Chapter 5

Single species models

Learning outcomes

By the end of this chapter you should be able to:

- derive the exponential (Malthusian) population model from first principles;
- derive and solve the logistic model, including nondimensionalisation;
- find equilibrium points of autonomous ODEs and determine their stability using linearisation;
- analyse the effect of constant harvesting on a population model, including critical harvesting rates and bifurcation diagrams.

5.1 Introduction

In this part of the course we examine models that describe the behaviour of populations of a single species in terms of population size. In most cases the real population is measured in discrete units (it does not make much sense to have a third of a rabbit), but the equations we derive describe the behaviour in some average sense and we treat population size as a continuous variable. This is a subtlety worth bearing in mind when we construct mathematical models.

5.2 The exponential model

We discussed this simple model in the introductory chapter, now we will motivate it from first principles, for example consider a colony of rabbits with plenty of space and food. Rabbits do not migrate into or out of the colony and there are no predators.

Variables and parameters. Let $N(t)$ denote the number of rabbits at time t, measured in appropriate units (weeks or months). In a time interval $[t,\ t+h]$, the change in population is entirely due to births and deaths:

$$N(t+h) - N(t) = \text{births in } [t, t+h] - \text{deaths in } [t, t+h].$$

The **birth rate** β is the average number of births per unit time per member of the population. The **death rate** δ is defined analogously. In any time interval, the number of births or deaths is (on average)

$$\text{length of interval} \times \text{rate} \times \text{population size}.$$

Forming the model. With birth rate β and death rate δ, the change in population between times t and $t+h$ is

$$N(t+h) - N(t) = \beta\, N(t)\, h - \delta\, N(t)\, h = \alpha\, N(t)\, h,$$

where $\alpha := \beta - \delta$ is the **growth rate**. Dividing by h and taking the limit $h \to 0$ using the definition of the derivative gives the ODE

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \alpha\, N. \tag{5.1}$$

This is the **exponential** or **Malthusian** population model.[1]

Solving the model. As we saw earlier equation (5.1) is separable. For $N \neq 0$:

$$\int \frac{\mathrm{d}N}{N} = \int \alpha\, \mathrm{d}t \qquad \Longrightarrow \qquad \log N = \alpha t + C.$$

With the initial condition $N(0) = N_0$, we find $C = \log N_0$, giving

$$\boxed{N(t) = N_0\, e^{\alpha t}.} \tag{5.2}$$

The solution depends on two parameters: the growth rate α and the initial population N_0.

Example World population

The estimated world population in 1961 was 3.06×10^9 and the growth rate was estimated at 2% per annum. Using the exponential model, the predicted population in 2000 ($t = 39$) is

$$N(39) = 3.06 \times 10^9 \times e^{39 \times 0.02} \approx 6.67 \times 10^9.$$

This is a slight overestimate, the actual population reached 6 billion around 1999. The main reason is that the growth rate has not been constant; it has been falling since 1961, mainly due to more widespread use of birth control.

5.3 Variations on the exponential model

A more general exponential model is

$$\frac{\mathrm{d}N}{\mathrm{d}t} = (\beta(N,t) - \delta(N,t))\, N, \tag{5.3}$$

where β and δ can now be functions of population size and/or time. This allows us to model many interesting real-world phenomena that are not captured by constant birth/death coefficients.

5.3.1 Worked example: periodic growth

Consider the model

$$\frac{\mathrm{d}N}{\mathrm{d}t} = -\alpha \cos(\omega t)\, N, \qquad N(0) = N_0.$$

What could this model be used to describe? What are the maximum and minimum growth rates? What is the period of the growth rate? Solve the model using the initial condition $N(0) = N_0$. What are the minimum and maximum values of the population size?

[1] Named after Thomas Malthus (1766–1834), author of *An Essay on the Principle of Population* (1798).

