Lecture 1
Single species population models

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Population ecology is the study of how populations of plants, animals, or any other organisms change over time and space and interact with each other and their environment. Populations are groups of organisms of the same species living in the same area at the same time. They are described by characteristics that include: size, density, growth and death rates.

The study of this science can help predict how a population will change due to changing conditions. This knowledge informs other disciplines such a biodiversity studies, or even climate change as a result of changes in human population.

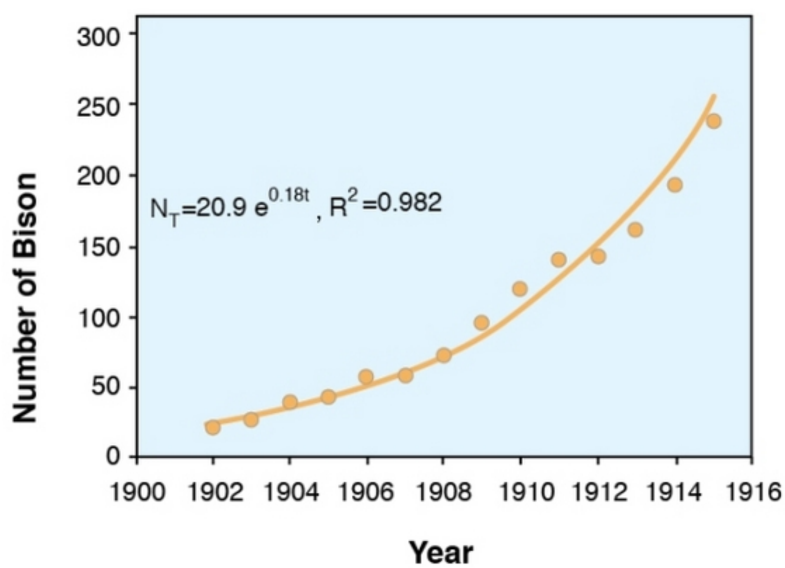


Figure 1: The American bison population in northern Yellowstone National Park grew exponentially between 1902 and 1915. After being driven nearly to extinction in the 1800s, the population began growing again due to conservation efforts implemented by governments and private landowners in the early 1900s. Image credit: Snider, & Brimlow, "*An Introduction to Population Growth*". Nature Education Knowledge **4**, 3 (2013)

1 Single species population models

These models are based on the idea

$$\text{rate of change of population} \quad = \quad \text{rate of birth (B)} \quad + \quad \text{rate of death (D)}.$$

Let

$$N(t) \;=\; \text{the population at time } t,$$

we can expect that, in general, the **birth rates**, B, and **death rates**, D, are functions of N (more $N \Rightarrow$ more breeding individuals and $\Rightarrow$ more competition for resources) and t (e.g. seasonal effects). The general equation for population growth of a single species is

$$\frac{dN}{dt} = B(N,t) \ - \ D(N,t)\,, \qquad \text{or} \qquad \frac{dN}{dt} = f(N,t),$$

where $f(N,t) = B(N,t) - D(N,t)$. **Throughout this module, we will neglect explicit temporal dependence of birth and death rates**, and therefore for this Section assume $f(N,t) = f(N)$, i.e. the growth rate is only dependent on the current population, hence we will be considering ODEs of the form

$$\boxed{\frac{dN}{dt} \ = \ f(N)\,.} \tag{1}$$

Very Big Note 1.1A: $N(t)$ **is a physical quantity** and is therefore **non-negative** ($N \geq 0$). This will be assumed throughout the section and module.

Figure 1 shows real-world data of the American bison population in the early XX century growing after centuries of hunting. The data show a clear trend that can be fit with a simple exponential function of time. In the next section we will develop and study a model that can describe these dynamics.

