Mathematical Ecology and Epidemiology

Lecture notes for Spring 2024

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Welcome

This site will contain the lecture notes and problem sheets for the Ecology and Epidemiology part of the "Mathematical Ecology, Epidemiology and Evolution" module as taught at the University of York in the Spring of 2024. The mathematics used in Mathematical Ecology and in Mathematical Epidemiology are quite similar, whereas the mathematics used in Mathematical Evolution has a different flair and that part is taught by a different lecturer, George Constable.

This part is taught in three two-week blocks, with each block consisting of 6 lectures, one problem sheet, one examples class and one small-group seminar. Between each block there will be a two-week block of Mathematical Evolution.

The notes will be created after each lecture and will continue to be periodically revised. Whenever you spot something that is not quite right, please email me at gustav.delius@york.ac.uk or submit your correction in the correction form at https://forms.gle/w17c19vWnM7wpLpz7.

1 Continuous-time population models

We are interested in modelling the time evolution of the population number $N(t)$, starting with the current population number $N(0) = N_0$. Thinking about the processes by which the population number can change, we see that we can write the rate of change in the population number as

$$\frac{dN}{dt} = \text{birth rate} - \text{death rate} + \text{immigration rate} - \text{emigration rate}. \tag{1.1}$$

The idea behind this approach is that if we understand how these processes depend on the population number N, then we can find $N(t)$ by solving the above differential equation. Different assumptions about the individual rates will give us different models for N(t). We will look at some influential models now.

1.1 Exponential model

This is the simplest and oldest model, introduced by Thomas Robert Malthus in 1798. If we assume that the per-capita birth rate b and the per-capita death rate d are fixed constants, then the general differential equation Eq. 1.1 becomes the linear equation

$$\frac{dN}{dt} = bN - dN = rN, \tag{1.2}$$

where we introduced the new parameter $r = b - d$. This equation is easy to solve:

$$N(t) = N_0 e^{rt}. \tag{1.3}$$

So if the birth rate exceeds the death rate and hence $r > 0$, the model predicts exponential growth. In the opposite case of lower birth rate than death rate the model predicts exponential decay of the population number towards extinction. Only when birth and death rates are perfectly equal can the population stay steady over time. We illustrate that in Figure 1.1.

1.2 Logistic model

Exponential population growth can not be maintained for ever. There will be a limit to the size of population that an ecosystem can maintain. When the population gets closer to this limit its growth rate will decrease, for example due to competition for limited food sources

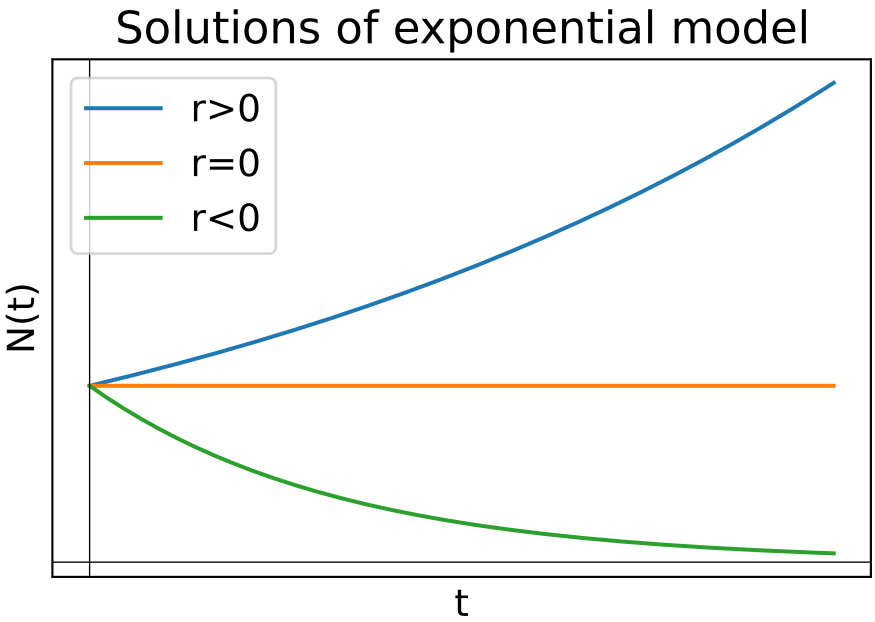

Figure 1.1: Solutions to the exponential model.

