Mathematical Ecology and Epidemiology

Lecture notes for Spring 2024

Gustav Delius

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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.

The Mathematical Ecology and Epidemiology 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

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

The idea behind this approach is that if we understand how the rates at which these processes take place 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

$$\frac{dN}{dt} = bN - dN = rN, \qquad (1.2)$$

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

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

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
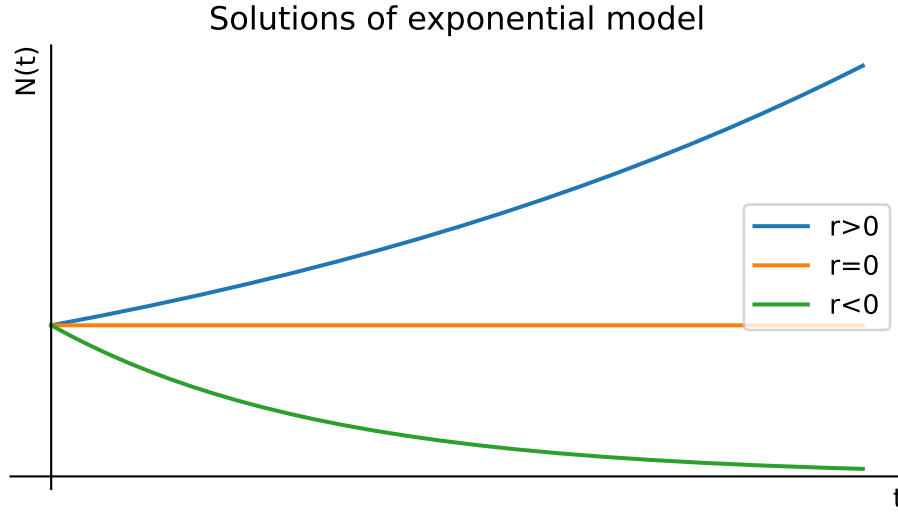
Figure 1.1: Solutions to the exponential model.

limit its growth rate will decrease, for example due to competition for limited food sources or space, or due to disease. This decrease in the growth rate is captured by the logistic equation

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

where K is the carrying capacity of the environment. The extra factor of $1 - N/K$ decreases the growth rate towards zero as the population number N approaches the carrying capacity K.

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. While that figure was created by the computer, the plot is easy to sketch by hand because the function we want to sketch is simply an upside-down parabola. The maximum of the parabola is at $N = K/2$ and the parabola crosses the N-axis at $N = 0$ and $N = K$. This means that the population growth rate is zero at $N = 0$ and $N = K$, and it is maximal at $N = K/2$.

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

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

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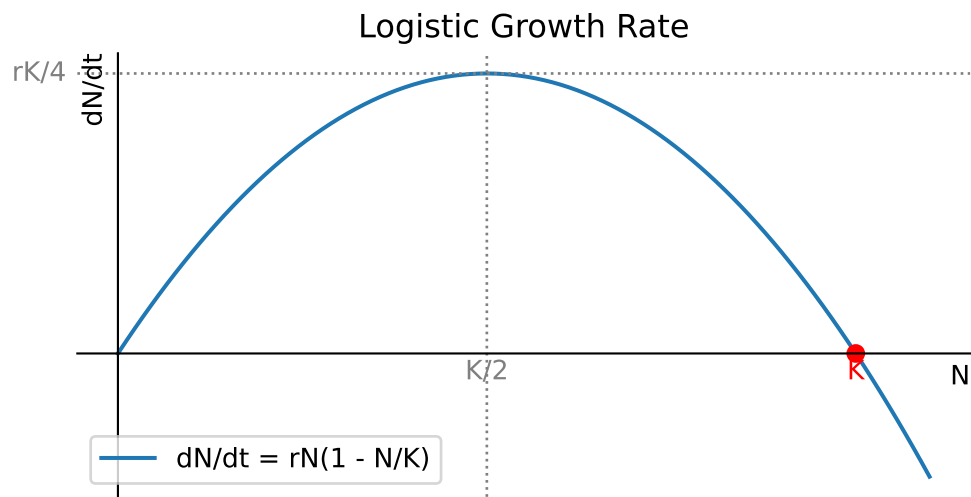
Figure 1.2: The logistic growth rate as a function of the population number.
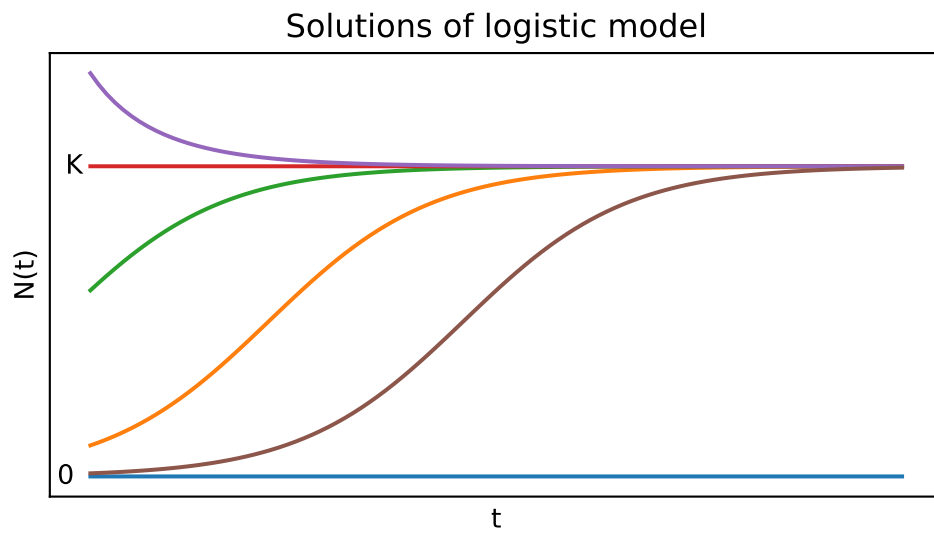
Figure 1.3: Solutions to the logistic equation.

1.3 Allee effect

Warder Clyde Allee (1885-1955) was an American ecologist who studied the effects of population density on the growth rate of a population. He found that in some cases the per-capita growth rate can increase with N. This is called the Allee effect. It can occur when the population is too small to find a mate, to find food, or to avoid predators.

Figure Figure 1.4 shows the per-capita growth rate as a function of the population number for exponential growth in black, for logistic growth in blue and two different growth rates exhibiting the Allee effect in green and red.
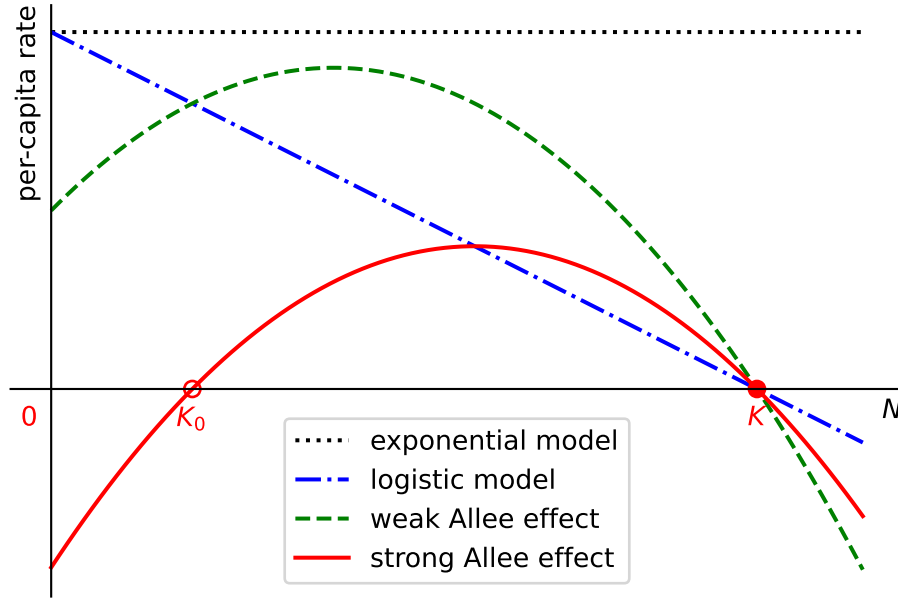
Figure 1.4: The per-capita growth rate as a function of the population number.

The green curve in Figure 1.4 shows a weak Allee effect, where the per-capita rate is small but possitive for small population sizes, then initially increases with the population size before then decreasing again as the population approaches its carrying capacity. The red curve shows a strong Allee effect, which is similar but so strong that the growth rate starts out not just small but actually negative for small N.

