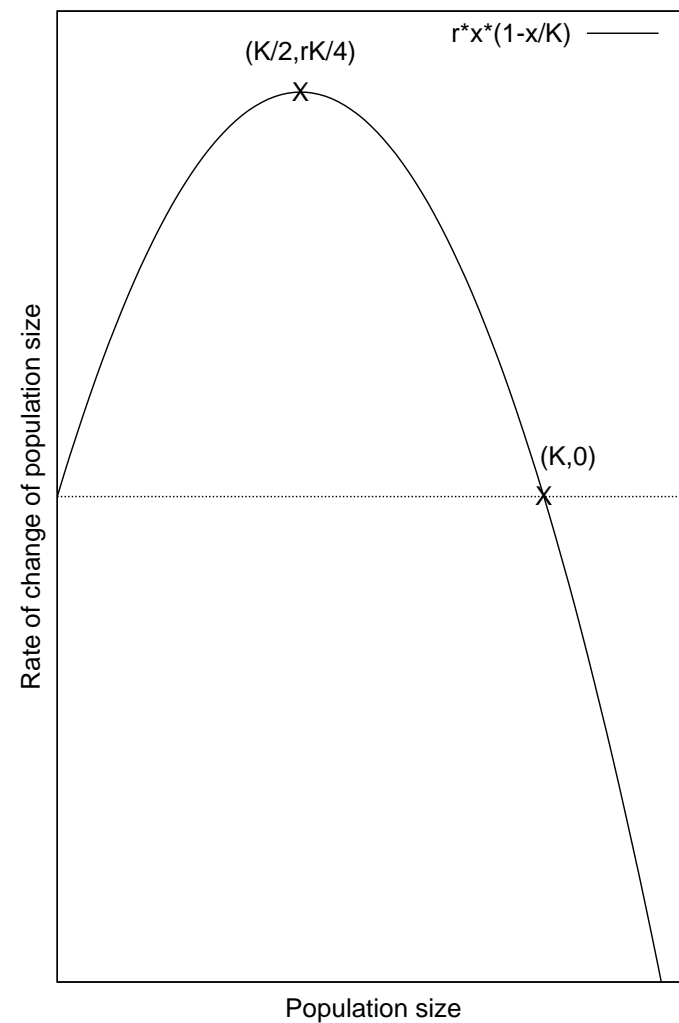


Figure 11.1: $y = rx(1 - x/K)$.

We can also use figure 11.1 to sketch how the solution of the logistic differential equation evolves with time.

Question 1.8 *Sketch the dynamic evolution of the logistic differential equation with*

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

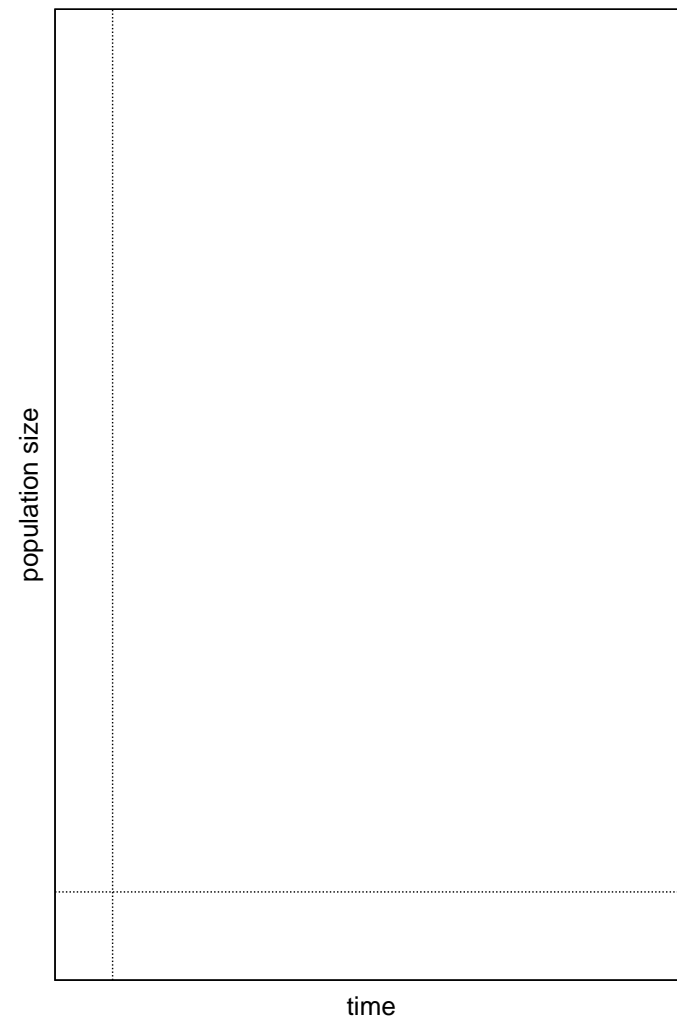


Figure 11.2: (a) $0 < x_0 < \frac{K}{2}$.