or space, or due to disease. This decrease in the growth rate is captured by the logistic equation

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right), \tag{1.4}$$

where K is the carrying capacity of the environment. To see how the logistic equation captures the idea of a carrying capacity, we can look at the two limiting cases. When $N \ll K$, the logistic equation reduces to the exponential equation Eq. 1.2. When $N \approx K$, the growth rate is approximately zero.

In Figure 1.2 make a plot of the right-hand side of the logistic equation Eq. 1.4 to see how the growth rate depends on the population number.

From the plot we see that the growth rate is zero at $N = 0$ and $N = K$, and it is maximal at $N = K/2$. By realising that dN/dt is the slope of the graph of $N(t)$ we can sketch a few solutions to the logistic equation Eq. 1.4 in Figure 1.3.

The logistic equation Eq. 1.4 can be solved analytically to give

$$N(t) = \frac{K}{1 + \left(\frac{K}{N_0} - 1\right) e^{-rt}} = \frac{N_0 K e^{rt}}{K + N_0(e^{rt} - 1)}. \tag{1.5}$$

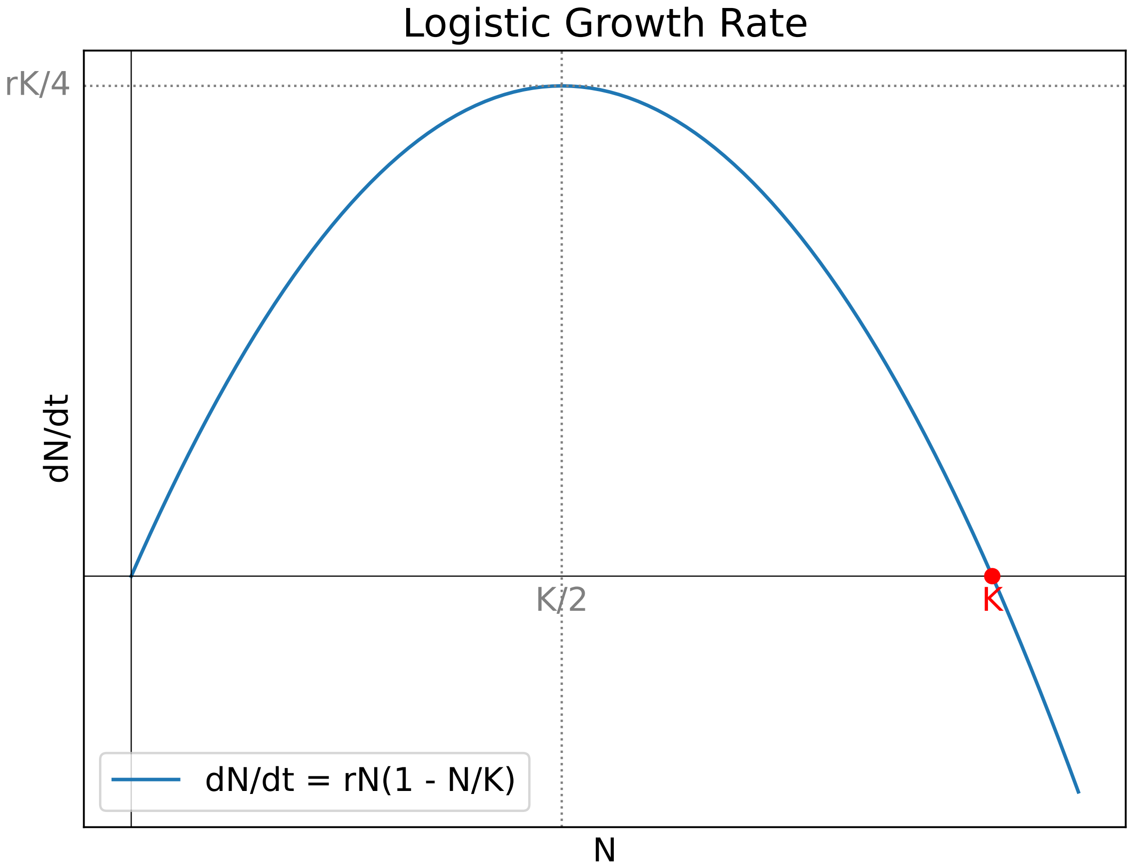

Figure 1.2: The logistic growth rate as a function of the population number.

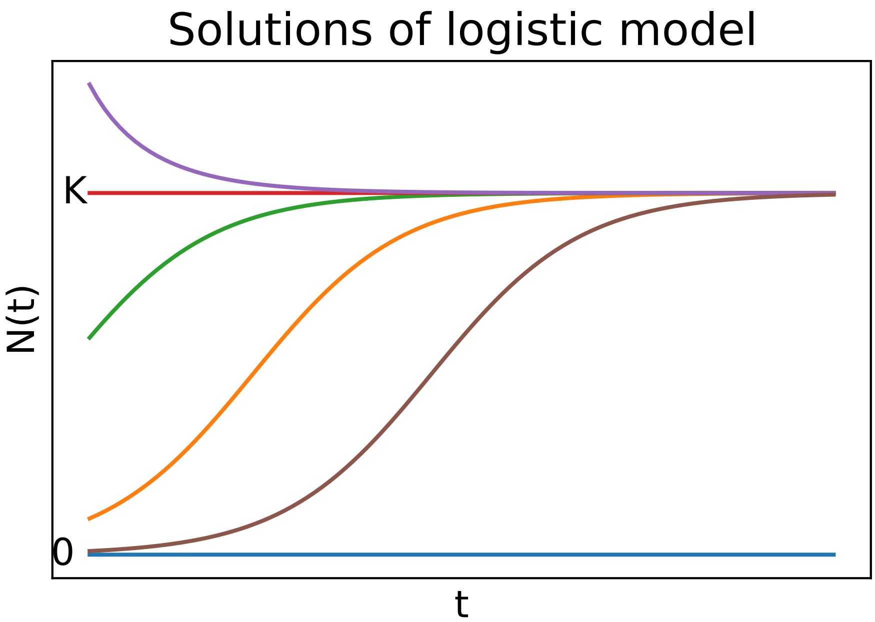

Figure 1.3: Solutions to the logistic equation.

Problem sheet 1

Exercises marked with a * are essential and are to be handed in. Exercises marked with a + are important and you are urged to complete them. Other exercises are optional but recommended.

The * and + markup will only be applied to exercises once the material you need to solve them has been covered in the lectures.

*Sketching solutions

Exercise 1.1. Consider the population model with carrying capacity and Allee effect given by the differential equation

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)\left(\frac{N}{K_0} - 1\right).$$

Here $r > 0$, $K > K_0 > 0$ are constants. Simply by considering the shape of the right hand side, sketch a graph with several solutions for different initial conditions. Choose two initial conditions between 0 and K_0, two initial conditions between K_0 and K and one initial condition larger than K. Note that the graph only needs to be qualitatively correct, similar to the rough sketch for the solutions of the logistic model sketched in the first lecture.

+Von Bertalanffy growth

Exercise 1.2. Assume the weight $w(t)$ of an individual fish at time t is governed by the differential equation

$$\frac{dw}{dt} = \alpha\, w^{2/3} - \beta w$$

with initial condition $w(0) = w_0$ (the weight at birth), and where α and β are positive parameters depending on the fish species.

i) Without solving the differential equation, just thinking about fixed points and their stability, determine $\lim_{t\to\infty} w(t)$.

ii) Derive the linear first order ODE for $u = w^{1/3}$ and solve it.

iii) Use the solution for u to find the solution for w.

