MATH3565 - Mathematical Biology

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2024

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Part I

Dynamics of a single population

Chapter 1

Exponential growth

1.1 Exponential growth

Suppose we have one variable, $N(t)$, that represents the size of a population as a function of time. We can describe how $N(t)$ changes with time by means of an ordinary differential equation (ODE) of the form

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \text{“birth”} - \text{“death”}. \tag{1.1}$$

One of the first people to try this was Robert Malthus, about 1798, who considered the world's human population with the ODE

$$\frac{\mathrm{d}N(t)}{\mathrm{d}t} = bN(t) - dN(t) = (b-d)N(t), \tag{1.2}$$

where b and d are positive constants. The solution of the equation is

$$N(t) = N(0)\mathrm{e}^{(b-d)t}. \tag{1.3}$$

The population will grow exponentially, if $b > d$, or decrease exponentially, if $b < d$.

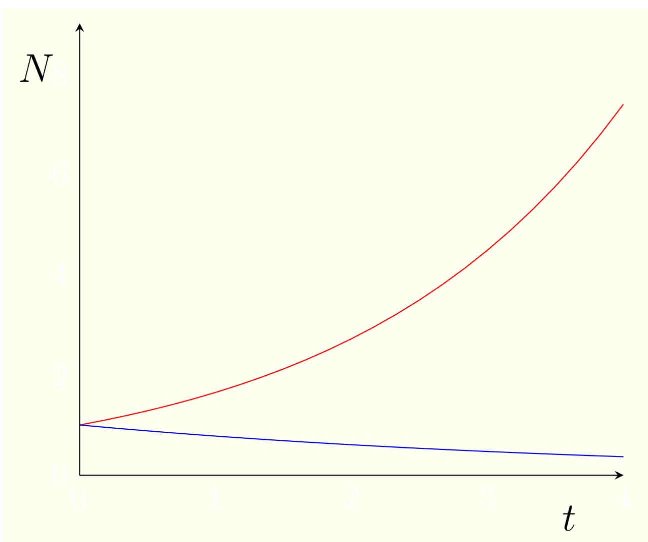

Figure 1.1: Population increasing exponentially (red).
Population decreasing exponentially (blue).

In the nineteenth century, based on simple ideas of this type, some people concluded that high birth rates in a population would inevitably cause a huge increase in population followed by catastrophic famine. The model is too simple to draw accurate conclusions about real populations, but the concept of exponential growth (or decay) is important.

1.2 Dimensions

We use (1.2) to introduce the idea of dimensions. Two quantities have the same dimensions if they could be measured in the same units. For example, the average age of students taking this course and the time it takes to walk from my office to the lecture theatre are two quantities with the same dimensions. They are both times; we say they have dimensions T. We could choose to measure both quantities in units of seconds (although we usually wouldn't). On the other hand, the distance from my office to the lecture theatre has dimensions L; we may choose to measure it in metres or miles, but not in seconds.

We start by writing

$$\left[\frac{\mathrm{d}N}{\mathrm{d}t}\right] = \text{ dimensions of } \frac{\mathrm{d}N}{\mathrm{d}t} = [N]T^{-1}.$$

When you see square brackets, read it as "the dimensions of". Thus, $[N]$ means "the dimensions of N". In a correct equation:

- the dimensions of the left-hand and right-hand side are equal,
- all the quantities in a sum have the same dimensions,
- and the dimensions of a product is the product of the dimensions of each factor.

Looking at (1.2), we write

$$[N]T^{-1} = [b][N] = [d][N].$$

Thus we conclude that

$$[b] = [d] = T^{-1}. \tag{1.4}$$

The dimensions of the rates, b and d, are "inverse time" because, if we want to specify their values we need to use a unit: for example per day or per year (I write this as day^{-1} or year^{-1}).

In many situations, a quantity is just a number (a number of people, or the ratio of the circumference of a circle to its radius, for example). Then, we don't need to introduce a unit. A number is considered to be "dimensionless", which is written as:

$$[N] = 1.$$

If $N(t)$ is a density or weight of some quantity, it will not be dimensionless, but that will not change (1.4).