The simplest model for the Allee effect is the logistic equation with a modified growth rate that includes another factor that decreases the growth rate for small N:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)\left(\frac{N}{K_0} - 1\right). \tag{1.6}$$

If $0 < K_0 < K$, this exhibits the strong Allee effect because the growth rate is negative when $N < K_0$. This means that the population will be driven towards extinction when it is below

the threshold size K_0 and it will grow towards its carrying capacity when it is above K_0. This is illustrated in Figure 1.5.
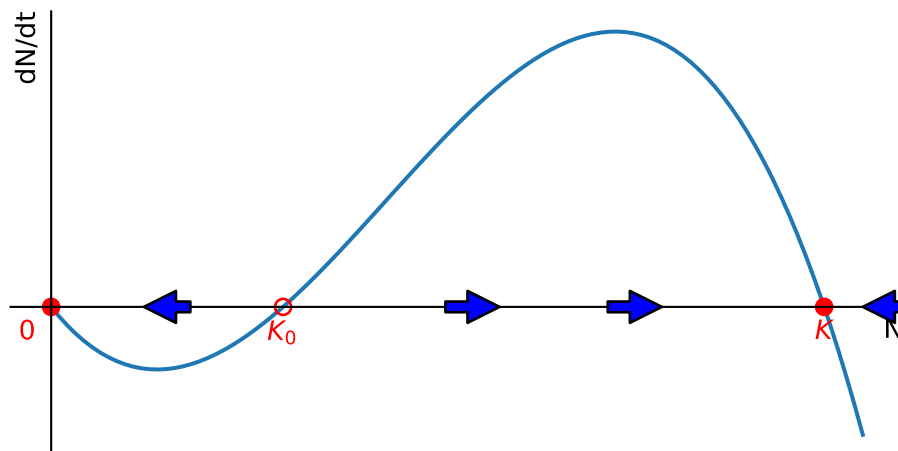
Figure 1.5: The Allee growth rate as a function of the population number.

This phenomenon is important for conservation biology because it means that small populations are particularly vulnerable to extinction. It is also important for fisheries management because it means that the population can collapse if it falls below a certain threshold size. The phenomenon is called "critical depensation". We will meet it again when we discuss harvesting later in this section.

1.4 General autonomous ODE model

The logistic model is a special case of a general autonomous ordinary differential equation (ODE) model

$$\frac{dN}{dt} = f(N), \tag{1.7}$$

where $f(N)$ is a function of N only, not t. The logistic equation Eq. 1.4 is an example of such a model with

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

If f is Lipschitz continuous, then, given $N(0) = N_0$, there exists a unique solution $N(t)$ to the initial value problem Eq. 1.7. This is a consequence of the Picard-Lindelöf theorem.

We are interested in the steady states of the model, i.e. the values N^* for which $f(N^*) = 0$. These are the values of N for which the population number does not change. To determine

the stability of the steady states, we can look near N^* by writing $N(t) = N^* + n(t)$ with $n(t)$ small. Then

$$\frac{dN}{dt} = \frac{dN^*}{dt} + \frac{dn}{dt} = f(N^* + n(t)) \approx f(N^*) + f'(N^*)\, n(t).$$

We now use that $dN^*/dt = 0$ and $f(N^*) = 0$ to find

$$\frac{dn}{dt} \approx f'(N^*)\, n(t).$$

This is a linear equation for $n(t)$ with solution

$$n(t) = n(0)e^{f'(N^*)t}$$

and we can use the sign of $f'(N^*)$ to determine the stability of the steady state:

- If $f'(N^*) < 0$, then $n(t)$ will decrease towards zero, and the steady state is stable.

- If $f'(N^*) > 0$, then $n(t)$ will increase away from zero, and the steady state is unstable.

If $f'(N^*) = 0$, then we need to look at higher order terms to determine the stability.

We illustrate this in the example of the logistic model. The fixed points are $N^* = 0$ and $N^* = K$. The derivative of $f(N)$ is

$$f'(N) = r\left(1 - \frac{2N}{K}\right).$$

So we find that $f'(0) = r > 0$ and $f'(K) = -r < 0$. This means that the steady state $N^* = 0$ is unstable and the steady state $N^* = K$ is stable. This agrees with what we had already seen graphically in Figure 1.2 and Figure 1.3.

1.5 Harvesting a renewable resource

Ecologists model populations not only out of academic interest but also for practical purposes. Humans are interested in exploiting the natural resources. They want o harvest fish from the sea, to hunt deer in the forest, and to cut down trees in the jungle. They want to do this in a way that is sustainable, i.e. that does not lead to the extinction of the resource, while at the same time giving the highest yield.

My personal interest is in understanding how fish populations react to different kinds of fishing. I use coupled partial integro-differential equations for that purpose, but most fisheries management is based on simpler models and we get a good first idea by using the logistic model, which we will now modify to include harvesting.

1.5.1 Harvesting with fixed effort

We assume that in the absence of fishing the fish population number $N(t)$ is governed by the logistic equation Eq. 1.4. We also assume that the fish are harvested at a rate $EN(t)$, where E is the harvesting rate, which is determined by the effort that is put into fishing. This means that the rate of change in the fish population number is given by

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - EN = f(N). \tag{1.8}$$

We can rewrite this equation in the form of a logistic equation with modified parameters:

$$\frac{dN}{dt} = rN\left(\left(1 - \frac{E}{r}\right) - \frac{N}{K}\right). \tag{1.9}$$

This makes it easy to read off the fixed points $N^* = 0$ and $N^* = K\left(1 - \frac{E}{r}\right)$. The nonzero fixed point gets smaller when fishing effort E increases. This is illustrated in Figure 1.6.
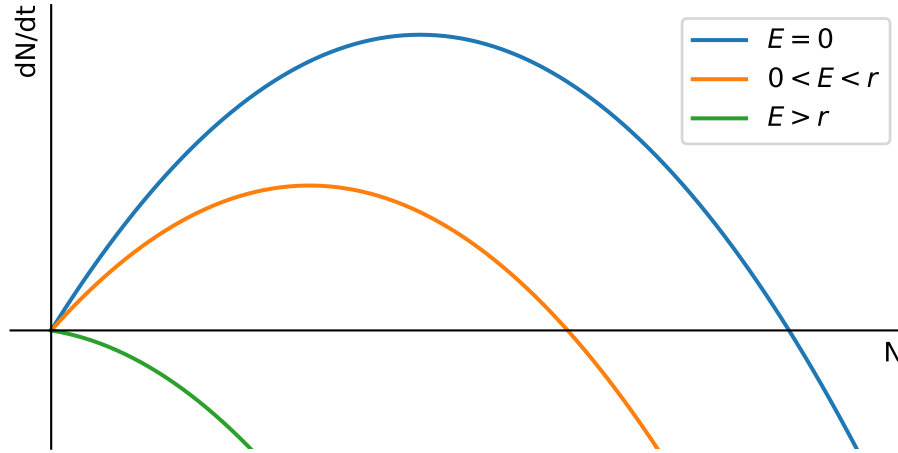
Figure 1.6: Growth rate when harvesting with fixed effort.

We are now interested in finding out at what level we should fish in order to achive the maximum sustainable yield (MSY). This is the level of fishing effort that gives the highest possible yield that can be sustained indefinitely. So we are interested in the yield at the non-zero fixed point $N^* = K\left(1 - \frac{E}{r}\right)$. The yield is the amount of fish that can be harvested per unit time, and it is given at the fixed point by

$$Y = EN^* = EK\left(1 - \frac{E}{r}\right).$$

We can find the maximum of Y by differentiating with respect to E and setting the derivative equal to zero:

$$\frac{dY}{dE} = K\left(1 - \frac{2E}{r}\right) = 0.$$

We can solve this equation for E to find the optimal fishing effort E^*:

$$E^* = \frac{r}{2}.$$

The resulting maximum sustainable yield is

$$MSY = \frac{r}{2}K\left(1 - \frac{r}{2r}\right) = \frac{rK}{4}.$$

1.5.2 Harvesting with fixed quote

Fisheries managers in the Mediterranean are aiming to control the fishing effort in order to achieve the maximum sustainable yield, and we have seen how to model that in the previous section. Fisheries in the North Sea or the North Atlantic however are instead managed by setting the total allowable catch (TAC) for the whole fleet. This is a fixed quota for the total amount of fish that can be harvested in a year. To model that policy we use the logistic equation with harvesting, but we replace the harvesting rate EN by a harvesting quota Q:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - Q. \tag{1.10}$$

This is visualised in Figure 1.7.
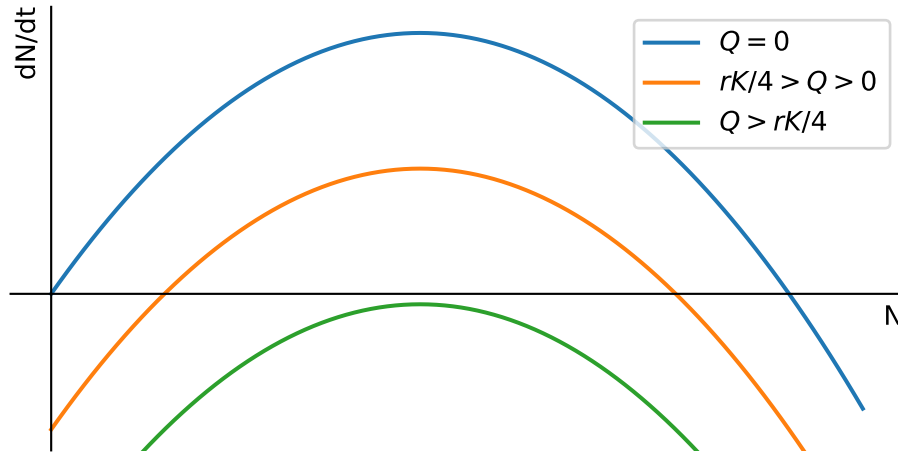
Figure 1.7: Growth rate when harvesting with fixed quota.