Solving logistic equation

Exercise 1.3. By using separation of variables and partial fractions, solve the logistic equation

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

with initial condition $N(0) = N_0$.

Harvesting with fixed effort

Exercise 1.4. Consider a population $N(t)$ that is described by the logistic model with carrying capacity K and initial growth rate r. You want to harvest this population, for example by hunting or fishing, with some effort E. The rate at which you harvest individuals (which removes them from the population and hence results in an additional source of death) is proportional to the size of the population: $H = EN$. This is called the yield. Write down the differential equation for $N(t)$ including this harvesting term. Determine the fixed points and their stability. Find the maximum sustainable harvest rate H, i.e., the maximum harvest rate that can be sustained indefinitely.

Harvesting with fixed quota

Exercise 1.5. As in Exercise 1.4, consider a population $N(t)$ that is described by the logistic model with carrying capacity K and initial growth rate r. Imagine that this describes a fish population in a lake where fishing is going to be introduced, and that you are tasked with setting the quota that limits the rate at which the fishers are allowed to take fish out of the lake. The fishers demand that you set the quota to the maximum sustainable level. What is the maximum sustainable quota according to the model? Would it be wise to give in to the demand of the fishers and set the quota at this level?

Harvesting in Gompertz model

Exercise 1.6. Repeat exercises 1.4 and 1.5 but with the logistic model replaced by the Gompertz model

$$\frac{dN}{dt} = \alpha N \log \frac{K}{N},$$

where α and K are positive constants.

Spruce budworm

Exercise 1.7. In the spruce budworm model that you explored in the module Dynamical Systems,

$$\frac{du}{dt} = ru\left(1 - \frac{u}{q}\right) - \frac{u^2}{1+u^2},$$

suppose that the carrying capacity q is fairly large and that the growth rate r assumes some value consistent with there being three (non-zero) steady states. Suppose also that the population u is at the outbreak steady state u_3. Keeping q fixed, imagine that r is decreased to a very small value. What happens to the population? If r is later restored to its original value, what does the population tend to, and why?

Wasps

Exercise 1.8. In a colony of the European Hornet there is a single queen that produces all the offspring. It produces two kinds of offspring: workers and reproducers. We'll denote the number of workers alive at time t by $n(t)$ and the number of reproducers by $N(t)$. The workers are responsible for collecting food. They can't breed themselves and they die in the winter. However they are necessary to allow the queen to reproduce because without the food that they are collecting the queen would have nothing to eat. So we need workers. But because they die in winter, they don't help the survival of the colony in the long run. That's where the reproducers come in. They don't do any work, but they can, if they survive the winter, breed in the next spring as new queens.

So the queen now has a strategy of how to proceed: It first of all needs to produce workers, and from time zero to time t_c it only produces workers. We assume that the birth rate is proportional to the number of workers, so that the total birth rate of workers is $rn(t)$ for some constant $r > 0$. The queen then switches to producing only reproducers from time t_c up to the start of winter at time T and we assume that the total birth rate of reproducers is $Rn(t)$ for some constant $R > 0$. We also assume that until the start of winter there are no deaths.

What is the optimal time t_c at which the queen should switch from producing workers to producing reproducers in order to achieve the largest number of producers $N(T)$ at the start of the winter and therefore to the largest number of wasps in the following year.

Wasps with death

Exercise 1.9. In the wasp example from question 1, assume that the worker wasps die at a constant per-capita rate d but the reproducers do not die. Also assume that at time t=0 there is one worker, n(0)=1. Keep the birth rates as in Exercise 1.8. Determine the number of workers $n(t)$ for any time between t_c and T. Determine the number of reproducers at the onset of winter at time T. Derive the optimal time for the switchover time t_c.