The first part of what is called dimensional analysis is to make sure that both sides of an equation have the same dimensions. We *cannot* postulate, for example, that

$$\text{“ number of cells in an experiment } = \text{ average lifetime of a cell ''},$$

because the LHS and RHS have different dimensions: $1 \neq T$. On the other hand, we may write

$$\text{number of cells in an experiment } = \text{ rate of cell division } \times \text{ average lifetime of a cell },$$

because $1 = T^{-1} \times T$. This does not prove that the equation is a correct description of reality, but at least it makes sense. Dimensional analysis is a sort of mathematical modelling grammar.

The arguments of functions, such as the exponential and sine functions, are always dimensionless. Therefore, in this course you will see expressions like $\exp(rt)$ and $\sin(kx)$, where $[r] = 1/T$ and $[k] = 1/L$, but not simply $\exp(t)$ or $\sin(x)$.

1.3 Doubling time

If $b > d$ then we can consider the doubling time of the population. It is denoted by τ and satisfies

$$N(t+\tau) = 2N(t). \tag{1.5}$$

We use the solution (1.3):

$$\begin{aligned} N(0)\mathrm{e}^{(b-d)(t+\tau)} &= 2N(0)\mathrm{e}^{(b-d)t} \\ \mathrm{e}^{(b-d)\tau} &= 2 \\ \tau &= \frac{\log 2}{b-d}. \end{aligned}$$

(Notice that t drops out because the growth is exponential.)

Now $\log 2$ is just a number, so $[\log 2] = 1$ and $[\tau] = [\frac{1}{b-d}] = T$.

That is, τ is indeed a time; it will have units of years if b and d have units of year^{-1}. On the other hand, if $b < d$ then we can describe the decay of the population by calculating a "half life".

1.4 Immigration

In 21st century rich countries, there are more deaths than births per year. In such a scenario, the population can be maintained by immigration. Suppose that immigrants arrive at rate γ. Then

$$\frac{\mathrm{d}N(t)}{\mathrm{d}t} = -(d-b)N(t) + \gamma,$$

with $d > b$. The solution is

$$N(t) = \frac{\gamma}{d-b}(1 - \mathrm{e}^{-(d-b)t}) + N(0)\mathrm{e}^{-(d-b)t}.$$

As $t \to \infty$, $N \to \frac{\gamma}{d-b}$. So, assuming that $d-b$ and γ are constant, we say that the population approaches a "steady state".

Chapter 2

Dynamics of a single population

2.1 Logistic growth

In 1838, Verhulst proposed a model where the population grows in a way that seems exponential for a time, but cannot exceed a maximum value, or "carrying capacity", K. The ODE is

$$\frac{\mathrm{d}N(t)}{\mathrm{d}t} = rN(t)\left(1 - \frac{N(t)}{K}\right). \tag{2.1}$$

The constant r can be thought of as the difference $b - d$, and we assume it is positive, but the constant K has no equivalent in (1.2). Let's begin by looking at dimensions. We need

$$\left[\frac{\mathrm{d}N}{\mathrm{d}t}\right] = [rN] = \left[\frac{r}{K}N^2\right].$$

Thus, $[r] = T^{-1}$, as we would expect. To balance the dimensions, we need the dimensions of K to be the same as those of N. If $[N] = 1$ then $[K] = 1$. That is, K is a number of individuals.

We can solve (2.1), using separation of variables and assuming that $0 < N(t) < K$:

$$\begin{aligned}
\int \frac{\mathrm{d}N}{N(1-\frac{N}{K})} &= \int r\mathrm{d}t \\
\int \frac{1}{N}\mathrm{d}N + \int \frac{1}{K-N}\mathrm{d}N &= \int r\mathrm{d}t \\
\log N - \log(K-N) &= rt + c \\
\log\frac{N}{K-N} &= rt + c.
\end{aligned}$$

To find c, we set $t = 0$:

$$e^c = \frac{N(0)}{K - N(0)}.$$

Now we can write the solution

$$\begin{aligned}
N(t) &= \frac{K\mathrm{e}^{rt}\mathrm{e}^c}{1 + \mathrm{e}^{rt}\mathrm{e}^c} && (2.2) \\
&= \frac{KN(0)\mathrm{e}^{rt}}{K - N(0) + N(0)\mathrm{e}^{rt}}. && (2.3)
\end{aligned}$$

The solution (2.3) is plotted in Figure 2.1, for different values of $N(0)$. The value K is shown as a dotted line. As $t \to \infty$, $N(t) \to K$, for any initial value $N(0) > 0$.