2 The simplest model

The most famous early example of population modelling is due to Malthus (1789), who assumed that the rates of birth, $B(N)$, and death, $D(N)$, are simply $\propto N(t)$, i.e. i.e. $B(N) = bN$ and $D(N) = dN$, where b and d are constants, hence

$$\frac{dN}{dt} = bN - dN = (b-d)N \Rightarrow N(t) = N_0 e^{(b-d)t}\,, \tag{2}$$

where N_0 is the **initial population at** $t = 0$, i.e. $N(0) = N_0$. Some remarks:

- $b > d \;\Rightarrow\;$ exponential population growth

  $b < d \;\Rightarrow\;$ exponential decay (i.e. eventual extinction).
- For $b > d$ the **population doubles in time** $\frac{\ln 2}{b-d}$ (exercise!).
- Malthus predicted that population growth will far out pace advancements in food production; representing his thoughts graphically,
- Malthus's solution:

  he proposed restricting the family sizes of the lower classes! This partly inspired Darwin towards his theory of evolution:
- Malthus's work partly inspired Darwin towards his theory of evolution:

  Limited Resources $\Rightarrow$ Competition
  $\Rightarrow$ Survival of the fittest.

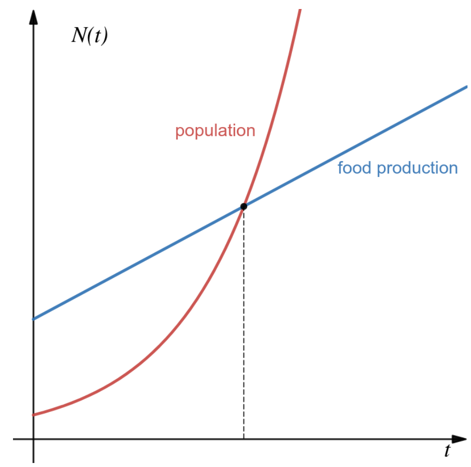


Figure 2: Sketch of the Malthusian exponential growth of a population, and linear growth of food production. Beyond the intersection point, famine and war (*Malthusian catastophe*) are predicted in this simplistic model.

Critique of this model. This model is ok if there are **lots of resources or if the population is small**, but in most situations in biology/ecology it rapidly becomes inaccurate. Populations do not continuously grow, limitations in food availability, physical space etc. will ultimately have an impact and restrict growth. We need a new model to that provides a better description in most cases.

- The model is ok if there are lots of resources or if the population is small.
- When $b > d$ the population will grow exponentially for all time – not likely.

This model is too simplistic for real problems, populations can never grow continuously, being limited by food availability, physical space etc.

3 The logistic model

This better, frequently used model was proposed by Verhulst in 1836. The variable $N(t)$ can be considered the population numbers, but it is usual to take $N(t)$ as being the "**population density**" (e.g. population/area). The model assumes:

- $B(N) = b\,N$, as with Malthus

- $D(N) = d\,N + c\,N^2$,

where the term $\propto d$ represents the "natural death rate", and the term $\propto c$ represents the death rate due to resource limitations (which is proportional to the rate of physical contacts between two individuals). Hence,

$$\frac{dN}{dt} \;=\; B(N) - D(N) \;=\; bN \,-\, dN \,-\, cN^2 \;=\; (b-d)N \,-\, cN^2. \tag{3}$$

In Eq. (3), **it is assumed that** $b - d > 0$ (otherwise extinction is guaranteed). To write this equation in its "usual" form, we let $r = b - d$ and $K = (b-d)/c = r/c$ so that

$$\frac{dN}{dt} \;=\; rN\left(1 - \frac{N}{K}\right). \tag{4}$$

This is called the **logistic ordinary differential equation** (or simply "the logistic equation").

The term r is called the **intrinsic growth rate** and has units of $(\text{time})^{-1}$. We note that when N is small (neglect N^2 term), then $\frac{dN}{dt} \approx rN \;\Rightarrow\; N \approx N_0 e^{rt}$ (as with Malthus's model).

The constant $K > 0$ is called the **carrying capacity** and has the same units as $N(t)$ (typically it is a population density). If $N = K$ then $\frac{dN}{dt} = 0$, so the population will remain at $N = K$. K represents the maximum population density that the resources/environment can accommodate.

Very Big Note 1.3A: The logistic equation is and only is an ODE of the form

$$\frac{dN}{dt} \;=\; \alpha N - \beta N^2.$$

where $\alpha > 0$ and $\beta > 0$ are constants. No other form of an ODE is logistic.

