MATH1134 - Lecture 3

Mr. Tony Mann, Dr. Erwin George, Department of Mathematical Sciences, University of Greenwich

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TIPS

1. Invest time learning the *language* of Mathematics (with all of its special cases and exceptions and conventions).
2. Review constantly.
3. Do assignments, tutorials, etc. Practise, practise, practise. Read textbook/supplementary notes. Ideally read the textbook/supplementary notes material on a topic *before* the relevant lecture. You will have to do significant work outside of the classroom to master the material.
4. Attend and engage with lectures and tutorials. This represents the most efficient way to learn the material. Come prepared and ask questions if you do not understand something.
5. Speak to me as soon as you feel you may be falling behind.
6. In summary: KEEP UP. This will be a very fast-paced class and falling behind is **very unwise**. Mathematics is very hierarchical and you generally progress only by first knowing well what went before.

Here we begin to look at building and extending mathematical models of biological systems, with a focus on modelling the time evolution of the "population" of various species.

As in most of mathematics and life, you will not likely become an expert in mathematical modelling overnight. However by keeping a focus on the big picture, you will gradually see the key features which go into developing a good model and become better and better at modelling. Practice and experience will be two of your key allies in becoming proficient in the application of mathematics to the life sciences. Try not to be too distracted by the "processes" but instead focus on the "concepts".

Continuous Population Models for Single Species - Introduction

``The motivation for modelling ... is to further our understanding of the underlying processes since it is only in this way that we can make justifiable predictions.'' from *Mathematical Biology 1: An Introduction* by J.D. Murray.

- When creating and analysing mathematical models, some of the key ingredients are:
  - A good *understanding* of differential and integral calculus;
  - A good understanding of the biological/physical etc problem being modelled, and a clear idea of what you want the model to tell you about that problem *(although it could be argued this is not always necessary)*.
  - Common sense.
  - Patience - as with most things in mathematics, you get better at modelling the more you do it.
- We typically start with simple models with simplifying assumptions and then adjust to more "complex" models as those assumptions are relaxed. This is the pattern we will largely follow in this course.
- It is important to always keep in mind the assumptions (including hidden ones) which go into a model so that you have some idea of its limitations.

- There are many books on mathematical modelling which you can consult to find out more.
- For example, the book **Elementary Differential Equations** by William Boyce and Richard DiPrima *(Wiley)* has a nice summary of typical steps in the modelling process, which I have included (paraphrased and slightly modified) in the appendix - Appendix A.
- However, I think it might be better for now to keep things fairly simple and focus on the big picture: try to understand the models presented, and use them as examples of how to construct your own models. AND USE COMMON SENSE.

$\rightsquigarrow$ Vocabulary Alert: *per capita* means (average) *for each individual*. E.g. the per capita birth rate is the average number of births for each individual in a population. You will see the term *per capita* often in what follows.

Aside 1 - Dimensional Analysis

Primary Dimension		SI Unit	
Mass	M	kilogram	kg
Length	L	metre	m
Time	T	second	s
Temperature	T, q, Θ	Kelvin	K
Electric current	I	Ampere	A
Amount of light	C	candela	c
Amount of matter	N	mole	mol

- $\mapsto$ When setting up model equations, one important check is to ensure that the dimensions on both sides of each equation match.
- $\mapsto$ The standard notation for indicating the dimension of a quantity is to **put square brackets around it**.
- $\mapsto$ E.g. from Newton's law **Force = mass** $\times$ **acceleration** or $\boldsymbol{F = ma}$. Thus

$$[F] = ML/T^2 \quad \textit{so in SI unit is} \quad kg\ m/s^2.$$

- $\mapsto$ **Note in mathematical models of population, the population may be measured directly in the number of members of a species or less directly as in a density or concentration.**

The Exponential Growth (Malthusian) Model

- A very simple model of the growth of the population of a species, e.g. bacteria, *under ideal conditions - e.g., unlimited space, no disease, no predators*.
- Thomas Malthus observed (in 1798) that *(over relatively small time frames)*, under the assumptions above, the population of a species (bacteria, humans, other animals, etc.) grew at a rate which is proportional to the size of the current population.
- Define appropriate dependent and independent variables, and write out the last observation as a mathematical equation:

  ANSWER Let $N = N(t)$ (dependent variable) be the population at time t (independent variable). Then

  $$\frac{dN}{dt} = rN, \text{ where } r \text{ is a constant.}$$

- This is both a linear and separable ODE, and with initial condition $N(t_0) = N_0$, the solution is

  $$N(t) = N_0 e^{r(t-t_0)} \quad or \ N(t) = N_0 e^{rt} \ if \ t_0 = 0,$$

  hence the name *the exponential model*. **r is called the net per capita growth rate or Malthusian parameter** $\rightsquigarrow$ see alternative derivation next for reason.

Alternative Derivation A

- For variety, here is another way the Malthusian ODE could have been derived.

- Let $N(t)$ be the population at time t and consider a small time increment δt.
- Let b be the per capita birth rate - so b is the number of births to an individual per unit time *(NOTE b would typically NOT be a whole number since it is an average)*. Thus $b\delta t$ is the total number of births to each individual from time t to $t + \delta t$.
- Similarly, let d be the per capita death or mortality rate. Thus $d\delta t$ is the total number of deaths to each individual from time t to $t + \delta t$.
- Finally, assume there is no net migration, so that births and deaths are the only way the population changes. Then

$$N(t+\delta t) = N(t) + b\delta t N(t) - d\delta t N(t) \quad \Rightarrow \quad \frac{N(t+\delta t) - N(t)}{\delta t} = (b-d)N(t)$$

and taking limits as $\delta t \to 0$, letting $b - d = r$, which is clearly the **net per capita growth rate** (if > 0) or decline (if < 0), we again get the Malthusian ODE

$$\frac{dN}{dt} = rN,$$

Alternative Derivation B

- Yet another approach to deriving the Malthusian ODE involves starting with the basic *conservation equation* for a population at time t, $N(t)$: the rate of change

$$\frac{dN}{dt} = \text{rate in} - \text{rate out} \quad = \quad \text{rate of births} - \text{rate of deaths} + \text{rate of migration}$$

- The Malthusian ODE follows from making the simplifying assumptions that:
  - there is no migration (a closed system), and
  - the birth and death rates at any time t are both proportional to the population at time t, $N(t)$.
- Thus taking those proportionality coefficients to be b and d respectively, we again get

$$\frac{dN}{dt} \quad = \quad bN - dN \quad = \quad (b-d)N \quad = \quad rN$$

where $r = b - d$

- ASIDE: Dimensional Analysis

- $\rightarrow$ Use dimensional analysis to determine the dimensions of r in $N(t) = N_0 e^{r(t-t_0)}$
- $\rightarrow$ $\boxed{\text{ANSWER}}$ Loosely speaking,

$$[N] = \text{“}\mathit{Number\ of\ individuals}\text{''} \text{ or } \text{“}\mathit{Population}\text{''}$$

which is the same as $[N_0]$, so for the equation to be consistent $e^{r(t-t_0)}$ must be a dimensionless (pure) number.
That is only possible if $[r] = 1/[t - t_0]$ thus $[r] = 1/T$.
- $\rightarrow$ Note you could have come to the same conclusion performing the dimensional analysis on $\frac{dN}{dt} = rN$ instead.