What is the value of ω if we wish to model a seasonal phenomenon and t is measured in days?
A colony of wasps is reduced to size 250 in the depths of winter (when the growth rate of the colony is minimum), at what point in the year is the maximum growth rate? At what point in the year does the maximum population size occur? If the maximum growth rate of the colony is 1 per week, what is the maximum population size? [2]
Solution: The model could be used to describe a seasonal growth rate in a population. The minimum growth rate is $-\alpha$ and the maximum growth rate is α . The period of the growth rate is $T = 2\pi/\omega$. The differential equation is separable and the solution is:

$$\boxed{N(t) = N_0 \exp\left(-\frac{\alpha}{\omega}\sin\omega t\right).}$$

The population oscillates between a minimum of $N_0 e^{-\alpha/\omega}$ and a maximum of $N_0 e^{\alpha/\omega}$. For a yearly seasonal variation with t in days, $\omega = 2\pi/365 \approx 0.0172$ day^{-1}. If a colony of wasps is reduced to $N_0 = 250$ in the depths of winter (when the growth rate is minimum, at $t = 0$), the maximum growth rate occurs mid-year (June/July) and the maximum population size occurs in September/October (out of phase with the growth rate). If the maximum growth rate is $\alpha = 1/7$ day^{-1}, the peak population is

$$N_{\max} \approx 250\, e^{(1/7)/0.0172} \approx 10^6.$$

Exercise 5.1

Suppose the growth rate is

$$\alpha(t) = \alpha_0(1 - a\cos\omega t),$$

where $\alpha_0 > 0$, $a > 0$ and $\omega > 0$. Describe what this growth rate could represent, making explicit reference to the physical significance of α_0, a and ω. Solve the model in this case, using the initial condition $N(0) = N_0$. Sketch, on the same axes, the population size as a function of time in the cases $a = 0$, $0 < a < 1$ and $a > 1$.

5.4 The logistic model

The exponential model assumes unlimited resources. In reality, there is a maximum population size that the environment can support, the **carrying capacity** M. As the population approaches M, the growth rate must approach zero. The simplest way to model this is

$$\alpha(N) = \alpha\left(1 - \frac{N}{M}\right),$$

where α is the **linear growth rate** (the growth rate when $N \ll M$). This gives the **logistic model**:

$$\boxed{\frac{\mathrm{d}N}{\mathrm{d}t} = \alpha\left(1 - \frac{N}{M}\right)N,} \tag{5.4}$$

where $\alpha > 0$ and $M > 0$ are constants. This model was first studied by the Belgian mathematician Pierre François Verhulst in the mid-19th century.

Note two important limits:

[2] Note that this is a very crude model of wasp population. In particular it does not incorporate hibernation or the role of the queen wasp. You must always be prepared to evaluate any population model critically and be aware of its limitations.

- As $M \to \infty$ (for fixed N), the growth rate $\alpha(N) \to \alpha$, recovering the exponential model with infinite resources.
- For $N \ll M$, the growth rate is close to α, resources appear plentiful. The finiteness of resources only becomes noticeable when N is comparable to M.

Solving the logistic model. Rewrite (5.4) as $M\,\mathrm{d}N/\mathrm{d}t = \alpha(M-N)N$. The equilibrium solutions are $N(t) = 0$ and $N(t) = M$. For $N \neq 0, M$, separate variables and use partial fractions:

$$\int \frac{M\,\mathrm{d}N}{(M-N)N} = \int \alpha\,\mathrm{d}t \qquad \Longrightarrow \qquad \int \left(\frac{1}{N} + \frac{1}{M-N}\right)\mathrm{d}N = \alpha t + C.$$

Evaluating:

$$\log\left|\frac{N}{M-N}\right| = \alpha t + C.$$

Applying the initial condition $N(0) = N_0$ and noting that $N/(M-N)$ does not change sign along an orbit, we obtain

$$\boxed{N(t) = \frac{MN_0}{(M-N_0)\,e^{-\alpha t} + N_0}.} \tag{5.5}$$

This includes the equilibrium solutions ($N_0 = 0$ gives $N = 0$; $N_0 = M$ gives $N = M$). The solutions depend on three parameters: N_0, M and α. The resulting curves are called **logistic curves**.