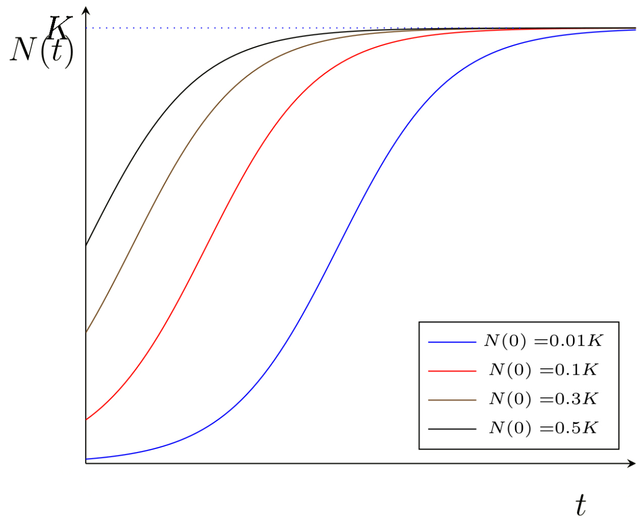

Figure 2.1: Solutions of the logistic growth model (2.1). Given any $N(0) > 0$, we find that $N(t) \to K$ as $t \to \infty$.

2.2 General models for a single population

Many different models of populations have been proposed, where the RHS of (2.1) is replaced by something more complicated. Whether or not we can find an explicit solution of the ODE, we can deduce important features of the dynamics by writing the ODE as

$$\frac{\mathrm{d}N(t)}{\mathrm{d}t} = f(N(t)), \tag{2.4}$$

and plotting $f(N)$ as a function of N.

Because the rate of change of N depends on N itself, but not on time (that is, we have a function $f(N(t))$ and not $f(t, N(t))$), the set of possible trajectories can be easily classified. Either $N(t)$ always increases, or $N(t)$ always decreases, or $N(t)$ remains constant, as a function of time. Which one is found depends on the shape of the function N and on the initial condition $N(0)$. Another restriction is common in mathematical biology: N represents a population, so it cannot be less than 0. Therefore, $f(0) \geq 0$.

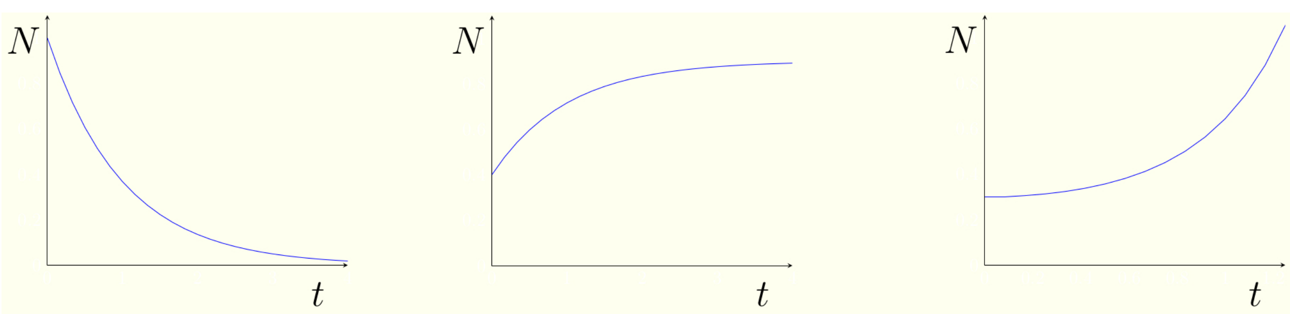

Figure 2.2: Possible trajectories for $N(t)$.