Modified Fibonacci

Exercise 1.10. Modify Fibonacci's model for the population of rabbits that was discussed in the lecture to model the case where at the end of each month some of the rabbits die, so that only a fraction r of the pairs of rabbits that are alive in month t survives to the next month. Assume that reproduction takes place before this mortality and that the offspring all survive. Solve this to give the number N_t of pairs after t months given that initially there are c pairs. (Ignore the issue that fractional numbers of pairs don't really make sense, because if c is large this fractional part makes little difference.)

Discrete logistic model

Exercise 1.11. For some choices of the parameters, the discrete logistic model

$$N_{t+1} = rN_t\left(1 - \frac{N_t}{K}\right)$$

can lead to negative population numbers even when initially starting with a positive population below its carrying capacity. Derive the condition on the parameters for this to happen. One good way to approach this is to think about what the cobweb diagram would have to look like for such a scenario.

Discrete time model

Exercise 1.12. Consider the discrete time model

$$N_{t+1} = \frac{rN_t}{1 + (N_t/K)^b}$$

where r, b and K are positive parameters with $b > 1$. Show that the model has two steady states. Investigate the stability of the trivial steady state. Show that the non-trivial steady state can lose stability through a period doubling bifurcation at $b = 2r/(r-1)$, or a tangent bifurcation at $r = 1$. Show also that, after a sufficient amount of time,

$$\frac{Kr^2 b^{b-1}(b-1)^{(b-1)/b}}{b^b + r^b(b-1)^{b-1}} \leq N_t \leq \frac{rK}{b}(b-1)^{(b-1)/b}.$$

Sex ratio

::: {#exr-sex_ratio} As in the lecture, consider the sex-structured population model

$$\frac{dF}{dt} = -\mu_F F + b_F\phi(F, M), \quad \frac{dM}{dt} = -\mu_M M + b_M\phi(F, M),$$

where $F(t)$ denotes the number of females and $M(t)$ the number of males and μ_F, μ_M, b_F, b_M are positive constants. Unlike in the lecture make the choice

$$\phi(F, N) = \sqrt{FM}.$$

Determine the asymptotic sex ratio. ::

Spotted Owl

Exercise 1.13. The Spotted Owl (Strix occidentalis) has the following population parameters:

$$m_a = \begin{cases} 0 & a < 2 \\ m & a \geq 2 \end{cases}, \quad l_2 = l, \quad l_{a+1} = p\, l_a \text{ if } a \geq 2.$$

where m_a is the number of females born, on average, to a female of age a, l_a is the fraction of females surviving from birth to age a. Here m, l and p are constants and age a is integer valued.

We model the number B_t of female births at time t by the difference equation

$$B_t = \sum_{a=2}^{\infty} B_{t-a}\, l_a\, m_a.$$

Here the time t and the age a are integer valued.

a) Using the Ansatz $B_t = c\,\lambda^t$, show that this is a solution if λ satisfies the equation $\psi(\lambda) = 1$, where

$$\psi(\lambda) = \sum_{a=2}^{\infty} \lambda^{-a}\, l_a\, m_a.$$

b) Use the formula for the geometric series to show that

$$\psi(\lambda) = \frac{l\,m}{\lambda(\lambda - p)}.$$

c) Solve the equation $\psi(\lambda) = 1$ to find the possible values of λ and use that to write the general solution for B_t.

Reaction-diffusion equation on strip

Exercise 1.14. Consider the partial differential equation

$$\frac{\partial u}{\partial t} = f(u) + D\frac{\partial^2 u}{\partial x^2}$$

where $f(0) = 0$ and $f'(0) > 0$. Assume that u is small and show that under this assumption the equation can be approximated by

$$\frac{\partial u}{\partial t} = f'(0)\, u + D\frac{\partial^2 u}{\partial x^2}.$$

With Dirichlet type boundary conditions $u(0, t) = u(L, t) = 0$ show that if the population is not to be driven to extinction we must have $L > \pi\sqrt{D/f'(0)}$.