- NOTE the Malthusian ODE $\dfrac{dN}{dt} = rN$ is clearly **autonomous** and it is also easy to see that there is only one *equilibrium solution*, $N(t) = 0$, which is *unstable* if $r > 0$ and *stable* if $r < 0$.
- $\boxed{\text{EXAMPLE 1}}$ The UK population was 57 439 000 in 1991 and 59 113 000 in 2001. Use this information and a Malthusian model of population growth to estimate the population in 2011 and compare your calculated result with the actual figure of 63 182 000.
- $\boxed{\text{ANSWER}}$ First we need the per capita growth rate, r, over the period 1991 to 2001 and will assume it is the same over the next ten years. For simplicity we take 1991 to be year 0 so $t_0 = 0$ and

$$N(t) = N_0 e^{rt} = 57439000e^{rt},\ so\ t = 10\ (year\ 2001) \Rightarrow N(10) = 57439000e^{10r} = 59113000.$$

To estimate r we take ln of both sides:

$$\ln(57439000)+10r = \ln(59113000) \Rightarrow r = \frac{\ln(59113000) - \ln(57439000)}{10} \approx 0.00287273512644$$

Thus in 2011 we expect the population to be
$N(20) = 57439000e^{0.00287273512644255(20)} \approx 60\ 835\ 787 \rightsquigarrow$ relative error 0.0371341997496619, so not bad but not great.
- Any ideas about why this estimate is a bit low? *Higher immigration in the 2001-2011 period as compared to 1991-2001 is likely a factor, hence a larger r should have been used.*

- So a simple change would be to modify our assumption that r was constant over the period 1991 to 2001 and assume that it depended on t, so $\boldsymbol{r = g(t)}$ - beginning with the simplest assumption that it is *linear* over this period and continued growing at the same rate over the period 2001 to 2011. We assume $g(t=0) = 0$ since evaluating $N(t=0)$ gives us no insight into the value of g, so $g(t) = \alpha t$ for some constant α which we will now find.
- This means that we have to solve the IVP with linear ODE $\dfrac{dN}{dt} = \alpha t N, \quad N(0) = 57439000 \ldots \Rightarrow N(t) = 57439000e^{\alpha t^2/2}$, but then

$$N(10) = 57439000e^{50\alpha} = 59113000 \Rightarrow \alpha = \frac{\ln(59113000/57439000)}{50} \approx 0.000574547025288529$$

$$\text{So the linear function } \; g(t) = 0.000574547025288529\, t \;\Rightarrow\; \frac{dN}{dt} = 0.000574547025288529\, tN.$$

$$\text{And the solution to this linear ODE is} \quad N(t) = 57439000e^{0.000574547025288529t^2/2}.$$

So, as expected, in 2001 $N(10) = 59113000$ (exact answer). And in 2011, $\boxed{N(20) \approx 64\ 433\ 451}$ for a relative error of 0.0198070775144054.

- So the estimate is better now - relative error reduced by about one-half.

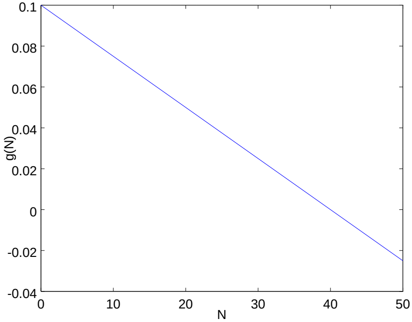
The Logistic Growth Model $\rightsquigarrow$ More realistic population modelling

- $\rightsquigarrow$ The exponential growth/decay model is not very practical over long time frames since the "ideal conditions" of its assumptions are simply typically not present. If $r > 0$ the population grows forever while if $r < 0$ the population eventually dies out.
- $\rightsquigarrow$ Note even the modified ODE with the linear growth rate $g(t)$, $\dfrac{dN}{dt} = 0.000574547025288529\ tN$, is not very realistic since $\lim_{t\to\infty} N(t) = \infty$, *i.e.*, the population grows forever.
- $\rightsquigarrow$ It is reasonable to expect that the growth rate, r, DOES depend on the current population, $r = g(N) \Rightarrow \frac{dN}{dt} = g(N)N$, *(as opposed to depending directly on t)* but a more realistic model for g is needed which matches *empirical observations* (real-life observations).
- $\rightsquigarrow$ The **Logistic Growth Model** is an attempt to derive a *simple* $\boldsymbol{g(N)}$ which reflects key empirical observations about population growth.

- Realistically, based on observations, a given population will often initially grow (or decline) quickly: $\frac{dN}{dt} \approx \ constant \times N = rN$ for N "small").
- However, due to limited resources, disease, etc., the population levels off when it reaches its *carrying capacity* $K > 0$, and stays at that level for awhile.
  - Thus we want that if the population $N < K$ then the population *increases* towards N so $\frac{dN}{dt} > 0$, AND if $N > K$ then the population *decreases* towards K so $\frac{dN}{dt} < 0$.
  - Can you think of a simple *LINEAR* expression for $g(N)$ which has the required property that for small N it causes the population to initially grow but for $N > K$ it causes the population to decline and for $N = K$ it causes the population to stay constant?
  - For g, we essentially want a linear function of N which is positive for $N < K$, is 0 at $N = K$, and negative for $N > K$. Hence we want a *decreasing* linear function of N.
- If we make the logical assumption that if $N = 0$ then the value of $g(N)$ should be at its largest - which we will denote $r(> 0)$, then the problem of finding $g(N)$ becomes one of finding the equation of a line which passes through the points $\mathbf{(0, r)}$ and $\mathbf{(K, 0)}$. That line is determined as follows:
  - The line has gradient $-\frac{r}{K}$ so that $g(N) = -\frac{r}{K}N + C$ for some constant C. To determine C we use either of the points $(0, r)$ or $(K, 0)$ in the equation for $g(N)$. For example, using $(0, r)$, we get $g(0) = r \Rightarrow C = r$ so

$$g(N) \quad = \quad -\frac{rN}{K} + r \quad = \quad r\left(1 - \frac{N}{K}\right).$$

Here is a plot of this population growth rate $g(N)$ versus population N for the case *(without loss of generality)* of $r = 0.1$ and $K = 40$, showing that the population growth rate $g(N)$ is positive for $N < 40$ but negative for $N > 40$.



DEFINITION The Logistic model is called **compensatory** since its *net per capita growth rate* $g(N)$ is a MONOTONICALLY DECREASING function of N. A **depensatory** model is one in which $g(N)$ is an INCREASING function of N over *SOME* range of N values.