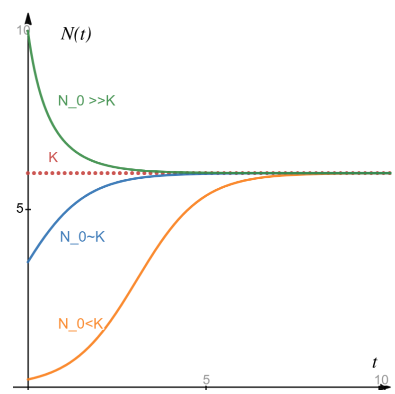


Figure 3: Sketch of the solutions of the logistic model for different initial values of N_0 compared to K.

The logistic equation can be solved (separation of variables, exercise!) to give

$$N(t) \;=\; \frac{N_0 K\, e^{rt}}{K + N_0(e^{rt} - 1)}. \tag{5}$$

using $N(0) = N_0$. Plotting N against t (see **Maple file M1.1** on Learn).

Note 1.3B: For any $N_0 > 0$, $N \to K$ as $t \to \infty$.

3.1 Steady-states and their stability

Definition 3.1. Any value N^* satisfying $f(N^*) = 0$, so that $\frac{dN}{dt} = 0$ at $N = N^*$, is called a **steady-state**. For the logistic equation $f(N^*) = rN^*(1 - N^*/K) = 0 \Rightarrow N^* = 0$ and $N^* = K$ are steady-states. These are very important in determining how N will behave as $t \to \infty$.

See now Appendix A.

Using the ideas of App. A on the Logistic equation:

Clearly see that $N \to K$ for any $N(0) = N_0 > 0$, so $N^* = K$ is a stable steady-state. Note also from the diagram that inside the parabola $f'(0) > 0$, whereas outside $f'(K) < 0$.

Linear stability analysis. Let $f(N) = rN(1 - N/K)$, we have

$$f'(N) = r - \frac{2rN}{K}$$

and for each of the 2 steady states we have

- $N^* = 0$: $f'(0) = r > 0 \;\Rightarrow\; N^* = 0$ is **unstable**.
- $N^* = K$: $f'(K) = r(1 - 2K/K) = -r \;\Rightarrow\; N^* = K$ is **stable**.

Both analyses are in agreement and expect $N \to K$ as $t \to \infty$.

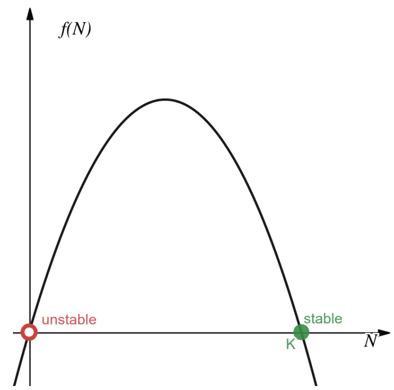


Figure 4: Sketch of the solutions of the logistic model for different initial values of N_0 compared to K.

4 Dimensionality and non-dimensionalisation

A **dimension** is the description of the fundamental attribute by which a quantity is measured, that is, length, time, mass, charge, mole of substance, temperature, light intensity. For example, for the logistic ODE

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right), \quad \text{with} \quad N(0) = N_0,$$

the dimension of N is "population density", t is "time"; the parameters r has units of time^{-1}, and K and N_0 = population density. In contrast, **units** describes specifically what a quantity is measured by, e.g. for "time" it could be seconds, months, years etc. and "population density" could be pop/ml=pop/cm^3, pop/km^2 etc.

for any equation (ODEs, PDEs etc.) to make sense, **the dimension/units on either side of the "=", "+" and "–" symbols must be the same**.

Denoting $[A]$ for the "dimension of A" then

- N/K must have same dimension as 1 (dimensionless) which means $[K] = [N]$.
- $\dfrac{dN}{dt}$ has dimension $[N]/[t]$ meaning that $[r][N] = [N]/[t] \Rightarrow [r] = 1/[t]$.
- From $N_0 = N(0)$, it is clear that $[N_0] = [N]$.

Quantities with different dimension or units cannot be compared; questions like "is 10^6 miles bigger than 3 seconds?" do not make sense.