Age structured population

Exercise 1.15. In the age structured population model of section 2.1, show that if $b(a) = b$ and $\mu(a) = \mu$ are both constant then the condition for growth of the population reduces to what you would expect. For this purpose, start from the equations of the age-structured model and the Ansatz $n(t, a) = e^{\gamma t} r(a)$ for unknown $r(a)$ and γ. Give the expression for $r(a)$ in terms of γ. Calculate the expected number $\phi(0)$ of offspring that an individual produces during their lifetime. Then compare what this tells you about whether the population goes extinct or explodes to the corresponding condition in the Malthus model.

Age structured fish population

Exercise 1.16. We model a fish population with the age structured population model of section 2.1. Let us assume that the birth rate is constant for all fish above a maturity age a_m and zero for younger fish. Let us assume a constant natural mortality rate μ_0. Then impose a constant fishing mortality μ_f on all fish above maturity age. What is the maximum value for the fishing mortality at which the population can be maintained? What is the maximum sustainable yield?

House finches

Exercise 1.17. *[Note: in this problem we combine a continuous time model for the dynamics within a single year with a discrete model for the dynamics from one year to the next. The subscript $t \in \mathbb{Z}$ refers to the discrete year t, whereas $\tau \in \mathbb{R}$ will indicate the continuous time within a single year.]*

A population of house finches resides in an isolated region in North America. In this problem you want to find out about the long-term prospects for the population.

Each year the males and females begin their search for mates at the beginning of winter with a combined population number N_t in year t, and form P_t breeding pairs by the end of this search period, the start of the breeding season.

The mate search period lasts from within-year time $\tau = 0$ to the end of the search period at within-year time $\tau = T$. Assume that there is a 1:1 sex ratio and that males $M(\tau)$ and females $F(\tau)$ locate one another randomly to make a pair at rate σ, such that the number $M(\tau)$ of males that are not in a pair at time τ satisfies

$$\frac{dM}{d\tau} = -\sigma \, M \, F$$

and similarly the number F of females that are not in a pair at time τ satisfies

$$\frac{dF}{d\tau} = -\sigma \, M \, F.$$

You are given that the number of breeding pairs that establish a nest and breed successfully is $G(P_t)P_t$, where the fraction $G(P_t)$ takes the particular form

$$G(P_t) = \frac{1}{1 + P_t/\delta},$$

where δ represents the density of available nesting sites. Each pair that reproduces successfully has a mean number c of offspring.

The probability that a bird will survive from one year to the next is s.

a) Show that the number $n(\tau) = M(\tau) + F(\tau)$ of birds *not* in a pair is governed by

$$\frac{dn}{d\tau} = -\frac{\sigma}{2}n^2, \quad n(0) = N_t.$$

b) Using the above, show that the number $n(T)$ of birds that have not found a mate at the start of the breeding season in year t is

$$n(T) = \frac{r\,N_t}{r + 2N_t}$$

where N_t is the number of birds at the start of the season in that particular year and where $r = 4/(\sigma T)$.

c) Explain why the number of pairs $P(\tau)$ is governed by

$$\frac{dP}{d\tau} = -\frac{1}{2}\frac{dn}{d\tau}, \quad P(0) = 0.$$

d) Use the above to show that the number of breeding pairs at the start of the breeding season in year t is

$$P_t := P(T) = \frac{N_t^2}{r + 2N_t}.$$

e) Show that the population N_{t+1} at the beginning of winter in year $t+1$ is given by

$$N_{t+1} = s\,N_t + \frac{c\,N_t^2}{r + 2N_t + N_t^2/\delta}. \tag{1.6}$$

f) Find the realistic steady states of the model in Eq. 1.6 for the case that

$$\frac{c}{1-s} - 2 \geq \sqrt{\frac{4r}{\delta}}.$$

g) Draw a cobweb diagram to illustrate the stability of the steady states in the case that there are two positive steady states, labelling key features of the curves.

h) What type of bifurcation occurs when there is equality in the condition in part f)?