$\hookrightarrow$ With this choice of $g(N) = r\left(1 - \frac{N}{K}\right)$ we get a DE which more accurately reflects realistic population trends, called the **Logistic (or Verhulst) differential equation**

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

whose solution is said to represent LOGISTIC GROWTH.

$\hookrightarrow$ DEFINITION In this **Logistic** DE $\frac{dN}{dt} = g(N)N = r\left(1 - \frac{N}{K}\right)N$, the right hand side of the differential equation, $\boldsymbol{f(N) = rN\left(1 - \frac{N}{K}\right)}$, is called `the net growth rate of the population` of size N and $\boldsymbol{g(N) = r\left(1 - \frac{N}{K}\right)}$ is called `the net per capita growth rate of the population`. MAKE SURE YOU KNOW WHY *(for example, use dimensional analysis)*.

↪ The **Logistic (or Verhulst) differential equation**

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

is a first order, nonlinear, separable differential equation. See **Tutorial 3** for how to solve it.

- NOTE we can figure out several things about the general behaviour of solutions to the **Logistic ODE** just by looking at the ODE

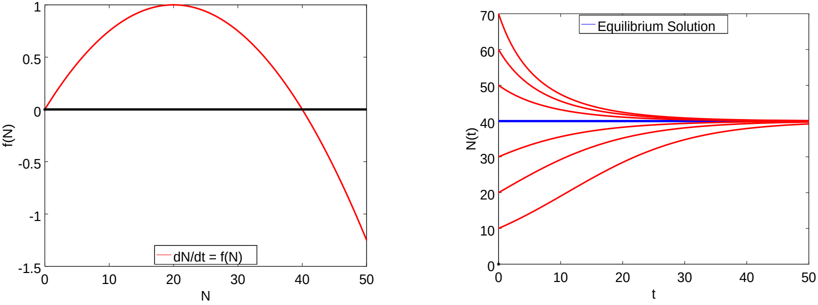
$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \quad = \quad f(N)$$

- Equilibrium Solutions: These are clearly $\boldsymbol{N(t) = 0}$ and $\boldsymbol{N(t) = K}$.

$$\frac{df}{dN} \quad = \quad r\left(1 - \frac{N}{K}\right) - \frac{rN}{K} \quad = \quad r - \frac{2rN}{K}.$$

Thus $f'(0) = r$ and $f'(K) = -r$ and so if $r > 0$, $N(t) = 0$ is an *unstable equilibrium solution* and $N(t) = K$ is a *stable equilibrium solution* *(or vice versa if $r < 0$)*.

Below is a graph of $f(N)$ versus N along with corresponding graphs of $N(t)$ versus t in the **Logistic ODE** for the case *(without loss of generality)* of $r = 0.1$ and $K = 40$.



The fact that $N(t) = 40$ is a stable equilibrium point is obvious, and one can also deduce that $N(t) = 0$ is unstable (although I have not plotted anything for $N < 0$ since it makes no physical sense for a population).

↪ So we see from the plot of $f(N)$ versus N which informs the plots of $N(t)$ versus t that solutions to the **Logistic** differential equation

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

behave as follows:

- If the population starts out above zero but below the *carrying capacity* K, then it increases towards the carrying capacity (but does not cross it) as $t \to \infty$.
- If the population starts out above the *carrying capacity* K, it decreases towards the carrying capacity (but does not cross it) as $t \to \infty$.

- The same conclusions could have been arrived at by looking at a direction field plot for the **Logistic** DE which included the equilibrium solutions.

↪ DEFINITION r is called the **intrinsic growth rate** and is the growth rate in the absence of any limiting factors.

- The general solution of the Logistic ODE is *(see* **Tutorial 3***)*

$$N(t) = \frac{K}{1 + Ae^{-rt}},$$

where A is an arbitrary constant.

⇝ If we take the initial condition $\boldsymbol{N(0) = N_0}$, then $\boldsymbol{A = \frac{K}{N_0} - 1}$ so

$$N(t) = \frac{K}{1 + \left(\frac{K}{N_0} - 1\right) e^{-rt}} = \frac{N_0 K}{N_0 + (K - N_0)e^{-rt}} = \frac{N_0 K e^{rt}}{K - N_0 + N_0 e^{rt}} \; (CHECK!)$$

↪ More generally, if $N(t_0) = N_0$ then

$$N(t) = \frac{K}{1 + \left(\frac{K}{N_0} - 1\right) e^{-r(t-t_0)}} = \cdots = \frac{N_0 K e^{r(t-t_0)}}{K - N_0 + N_0 e^{r(t-t_0)}}$$

- The **Logistic** model has been applied successfully to a variety of scenarios, including modelling bacteria growth and animal (including human, fish, etc.) population growth and decline. For example, see page 14 of `Essential Mathematical Biology` by Nicholas Britton, or the discussion in Chapter 1 and associated bibliography of `Mathematical Biology: 1 An Introduction, Third Edition` by J.D. Murray or the 1981 paper `Polynomial models of biological growth` by R. Lamberson and C. Biles, *UMAP Journal, 2(2), 9–25*.

- We will do an example which uses the following USA population data table (see also **Tutorial 3**):

YEAR	POPULATION	YEAR	POPULATION	YEAR	POPULATION
1790	3,929,214	1870	38,558,371	1950	151,325,798
1800	5,308,483	1880	50,189,209	1960	179,323,175
1810	7,239,881	1890	62,979,766	1970	203,211,926
1820	9,638,453	1900	76,212,168	1980	226,545,805
1830	12,866,020	1910	92,228,496	1990	248,709,873
1840	17,069,453	1920	106,021,537	2000	281,421,906
1850	23,191,876	1930	123,202,624	2010	308,745,538
1860	31,443,321	1940	132,164,569	2020	???

- EXAMPLE 2 Use the data from the USA population table in the years 1800, 1850, and 1900 to determine a **Logistic** growth population model $N(t)$ which is exact for those three years. Use this model to predict the populations in 1940 and 1950 and comment on the accuracy.

- *HINT:* Why are *THREE* years' worth of data needed to correctly determine an appropriate Logistic model?
  Because the solution $N(t) = \frac{K}{1+\left(\frac{K}{N_0}-1\right)e^{-rt}}$ has THREE *parameters* which determine it uniquely: N_0 the initial population, K the carrying capacity, and r the intrinsic growth rate.