Quantities in equations with dimension and units can make some forms of analysis awkward, so a common practice in applied mathematics is to get rid of them by **non-dimensionalising** the system. There are two main reasons:

1. End up with a system with fewer parameters.
2. Dimensionless quantities are simply numbers and can be compared, so we can systematically reduce, by neglecting small valued terms, an analytically unsolvable system to a simpler, solvable one that approximates well the solutions of the full one (asymptotic analysis).

4.1 Non-dimensionalisation

Using the logistic equation as example, the process follows a three step recipe,

1. **Rescale all variables:** the logistic equation has two variables $N(t)$ (dependent) and t (independent). To **rescale** we write

$$N = n_0 u\,, \quad t = t_0 \tau\,,$$

where the n_0 and t_0 are constants with the same units as N and t, respectively, and u and τ are **dimensionless** versions of N and t. On substitution

$$\frac{dN}{dt} = \frac{dn_0u}{dt} = \frac{d\tau}{dt}\frac{dn_0u}{d\tau} = \frac{n_0}{t_0}\frac{du}{d\tau} = rn_0u\left(1 - \frac{n_0u}{K}\right) = rn_0\,u - \frac{rn_0^2}{K}\,u^2,$$

and $n_0u(0) = N_0$. (we choose n_0 and t_0 in step 3).

2. **Grouping the constants** so that all expressions either side of "=", "+" and "–" are dimensionless quantities. No unique way of doing it; usually we multiply through by a set of parameters so that one of the terms has no parameters. Here, it is usual to multiply through by t_0/n_0 to get

$$\underbrace{\frac{du}{d\tau}}_{\text{clearly dimensionless}} = \underbrace{rt_0\,u - t_0\frac{rn_0}{K}\,u^2}_{\text{also dimensionless}}, \tag{6}$$

and $u(0) = N_0/n_0$.

3. **Choose rescaling constants:** usually, the aim is to minimise the number of parameters that remain. For the logistic equation it is usual to let

$$t_0 = 1/r \quad \text{and} \quad n_0 = K$$

so that,

$$\frac{du}{d\tau} = u(1-u), \tag{7}$$

and $u(0) = u_0 = N_0/K$. The ODE now has just one parameter (u_0) instead of 3.

Big Note 1.4A: non-dimensionalisation is not a unique process, e.g. we can choose $n_0 = N_0$ giving

$$\frac{du}{d\tau} = u\left(1 - \frac{u}{\widehat{K}}\right),$$

where $\widehat{K} = K/N_0$ and $u(0) = 1$. The "best" choice for the rescalings depends on the context and is not always obvious.

In the remainder of the course we will routinely non-dimensionalise the models.

Appendix

A Steady-state analysis - single ODE

Note: For the exam, you are expected to be able find the solution of routine first order ODEs using integrating factors and separation variables. Furthermore, you will be expected to be able to find all **biologically relevant** steady-states and apply the two methods described in Sections A.2 and A.3 to determine their stability.

A.1 Solutions for general $f(N)$

Consider the ODE

$$\frac{dN}{dt} \;=\; f(N) \tag{8}$$

with $N(0) = N_0$. This is variable separable and it can be rewritten as an integral equation

$$\int \frac{1}{f(N)}\, dN \;=\; \int dt \;=\; t + c\,, \tag{9}$$

where c is the constant of integration found by imposing $N(0) = N_0$. Ideally, we would like to determine the integral and write the solution of the ODE **explicitly** in the form of

$$N \;=\; g(t),$$

where $g(t)$ involves standard functions (e.g. polynomials, exponentials, trigonometric functions etc.) satisfying equation (8) and is easily computable for any t. However, in practice, there are 3 possible outcomes from this integral equation:

1. The **left-hand side** of (9) **can be integrated** and the resulting equation **can** be manipulated to get explicitly $N = g(t)$. E.g. the logistic equation, $f(N) = rN(1 - N/K)$, with solution
$$N(t) \;=\; \frac{N_0 K\, e^{rt}}{K + N_0(e^{rt} - 1)}.$$

2. The **left-hand side** of (9) **can be integrated**, but the resulting equation **cannot** be manipulated to get explicit $N = g(t)$. E.g. using a growth term *similar* to the logistic form $f(N) = rN^2(1 - N/K)$ (a cubic in N) has the **implicit** solution
$$\frac{1}{N} + \frac{1}{K}\ln\!\left(\frac{N}{K-N}\right) \;=\; r\,t + \frac{1}{N_0} + \frac{1}{K}\ln\!\left(\frac{N_0}{K-N_0}\right),$$
and there is no way of unwrapping this equation to express this in the explicit form of $N = g(t)$ in terms of simple/standard functions of t.