If the population obeys a single ODE like (2.4), then we may have behaviour like in Figure 2.2, but trajectories in Figure 2.3 are not possible. Since $N(t)$ is non-negative and real, we can imagine that it moves along a single axis.

- if $f(N) > 0$, N increases (moves to the right);
- if $f(N) < 0$, N decreases (moves to the left).

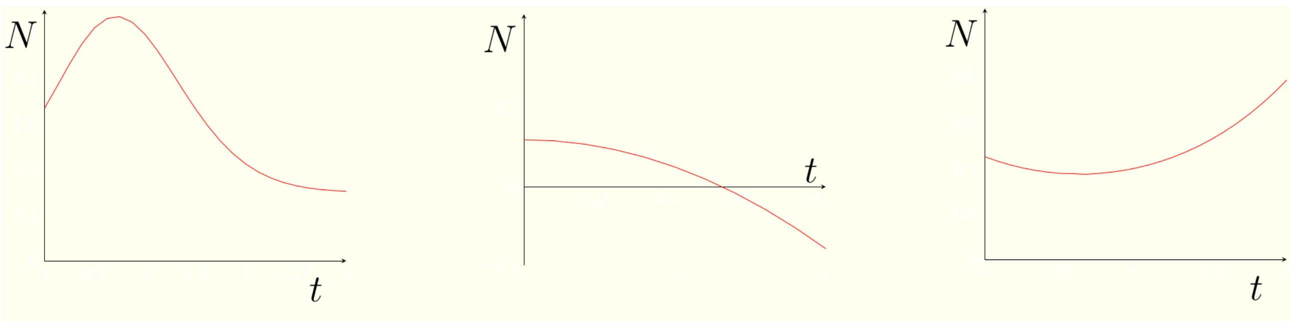

Figure 2.3: Impossible trajectories for $N(t)$.

For the logistic equation (2.1), $f(N) = rN(1 - \frac{N}{K})$, we plot the function (versus N) in Figure 2.4. Thus, if we choose $N(0)$ between 0 and K, then $f(N(0)) > 0$ and we deduce that $N(t)$ moves to the right, towards K. Interestingly, for a small initial population ($N(0) \approx 1$), the rate of growth is slow at the beginning, increasing until it reaches a peak, and then decreasing again as $N(t)$ approaches K.

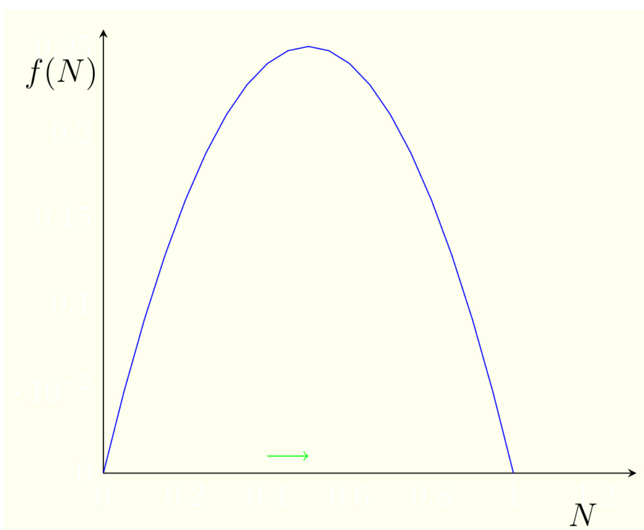

Figure 2.4: $f(N)$ as a function of N.

2.3 Steady states and their stability: single population

Special values of N are those where $f(N)$ is actually equal to 0. We say there is a steady state at $N = N^*$ if $f(N^*) = 0$. Usually, there is more than one such N^*.

We note that $f(N^*) = 0$ means that, if a population starts at size N^*, it will stay at size N^*. But, what if the population starts close to N^*? Roughly speaking, we say that the steady state N^* is "stable" if after a small perturbation in the system (i.e., it moves from N^* somewhere very close), the population goes back to N^*. On the other hand, we say that the steady state is "unstable" if after a small perturbation, the system moves away from the steady state. Graphically, we can see that:

- If $f'(N^*) > 0$, then the steady state at N^* is unstable; we are in the situation shown in Figure 2.5. In this situation, if $N(0)$ is slightly larger than N^* then $f(N(0)) > 0$. The population increases, taking it further away from N^*. If $N(0)$ is slightly smaller than N^* then $f(N(0)) < 0$. The population decreases, taking it further away from N^*.