- ANSWER Letting $t = 0$ coincide with the year 1800, we have $N(0) = N_0 = 5,308,483$ so that

$$N(t) = \frac{K}{1 + \left(\frac{K}{5{,}308{,}483} - 1\right) e^{-rt}}.$$

- ANSWER continued To find the other two parameters we use the fact that we know the values of $N(50)$ and $N(100)$ to come up with two (nonlinear) equations in two unknowns:

$$N(50) = 23,191,876 = \frac{K}{1+\left(\frac{K}{5,308,483}-1\right)e^{-50r}} = \frac{5,308,483K}{5,308,483+(K-5,308,483)\,e^{-50r}} \qquad AND$$

$$N(100) = 76,212,168 = \frac{K}{1+\left(\frac{K}{5,308,483}-1\right)e^{-100r}} = \frac{5,308,483K}{5,308,483+(K-5,308,483)\,e^{-100r}}$$

  - Solving this *nonlinear* system is tricky. One could use the in-built Matlab function `fsolve` *(see Tutorial 3)* or the systems version of **Newton's Method**, for example. *See* ***Appendix B*** *for this and note that this is important even if it appears in an appendix*.
    Here is an approach which leads to two single-variable nonlinear equations:

$$N(50) = 23,191,876 = \frac{5,308,483K}{5,308,483+(K-5,308,483)e^{-50r}} \Rightarrow$$

$$(23,191,876)(5,308,483)+23,191,876e^{-50r}K-(23,191,876)(5,308,483)e^{-50r} = 5,308,483K$$

$$\Rightarrow K = \frac{(23,191,876)(5,308,483)[1-e^{-50r}]}{5,308,483-23,191,876e^{-50r}}$$

- $\boxed{\text{ANSWER continued}}$ Also

$$N(100) = 76,212,168 = \frac{5,308,483K}{5,308,483 + (K - 5,308,483)e^{-100r}} \Rightarrow$$

$$(76,212,168)(5,308,483) + 76,212,168e^{-100r}K - (76,212,168)(5,308,483)e^{-100r} = 5,308,483K$$

$$\Rightarrow K = \frac{(76,212,168)(5,308,483)[1 - e^{-100r}]}{5,308,483 - 76,212,168e^{-100r}}$$

- So setting these two values of K equal we get an equation in terms of r only:

$$\frac{(76,212,168)(5,308,483)[1 - e^{-100r}]}{5,308,483 - 76,212,168e^{-100r}} = \frac{(23,191,876)(5,308,483)[1 - e^{-50r}]}{5,308,483 - 23,191,876e^{-50r}}$$

- This is difficult to solve by hand but an approximation technique such as the *Bisection method* or *Secant method* leads to a solution of

$$\boldsymbol{r \approx 0.0315482567314}$$

- $\boxed{\text{ANSWER continued}}$ We can now use this r value in either of the two earlier equations for K (corresponding to $N(50)$ or $N(100)$) to find K. For example,

$$K = \frac{(76,212,168)(5,308,483)[1 - e^{-100r}]}{5,308,483 - 76,212,168e^{-100r}} = \frac{(76,212,168)(5,308,483)[1 - e^{-3.15482567314}]}{5,308,483 - 76,212,168e^{-3.15482567314}}$$

$$\Rightarrow \quad K \quad \approx \quad \mathbf{188,168,898}$$

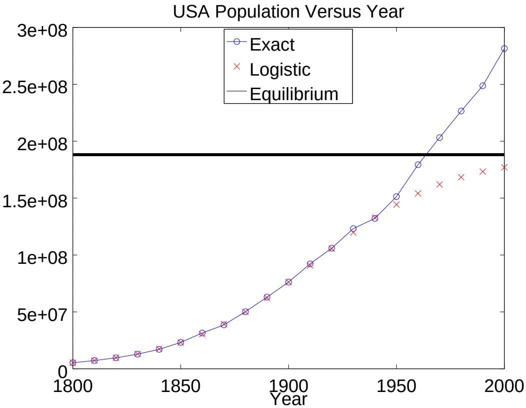
- So

$$N(t) = \frac{188,168,898}{1 + \left(\frac{188,168,898}{5,308,483} - 1\right) e^{-0.0315482567314t}}.$$

  and it is easy to check (for example, using a function handle in Matlab) that $N(0) = 5,308,483$, $N(50) = 23,191,876$, and $N(100) = 76,212,168 \rightsquigarrow$ the *exact* values.

- $N(140) = 132,898,138$ versus the real 1940 population of $132,164,569$ for an absolute error of only 733 569 and a relative error of 0.00555 $\rightsquigarrow$ AN EXCELLENT ESTIMATE!
- $N(150) = 144371704$ versus the real 1950 population of $151,325,798$ for an absolute error of 6 954 093 and a relative error of 0.04595 $\rightsquigarrow$ not so good this time!

- The figure below shows how this particular Logistic model is quite good at predicting the USA population from 1800 until about 1950, but not afterwards. The model doesn't properly capture the *baby boom* from the mid 1940's to the mid 1960's.



EXERCISE Do EXAMPLE 2 with the exponential growth model instead, using data from the years 1800 and 1900 to calculate r.

$\hookrightarrow$ Note when we multiply out the right-hand-side of the Logistic DE $\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$ we get

$$\frac{dN}{dt} = rN - \frac{r}{K}N^2$$

which makes it "easier" to see that it can be interpreted as model showing intraspecific competition.

- Since individuals within a species often compete for food, water, space, mates, and other scarce resources, then in over-crowded conditions there might be an increase in the net population mortality.
- This will particularly be the case if individuals encounter each other frequently.
- When written as it is above, the Logistic DE shows an exponential growth rate rN *(a growth rate proportional to the population)* which is then adjusted down by a mortality term which is proportional to the number of paired encounters between individuals in the population.

The Logistic Equation With Harvesting $\rightsquigarrow$ Constant Harvesting

Following courtesy of Professor Kevin Parrott's 2010 MATH1106 notes

4.2.2 Logistic equation with harvesting

The logistic equation is frequently used to model a population that is being hunted to establish the stability of the population. A good example is that of the EU policy of fishing where the EU prescribes a limit on how many fish can be caught in a given year for specific species such as cod. A stability analysis is needed to decide whether the new equilibrium population is stable or not. The following problem addresses this question.

Analyse the stability of the equilibrium points of the logistic equation with harvesting (H is the cap on the rate at which the population can be harvested)

$$\frac{dy(t)}{dt} = ay(t)(1 - y(t)/K) - H, \qquad a, K, H > 0, \qquad t \geq 0$$

What is the smallest value of the harvesting rate H for which the population is stable and non-zero!