Key idea

While the population is small relative to the carrying capacity, the actual growth rate is close to the base growth rate α. This can be used to estimate α from early-stage population data. As $t \to \infty$, all solutions with $0 < N_0 < M$ approach M; the population saturates at the carrying capacity.

Nondimensionalisation. The logistic model has four dimensional quantities: α (dimensions $[\mathrm{T}]^{-1}$), N and M (dimensions [N]), and t (dimensions [T]). The natural time scale is α^{-1} and the natural population scale is M. Define

$$\hat{t} = \alpha t, \qquad \hat{N} = \frac{N}{M}.$$

The equation becomes

$$\frac{\mathrm{d}\hat{N}}{\mathrm{d}\hat{t}} = \hat{N}(1-\hat{N}), \qquad \hat{N}(0) = \hat{N}_0 = \frac{N_0}{M}.$$

The only remaining parameter is $\hat{N}_0$, the initial population as a fraction of the carrying capacity. All logistic solutions are essentially the same, the only differences are in scale.

Example Protozoa population

A population of protozoa has an estimated growth rate of $\alpha = 2.31\ \mathrm{day}^{-1}$ and saturates at $M = 375$ cells after 6 days, starting from $N_0 = 5$. The logistic curve is

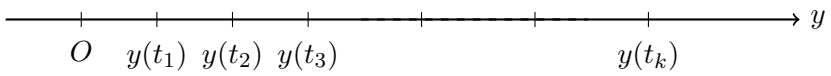
$$N(t) = \frac{375 \times 5}{(375-5)\,e^{-2.31t} + 5} = \frac{375}{74\,e^{-2.31t} + 1}.$$

5.5 Qualitative analysis of autonomous ODEs

In this section we will introduce some terms and ideas that are particularly useful when we move on to consider systems of differential equations that model populations of two or more species, or more generally systems of ODEs. Introducing these ideas in the simpler context of single species models will allow us to test the results against the previously obtained exact solutions. Consider a general autonomous first-order ODE

$$\frac{\mathrm{d}y}{\mathrm{d}t} = f(y). \tag{5.6}$$

The value $y(t)$ can be represented as a point on the real line, which we call the **phase space**. An **orbit** is the set of all points visited by the solution: $\{y(t) : t \in \mathbb{R}\}$.

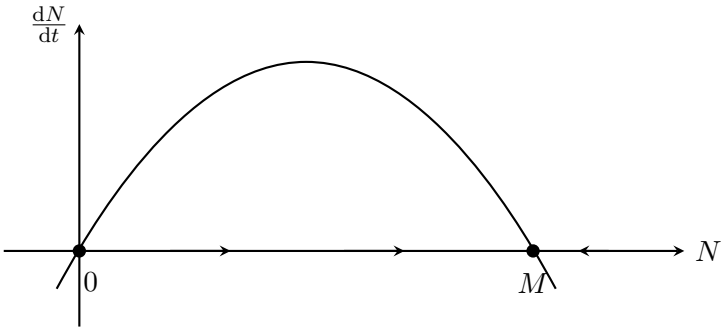


To determine the direction of motion along an orbit, note that for small $h > 0$:

- $\dot{y} > 0 \implies y(t+h) > y(t)$ (moves to the right);
- $\dot{y} = 0 \implies y(t+h) = y(t)$ (stationary);
- $\dot{y} < 0 \implies y(t+h) < y(t)$ (moves to the left).

The sign of $\dot{y}$ is determined directly from the ODE, since $\dot{y} = f(y)$.