We see that any non-zero quota leads to critical depensation, i.e., it introduces a critical threshold below which the population will collapse. This is a well-known problem in fisheries management, and it is the reason why the TAC is set to zero for some fish stocks. As the fishing quota is increased, the critical depensation threshold moves to higher population numbers and the stable steady state moves to lower population numbers. Eventually all non-zero fixed points disappear and the population collapses.

1.6 Exercises

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.

1.6.0.1 *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.

1.6.0.2 +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.

1.6.0.3 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 $N(0) = N_0$.

1.6.0.4 * Harvesting with fixed effort

Exercise 1.4. Consider a population $N(t)$ that is described by the by the Gompertz model

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

where α and K are positive constants. 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: $Y = EN$. 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 yield, i.e., the maximum yield that can be sustained indefinitely.

1.6.0.5 Harvesting with fixed quota

Exercise 1.5. As in Exercise 1.4, consider a population $N(t)$ that is described by the Gompertz model. 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?

1.6.0.6 Wasps

Exercise 1.6. 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.

1.6.0.7 Wasps with death

Exercise 1.7. 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 1.6. 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.

2 Discrete-time population models

So far we have assumed that the rate of change of the population number has no explicit time dependence. However births and also deaths often happen on an annual cycle. Many fish have their spawning season in the spring, and many birds breed in the summer and annual plants produce their seed and then die in winter. In this case, the rate of change of the population number is not constant, but depends on the time of the year. We can model this by introducing a time dependence in the birth and death rates. However this will lead to equations that will be difficult to analyse. Instead we can give up on the idea of modelling the population numbers continuously through time and instead only follow how the population changes from year to year.

So we will use models of the form

$$N_{t+1} = f(N_t) \tag{2.1}$$

where N_t is the population number at time t and f is some function. Time t now takes on only integer values, and the population number is only defined at these times. This is called a discrete-time model. Given the initial population number N_0, we can calculate the population number at any future time t by iterating the function f: $N_1 = f(N_0)$, $N_2 = f(N_1) = f(f(N_0)), \dots N_t = f(f(\dots f(N_0) \dots))$.

2.1 Exponential model

The simplest discrete-time model is the exponential model

$$N_{t+1} = RN_t \tag{2.2}$$

where $R > 0$ is the growth factor. This is the discrete-time version of the continuous-time exponential model. The solution to this equation is

$$N_t = N_0 R^t. \tag{2.3}$$

It is important to stress that R is not a growth *rate* but a dimensionless growth factor. Comparing the discrete-time solution to the continuous-time solution $N(t) = N_0 \exp(rt)$ we see that they agree at integer times t if we measure time in years and set

$$R = \exp(r \cdot 1 \text{ year}). \tag{2.4}$$

If you are confused by the units, remember that the exponential function is dimensionless, so the argument of the exponential function must be dimensionless. We need the extra factor of 1 year because r is a rate and has dimension 1/time.

The population number grows exponentially with time if $R > 1$ and declines exponentially if $R < 1$. To get more realistic models we again need to introduce a limited carrying capacity.

2.2 Models with limited carrying capacity

Recall how we introduced the logistic model by assuming that the per-capita birth rate declines linearly with the population number and vanishes when the population reaches its carrying capacity. This gave us the equation

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) \tag{2.5}$$

where r is the per-capita growth rate and K is the carrying capacity.

It turns out that there are several models which all deserve to be called the discrete-time logistic model.

2.2.1 Verhulst model

The most famous discrete-time logistic model is the Verhulst model.

$$
\begin{aligned}
N_{t+1} &= (R_0 + 1)N_t \left(1 - \frac{N_t}{K(R_0 + 1)/R_0} \right) \\
&= N_t + R_0 N_t \left(1 - \frac{N_t}{K} \right) = f(N_t).
\end{aligned} \tag{2.6}
$$

Again it is important to stress that R_0 is not a growth *rate* but a dimensionless growth factor.

We have written the model in two alternative forms because the first form makes the analogy with the continuous-time logistic model more obvious, while the second form makes it easier to read off the fixed point.

The fixed point is a value for which $N_{t+1} = N_t$, i.e. a value of N for which the population number does not change from year to year. Thus it is a value N^* for which $f(N^*) = N^*$. Using the second form of the model, we can see easily that the fixed points are $N^* = 0$ and $N^* = K$, so K is the carrying capacity.

A problem with the Verhulst model is that it can give rise to negative population numbers. This is not realistic, so we are motivated to modify the model to prevent this.

2.2.2 Ricker model

The Ricker model is a modification of the Verhulst model that prevents negative population numbers. It is given by

$$N_{t+1} = N_t\, e^{R_0\left(1 - \frac{N_t}{K}\right)}. \tag{2.7}$$

By moving the logistic factor inside the exponential, the Ricker model prevents negative population numbers. The fixed points are still $N^* = 0$ and $N^* = K$. Ricker introduced this model to describe salmon populations.

2.2.3 Beverton-Holt model

The Beverton-Holt model is another modification of the Verhulst model which prevents negative population numbers. It is given by

$$N_{t+1} = \frac{RN_t}{1 + \frac{R-1}{K}N_t}. \tag{2.8}$$

This has been a very influential model in fisheries science. On the face of it the model does not look very similar to the logistic model, but we will see the relationship when we solve the model. The Beverton-Holt model is one of the rare cases where a non-linear model can be solved exactly. The trick is to make a change of variables from N_t to $u_t = 1/N_t$. Then we have

$$u_{t+1} = \frac{1}{N_{t+1}} = \frac{1 + \frac{R-1}{K}N_t}{RN_t} = \frac{u_t}{R} + \frac{R-1}{RK}. \tag{2.9}$$

This is a linear equation for u_t, and linear equations are easy to solve. The easiest way to proceed is to look at the first few terms of the sequence u_t and guess the general form of the solution. We find

$$\begin{aligned}
u_1 &= \frac{u_0}{R} + \frac{R-1}{RK}, \\
u_2 &= \frac{u_0}{R^2} + \frac{R-1}{RK}\left(1 + \frac{1}{R}\right), \\
u_3 &= \frac{u_0}{R^3} + \frac{R-1}{RK}\left(1 + \frac{1}{R} + \frac{1}{R^2}\right), \\
&\;\;\vdots \\
u_t &= \frac{u_0}{R^t} + \frac{R-1}{RK}\left(1 + \frac{1}{R} + \frac{1}{R^2} + ... + \frac{1}{R^{t-1}}\right).
\end{aligned} \tag{2.10}$$

The sum in the second term is a geometric series. We know the general formula for a geometric series:

$$1 + x + x^2 + ... + x^{t-1} = \frac{1 - x^t}{1 - x}. \tag{2.11}$$

We can use this with $x = 1/R$ to sum terms in the second term. We find

$$u_t = \frac{u_0}{R^t} + \frac{R-1}{RK}\frac{1-(1/R)^t}{1-1/R}.$$

We simplify this a bit and bring everything on the same denominator.

$$u_t = \frac{u_0}{R^t} - \frac{(1/R)^t - 1}{K} = \frac{Ku_0 - 1 + R^t}{KR^t}. \tag{2.12}$$

We can now change back to $N_t = 1/u_t$ to find the solution to the Beverton-Holt model. We find

$$\begin{aligned} N_t &= \frac{1}{u_t} = \frac{KR^t}{Ku_0 - 1 + R^t} \\ &= \frac{K/u_0}{KR^{-t} - R^{-t}/u_0 + 1/u_0} \\ &= \frac{KN_0}{N_0 + (K - N_0)R^{-t}}. \end{aligned} \tag{2.13}$$

This is the solution to the Beverton-Holt model. Comparing this to the solution of the continuous-time logistic model

$$N(t) = \frac{KN_0}{N_0 + (K - N_0)\exp(-rt)} \tag{2.14}$$

we see that they agree at integer times t if we measure time in years and set $R = \exp(r \cdot 1\text{ year})$.

2.3 Stability and Cobwebs

We now want to study the stability of the fixed points in discrete-time models. As discussed, fixed points N^* satisfy the equation $N^* = f(N^*)$. We study the stability of the fixed points by looking at the sequence N_t for t close to the fixed point. That means we write $N(t) = N^* + n_t$ for $n_t \ll 1$. We then have

$$N_{t+1} = N^* + n_{t+1} = f(N_t) = f(N^* + n_t) = f(N^*) + f'(N^*)n_t + ... \tag{2.15}$$

where we have used the Taylor expansion of f around N^*. Because N^* is a fixed point, we have $f(N^*) = N^*$. Thus we find that

$$n_{t+1} \approx f'(N^*)n_t \tag{2.16}$$

where we neglected the higher order terms in the Taylor expansion. This is a linear equation for n_t that we know how to solve:

$$n_t = n_0(f'(N^*))^t. \tag{2.17}$$

So we have found that:

- If $|f'(N^*)| < 1$, then n_t will decrease with time and the fixed point is stable.