Solution

Denote the RHS of this ODE by $f(y)$. If y_0 is an equilibrium point for this problem then we must have that

$$f(y_0) = ay_0(1 - y_0/K) - H = 0$$

i.e.

$$ay_0 - ay_0^2/K - H = 0$$

re-arranging

$$\frac{a}{K}y_0^2 - ay_0 + H = 0$$

Solving the quadratic using

$$x = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a} \quad if\ ax^2 + bx + c = 0 \text{ (don't confuse the } a\text{'s!!!!)}$$

results in

$$y_0 = \frac{a \pm \sqrt{a^2 - 4\frac{a}{K}H}}{\frac{2a}{K}}$$

helps to simplify so multiply top and bottom by K/a (turns into $\left(\frac{K}{a}\right)^2$ inside $\sqrt{}$)

$$= \frac{K \pm \frac{K}{a}\sqrt{a^2 - 4\frac{a}{K}H}}{2} = \frac{K \pm \sqrt{K^2 - \frac{4K}{a}H}}{2} = \frac{K \pm K\sqrt{1 - \frac{4H}{Ka}}}{2}$$

The population must be *real* so there will be no equilibrium points unless

$$K^2 - \frac{4K}{a}H > 0 \quad \text{i.e.} \quad H < \frac{aK}{4} = H_{max}$$

This is interesting as it means that there is an upper limit H_{max}on the harvesting rate for this population (e.g. the catch rate for a fish population) without which there can be NO equilibrium population. The two roots of the quadratic can be written in terms of the fraction of the maximum catch rate $\alpha = H/H_{max} < 1$

$$y_0 = \frac{K \pm K\sqrt{1 - \frac{4H}{Ka}}}{2} = \frac{1}{2}K\left(1 \pm \sqrt{1 - H/H_{max}}\right) = \frac{1}{2}K\left(1 \pm \sqrt{1-\alpha}\right)$$

PHEW! (but really all we did was solve a quadratic)

Now to check for stability. The first step is the same as problem 6.1 since the constant harvesting rate H drops out when differentiated so that

$$f'(y) = a - \frac{2ay}{K}$$

Equilibrium point 1: $y_0 = \frac{1}{2}K\left(1 + \sqrt{1-\alpha}\right)$

$$f'(y_0) = a - \frac{2ay_0}{K} = a - a\left(1 + \sqrt{1-\alpha}\,\right) = -a\sqrt{1-\alpha} < 0$$

Equilibrium point 2: $y_0 = \frac{1}{2}K\left(1 - \sqrt{1-\alpha}\,\right)$

$$f'(y_0) = a - \frac{2ay_0}{K} = a - a\left(1 - \sqrt{1-\alpha}\,\right) = +a\sqrt{1-\alpha} > 0$$

So the first point is unstable (population lower than the original equilibrium population K) and the second point is stable (population is even lower than the original equilibrium population K). Try $\alpha = 0.5$ and check the two equilibrium populations.

The Logistic Equation With Harvesting $\rightsquigarrow$ Non-Constant Harvesting

- There are other more sophisticated fisheries models in which the harvesting is more realistically non-constant but the same issues about determining a sustainable level of harvesting is considered.

- Interested students should read up on the *Schaefer Model* which is covered in places such as

https://en.wikipedia.org/wiki/Gordon-Schaefer_Model

Growth with a Critical Threshold - A Minor Modification of the Logistic Equation

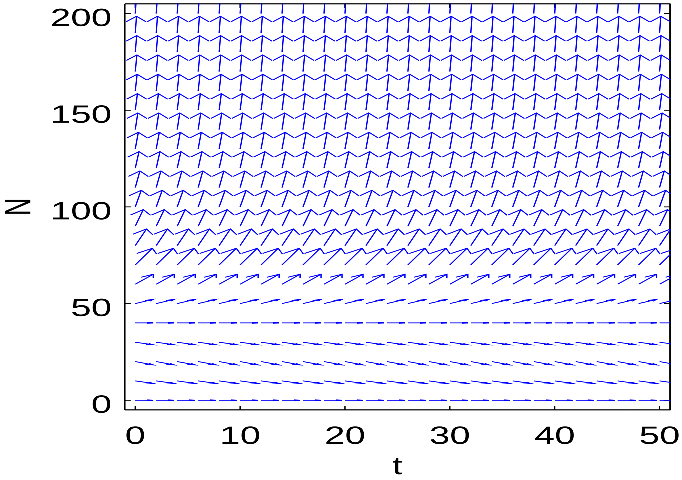
- If we modify the Logistic growth DE $\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$ by putting a minus sign in front of the right-hand-side and renaming K as T, we get the following equation which *looks* very similar to the Logistic DE but whose solution *behaves very differently*:

$$\boldsymbol{\frac{dN}{dt} = -rN\left(1 - \frac{N}{T}\right), \quad r > 0.}$$

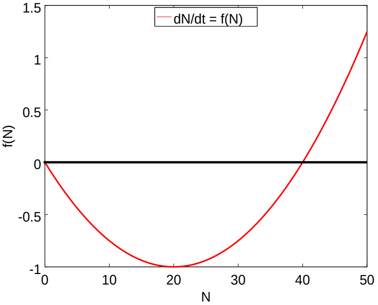
- NOTE the *per capita growth rate* $g(N) = -r\left(1 - \frac{N}{T}\right)$ is an *increasing* function of N, hence this model is **depensatory**.
- It's easy to see that its equilibrium solutions are $N = 0$ and $N = T$.

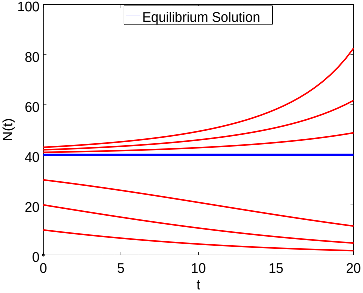
- And if we let $f(N)$ be the right-hand-side of this DE, then $f'(N) = -r\left(1 - \frac{N}{T}\right) + \frac{rN}{T} = -r + \frac{2rN}{T}$, so $f'(0) = -r < 0 \Rightarrow N(t) = 0$ is a **stable** equilibrium point, and $f'(T) = r > 0 \Rightarrow N(t) = T$ is an **unstable** equilibrium point. This is illustrated in the following graphs *(without loss of generality $r = 0.1$ and $T = 40$).*

Direction Field for $\frac{dN}{dt} = -rN\left(1 - \frac{N}{T}\right)$



Below is a graph of $f(N)$ versus N along with corresponding graphs of $N(t)$ versus t for the DE $\frac{dN}{dt} = -rN\left(1 - \frac{N}{T}\right)$ for the case *(without loss of generality)* of $r = 0.1$ and $T = 40$.





The fact that $N(t) = 40$ is an unstable equilibrium point is obvious, and one can also deduce that $N(t) = 0$ is stable (although I have not plotted anything for $N < 0$ since it makes no physical sense for a population).

- In practical terms, T is a **threshold level** below which no growth occurs, and in fact a population dies out. Above this level, the population takes off *(unrealistically quickly for "large" t)*.

- Some species show this population growth pattern such as the now extinct passenger pigeon: if there are "enough" of them they will thrive but if there are too few the population dies out *('though there is a modification to this model which more accurately captures the passenger pigeon plight)*.

- In the case of the passenger pigeon, it was heavily hunted for food and sport over a period of years causing the population to fall below the critical threshold level for survival circa the 1880s and they died out in 1914.