Any point y_e where $f(y_e) = 0$ is called an **equilibrium point** (or fixed point), since a solution at y_e remains there for all time. The information about equilibrium points and the direction of orbits is displayed in a **phase portrait**: equilibrium points are marked by dots and arrows indicate the direction of motion.



The logistic model. For $\mathrm{d}N/\mathrm{d}t = \alpha(1 - N/M)N$, we have $f(N) > 0$ for $0 < N < M$ and $f(N) < 0$ for $N > M$. The equilibrium points are $N = 0$ and $N = M$. From the phase portrait:

Initial condition	Behaviour	Orbit
$N_0 = 0$	$N(t) = 0$ for all t	$\{0\}$
$0 < N_0 < M$	$N \to 0$ as $t \to -\infty$, $N \to M$ as $t \to \infty$	$(0, M)$
$N_0 = M$	$N(t) = M$ for all t	$\{M\}$
$N_0 > M$	$N \to \infty$ as $t \to -\infty$, $N \to M$ as $t \to \infty$	(M, ∞)

5.6 Stability and linearisation

For the general autonomous ODE (5.6), let y_e be an equilibrium point. We say y_e is:

- **stable** if all solutions starting close to y_e remain close for all t;
- **asymptotically stable** if all solutions starting close to y_e satisfy $y(t) \to y_e$ as $t \to \infty$;
- **unstable** otherwise.

For the logistic model, M is asymptotically stable and 0 is unstable.

Linearisation. Let y_e be an equilibrium point with $f(y_e) = 0$. Define the perturbation $\tilde{y} = y - y_e$. Taylor-expanding $f(y)$ about y_e:

$$f(y) = f(y_e) + (y - y_e)\, f'(y_e) + \tfrac{1}{2}(y - y_e)^2\, f''(y_e) + \cdots = f'(y_e)\, \tilde{y} + \text{h.o.t.}$$

Since $\mathrm{d}\tilde{y}/\mathrm{d}t = \mathrm{d}y/\mathrm{d}t$, for $\tilde{y}$ small we obtain the **linearisation** of (5.6) about y_e:

$$\frac{\mathrm{d}\tilde{y}}{\mathrm{d}t} = f'(y_e)\, \tilde{y}. \tag{5.7}$$

This is a linear ODE with solution $\tilde{y}(t) = \tilde{y}(0)\, e^{f'(y_e)\, t}$. Provided $f'(y_e) \neq 0$, the stability is determined entirely by the sign of $f'(y_e)$:

Key idea

Linearised stability criterion: For the autonomous ODE

$$\dot{y} = f(y)$$

with equilibrium point y_e:

$$f'(y_e) < 0 \implies y_e \text{ is asymptotically stable}, \quad f'(y_e) > 0 \implies y_e \text{ is unstable.}$$

If $f'(y_e) = 0$, the linearisation is inconclusive and higher-order terms must be retained.

Example Linearisation of the logistic model

For the logistic model, $f(N) = \alpha(1 - N/M)N$, so

$$f'(N) = \alpha\left(1 - \frac{2N}{M}\right).$$

At $N = 0$: $f'(0) = \alpha > 0$, so $N = 0$ is **unstable**. The linearisation is $\mathrm{d}\tilde{N}/\mathrm{d}t = \alpha\tilde{N}$. At $N = M$: $f'(M) = -\alpha < 0$, so $N = M$ is **asymptotically stable**. The linearisation is $\mathrm{d}\tilde{N}/\mathrm{d}t = -\alpha\tilde{N}$.

Exercise 5.2

Suppose a population evolves according to

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \alpha N\left(\frac{N}{m} - 1\right)\left(1 - \frac{N}{M}\right),$$

with $\alpha > 0$ and $0 < m < M$. Find all equilibrium points. Calculate $f'(N)$ at each equilibrium point and hence deduce the stability of each equilibrium point. Sketch the phase portrait and some representative solutions for different N_0.