- If $|f'(N^*)| > 1$, then n_t will increase with time and the fixed point is unstable.

If $|f'(N^*)| = 1$, then we cannot say anything about the stability of the fixed point from this analysis.

In the continuous-time case we also had a graphical way to see the stability of fixed points. We will now introduce a graphical method for studying the stability of fixed points in discrete-time models, called the cobweb method.

We plot the function $f(N_t)$ and the line $N_{t+1} = N_t$. The fixed points are the intersection points of the function and the line. We then draw the graph of the sequence N_t by starting at the initial population number N_0 and iterating the function $f(N_t)$ to find N_1, then iterating the function again to find N_2, and so on. The graph of the sequence N_t is called the cobweb. The stability of the fixed points can be read off from the cobweb. If the cobweb spirals into the fixed point, as shown in Figure 2.1, then the fixed point is stable. If the cobweb spirals out of the fixed point, as shown in Figure 2.2, then the fixed point is unstable. You have to press the play button below the figures to see the cobweb diagrams in action.

<IPython.core.display.HTML object>

Figure 2.1: Cobweb diagram for a stable fixed point.

<IPython.core.display.HTML object>

Figure 2.2: Cobweb diagram for an unstable fixed point.

The oscillatory nature of the sequence N_t, hopping from one side of the fixed point to the other, that creates the cobweb pattern is due to the fact that the slope of f is negative at the fixed point. The graphical method for visualising the iterations will work also when the slope is positive at the fixed point, but it will not look like a cobweb. Figure 2.3 shows the cobweb for a stable fixed point with positive slope.

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Figure 2.3: Cobweb diagram for a fixed point with positive slope.

2.4 Discrete-time harvesting model

We will now look at an example of a discrete-time model with harvesting and apply the techniques we have learned. The model has the standard discrete-time model form $N_{t+1} =$

$f(N_t)$, where f in our example is

$$f(N) = \frac{bN^2}{1 + N^2} - EN.$$

The constant $b > 2$ determines the growth rate of the population and the harvesting rate is determined by the harvesting effort E.

We start by studying the model without harvesting, so we set $E = 0$ for now. As usual, we start by looking at the steady states of the model. The fixed points are the solutions to the equation

$$N^* = \frac{b\,N^{*2}}{1 + N^{*2}}.$$

There is the obvious solution $N^* = 0$. We can then find the non-zero solutions by dividing both sides by N^* and multiply them by $1 + N^{*2}$ to get the equation

$$1 + N^{*2} = bN^*.$$

This is a quadratic equation for N^*, which we could rewrite in the more convential form

$$N^{*2} - bN^* + 1 = 0.$$

The solutions to this equation are

$$N^*_\pm = \frac{b \pm \sqrt{b^2 - 4}}{2}.$$

The solutions are real if $b^2 - 4 \geq 0$, i.e. if $b \geq 2$, which we have stipulated earlier. Both solutions are positive.

We now have enough information to draw a good sketch to understand the dynamics of the model. We can draw the function $f(N)$ and the line $N_{t+1} = N_t$. It may not be immediately obvious what the sketch of $f(N) = bN^2/(1 + N^2)$ looks like. We'll reason ourselves through this in steps:

- First let us consider what happens near $N = 0$. There the function is approximately $f(N) \approx bN^2$. This is a parabola that opens upwards. The function is zero at $N = 0$ and increases quadratically with N.

- Next we consider what happens as N becomes large. There the function is approximately $f(N) \approx b$. So the graph has a horizontal asymptote at $y = b$.

- We know that in between there are two fixed points. That means the graph needs to cross the diagonal line $y = N$ twice.

- Finally we observe that the function is monotonically increasing.
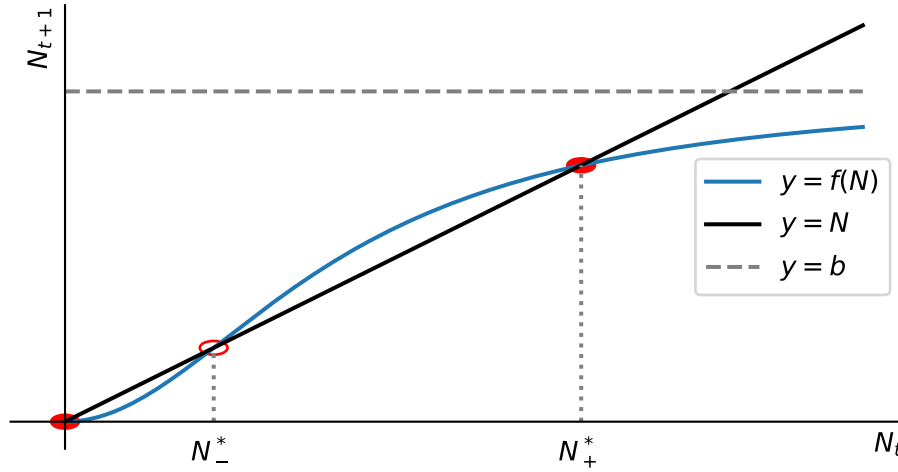
Figure 2.4: Graph of the function $f(N) = \frac{bN^2}{1+N^2}$.

If we now draw something that has all these features, we will have a sufficiently good sketch of the function for our purpose of understanding the dynamics of the model. We will necessarily end up with something that qualitatively looks like the graph in Figure 2.4.

Using our cobweb technique, or simply looking at the slope of f at the fixed points, we can easily convince ourselves that the extinction fixed point is stable, the smaller non-zero fixed point N_-^* is unstable and the larger fixed point N_+^* is stable. in Figure 2.4 we have indicated the stable fixed points by solid circles and the unstable fixed points by open circles. So when the population number is larger than N_-^* it will grow towards N_+^*, and when it is smaller than N_-^* it will go extinct. So this model exhibits a strong Allee effect with critical depensation. N_-^* is the smallest viable population size.

We can now add harvesting to the model. The extra term in the function $f(N)$ is $-EN$. This lowers the graph of $f(N)$ by an amount that grows linearly with N. This is illustrated in Figure 2.5.

We see that as the harvesting effort E increases, the two fixed points move closer together. At a critical value E_c the two fixed points merge and disappear. The population number will then go extinct for all initial population numbers.

Let us find the critical value E_c. For that we first determine the location of the fixed points in the presence of harvesting. So we solve the equation

$$N^* = \frac{b\,N^{*2}}{1+N^{*2}} - EN^*.$$

Again this has a solution $N^* = 0$. We can then find the non-zero solutions by dividing both
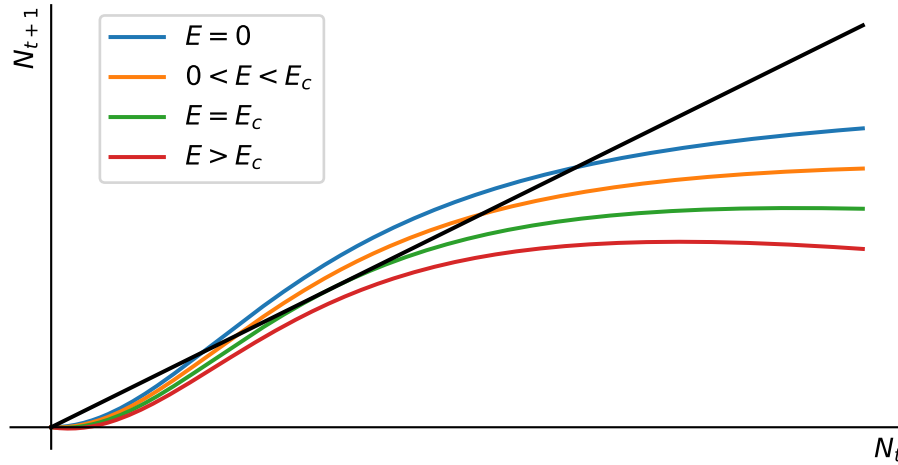
Figure 2.5: Graph of the function $f(N) = \frac{bN^2}{1+N^2} - EN$.

sides by N^* and multiply them by $1 + N^{*2}$ to get the equation

$$(1 + E)N^{*2} - bN^* + 1 + E = 0.$$

This is solved by

$$N^*_\pm = \frac{\frac{b}{1+E} \pm \sqrt{\left(\frac{b}{1+E}\right)^2 - 4}}{2}.$$

We see that these solutions are real only if $\left(\frac{b}{1+E}\right)^2 - 4 \geq 0$, i.e., if $E < \frac{b-2}{2}$. Thus the critical effort is $E_c = \frac{b-2}{2}$. Fishing above this level will lead to extinction of the population. But even fishing just near this level is risky because the population number will be very close to the minimum viable population and a small disturbance could lead to extinction.

2.5 Bifurcations

A bifurcation is a change in the existence and/or stability of the fixed points as the parameters of the model are varied.

You have met bifurcations in continuous-time models already in your Dynamical Systems module. You have seen there that in one-dimensional systems described by a single ODE there are three different types of bifurcation: saddle-node, pitchfork, transcritical. The same types of bifurcations can occur in discrete-time models but there is also one more type: the period-doubling bifurcation.