- One could solve this DE in very much the same way as one solves the Logistic DE *(see* **Tutorial 3)**. However, one could also get the solution by replacing K with T and r with $-r$ in the solution to the Logistic DE. Thus, with initial condition $N(0) = N_0$ we get:

$$N(t) = \frac{T}{1 + \left(\frac{T}{N_0} - 1\right) e^{rt}}.$$

- Note in this solution we observe something which we couldn't easily tell from the earlier analytical classification of the two equilibrium solutions *(but which might have been suggested by the direction field)*: If $N_0 > T$ so that $\frac{T}{N_0} - 1 < 0$, then we can find a *FINITE* t value, $t*$, for which the denominator $1 + \left(\frac{T}{N_0} - 1\right) e^{rt} = 0$ and thus the solution $N(t)$ is unbounded.

- To find $t*$ we solve $1 + \left(\frac{T}{N_0} - 1\right) e^{rt*} = 0 \Rightarrow N_0 + (T - N_0)e^{rt*} = 0 \Rightarrow$

$$e^{rt*} = -\frac{N_0}{T - N_0} \quad \Rightarrow \quad t* \quad = \quad \frac{1}{r} \ln\left(\frac{N_0}{N_0 - T}\right).$$

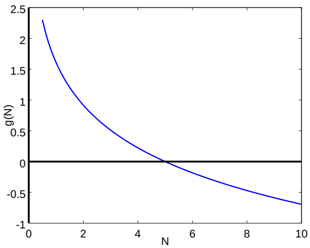
- NOTE this is a case in which the solution provided more detail than just the geometrical analysis.

- Critical thresholds or *tipping points* occur in other instances such as:
  - in laminar (smooth) flow of a fluid, a small disturbance might have a critical amplitude above which the flow becomes turbulent;
  - in infectious disease control, there may be a critical percentage of the population which, if vaccinated, causes an infectious disease to die out;
  - inside a computer's central processing unit (CPU) there may be fail-safe devices *(automatic control devices)* designed to safely shut down the CPU if a critical maximum temperature is reached.

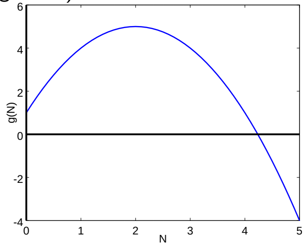
Two Other Famous Density-Dependent Intrinsic Growth Rate Models

↪ Two other well-known $g(N)$ for population models of the type $\boldsymbol{\frac{dN}{dt} = g(N)N}$ are:

1. **The Gompertz law** where $g(N)$ is a negative logarithmic function of N - for example, $g(N) = r \ln\left(\frac{K}{N}\right)$ where $r, K > 0$, leading to the **Gompertz equation**, $\boldsymbol{\frac{dN}{dt} = rN \ln\left(\frac{K}{N}\right)}$
   - Like the Logistic DE this is *compensatory* but since $\ln(0)$ is not defined this model is not valid for small populations.
   - *This is used to model self-limiting population growth, notably the growth of tumours.*



2. **The Allee effect** (Warder Clyde Allee)
   - $g(N)$ in this case initially increases, reaches a peak at an intermediate value of N, then decreases (see example graph below).
   - This models populations in which the growth rate increases with the population - at least, until a certain point where the population density becomes too high and the population declines. It is the increase of population growth rate with increasing population specifically which is called the *Allee effect*.
   - This *Allee effect* is typically due to cooperation within the individuals in the population - for example, fighting off predators or collecting food (the more individuals there are to do these, the greater the success of the group in doing them).



Aside 2 - Non-dimensionalisation (and Scaling) of Equations

- There are several very good reasons to (re)write and study the differential equations we derive in these models so that they involve *dimensionless* quantities. Some of the benefits are:
  - It can help to ensure that both sides of the equation are dimensionally consistent.
  - Units of measurement are no longer important and it is "easier" to compare the relative sizes of quantities in the model - "large" and "small" take on a clearer meaning.
  - It typically uncovers key dimensionless quantities that govern the dynamics and in the process reduces the number of parameters in the equation.
- You can read a good article on this, *Simplification and Scaling* written by Lee A. Segel in `SIAM Review, vol. 14, no. 4, pp 547--571` (1972).
- There is no unique way to do this but with some practice and thought it becomes easier to decide what an appropriate non-dimensionalisation/scaling of a model might be. For some models, the approach typically used is established and standard.

Non-dimensionalisation of the Logistic DE

- For the Logistic DE, $\boldsymbol{\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)}$ we observe the presence of the *dimensionless* (WHY?) ratio $\frac{N}{K}$ which suggests that we divide both sides of the equation by K *(ASIDE: dividing by N_0 would also have been a possibility)*:

$$\frac{1}{K}\frac{dN}{dt} = r\frac{N}{K}\left(1 - \frac{N}{K}\right) \quad \Rightarrow \quad \frac{d}{dt}\left(\frac{N}{K}\right) = r\frac{N}{K}\left(1 - \frac{N}{K}\right).$$

- This form of the equation reveals that $N(t)$ really only appears in the *dimensionless* ratio $\frac{N}{K}$, so we can define a new *dimensionless* variable

$$y(t) = \frac{N(t)}{K}$$

which is the *population as a multiple (or fraction) of the carrying capacity, K.*

- Thus taking this and substituting $N(t) = Ky(t)$ into the original Logistic DE we get

$$\frac{dy}{dt} = ry(1 - y)$$

REMINDER $\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$ with substitution $y(t) = \frac{N(t)}{K}$ becomes $\frac{dy}{dt} = ry(1-y)$.

- This is good but the equation is still not completely dimensionless ... it has dimension $1/T$ - essentially we haven't really non-dimensionalised the independent variable, t (time).
- Thus we would like to scale both sides of the equation by a quantity with dimension T to arrive at a truly dimensionless DE.
- One way is to introduce a dimensionless variable related to time: one may ask what variable(s) in the current equation can we multiply or divide t by to get a dimensionless variable. The "obvious" choice is to multiply by r so we get the *dimensionless* $\tau = rt$ so that $t = \frac{\tau}{r}$ and $y(t) = y\left(\frac{\tau}{r}\right)$ thus by the chain rule $\dfrac{dy}{dt} = \dfrac{dy}{d\tau}\dfrac{d\tau}{dt} = \dfrac{dy}{d\tau}r$ and modified Logsitic DE becomes

$$\frac{dy}{d\tau}r = ry(1-y) \quad \Rightarrow \quad \frac{dy}{d\tau} = y(1-y).$$

- Thus this form of the Logistic equation is *dimensionless* and has only ONE (or TWO) parameter(s), $\boldsymbol{y}$ (and $\boldsymbol{\tau}$) as opposed to the original equation which had THREE (or FOUR), $\boldsymbol{N}$, $\boldsymbol{r}$, $\boldsymbol{K}$, (and $\boldsymbol{t}$).
- NOTE if we solve the dimensionless form of the Logistic DE $\frac{dy}{d\tau} = y(1-y)$ for $y(\tau)$ then we can recover the solution in terms of the original dependent variable $N(t)$ by observing that $N(t) = Ky(\tau(t)) = Ky(rt)$ *(CHECK!)*

A general rough guide to nondimensionalisation of an equation:

- Identify the dependent and independent variables.
- Where possible replace each variable by a quantity scaled relative to some base unit of measurement.
- Rewrite the equation with these scaled/dimensionless variables.