5.7 Harvesting

To describe the effects of hunting, predation or migration out of a population, we add a **harvesting term**:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \alpha(N)\, N - H(N,t), \tag{5.8}$$

where $H(N,t)$ represents the number of members removed per unit time. Common choices include:

- $H = H_0$ (constant): a fixed number removed per unit time.
- $H = H_1 N$ (proportional): a fixed fraction of the population removed.
- $H = BN^2/(A^2 + N^2)$ (saturating): harvesting that "switches on" when N reaches A and saturates at rate B.

5.8 Worked example: constant harvesting

Example Shrimp harvesting

A shrimp population has unlimited resources, grows at 10% per month, and starts at $N_0 = 10^6$. How many shrimp may be caught each month without exhausting the population?
The model is

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \alpha N - H, \qquad N(0) = N_0,$$

with $\alpha = 0.1$ and H to be determined.
Method 1 — exact solution. This is separable:

$$\int \frac{\mathrm{d}N}{\alpha N - H} = \int \mathrm{d}t \qquad \Longrightarrow \qquad N(t) = \frac{H + (\alpha N_0 - H)\, e^{\alpha t}}{\alpha}.$$

For the population to survive ($N > 0$ for all t), we need $\alpha N_0 - H \geq 0$, giving a maximum harvesting rate of $H = \alpha N_0 = 100{,}000$ per month.
Method 2 — phase portrait. The equilibrium point is $N = H/\alpha$, which is unstable. The population survives only if $N_0 \geq H/\alpha$, giving the same answer. This method is preferred because it adapts easily to other models.

5.9 Constant harvesting of the logistic model

Consider the logistic model with constant harvesting:

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \alpha\left(1 - \frac{N}{M}\right)N - H, \qquad H \geq 0. \tag{5.9}$$

The equilibrium points are the roots of $N^2 - MN + MH/\alpha = 0$, which has discriminant $\Delta = M^2 - 4MH/\alpha$. Three cases arise:

Moderate harvesting ($H < M\alpha/4$). Two equilibrium points exist:

$$E_\pm = \frac{M \pm \sqrt{M^2 - 4MH/\alpha}}{2}.$$

From the phase portrait, E_+ is asymptotically stable and E_- is unstable. For all $N_0 > E_-$, the population approaches E_+. If $N_0 < E_-$, the population goes extinct.

Critical harvesting ($H = M\alpha/4$). There is a single equilibrium at $E = M/2$. This is a borderline case and conclusions drawn from it are unreliable since the model is itself an approximation.

Excessive harvesting ($H > M\alpha/4$). No equilibrium points exist. For all initial populations, $N(t) \to 0$, the population goes extinct.

Key idea

The **critical harvesting rate** is $H_c = M\alpha/4$. If the harvesting rate exceeds this value, the population will inevitably go extinct regardless of the initial population size. More generally, for an autonomous model $\dot{N} = f(N) - H$, the critical rate is $H_c = \max_{N \geq 0} f(N)$.

Example Deer herd

A forest supports a herd of $M = 500$ deer with linear growth rate $\alpha = 0.2$ year^{-1}. The logistic model with harvesting is

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \frac{1}{5}\left(1 - \frac{N}{500}\right)N - H.$$

The equilibrium equation is $N^2 - 500N + 2500H = 0$ with $\Delta = 10000(25 - H)$.
(a) The maximum sustainable hunting rate is $H_c = M\alpha/4 = 25$ deer per year.
(b) To maintain the herd at $E_+ = 300$, we need $300 = 250 + 50\sqrt{25 - H}$, giving $\sqrt{25 - H} = 1$, so $H = 24$ deer per year. The minimum initial herd size is $N_0 > E_- = 250 - 50\sqrt{25 - 24} = 200$.
(c) With $H = 24$: $E_- = 200$ (unstable) and $E_+ = 300$ (stable). Populations starting above 200 converge to 300; populations starting below 200 go extinct.