We have already seen a bifurcation in the discrete-time harvesting model. The bifurcation was a saddle-node bifurcation, where two fixed points merge and disappear. This is also sometimes

referred to as a tangent bifurcation, because at the critical value of the parameter the curve $y = f(N)$ is tangent to the line $y = N$ at the fixed point.

In the period-doubling bifurcation the stability of the fixed point changes as the parameter is varied. The fixed point changes from stable to unstable, and at the same time a stable period-2 orbit appears, where the population number oscillates between two values. The period-2 orbit is stable in the sense that if the population number is close to the orbit it will converge to the orbit. This kind of bifurcation can obviously not arise in one-dimensional continuous-time models because a continuous orbit can not move from one side of a fixed point to the other.

In the lectures we drew diagrams illustrating three of the four types of bifurcations. For a discussion of all four types in a similar fashion, you can view the following video.

2.6 Exercises

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 exercise marked with an o will be worked through in the problems class.

2.6.0.1 + Verhulst model

Exercise 2.1. For some choices of the parameters, the Verhulst model

$$N_{t+1} = rN_t \left(1 - \frac{N_t}{K} \right) \tag{2.18}$$

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.

2.6.0.2 * Ricker model

Exercise 2.2. Find the fixed points in the Ricker model

$$N_{t+1} = N_t \, e^{R_0 \left(1 - \frac{N_t}{K} \right)}. \tag{2.19}$$

and investigate their stability. Do this both analytically and by drawing cobweb diagrams.

2.6.0.3 Beverton-Holt model

Exercise 2.3. Find the fixed points in the Beverton-Holt model

$$N_{t+1} = \frac{RN_t}{1 + \frac{R-1}{K}N_t}. \tag{2.20}$$

and investigate their stability. Do this both analytically and by drawing cobweb diagrams.

2.6.0.4 o House finches

Exercise 2.4. *[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 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

$$N_{t+1} = s\, N_t + \frac{c\, N_t^2}{r + 2N_t + N_t^2/\delta}. \tag{2.21}$$

f) Find the realistic steady states of the model in Eq. 2.21 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. Label key features of the curves.

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

2.6.0.5 Another model

Exercise 2.5. Consider the discrete time model

$$N_{t+1} = \frac{rN_t}{1 + (N_t/K)^b} \tag{2.22}$$

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

3 Sex-structured population models

Up to this point we have completely ignored that there are differences between the individuals making up a population. So we ignored all structure within a population. We will now start to remedy this. In this chapter we will start with the simplest possible structure by splitting the population into males and females. Keeping track of both the abundance of males and of females separately makes sense because

- birth and death rates depend on the sex

- both a male and a female are needed to produce offspring

So in this chapter instead of just looking at a single function $N(t)$ giving the total population number, we will look at two functions $M(t)$ and $F(t)$ giving the number of males and females respectively. We again describe them by differential equations that capture that the numbers can decrease due to deaths and increase due to births.

$$
\begin{aligned}
\frac{dF}{dt} &= -\mu_F F + b_F \, \varphi(F, M) \\
\frac{dM}{dt} &= -\mu_M M + b_M \, \varphi(F, M).
\end{aligned}
\tag{3.1}
$$

Here μ_F and μ_M are the death rates of females and males respectively. The rate of births now depends both on the number of females and the number of males, because both males and females are needed to produce offspring. We formulate that dependence on the number of females and the number of males as a function $\varphi(F, M)$. The functional dependence of the rate on F and M is the same for births of females and for births of males, but the extra factors b_F and b_M account for the differences between female and male birth rates.

3.1 Symmetric model

We first consider the simpler situation where birth and mortality rates are the same for males and females:

$$
\mu_F = \mu_M = \mu, \quad b_F = b_M = b.
\tag{3.2}
$$

In this case we can get a simple ODE for the difference $F - M$ between the number of females and males:

$$
\frac{d(F - M)}{dt} = -\mu(F - M).
\tag{3.3}
$$

This equation has the solution

$$F(t) - M(t) = (F(0) - M(0))e^{-\mu t}. \tag{3.4}$$

This means that the difference decreases exponentially over time. In particular, if we start with equal number females and males then the they will stay equal for all times.

To make further progress we need to make a concrete choice for the function $\varphi(F, M)$. We will consider the simplest possible choice

$$\varphi(F, M) = F M. \tag{3.5}$$

This choice is motivated by the fact that both a male and a female is needed to produce offspring. So the rate of births should increase if there are more females but also when there are more males. The simplest way to capture this is to multiply F and M.

A simple thing to note is that if $M(0) = 0$ then $M(t) = 0$ for all times. Then the number of females satisfies

$$\frac{dF}{dt} = -\mu F. \tag{3.6}$$

This has the solution

$$F(t) = F(0)e^{-\mu t}. \tag{3.7}$$

So if there are no males, the females have to die out as well.

We noted above that if initially $F(0) = M(0)$ then $F(t) = M(t)$ for all times. In that case the number of females satisfies

$$\frac{dF}{dt} = -\mu F + b F^2. \tag{3.8}$$

This is illustrated in Figure 3.1.

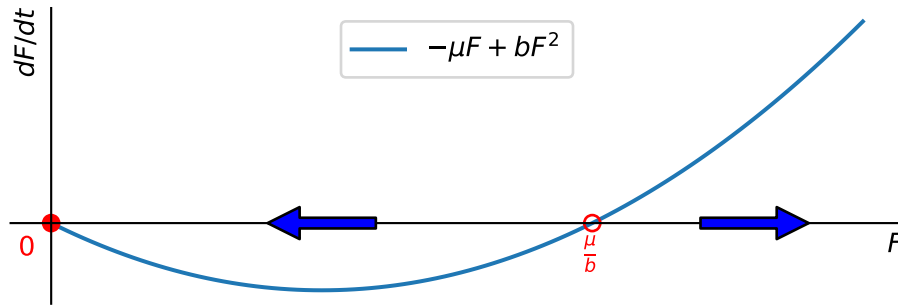Figure 3.1: Quadratically increasing growth rate.

Note that the non-zero fixed point at $F = \mu/b$ is unstable. If $F(0) < \mu/b$ then the females and hence the males go extinct. If $F(0) > \mu/b$ then the females and hence the males grow rapidly. In fact, they grow so rapidly that the population size becomes infinite in finite time, as we can see when we solve the ODE.

We can solve Eq. 3.8 by separation of variables:

$$\int \frac{dF}{-\mu F + bF^2} = \int dt.$$

We could do the integral on the left hand side by partial fractions. But to see the problem of the population size becoming infinite in finite time it is sufficient to consider the case of $F \gg 1$ where we can neglect the term $-\mu F$ in the denominator. Then we get

$$\int_{F(0)}^{F(t)} \frac{dF}{F^2} = \frac{1}{F(0)} - \frac{1}{F(t)} = \int_0^t b \, d\tilde{t} = bt.$$

and hence

$$F(t) = \frac{1}{1/F(0) - bt}. \tag{3.9}$$

So the population size becomes infinite at time $t = 1/(bF(0))$. So clearly this model is not ecologically sensible.

3.2 Female-limited reproduction

We will now consider a model where the birth rate depends only on the number of females:

$$\varphi(F, M) = F. \tag{3.10}$$

This is clearly a strong simplification but is reasonable for populations where there are always more than enough males to fertilize all females.

With this simplification, the ODE for F becomes

$$\frac{dF}{dt} = -\mu_F F + b_F F = (-\mu_F + b_F)F. \tag{3.11}$$

This has the solution

$$F(t) = F(0)e^{(-\mu_F + b_F)t}. \tag{3.12}$$

We can now use this in the equation for M:

$$\frac{dM}{dt} = -\mu_M M + b_M F = -\mu_M M + b_M F_0 \, e^{(-\mu_F + b_F)t}. \tag{3.13}$$

(We have used $F(0) = F_0$ to make the equation more readable.) This is a first-order linear ODE with time-dependent inhomogeneity. We can solve it by the method of integrating factors. We first rewrite it in the form

$$\frac{dM}{dt} + \mu_M M = b_M F_0 \, e^{(-\mu_F + b_F)t} \tag{3.14}$$

and then observe that the left-hand side is proportional to a total derivative:

$$\frac{dM}{dt} + \mu_M M = \frac{d}{dt}(e^{\mu_M t} M)e^{-\mu_M t} \tag{3.15}$$

Thus after multiplying both sides by $e^{\mu_M t}$ we get

$$\frac{d}{dt}(e^{\mu_M t} M) = b_M F_0 \, e^{(\mu_M - \mu_F + b_F)t}. \tag{3.16}$$

We can now integrate both sides to get

$$e^{\mu_M t} M(t) - e^{\mu_M t} M_0 = \frac{b_M F_0}{\mu_M - \mu_F + b_F} \left(e^{(\mu_M - \mu_F + b_F)t} - 1 \right). \tag{3.17}$$

This can be solved for $M(t)$:

$$M(t) = M_0 e^{-\mu_M t} + \frac{b_M F_0}{\mu_M - \mu_F + b_F} \left(e^{(-\mu_F + b_F)t} - e^{-\mu_M t} \right). \tag{3.18}$$

We have been able to fully solve this model. At this stage it is worth checking that the dependence of the solution on the parameters and on the initial conditions is reasonable.

