MATH1134 - Lecture 3

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Continuous (ODE) Models of Population Growth/Decline for Single Species
- Aside 1 - Dimensional Analysis

Preliminary Basic Single Species Population Models
- The Exponential Growth (Malthusian) Model
- The Logistic Model *(and related models)*
- Aside 2 - Nondimensionalisation of Equations

Metapopulations

Appendix

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".

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- 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.

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$\rightsquigarrow$ 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

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↦ **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.**

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  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.

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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

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

where $r = b - d$

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- → Note you could have come to the same conclusion performing the dimensional analysis on $\frac{dN}{dt} = rN$ instead.

- NOTE the Malthusian ODE $\frac{dN}{dt} = rN$ 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 $r < 0$.

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- 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.

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

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- $\rightsquigarrow$ The **Logistic Growth Model** is an attempt to derive a *simple* $\boldsymbol{g(N)}$ which reflects key empirical observations about population growth.

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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 $N > 40$.

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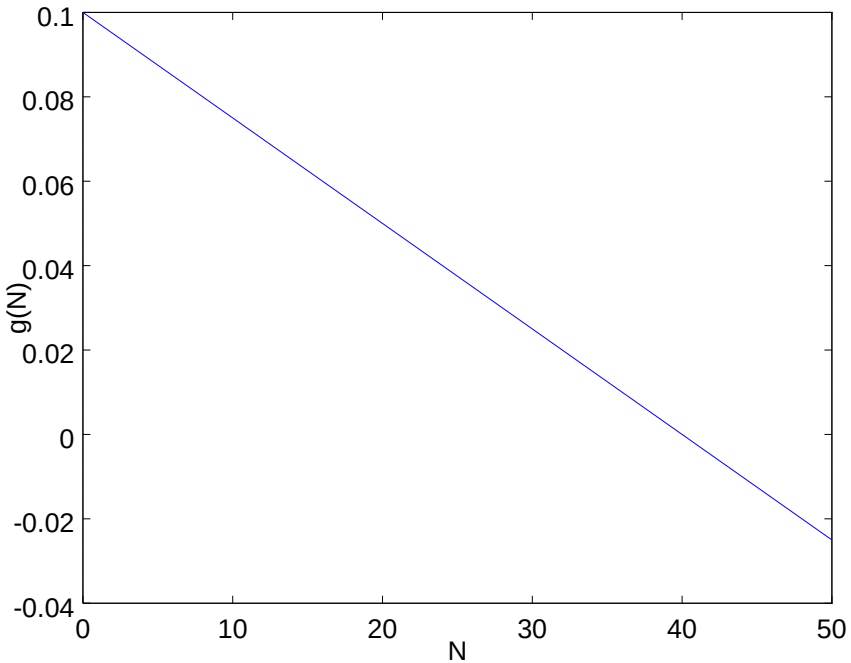

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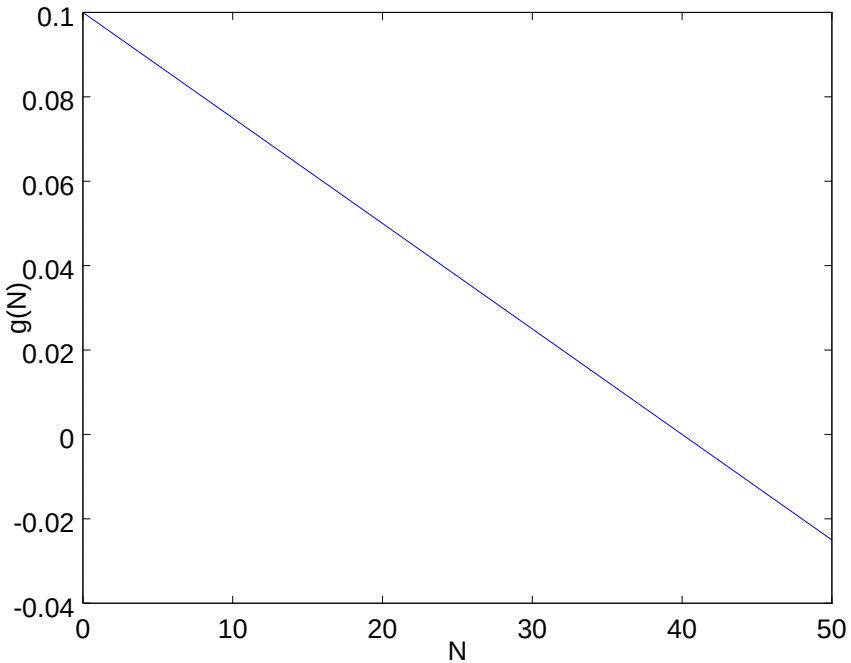