3. The **left-hand side** of (9) **cannot be integrated** to get a regular function. E.g. using an exponential growth law, $f(N) = rN(1 - \exp(N/K - 1))$, leads to
$$\int \frac{dN}{N(1 - e^{(N/K-1)})} \;=\; r\,t + c.$$
which can not be integrated in terms of the standard functions.

Key point: Any $f(N)$ under categories 2 and 3 poses problems in analysing the model. However, like the logistic model, population models typically predict $N \to N^*$ (N^* constant) as $t \to \infty$, and *finding such an N^* is often the main purpose of the investigation.*

- Fortunately, this can be done for any suitably continuous function $f(N)$ using (1) phase-line diagrams and/or (2) linear stability analysis ....

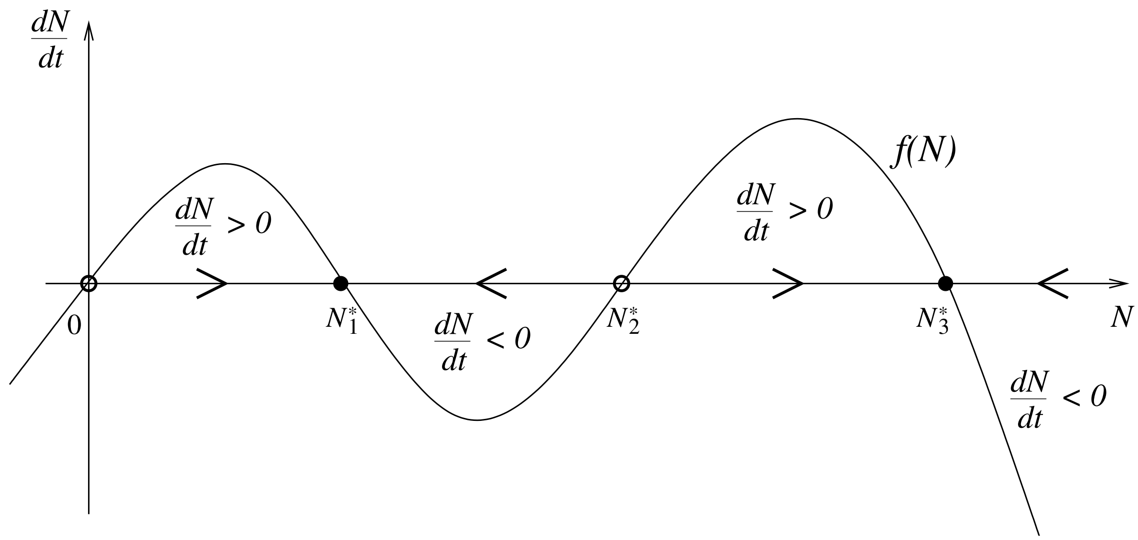
A.2 Phase-line plots

A quick way of determining how the solution of a single ODE will behave, particularly as $t \to \infty$, is to use **phase-line diagrams** (or phase diagram). The method works for any ODE of the form

$$\frac{dN}{dt} = f(N),$$

and consists simply of plotting $f(N)$ against N.

Example: Consider the following phase-line plot for the ODE $\frac{dN}{dt} = f(N)$:



Since $\frac{dN}{dt} = f(N)$, we can deduce from the picture

- Where $f(N) > 0$ then $\frac{dN}{dt} > 0 \quad \Rightarrow \quad N(t)$ is increasing.
- Where $f(N) < 0$ then $\frac{dN}{dt} < 0 \quad \Rightarrow \quad N(t)$ is decreasing.