$\rightsquigarrow$ **NOTE in Lecture 5 we outline a more systematic approach to non-dimensionalisation of equations.**

Metapopulations

(largely taken from `Essential Mathematical Biology` by Nicholas Britton)

- This isn't really different from the Logistic model - it's just that the approach and scenario are sufficiently different to merit (in my opinion) covering it. Also, we may use this approach later with interacting species.
- This allows us to incorporate a *spatial* element (implicitly) into our modelling of population dynamics, *while still using ordinary differential equations*.
- DEFINITION `A metapopulation is a group of spatially separated populations of the same species which interact in some way - i.e. there is some movement of individuals from one population to another`. Think for example of different populations of a given species of plant or animal (which can swim a bit or otherwise cross a body of water) living on a large group of nearby islands (archipelago).
- Was used by **Richard Levins** (inventor of the word "metapopulation") in 1969 to model population changes of insect pests in fields.
- BASIC ASSUMPTIONS In the *metapopulations* approach, we assume the set of potentially habitable *sites* (or *patches*) is large, the sites are identical, and they are all isolated from each other in the same way.
- We will look at the basic original model by **Levins** where the measure of population is simplified to the point that each habitable patch is considered at any point in time to be either occupied or unoccupied/vacant.

- ↪ Studies of patchy environments such as those assumed in the metapopulation model have shown that the overall species often manage to survive even through cycles of local *extinctions* and *recolonisations* in the different habitable patches. So if the population on a site becomes extinct there is a chance it could be recolonised by members of the species from other sites.
- → Assume a large set of K potentially habitable sites and let $p(t)$ be the fraction of sites occupied at time t *(so $1 - p(t)$ is the fraction of unoccupied sites at time t).*
  - ▶ Let $e\delta t$ be the probability that an occupied site becomes unoccupied in the next time interval δt. Thus e is a (local) **rate of extinction** *(a mean rate of extinction for each occupied patch)* ⇝ do a dimensional analysis of the dimensionless number $e\delta t$ to see this. This means that the mean fraction of sites which become unoccupied in the next time interval δt is $ep(t)\delta t$.
  - ▶ Let c be a constant rate of colonisation from each of the $p(t)$ fraction of occupied patches *(a mean rate of colonisation from each occupied patch)*. Then during the next time interval δt, the probability that an unoccupied site becomes occupied is $cp(t)\delta t$. This means that the mean fraction of sites which become newly occupied in the next time interval δt is $cp(t)\delta t(1 - p(t))$
- ⇝ *ASIDE: c above is often referred to as the rate of propagule generation from each of the $p(t)$ fraction of occupied sites. Propagule is a general term for any material used to propagate an organism - which may itself be different from the parent organism, such as the seeds or spores of plants.*

- Thus the net change in the fraction of sites occupied in the time interval from t to $t+\delta t$ is $p(t+\delta t) - p(t) =$

$$\textit{mean fraction of sites which become occupied} - \textit{mean fraction of sites which become unoccupied}.$$

$$\text{So } p(t+\delta t)-p(t) = cp(t)\delta t(1-p(t))-ep(t)\delta t = (cp(t)(1-p(t))-ep(t))\delta t \Rightarrow$$

$$\frac{p(t+\delta t)-p(t)}{\delta t} = cp(t)(1-p(t))-ep(t)$$

and taking the limit as $\delta t \to 0$ we get the basic **Levins** ODE model for metapopulations:

$$\frac{dp}{dt} = cp(t)(1-p(t)) - ep(t).$$

→ Note in this model, extinction of the population from a given occupied site is assumed to be independent of the number of other sites occupied, BUT colonisation of a given vacant site is a linear function of the number/fraction of sites available to provide colonists.

→ This equation is just a Logistic DE in disguise. I will for now leave it as an exercise for you to rewrite it in the form $\frac{dp}{dt} = rp\left(1-\frac{p}{K}\right)$ for appropriate r and K.

Reminder: $\frac{dp}{dt} = cp(t)(1 - p(t)) - ep(t)$.

- The critical parameter in the *metapopulation* ODE is the **basic reproduction ratio**, $R_0 = \dfrac{c}{e}$, which represents the number of sites an occupied site can expect to colonise before becoming extinct.
- Clearly there is a threshold when $R_0 = 1$. If $R_0 > 1$ and $p(0) > 0$ it can be shown that there is a stable equilibrium at $p(t) = 1 - \dfrac{1}{R_0} = 1 - \dfrac{e}{c}$ and therefore the population always persists and never dies out over the entire set of sites. If $R_0 < 1$, it can be shown that $p(t) \to 0$ as $t \to \infty$ so that the population eventually becomes extinct over the entire set of sites. Thus the dispersal/colonisation must be sufficiently large ($R_0 > 1 \Rightarrow c > e$) for the population to survive.
- A slight variation on this ODE can show the effect of habitat destruction on the survival chances of the species. Removal of a fraction D of the habitat leads to the modified equation

$$\frac{dp}{dt} = cp(t)(1-D - p(t)) - ep(t)$$

which contains the assumption that any attempted colonisation of a removed patch is unsuccessful and leads to the destruction of the propagules.

Reminder: $\frac{dp}{dt} = cp(t)(1 - D - p(t)) - ep(t)$.

- The **basic reproduction ratio** is changed now from $R_0 = \dfrac{c}{e}$ to $R_0' = \dfrac{c(1-D)}{e}$ since only the fraction $1 - D$ of the colonisations (assuming no habitat destruction) are now succesful.
- This means that the critical threshold is now

$$R_0' \quad = \quad 1 \quad \textit{or equivalently} \quad \left(\frac{c}{e}\right) \quad = \quad R_0 \quad = \quad \frac{1}{1-D}.$$

  Rearranging this equation to solve for D, we see that the critical threshold is reached when

$$D = 1 - \frac{1}{R_0}$$

  so extinction occurs when D is above this level.
- NOTE this critical value of D is the same as the steady state solution to the original metapopulation equation (when $D = 0$).
- Thus extinction occurs if only a fraction (depending on e and c) of the habitable sites are destroyed. An equivalent observation in epidemiology *("the study of the distribution and determinants of health-related states or events (including disease), and the application of this study to the control of diseases and other health problems")* is that one need only vaccinate a certain critical fraction of the susceptible population to eradicate a disease.

HOMEWORK:

- Review finding eigenvalues and eigenvectors of square matrices. For example, see the *Supplementary Lecture on Eigenvalues and Eigenvectors and Matrix/Vector Functions of a Single Variable* under the **Lecture 4** Section of the class Moodle page.