Next let us take a look at the sex ratio as $t \to \infty$. We find

$$\begin{aligned} s = \lim_{t \to \infty} \frac{M(t)}{F(t)} &= \lim_{t \to \infty} \frac{M_0 e^{-\mu_M t} + \frac{b_M F_0}{\mu_M - \mu_F + b_F} \left(e^{(-\mu_F + b_F)t} - e^{-\mu_M t} \right)}{F_0 e^{(-\mu_F + b_F)t}} \\ &= \frac{b_M}{b_F - \mu_F + \mu_M}. \end{aligned} \tag{3.19}$$

Just for fun let us check what this model would predict for the sex ratio in the population of the US, using data about births and deaths from 1992.

$$\begin{aligned} \mu_F &= 807/100,000/\text{year}, \quad \mu_M = 902/100,000/\text{year}, \\ b_F &= 1480/100,000/\text{year}, \quad b_M = 1550/100,000/\text{year}. \end{aligned} \tag{3.20}$$

Substituting these values into Eq. 3.19 we get $s \approx 0.9841$. The actual ratio in the US in 1992 was 0.953. Of course this is not to be taken seriously. To start with, human populations are not solely female-limited. But there are many other criticisms that can be made of this model when applied to human populations.

3.3 Harmonic mean model

We will now consider a model where the birth rate depends on both the number of males and the number of females. We choose to set $\varphi(F, M)$ to a weighted average of F and M:

$$\varphi(F, M) = D M + (1 - D)F \tag{3.21}$$

with some suitably chosen weighting factor D. We want to keep the feature that when there is an overabundance of males, then the birth rate is limited mostly by the number of females and vice versa. So we choose $D = M/(F + M)$, which is the relative abundance of males. This makes $1 - D = F/(F + M)$, which is the relative abundance of females. This gives

$$\varphi(F, M) = \frac{M}{F + M}F + \frac{F}{F + M}M = \frac{2FM}{F + M}. \tag{3.22}$$

We can now use this in the ODEs for F and M:

$$\begin{aligned}
\frac{dF}{dt} &= -\mu_F F + b_F \frac{2FM}{F + M}, \\
\frac{dM}{dt} &= -\mu_M M + b_M \frac{2FM}{F + M}.
\end{aligned} \tag{3.23}$$

We will not try to solve this coupled system of nonlinear ODEs. Instead we will directly look at the long-term sex ratio. We can derive an ODE for the sex ration M/F:

$$\frac{d}{dt}\frac{M}{F} = \frac{\frac{dM}{dt}F - M\frac{dF}{dt}}{F^2}. \tag{3.24}$$

Because we are only interested in the long-term behavior we look at the fixed point of this equation, hence we set the left-hand side to zero. We then get

$$\frac{dM}{dt}F - M\frac{dF}{dt} = 0. \tag{3.25}$$

We can now use the ODEs for F and M to get

$$\frac{dM}{dt}F - M\frac{dF}{dt} = \left(-\mu_M M + b_M \frac{2FM}{F + M}\right)F - M\left(-\mu_F F + b_F \frac{2FM}{F + M}\right) = 0. \tag{3.26}$$

We multiply by $F + M$ and divide by FM to get

$$-\mu_M(F + M) + 2b_M F + \mu_F(F + M) - 2b_F M = 0. \tag{3.27}$$

Collecting terms proportional to F and M we get

$$(-\mu_M + 2b_M + \mu_F)F = (\mu_M - \mu_F + 2b_F)M. \tag{3.28}$$

We can now solve this equation for the asymptotic sex ratio

$$s = \lim_{t \to \infty} \frac{M(t)}{F(t)} = \frac{\mu_M - \mu_F + 2b_F}{-\mu_M + 2b_M + \mu_F}. \tag{3.29}$$

Even though the sex ratio approaches a fixed point as $t \to \infty$, the population numbers themselves do not. Once the sex ratio has settled to the value s, we have $M = sF$ and we can use this to get a single ODE for F:

$$\begin{aligned}
\frac{dF}{dt} &= -\mu_F F + b_F \frac{2MF}{F + M} \\
&= -\mu_F F + \frac{2s}{s + 1}b_F F.
\end{aligned} \tag{3.30}$$

This is a linear equation and has the solution

$$F(t) = F_0 e^{(-\mu_F + \frac{2s}{s+1} b_F)t}. \tag{3.31}$$

Similarly we obtain

$$M(t) = M_0 e^{(-\mu_M + \frac{2}{s+1} b_M)t}. \tag{3.32}$$

So we have an exponential growth model for both F and M, but the exponent has a modified birth rate that takes the sex ratio into account.

To arrive at more realistic models we should introduce a carrying capacity into the model.

3.4 Exercises

3.4.0.1 * Geometric mean sex-structured model

Exercise 3.1. 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. Make the choice

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

Determine the asymptotic sex ratio

$$s = \lim_{t \to \infty} \frac{M(t)}{F(t)}?$$

What is the numerical value of s when $\mu_F = 2, \mu_M = 1, b_F = 1/2, b_M = 3/2$ per year?

4 Age-structured population model

4.1 Continuous time model

In the previous chapter we structured the population by a discrete variable, the sex of the individuals. This gave rise to a system of coupled ODEs, one ODE for each class of individuals. In this section we will structure the population by a continuous variable, the age of the individuals. This will give rise to a partial differential equation (PDE) for the age-dependent population density. We will solve this PDE and study the long-term behaviour of the population and its age distribution.

So instead of describing the population just by the total number of individuals $N(t)$, we will describe it by the density $n(t, a)$ of individuals at age a. The total number $N(t)$ of individuals in the population is then given by the integral of $n(at, a)$ over all ages. More generally, the total number of individuals in the population that are between age a_1 and a_2 is given by the integral of $n(t, a)$ over the interval $[a_1, a_2]$. You are familiar with the concept of density from probability theory, where continuous random variables are described by a probability density rather than a probability. You may also be familiar with the concept from physics, where the density of a material describes how the mass is distributed over space. Here, the density $n(t, a)$ describes how the individuals are distributed over ages.

To derive the PDE for the age-structured population density, we consider how the density changes over an infinitesimal time interval δt due to deaths:

$$n(t + \delta t, a + \delta t) = n(t, a) - \mu(a)n(t, a)\delta t. \tag{4.1}$$

Note how we had to take into account that over the time interval δt the age of the individuals has increased by δt. We now Taylor-expand the left-hand side around t and a:

$$n(t + \delta t, a + \delta t) = n(t, a) + \frac{\partial n}{\partial t}\delta t + \frac{\partial n}{\partial a}\delta t + \mathcal{O}(\delta t^2). \tag{4.2}$$

Cancelling the $n(t, a)$ terms on both sides and dividing by δt gives us the PDE for the age-structured population density:

$$\frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} = -\mu(a)n. \tag{4.3}$$

This equation captures the effect of individuals aging and dying, but it does not capture how they are born. Individuals are born with age 0. These offspring can be produced by parents

of any ages, but with an age-dependent rate $b(a)$. This gives

$$n(t, 0) = \int_0^\infty b(a)n(t, a)\, da. \tag{4.4}$$

This is a boundary condition for the PDE. It says that the density of individuals at age 0 is given by the total number of offspring produced by the individuals of all ages.

We will now solve the PDE for the age-structured population density by the method of separation of variables. We will make the Ansatz $n(t, a) = f(t)r(a)$. You have seen this trick for finding solutions of linear, homogeneous PDEs in other modules, like Waves and Fluids for example. Substituting this Ansatz into the PDE gives

$$f'(t)r(a) + f(t)r'(a) = -\mu(a)f(t)r(a). \tag{4.5}$$

Dividing by $f(t)r(a)$ gives

$$\frac{f'(t)}{f(t)} + \frac{r'(a)}{r(a)} = -\mu(a). \tag{4.6}$$

We now collect all terms that depend on t on the left-hand side and all terms that depend on a on the right-hand side:

$$\frac{f'(t)}{f(t)} = -\frac{r'(a)}{r(a)} - \mu(a). \tag{4.7}$$

Because the left-hand side is independent of a and the right-hand side is independent of t, both sides must be equal to a constant. We introduce the separation constant γ and write

$$\frac{f'(t)}{f(t)} = \gamma, \quad \frac{r'(a)}{r(a)} = -\gamma - \mu(a). \tag{4.8}$$

These are now linear ODEs and hence easy to solve. The first ODE has the solution

$$f(t) = f(0)e^{\gamma t} \tag{4.9}$$

and the second ODE has the solution

$$r(a) = r(0) \exp\left(-\int_0^a \mu(a')\, da' - \gamma a\right). \tag{4.10}$$

So altogether we have the population density

$$n(t, a) = n(0, 0)e^{\gamma t} \exp\left(-\int_0^a \mu(a')\, da' - \gamma a\right), \tag{4.11}$$

where $n(0, 0) = f(0)r(0)$ is the initial density of individuals at age 0.