The "direction" in which the solution $N(t)$ evolves are indicated by the ">" and "<" symbols on the N axis. When $f(N)$ is **continuous**, the following notes are relevant:

- The **steady-states** N^* of $\frac{dN}{dt} = f(N)$ satisfy $f(N^*) = 0$ and are thus the points at which $f(N)$ crosses the N axis.
- The solution of the ODE will necessarily tend either to a (**stable**) steady-state or infinity. (In the above picture, the ODE will tend to the stable steady-states N_1^* and N_3^*).

- There are some steady-states in which the solutions of the ODE move away from. These steady-states are **unstable**. (In the above picture, these are 0 and N_2^*).
- What happens as $t \to \infty$ depends on the initial condition $N(0) = N_0$. From the figure,
  - if $0 < N_0 < N_2^*$ then $N \to N_1^*$ as $t \to \infty$.
  - if $N_0 > N_2^*$ then $N \to N_3^*$ as $t \to \infty$.

  The **domains (or basins) of attraction** of each of the stable steady-states are divided either by an unstable steady-state (most common in population models) or a singular point of $f(N)$.

Big Big Note: The *stable* steady-states seem to satisfy $f'(N^*) < 0$ and the *unstable* ones $f'(N^*) > 0$. This can be proved with a little more rigour ....

A.3 Linear stability analysis for general $f(N)$

The stability of a steady-state N^* can also be established by using a method called **linear stability analysis**. This approach generalises better for systems consisting of multiple ODEs. The idea is to investigate the evolution of a small perturbation about a steady-state N^* by writing

$$N(t) \;=\; N^* + n(t), \tag{10}$$

where $\boxed{\boldsymbol{n(t)}\ \textbf{is a very small}}$ time dependent perturbation function (we write $|n(t)| \ll 1$). This assumption means that we can say

$$... \;\ll\; |n(t)|^3 \;\ll\; |n(t)|^2 \;\ll\; |n(t)|. \tag{11}$$

Substituting (10) into (8) gives

$$\begin{aligned} \frac{d(N^* + n(t))}{dt} \;&=\; f(N^* + n) \\ \Rightarrow\; \frac{dn}{dt} \;&=\; f(N^*) + nf'(N^*) + \frac{n^2}{2} f''(N^*) + O(n^3) \end{aligned} \tag{12}$$

using the Taylor's series of $f(N)$ about $N = N^*$ for the right-hand side. The trick now is to **exploit the fact that $\boldsymbol{n(t)}$ is very small**, which means we can **<u>linearise</u>** the equation to make it simpler, **i.e. <u>neglect</u> the terms that are of size $\boldsymbol{n^2, n^3}$ and smaller using (11)**, so that the remaining expression on the right-hand side is a linear function of $n(t)$. Since $f(N^*) = 0$, equation (12) can now be reduce to, on linearisation,

$$\frac{dn}{dt} \;\approx\; nf'(N^*)$$

which, because $f'(N^*)$ is constant, can be solved to give

$$\boxed{n \;\approx\; C\, e^{f'(N^*)t},} \tag{13}$$

where C is a constant of integration (which is small because $n(t)$ is small). This expression tells us how a perturbation from a steady-state N^* will evolve based on the sign of $f'(N^*)$:

- If $\boldsymbol{f'(N^*) > 0} \;\Rightarrow\;$ n grows $\Rightarrow N$ is moving away from $N^* \Rightarrow N = N^*$ is **unstable**.
- If $\boldsymbol{f'(N^*) < 0} \;\Rightarrow\;$ n decays $\Rightarrow N$ is moving towards $N^* \Rightarrow N = N^*$ is **stable**.
- If $\boldsymbol{f'(N^*) = 0}$ could be stable or unstable. Examine n^2 terms or use a phase-line diagram. (*These borderline cases will generally be ignored in this module*).

The first 2 bullet points confirm what was deduced from the phase-line diagram.

Recipe for the linear stability method:

1. Find all the physical steady-states N^* by solving $f(N^*) = 0$.
2. Evaluate $f'(N^*)$ to determine stability.
3. As $t \to \infty$, expect either $N(t) \to$ a *stable* steady-state or $N \to \infty$. (i.e. an N^* satisfying $f'(N^*) < 0$).