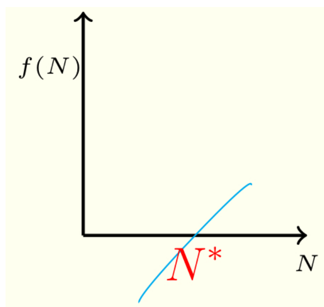

Figure 2.5: The steady state N^* is unstable because $f'(N^*) > 0$.

- If $f'(N^*) < 0$, then the steady state at N^* is stable; we are in the situation shown in Figure 2.6. In this situation, if $N(0)$ is slightly larger than N^* then $f(N(0)) < 0$. The population decreases, taking it closer N^*. If $N(0)$ is slightly smaller than N^* then $f(N(0)) > 0$. The population increases, taking it closer to N^*.

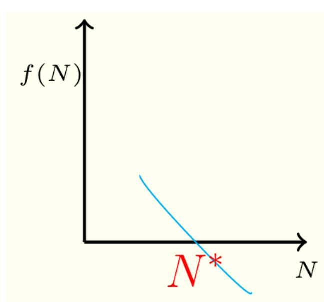

Figure 2.6: The steady state N^* is stable because $f'(N^*) < 0$.

This can also be proven analytically by expanding $f(N)$ in a Taylor series about N^*:

$$\begin{aligned} f(N) &= f(N^*) + f'(N^*)(N - N^*) + \frac{1}{2}f''(N^*)(N - N^*)^2 + \cdots \\ &= f'(N^*)(N - N^*) + \frac{1}{2}f''(N^*)(N - N^*)^2 + \cdots . \end{aligned}$$

If we define $U(t) = N(t) - N^*$, we note that $\frac{dU(t)}{dt} = \frac{dN(t)}{dt} = f(N)$ and

$$\frac{\mathrm{d}U}{\mathrm{d}t} = f'(N^*)U + \frac{1}{2}f''(N^*)U^2 + \cdots .$$

For small values of $U(t)$ (remember, we start somewhere near the steady state), $U(t) \propto \exp(f'(N^*)t)$. That is, the difference between the population size and its steady-state value increases or decreases (depending on the sign of $f'(N^*)$), exponentially. The exponent is the value of the derivative of f evaluated at N^*.

Extra: See the video for an explanation by Prof Lythe on this matter
`https://web.microsoftstream.com/video/9dc03972-823a-40e4-abdc-a758f814a055`

2.4 Harvesting

Imagine that a population (this time a good example would be a population of fish) obeys the logistic equation. Now imagine that we want to harvest some of the population (in this case, catch some fish). What is the optimal rate of harvesting and how does harvesting affect the population?

We include harvesting in the model by modifying (2.1) to

$$\frac{\mathrm{d}N(t)}{\mathrm{d}t} = rN(t)\left(1 - \frac{N(t)}{K}\right) - \alpha N(t) \;=\; rN(t)\left(1 - \frac{\alpha}{r} - \frac{N(t)}{K}\right). \tag{2.5}$$

The extra, harvesting, term is $-\alpha N$. (That is, the number of fish caught at any time is proportional to the number that are there.) Notice that $[\alpha] = T^{-1}$.

Let's look at $f(N)$, using (2.5). Two cases are shown below, one where $\alpha < r$ and one where $\alpha > r$.