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Thus $f'(0) = r$ and $f'(K) = -r$ and so if $r > 0$, $N(t) = 0$ is an *unstable equilibrium solution* and $N(t) = K$ is a *stable equilibrium solution* *(or vice versa if $r < 0$)*.

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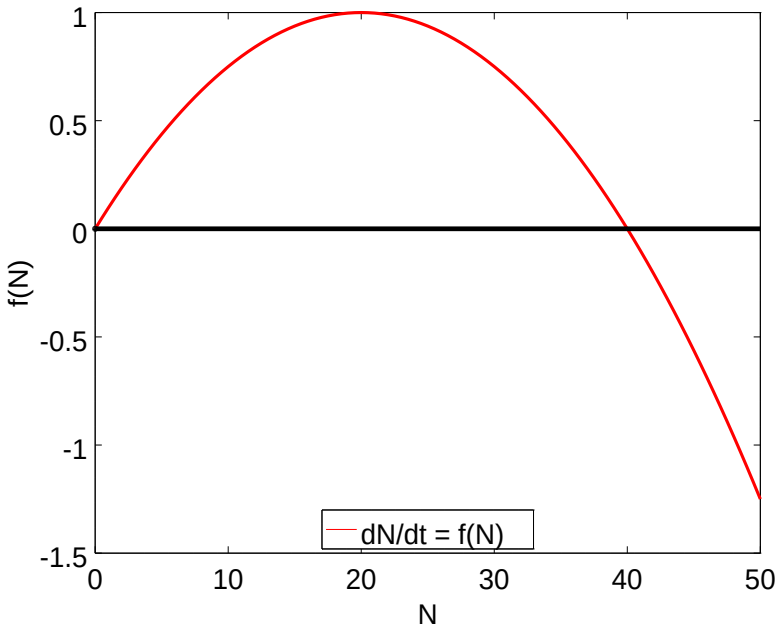