APPENDIX A - Constructing Mathematical Models

From section 1.1 of **Elementary Differential Equations** by Boyce and DiPrima *(Wiley)*, modified. The following steps are often involved in the modelling process:

1. Identify the dependent and independent variables and assign letters to represent them. In ODE models, the independent variable is often time.
2. Choose appropriate units of measurement for each variable. For example, depending on what you are modelling it might make more sense to measure time in seconds or years.
3. State the basic principle(s) which underlie(s) or govern(s) the problem you are investigating. This might be a widely-recognised physical law, such as Newton's law of motion, or a more speculative assumption based on observations. This step will typically require that you have some familiarity with the field in which the problem lies.
4. Express the principle or law in step 3 in terms of the variables you chose in step 1. This is typically where you obtain your differential (or other) equation(s) whose solution(s) are what you seek - the mathematical model of the problem. Note this may involve the use of physical constants or parameters and the choice of appropriate values for them, or it may involve the use of auxiliary/intermediate variables that must then be related to the primary variables.
5. Do a *dimensional analysis* of your equation(s) to ensure that both sides have the same unit(s) of measurement.

APPENDIX B - Newton's Method for Solving Systems of Nonlinear Equations

- The single variable Newton's method for solving a nonlinear equation $f(x) = 0$, $\boldsymbol{x_{k+1} = x_k - \frac{f(x_k)}{f'(x_k)} = x_k - [f'(x_k)]^{-1} f(x_k)}$ can be easily generalised to solve a nonlinear *SYSTEM* of n equations $\vec{F}(\vec{x}) = 0$, where $\vec{F}$ is an $n-$dimensional vector field.
- First recall that if $\vec{F}(\vec{x}) = [f_1(x_1, x_2, \dots, x_n),\ f_2(x_1, x_2, \dots, x_n),\ \dots,\ f_n(x_1, x_2, \dots, x_n)]^T$ is an $n-$dimensional vector field ($\vec{F} : \mathbb{R}^n \mapsto \mathbb{R}^n$), then the **Jacobian matrix** of $\vec{F}$ is denoted $\vec{F}\,'(\vec{x})$ and is the $n \times n$ matrix given by:

$$\vec{F}\,'(\vec{x}) = \begin{pmatrix} \frac{\partial f_1}{x_1} & \frac{\partial f_1}{x_2} & \frac{\partial f_1}{x_3} & \dots & \dots & \frac{\partial f_1}{x_n} \\ \frac{\partial f_2}{x_1} & \frac{\partial f_2}{x_2} & \frac{\partial f_2}{x_3} & \dots & \dots & \frac{\partial f_2}{x_n} \\ \frac{\partial f_3}{x_1} & \frac{\partial f_3}{x_2} & \frac{\partial f_3}{x_3} & \dots & \dots & \frac{\partial f_3}{x_n} \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\ \frac{\partial f_n}{x_1} & \frac{\partial f_n}{x_2} & \frac{\partial f_n}{x_3} & \dots & \dots & \frac{\partial f_n}{x_n} \end{pmatrix}$$

- Then to solve the *nonlinear system* of equations $\vec{F}(\vec{x}) = \vec{0}$, where $\vec{x} = [x_1, x_2, \ldots, x_n]^T$, $\vec{F}(\vec{x}) = [f_1(x_1, x_2, \ldots, x_n),\ f_2(x_1, x_2, \ldots, x_n),\ \ldots,\ f_n(x_1, x_2, \ldots, x_n)]^T$ is a vector field ($\vec{F} : \mathbb{R}^n \mapsto \mathbb{R}^n$), and $\vec{0}$ is the $n \times 1$ zero vector, we could use the systems version of *Newton's method* which resembles the scalar version:

$$\vec{x}^{(k+1)} = \vec{x}^{(k)} - [\vec{F}'(\vec{x}^{(k)})]^{-1}\vec{F}(\vec{x}^{(k)}).$$

where $\vec{F}'(\vec{x})$ is the $n \times n$ **Jacobian** matrix: with $\dfrac{\partial f_i(\vec{x})}{\partial x_j}$ being the $i-j$th entry of that matrix. *NOTE I'm using bracketed superscripts to indicate the iteration number in Newton's method.*

- ⇝ In practical terms, the systems version of *Newton's method* can also be written as

$$\vec{x}^{(k+1)} = \vec{x}^{(k)} + \vec{\delta}^{(k)}$$

where $\vec{\delta}^{(k)}$ is the solution to the *linear* system

$$\vec{F}'(\vec{x}^{(k)})\vec{\delta}^{(k)} = -\vec{F}(\vec{x}^{(k)}).$$

- A typical stopping criterion for this method is to stop when $\|\vec{x}^{(k+1)} - \vec{x}^{(k)}\| = \|\vec{\delta}^{(k)}\| < \epsilon$ for the first time, for some $\epsilon > 0$.
NOTE Matlab has an in-built `norm()` function for finding the norms of vectors.

↪ Example *(from Burden and Faires book)* for the following nonlinear system, identify $\vec{F}$ and the Jacobian matrix J:

$$\begin{aligned} 3x_1 - \cos(x_2 x_3) &= \frac{1}{2} \\ x_1^2 - 81(x_2+0.1)^2 + \sin x_3 &= -1.06 \\ e^{-x_1 x_2} + 20x_3 &= \frac{3-10\pi}{3}. \end{aligned}$$

$$\vec{F}(x_1,x_2,x_3) = \begin{pmatrix} 3x_1 - \cos(x_2x_3) - \frac{1}{2} \\ x_1^2 - 81(x_2+0.1)^2 + \sin x_3 + 1.06 \\ e^{-x_1x_2} + 20x_3 + \frac{10\pi-3}{3} \end{pmatrix} \quad \text{and}$$

$$J(x_1,x_2,x_3) = \begin{pmatrix} 3 & x_3\sin(x_2x_3) & x_2\sin(x_2x_3) \\ 2x_1 & -162(x_2+0.1) & \cos x_3 \\ -x_2e^{-x_1x_2} & -x_1e^{-x_1x_2} & 20 \end{pmatrix}$$

↪ Solving this system with my program *sysNewton.m*, with $\vec{x}_0 = (0.1, 0.1, -0.1)^T$ and requiring that $\|\vec{x}^{(k+1)} - \vec{x}^{(k)}\|_2 < 10^{-12}$, the method converges to the following solution after six iterations:

$$\vec{x} = [0.5, \quad 4.64018203058451 \times 10^{-18}, \quad -0.523598775598299]^T$$

$\hookrightarrow$ See the class Moodle page under **Lecture 3** for *sysNewton.m*.

- NOTE when using *sysNewton.m* for the system in **EXAMPLE 2** one has to start quite close to the solution for Newton's method to converge.

- For example, using $K = 200\,000\,000$ and $r = 0.1$, after 8 iterations the method converges to (with a tolerance for the norm of the difference of successive iterates set at 10^{-6})

$$K = 188\,168\,898 \quad AND \quad r = 0.031548256731400\bar{5}$$

as expected.

APPENDIX C - Key Terminology

Alot of what we have looked at in this lecture is essentially mathematical *ecology*.

- Ecology: A branch of biology which studies the interrelationship between different species and their environment/physical surrounding.