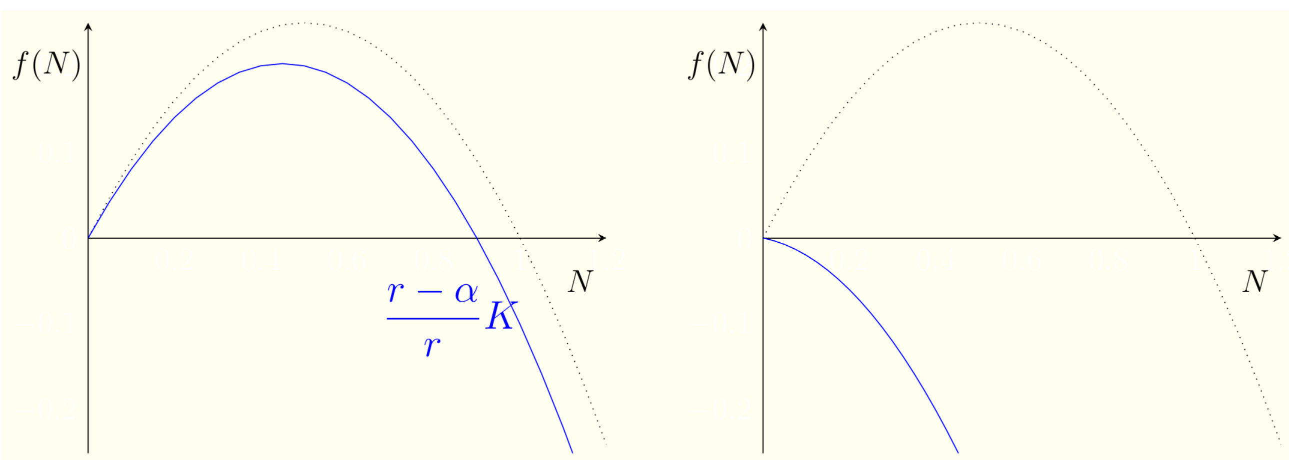

Figure 2.7: The function $f(N)$, according to (2.5), for two values of α. **Left.** $\alpha = 0.1r$. **Right.** $\alpha = 1.1r$.

- If $\alpha > r$ then $f(N) < 0$ and the population size always decreases. In the long run there are no fish! We can say that overfishing causes extinction.
- If $\alpha < r$ then there is a stable steady state. The size of the population in the long-term reaches $N^* = \frac{r-\alpha}{r}K$, which means that the steady-state rate of harvesting is

$$\alpha N^* = \alpha \frac{r-\alpha}{r} K.$$

What is the optimum value of α (if we want to sustainably catch as many fish as possible)? Let us define the steady-state rate of harvesting as a function of α:

$$h(\alpha) = \alpha \frac{r - \alpha}{r} K.$$

To find the maximum, take $h'(\alpha) = K - \frac{2K}{r}\alpha$. We conclude that the optimum value of alpha is $\alpha_{\max} = \frac{r}{2}$; see Figure 2.8.

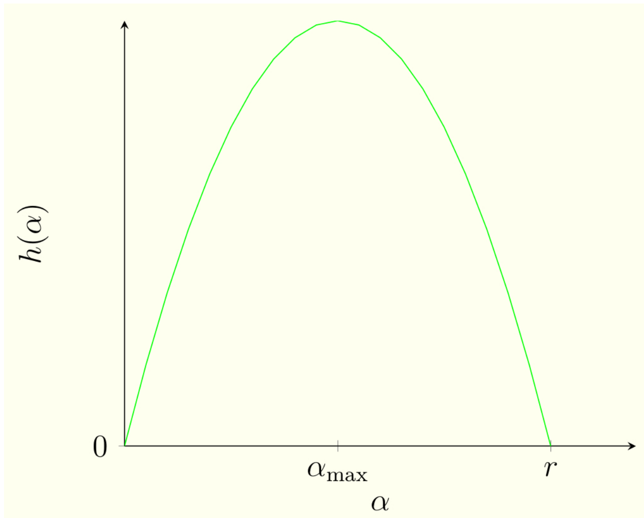

Figure 2.8: The value $\alpha_{max} = \frac{r}{2}$ maximises the steady-state rate of harvesting, $h(\alpha)$.

Does this all make sense? What is α? We know that α and r are rates with dimensions T^{-1}. The way to sustainably harvest the maximum from the population (to catch the most fish you can without driving the population to extinction) is to choose α to be half of r. In that case, the steady state size of the fish population will be half as big as if there were no fishing at all.

Extra: See the video for an explanation by Prof Lythe on this matter
`https://web.microsoftstream.com/video/c38bb76c-4928-4ea6-b844-d0dc30aa2f8b`