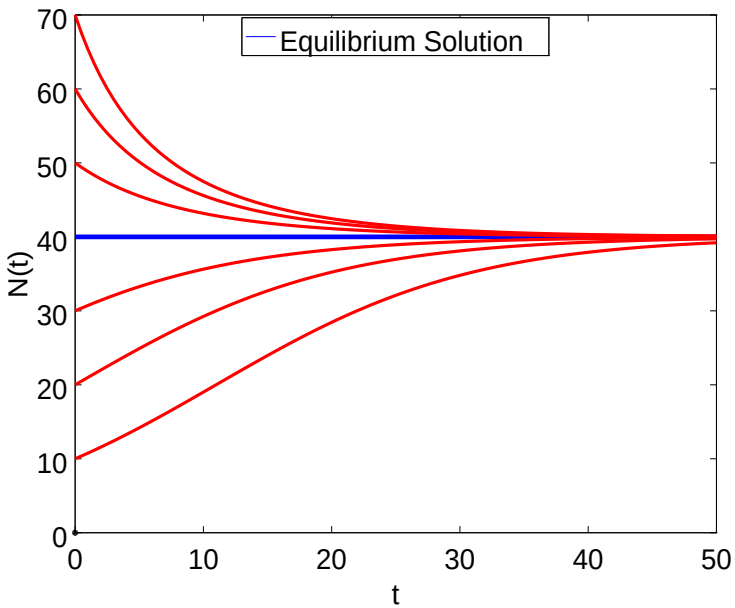

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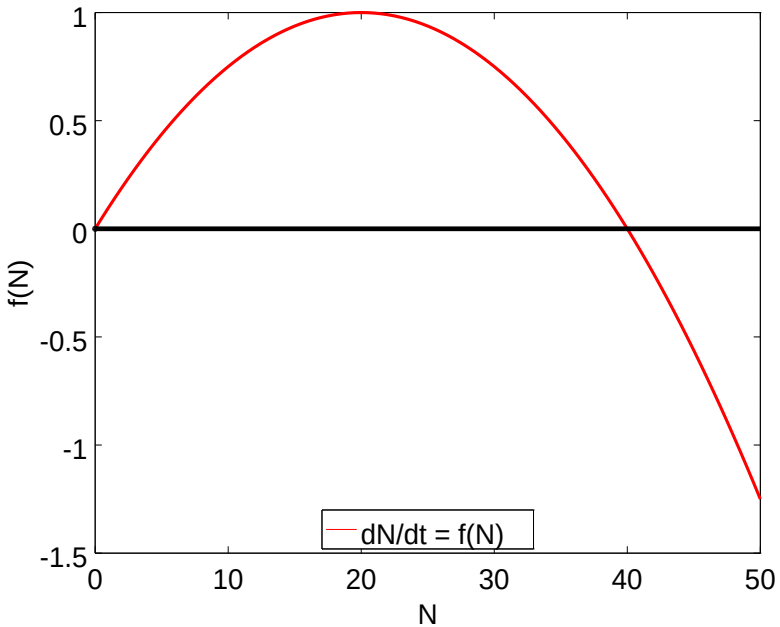

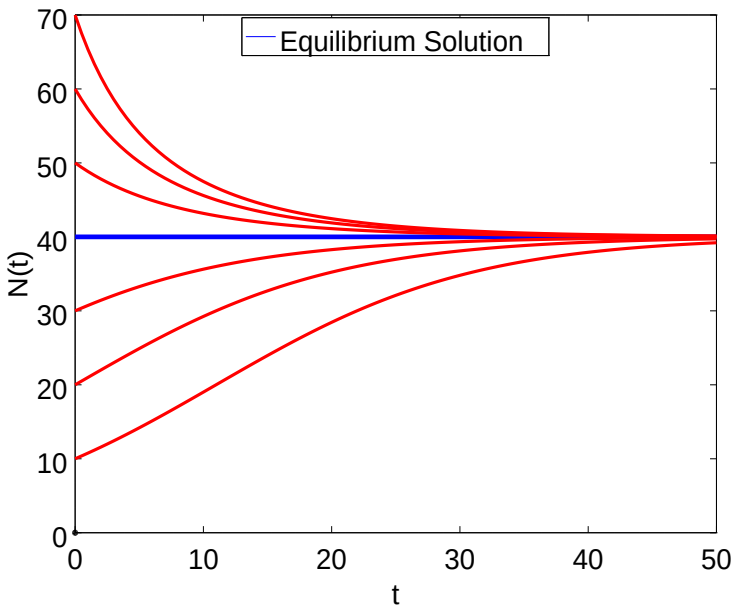

The fact that $N(t) = 40$ is a stable equilibrium point is obvious, and one can also deduce that $N(t) = 0$ is unstable (although I have not plotted anything for $N < 0$ since it makes no physical sense for a population).

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- 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*.

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- 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	???

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  - 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:

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

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

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

- ANSWER continued Also

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

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

- 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.

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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.