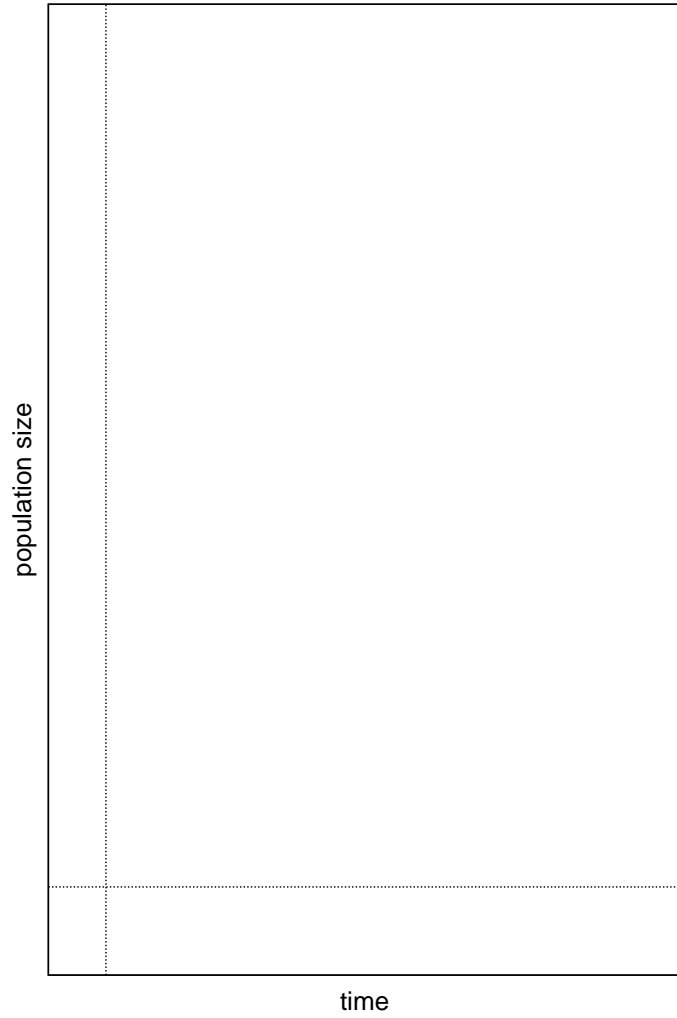


Figure 11.2: (b) $\frac{K}{2} < x_0 < K$.

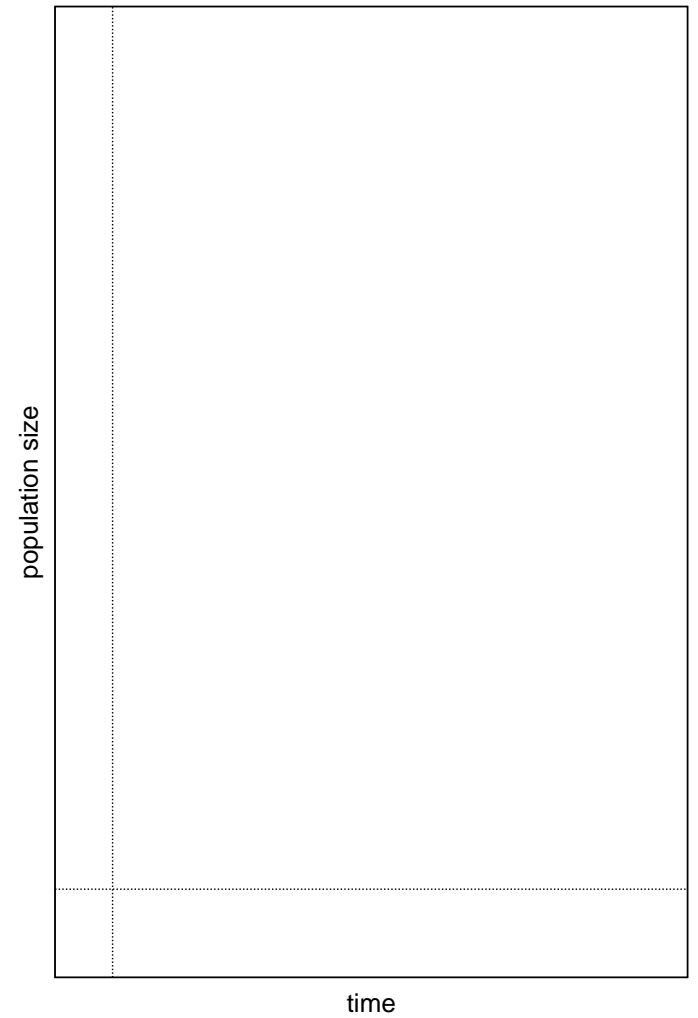


Figure 11.2: (c) $K < x_0$.

From figure 11.2 (a & b) we see that if $0 < x_0 < K$ then the solution is an increasing function of time with $x(t) \rightarrow K$ as $t \rightarrow \infty$.

From figure 11.2 (c) we see that if $K < x_0$ then the solution is a decreasing function of time with $x(t) \rightarrow K$ as $t \rightarrow \infty$.

Thus every solution with $x_0 > 0$ tends to K as $t \rightarrow \infty$, and we have obtained this information *without explicitly solving the differential equation*.

The above conclusions could have been obtained from the explicit solution (11.5). However, we can apply this *graphical technique* to problems that do NOT have explicit solutions.

1.6 Steady-state solutions

Points where

$$\frac{dx}{dt} = f(x) = 0 \quad (11.6)$$

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

Question 1.9

1. Why do you think steady-state's are called steady-state's?

Hint. Consider the problem

$$\frac{dx}{dt} = f(x), \quad x(t=0) = x^*,$$

where x^* is a steady-state of the function $f(x)$.

2. What does a steady-state represent biologically?

Question 1.10 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 1.11 *Gompertz (1825)* suggested the following form for the per-capita growth rate

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

Consider the associated population model

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

- (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. How do they differ from that of the logistic model?

1.7 Revision of key ideas

1.8 Concept map

Draw a concept map for this chapter relating the aims/key ideas of the chapter. If you are unfamiliar with the idea of a concept map see appendix A.