So far we don't yet know the value of the separation constant γ. This will be determined by the boundary condition. If we substitute the solution Eq. 4.11 into the boundary condition Eq. 4.4, we get

$$n(0,0)e^{\gamma t} = \int_0^\infty b(a)n(0,0)e^{\gamma t} \exp\left(-\int_0^a \mu(a')\,da' - \gamma a\right)\,da. \tag{4.12}$$

We can cancel the common factor $n(0,0)e^{\gamma t}$ on both sides to get the condition

$$1 = \int_0^\infty b(a)\exp\left(-\int_0^a \mu(a')\,da' - \gamma a\right)\,da = \phi(\gamma). \tag{4.13}$$

We have introduced the shorthand notation $\phi(\gamma)$ for the integral on the right-hand side. The condition Eq. 4.12 is a transcendental equation for γ. We cannot solve it analytically for γ. But we observe that ϕ is a monotonically decreasing function of γ. This observation alone allows us to make a statement about the sign of γ. According to Eq. 4.9 the sign of γ determines whether the total population grows expnentially or goes extinct.

If γ is positive, then the monotonicity of ϕ tells us that $\phi(0) > \phi(\gamma) = 1$ and vice versa. Conversely, if γ is negative, then $\phi(0) < \phi(\gamma) = 1$ and vice versa. So to determine the sign of γ we only have to look at the value of

$$\phi(0) = \int_0^\infty b(a)\exp\left(-\int_0^a \mu(a')\,da'\right)\,da. \tag{4.14}$$

- If $\phi(0) > 1$, then $\gamma > 0$ and the population grows exponentially.

- If $\phi(0) < 1$, then $\gamma < 0$ and the population goes extinct.

This result actually has a very intuitive explanation. The factor

$$\exp\left(-\int_0^a \mu(a')\,da'\right) =: l(a) \tag{4.15}$$

is the probability that an individual survives up to age a. Therefore $\phi(0)$ is the expected number of offspring produced by an individual during its lifetime. If this number is greater than 1, then the population grows exponentially. If it is less than 1, then the population goes extinct.

4.2 Discrete time model

In the continuous-time age-structured population model discussed in the previous section we had assumed that births take place continuously through time. If however reproduction is an annual event, taking place in a short breeding season for example, then it is more natural to model the population in discrete time. We will now derive the discrete-time version of the age-structured population model and then study the long-term behaviour of the population and its age distribution.

4.2.1 Model description

Both time and age will be discrete variables. We will take them to be integers counting years. We will describe the population by the numbers $N_{a,t}$ of individuals of age a at time t. The total number N_t of individuals in the population at time t is then given by the sum of $N_{a,t}$ over all ages.

The parameters of our model will be the probabilities S_a of surviving from age $a-1$ to age a and the number of offspring b_a produced by an individual when they reach age a. Because the number of individuals at age a at time $t+1$ is the number of individuals that a year earlier were at age $a-1$ and have survived to age a, we have

$$N_{a,t+1} = S_a N_{a-1,t}. \tag{4.16}$$

When individuals reach age a, they each produce b_a offspring. The total number of offspring produced at time t is therefore given by

$$N_{0,t} = \sum_{a=1}^{\infty} b_a N_{a,t}. \tag{4.17}$$

This is a boundary condition for the discrete-time model. It says that the number of individuals at age 0 at time t is given by the total number of offspring produced by the individuals of all ages at time t. This is the discrete-time analogue of the boundary condition Eq. 4.4 for the continuous-time model.

Note that in Eq. 4.17 both sides of the equation are at time t. That is because reproduction is taken to happen instantaneously at time t. It is conventional to use Eq. 4.16 to rewrite the boundary condition Eq. 4.17 as an equation for $N_{0,t+1}$:

$$N_{0,t+1} = \sum_{a=1}^{\infty} b_a N_{a,t+1} = \sum_{a=1}^{\infty} b_a S_a N_{a-1,t} = \sum_{a=1}^{\infty} F_a N_{a-1,t}, \tag{4.18}$$

where we have introduced the fecundity $F_a := b_a S_a$.

Eq. 4.16 and Eq. 4.18 are the equations for the discrete-time age-structured population model. They are a system of coupled difference equations, one equation for each age class. We would like to solve them to determine the numbers $N_{a,t}$ of individuals at each age at each time. Notice that Eq. 4.16 looks very simple and we could use it to determine $N_{a,t}$ for $a = 1, 2, 3, \dots$ in terms of $N_{0,t}$,

$$\begin{aligned} N_{a,t} &= S_a N_{a-1,t} = S_a S_{a-1} N_{a-2,t} = \cdots \\ &= S_a S_{a-1} \cdots S_1 N_{0,t} = l_a N_{0,t}, \end{aligned} \tag{4.19}$$

where we used that the product $S_a S_{a-1} \cdots S_1$ is the probability of surviving from age 0 to age a, which we denote by l_a. However Eq. 4.18 spoils the game because it tells us that we won't know $N_{0,t}$ until we know $N_{a,t}$ for all ages a. This is a typical feature of age-structured population models. The number of individuals at age 0 at time t depends on the number of individuals at all other ages at time t. Solving both Eq. 4.16 and Eq. 4.18 together is a non-trivial task.

4.2.2 Stable age distribution

In analogy to the continuous-time model, we will now look for a solution of the form

$$N_{a,t} = \lambda^t r(a) \tag{4.20}$$

This is a solution in which the age distribution $r(a)$ remains stable from one year to the next, but the total population grows or shrinks by a factor λ each year. This means in particular that for this solution $N_{a,t+1} = \lambda N_{a,t}$ for all ages a. For $a = 1$ this gives

$$N_{1,t+1} = \lambda N_{1,t} = S_1 N_{0,t} \tag{4.21}$$

and hence

$$N_{1,t} = \frac{S_1}{\lambda} N_{0,t}. \tag{4.22}$$

Similarly we can express $N_{2,t}$ in terms of $N_{0,t}$:

$$N_{2,t} = \frac{S_2}{\lambda} N_{1,t} = \frac{S_1 S_2}{\lambda^2} N_{0,t}. \tag{4.23}$$

We can continue this process to express $N_{a,t}$ in terms of $N_{0,t}$:

$$N_{a,t} = \frac{S_1 S_2 \cdots S_a}{\lambda^a} N_{0,t} = \frac{l_a}{\lambda^a} N_{0,t}. \tag{4.24}$$

Finally, for the newborns we have

$$N_{0,t+1} = \lambda N_{0,t} = \sum_{a=1}^{M} F_a N_{a-1,t} = \sum_{a=1}^{M} F_a \frac{l_{a-1}}{\lambda^{a-1}} N_{0,t}. \tag{4.25}$$

Dividing the equation by $\lambda N_{0,t}$ gives

$$1 = \sum_{a=1}^{M} F_a \frac{l_{a-1}}{\lambda^a}. \tag{4.26}$$

Using that $F_a = b_a S_a$ and $S_a l_{a-1} = l_a$ we can rewrite this equation as

$$1 = \sum_{a=1}^{M} b_a\, l_a\, \lambda^{-a} =: \psi(\lambda). \tag{4.27}$$

This is the Euler-Lotka equation for the stable age distribution. Compare it to the corresponding equation for the continuous-time model Eq. 4.13 with $e^\gamma = \lambda$. The only difference is that the continuous-time model has an integral over age, while the discrete-time model has a sum over age.

By the same argument as in the continuous case we can see that if the expected number of offspring produced by an individual during its lifetime, $\sum_{a=1}^{M} b_a\, l_a = \psi(1)$, is greater than 1 then the population grows exponentially. If it is less than 1, then the population goes extinct.

We will now determine the stable age distribution for a specific example.

Example 4.1. For the spotted owl the age-dependent reproduction numbers are

$$b_a = \begin{cases} 0 & \text{if } a < 2, \\ b & \text{if } a \geq 2 \end{cases} \tag{4.28}$$

for some constant b. The age-dependent survival probabilities are

$$S_a = \begin{cases} 1 & \text{if } a = 1, \\ l & \text{if } a = 2, \\ p & \text{if } a > 2 \end{cases} \tag{4.29}$$

for some constants l and p. Those values of the survival probabilities from year to year lead to the following values of the survival probabilities from birth to age a:

$$l_a = \begin{cases} 1 & \text{if } a = 1, \\ l\,p^{a-2} & \text{if } a \geq 2. \end{cases} \tag{4.30}$$

Substituting these values into the expression for $\psi(\lambda)$ in Eq. 4.44 gives

$$
\begin{aligned}
\psi(\lambda) &= bl \sum_{a=2}^{\infty} p^{a-2} \lambda^{-a} = lb\lambda^{-2} \sum_{n=0}^{\infty} \frac{p}{\lambda} \\
&= lb\lambda^{-2} \frac{1}{1 - \frac{p}{\lambda}} = \frac{lb}{\lambda(\lambda - p)},
\end{aligned}
\tag{4.31}
$$

where we made use of the formula for a geometric series, valid if $|p/\lambda| < 1$ [1]. In particular, the expected number of offspring produced by an individual in their lifetime is

$$\psi(1) = lb/(1 - p).$$

If this is greater than 1, then the population grows exponentially. If it is less than 1, then the population goes extinct.