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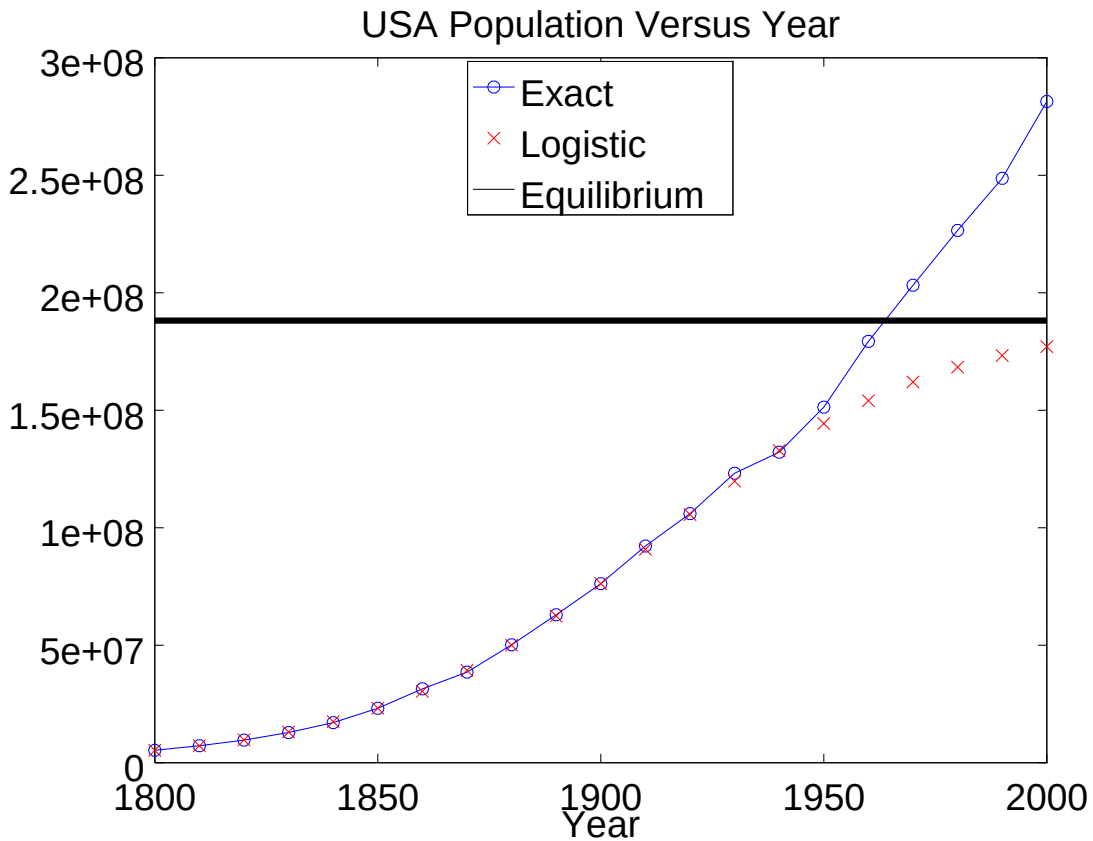
- $N(150) = 144371704$ versus the real 1950 population of $151,325,798$ for an absolute error of 6 954 093 and a relative error of 0.04595 $\rightsquigarrow$ not so good this time!

- 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.