5.10 Critical harvesting for general models

For a general autonomous model with constant harvesting,

$$\frac{\mathrm{d}N}{\mathrm{d}t} = f(N) - H, \tag{5.10}$$

if $f(N) - H < 0$ for all $N \geq 0$ then every population goes extinct. The **critical harvesting rate** is

$$H_c = \max_{N \geq 0} f(N).$$

Example Critical harvesting rate

For the model

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \alpha(N - m)\left(1 - \frac{N}{M}\right) - H,$$

with $0 < m < M$ and $\alpha > 0$, let $f(N) = \alpha(N - m)(1 - N/M)$. Then

$$f'(N) = \frac{\alpha}{M}(M + m - 2N),$$

which vanishes at $N^* = (M + m)/2$. The critical harvesting rate is

$$H_c = f(N^*) = \frac{\alpha}{4M}(M - m)^2.$$

5.11 Bifurcation diagrams

A **bifurcation diagram** displays the location and stability of equilibrium points as a function of a parameter. For the logistic model with constant harvesting, nondimensionalise by writing $N = Mn$ and $t = \tau/\alpha$:

$$\frac{\mathrm{d}n}{\mathrm{d}\tau} = n(1 - n) - h, \qquad h = \frac{H}{M\alpha}.$$

The single dimensionless parameter h controls the behaviour. The equilibrium points satisfy $n(1 - n) = h$, giving

$$n_\pm = \frac{1 \pm \sqrt{1 - 4h}}{2}.$$

The bifurcation diagram plots $n_\pm$ against h. For $h < 1/4$ there are two equilibria (n_+ stable, n_- unstable). At $h = 1/4$ they coalesce, this is a **saddle-node bifurcation**. For $h > 1/4$ there are no equilibria and all populations go extinct.

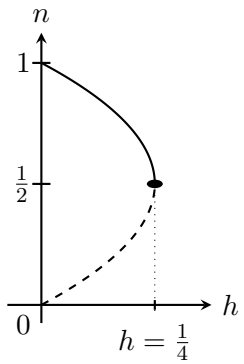


Figure 5.1: A simple bifurcation diagram for the logistic model with constant harvesting. The locations of the two equilibrium points are plotted against the parameter h. A solid line denotes a stable equilibrium; a dashed line denotes an unstable one. The critical harvesting rate $h = 1/4$ is marked, there are no equilibrium points beyond this point.

Key idea

The bifurcation diagram encodes, in a single picture, how the qualitative behaviour of the system changes as a parameter varies. The critical value $h = 1/4$ (equivalently $H = M\alpha/4$) marks a qualitative transition: below it the population can survive; above it, extinction is inevitable.

Exercise 5.3

A bacterial colony grows according to the exponential model with $\alpha = 0.5\ \text{hr}^{-1}$ and $N_0 = 100$.

(a) Find $N(t)$ and compute the population after 6 hours.

(b) At what time does the population reach 10^6?

(c) Explain why this model must eventually fail.

Exercise 5.4

A fish population obeys the logistic model with $\alpha = 0.4\ \text{year}^{-1}$ and $M = 10000$.

(a) Find the general solution $N(t)$ for initial condition $N(0) = N_0$.

(b) Nondimensionalise the equation and identify the single remaining parameter.

(c) What is the maximum sustainable constant harvesting rate?

(d) If 800 fish per year are harvested, find the equilibrium population sizes and their stability. What is the minimum initial population for the species to survive?

Exercise 5.5

Consider the autonomous ODE

$$\frac{\mathrm{d}N}{\mathrm{d}t} = N(1-N)(N-a), \qquad 0 < a < 1.$$

(a) Find all equilibrium points.

(b) Compute $f'(N)$ at each equilibrium point and determine the stability.

(c) Sketch the phase portrait.

(d) Describe in words how the population behaves for different ranges of N_0.

(e) What ecological phenomenon does the parameter a represent?