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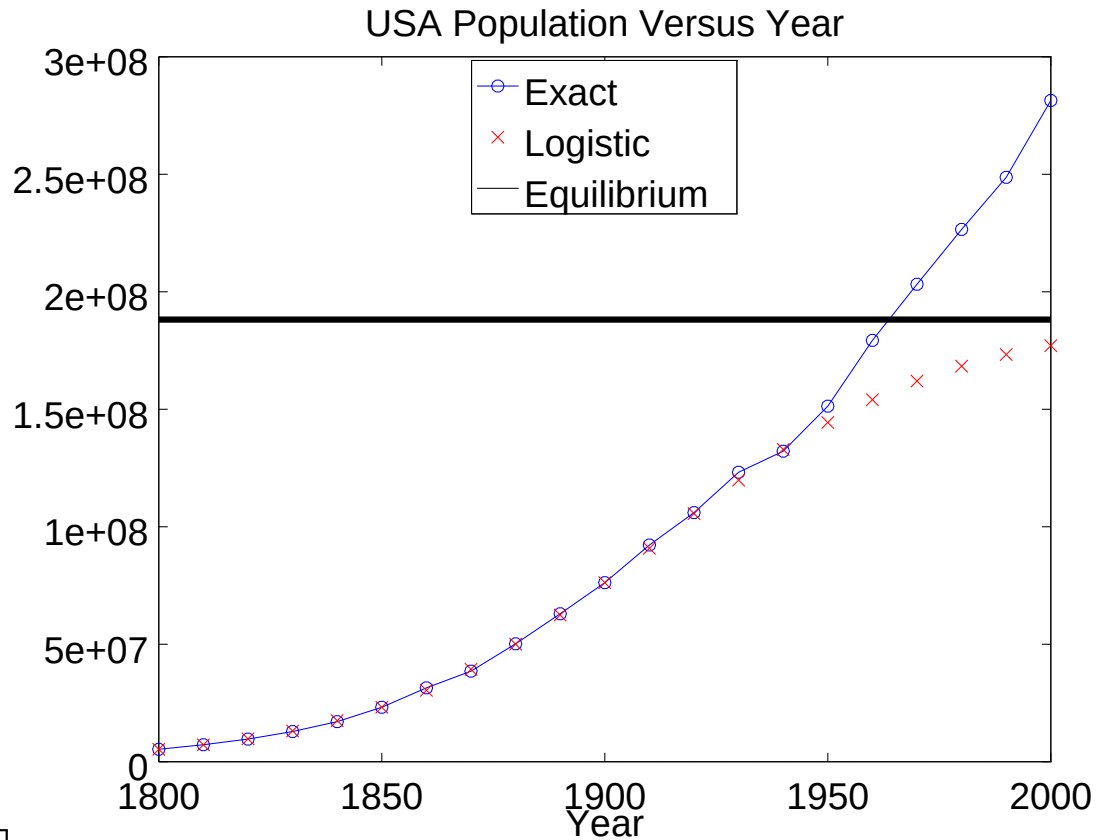

EXERCISE Do EXAMPLE 2 with the exponential growth model instead, using data from the years 1800 and 1900 to calculate r.

↪ 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

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

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- 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

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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

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

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 $\alpha = H/H_{max} < 1$

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

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

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

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.

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

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- 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*:

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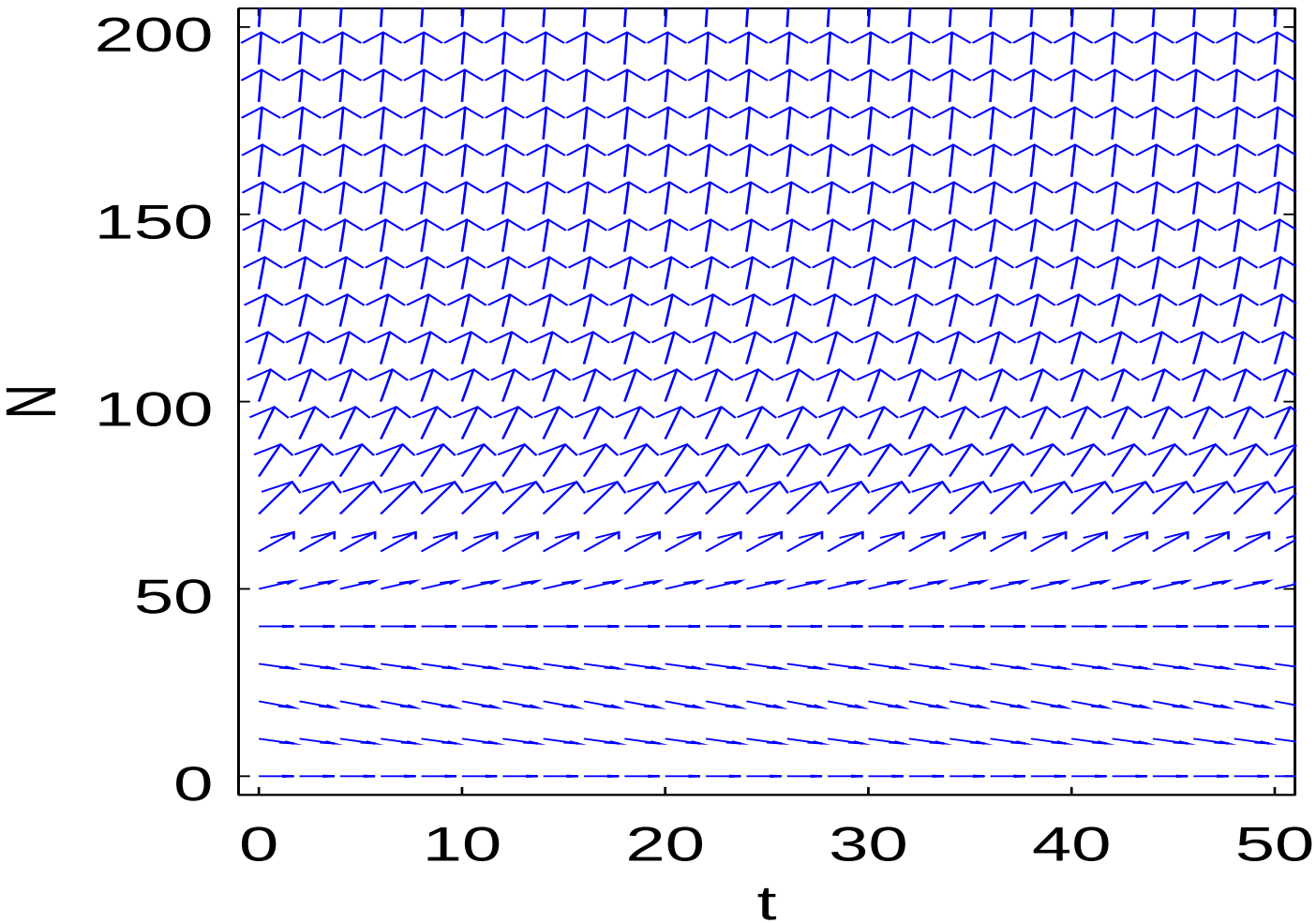
- And if we let $f(N)$ be the right-hand-side of this DE, then $f'(N) = -r\left(1 - \frac{N}{T}\right) + \frac{rN}{T} = -r + \frac{2rN}{T}$, so $f'(0) = -r < 0 \Rightarrow N(t) = 0$ is a **stable** equilibrium point, and $f'(T) = r > 0 \Rightarrow N(t) = T$ is an **unstable** equilibrium point. This 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 $T = 40$.

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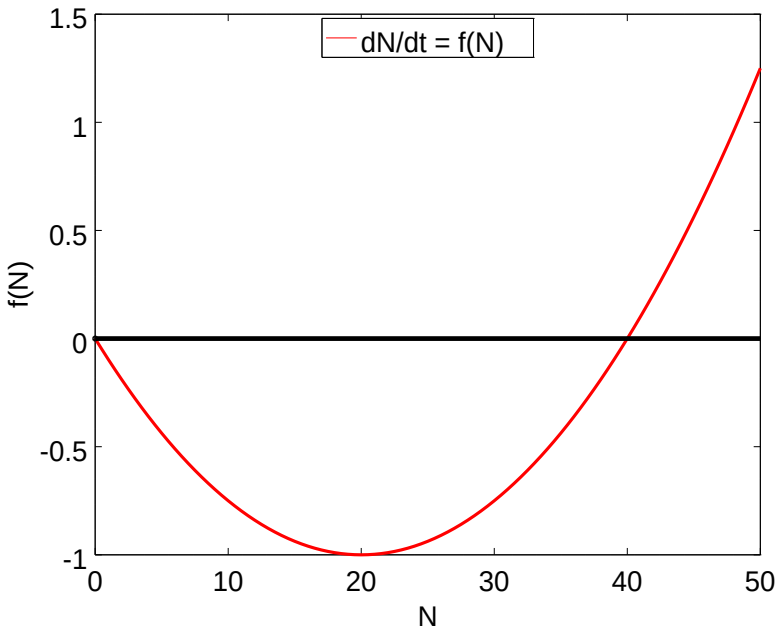

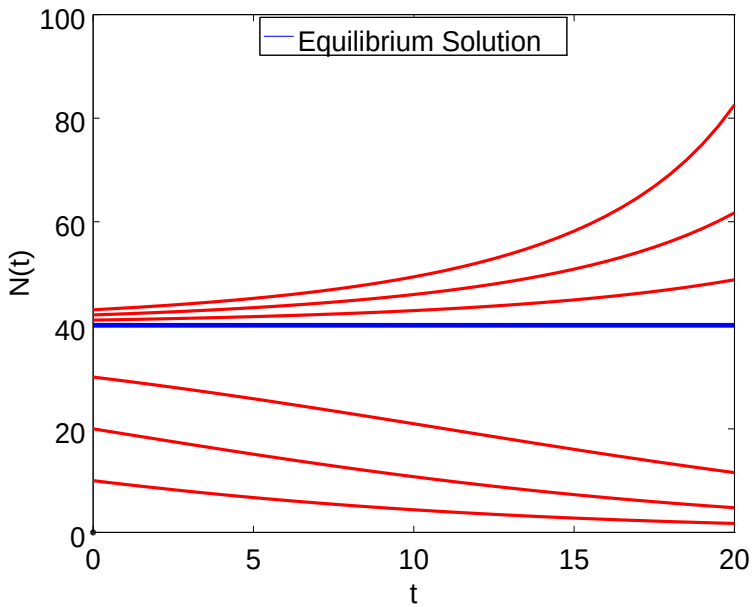

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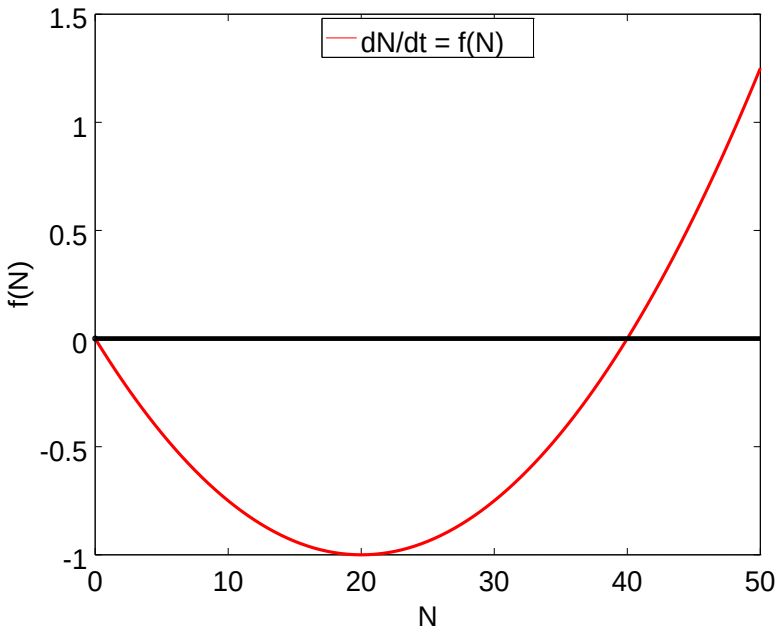

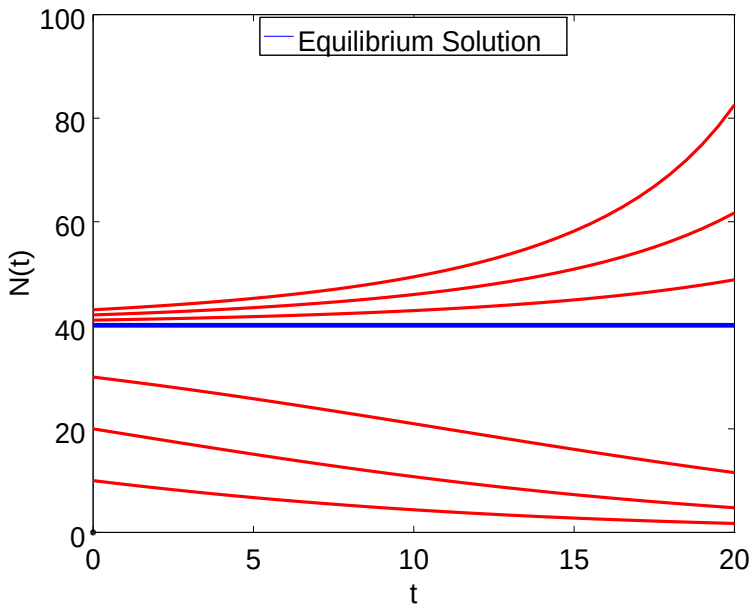

The fact that $N(t) = 40$ is an unstable equilibrium point is obvious, and one can also deduce that $N(t) = 0$ is stable (although I have not plotted anything for $N < 0$ since it makes no physical sense for a population).

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- 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:

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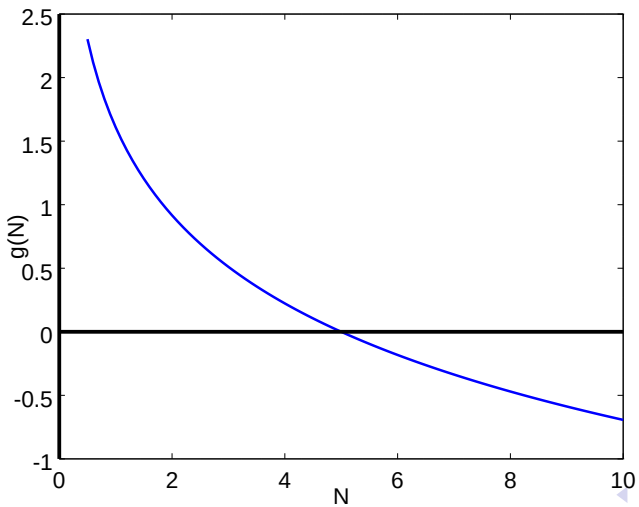

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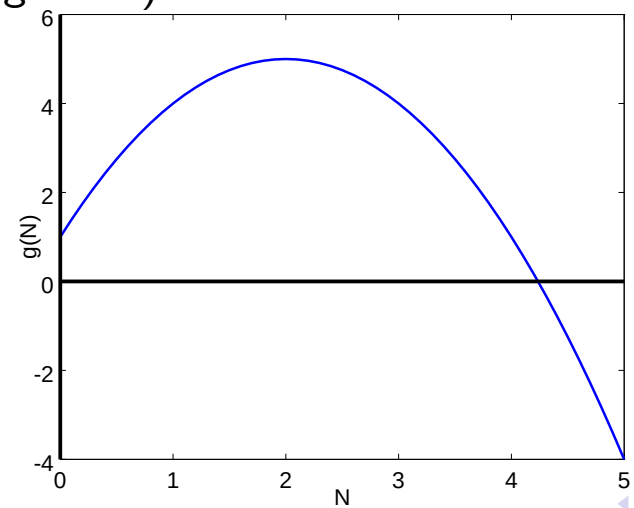
   - This *Allee effect* is typically due to cooperation within the individuals in the population - for example, fighting off predators or collecting food (the more individuals there are to do these, the greater the success of the group in doing them).



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- 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.

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- 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!)*

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

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(largely taken from Essential Mathematical Biology by Nicholas Britton)

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- 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.

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⇝ *ASIDE:* $\boldsymbol{c}$ *above is often referred to as the rate of propagule generation from each of the* $\boldsymbol{p(t)}$ *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.*

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

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

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  so extinction occurs when D is above this level.
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- 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

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- First recall that if $\vec{F}(\vec{x}) = [f_1(x_1, x_2, \ldots, x_n),\ f_2(x_1, x_2, \ldots, x_n),\ \ldots,\ f_n(x_1, x_2, \ldots, x_n)]^T$ is 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:

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

- 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,

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

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- ⇝ 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

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  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:

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

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

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

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

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- 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})

$$K = 188\ 168\ 898 \quad AND \quad r = 0.0315482567314005$$

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.