In this case the Euler-Lotka equation $\psi(\lambda) = 1$ becomes the quadratic equation for λ:

$$\psi(\lambda) = \frac{lb}{\lambda(\lambda - p)} = 1 \quad \Leftrightarrow \quad \lambda^2 - \lambda p - lb = 0. \tag{4.32}$$

The solutions are

$$\lambda_{\pm} = \frac{p \pm \sqrt{p^2 + 4lb}}{2}. \tag{4.33}$$

We are interested in the positive solution λ_+. Substituting this value for λ back into Eq. 4.42 and Eq. 4.20 we see that we have found the solution

$$N_{a,t} = \left(\frac{p + \sqrt{p^2 + 4lb}}{2} \right)^{t-a} l_a N_{0,0} \tag{4.34}$$

for any choice of $N_{0,0}$.

---

[1] If $\lambda \geq p$, then $\psi(\lambda)$ diverges and does not satisfy the Euler-Lotka equation $\psi(\lambda) = 1$.

4.2.3 Leslie matrix

In the case where there is a maximal age m beyond which there is no reproduction, either because $b_a = 0$ for $a > m$ or because there are not older individuals because $S_{m+1} = 0$, we can then collect the equations for $N_{a,t+1}$ for $a = 0, 1, 2, \ldots, m-1$ (Eq. 4.16 and Eq. 4.18) into a matrix equation:

$$
\begin{pmatrix} N_0 \\ N_1 \\ N_2 \\ \vdots \\ N_{m-1} \end{pmatrix}_{t+1}
=
\begin{pmatrix}
F_0 & F_2 & \cdots & F_{m-2} & F_{m-1} \\
S_1 & 0 & \cdots & 0 & 0 \\
0 & S_2 & \cdots & 0 & 0 \\
\vdots & \vdots & \ddots & \vdots & \vdots \\
0 & 0 & \cdots & S_{m-1} & 0
\end{pmatrix}
\begin{pmatrix} N_0 \\ N_1 \\ N_2 \\ \vdots \\ N_{m-1} \end{pmatrix}_{t} .
\tag{4.35}
$$

Note that we did not need to include the equation for $N_{m,t+1}$ in the matrix equation because $N_{m,t+1}$ is not needed to calculate the reproduction. Once the matrix equation Eq. 4.35 is solved, we can determine $N_{m,t+1}$ separately from Eq. 4.16 if we are interested, and similarly for all older age classes that do not reproduce, if any.

The matrix on the right-hand side of Eq. 4.35 is a so-called Leslie matrix. Let us denote it by L. The equation Eq. 4.35 is a matrix equation of the form

$$
\mathbf{N}_{t+1} = L \mathbf{N}_t,
\tag{4.36}
$$

where $\mathbf{N}_t$ is the column vector of the numbers $N_{a,t}$ and L is the Leslie matrix.

We now have the task of solving the homogeneous linear difference equation Eq. 4.36 with constant coefficients (the Leslie matrix L does not depend on time). You know from earlier modules that when confronted with a homogeneous linear *differential* equation with constant coefficients you can solve it with an exponential Ansatz. The same works for linear difference equations. We make the Ansatz

$$
\mathbf{N}_t = \lambda^t \mathbf{v}
\tag{4.37}
$$

and substitute it into Eq. 4.36. This gives

$$
\lambda^{t+1} \mathbf{v} = L \lambda^t \mathbf{v}.
\tag{4.38}
$$

Dividing by λ^t gives

$$
\lambda \mathbf{v} = L \mathbf{v}.
\tag{4.39}
$$

This means that our Ansatz works if we choose λ to be an eigenvalue of the Leslie matrix L and $\mathbf{v}$ to be the corresponding eigenvector.

In the case where all eigenvalues of the Leslie matrix are distinct[2], the general solution is the linear combination of the solutions for each eigenvalue.

$$\mathbf{N}_t = c_1 \lambda_1^t \mathbf{v}_1 + c_2 \lambda_2^t \mathbf{v}_2 + \cdots + c_m \lambda_m^t \mathbf{v}_m, \tag{4.40}$$

where $\lambda_1, \lambda_2, \ldots, \lambda_m$ are the eigenvalues of the Leslie matrix and $\mathbf{v}_1, \mathbf{v}_2, \ldots, \mathbf{v}_m$ are the corresponding eigenvectors. The constants $c_1, c_2, \ldots, c_m$ are determined by the initial conditions.

Example 4.2. Consider a population with the reproduction numbers b_a and the survival probabilities S_a given in the following table:

a	b_a	S_a	F_a
0	0	—	0
1	0	1	1/2
2	1	1/2	1
3	2	1/2	0
4	0	1/2	0

The final column in that table is calculated from the previous ones using $F_a := b_{a+1} S_{a+1}$. In this example the maximum age m beyond which there is no reproduction is $m = 3$. Hence the corresponding Leslie matrix is a 3×3 matrix. It is given by

$$L = \begin{pmatrix} F_0 & F_1 & F_2 \\ S_1 & 0 & 0 \\ 0 & S_2 & 0 \end{pmatrix} = \begin{pmatrix} 0 & 1/2 & 1 \\ 1 & 0 & 0 \\ 0 & 1/2 & 0 \end{pmatrix}. \tag{4.41}$$

Assume that the at time $t = 0$ we only have 10 individuals all of age 0, i.e.,

$$\mathbf{N}_0 = \begin{pmatrix} 10 \\ 0 \\ 0 \end{pmatrix}. \tag{4.42}$$

We can then calculate the numbers at the following times $t = 1, 2, 3, \ldots$ by repeated multiplication by the Leslie matrix L:

$$\mathbf{N}_1 = L\mathbf{N}_0 = \begin{pmatrix} 0 & 1/2 & 1 \\ 1 & 0 & 0 \\ 0 & 1/2 & 0 \end{pmatrix} \begin{pmatrix} 10 \\ 0 \\ 0 \end{pmatrix} = \begin{pmatrix} 0 \\ 10 \\ 0 \end{pmatrix},$$

---

[2] In the case where there are repeated eigenvalues, the general solution is just a bit more complicated. Luckily in ecology, we are rarely interested in that case, because the probability that a real ecosystem is exactly so that this special case arises is zero.

$$\mathbf{N}_2 = L\mathbf{N}_1 = \begin{pmatrix} 5 \\ 0 \\ 5 \end{pmatrix}, \quad \mathbf{N}_3 = L\mathbf{N}_2 = \begin{pmatrix} 5 \\ 5 \\ 0 \end{pmatrix}, \cdots.$$

Continuing like this (using a computer) we observe that the population converges to a stable age distribution.

$$\lim_{t \to \infty} \mathbf{N}_t = \begin{pmatrix} 4 \\ 4 \\ 2 \end{pmatrix}. \tag{4.43}$$

To understand this phenomenon we look for the eigenvalues and eigenvectors of the Leslie matrix. The eigenvalues are the solutions of the characteristic equation

$$0 = \det(L - \lambda I) = \begin{vmatrix} -\lambda & 1/2 & 1 \\ 1 & -\lambda & 0 \\ 0 & 1/2 & -\lambda \end{vmatrix} = -\lambda^3 + \frac{1}{2}\lambda + \frac{1}{2}$$
$$= (1 - \lambda)\left(\lambda^2 + \lambda + \frac{1}{2}\right) \tag{4.44}$$

We can read off that the solutions are

$$\lambda_) = 1, \quad \lambda_\pm = -\frac{1}{2} \pm \frac{1}{2}i. \tag{4.45}$$

Because the magnitude of the eigenvalues $\lambda_\pm$ is less than 1, we have that $\lim_{t \to \infty} \lambda_\pm^t = 0$. This means that the stable age distribution is given by the eigenvector corresponding to the eigenvalue $\lambda_0 = 1$:

$$\lim_{t \to \infty} \mathbf{N}_t = \lim_{t \to \infty} \left(c_0 \lambda_0^t \mathbf{v}_0 + c_+ \lambda_+^t \mathbf{v}_+ + c_- \lambda_-^t \mathbf{v}_-\right) = c_0 \mathbf{v}_0.$$

In general, if the Leslie matrix has a unique dominatn eigenvalue λ_0 with a corresponding eigenvector $\mathbf{v}_0$, then

$$\lim_{t \to \infty} \frac{\mathbf{N}_t}{\lambda_0^t} = c_0 \mathbf{v}_0,$$

where c_0 is a constant that depends on the initial conditions. This means that the population converges to a stable age distribution. The stable age distribution is given by the eigenvector corresponding to the dominant eigenvalue of the Leslie matrix.

Luckily, there is a theorem about the eigenvalues and eigenvectors of non-negative matrices that we can use to determine whether a Leslie matrix has a unique dominant eigenvalue. We start by associating the Leslie matrix with a directed graph. The graph has m vertices and a directed edge from vertex i to vertex j if and only if the Leslie matrix has a non-zero entry in column i and row j. The graph is called the Leslie graph. We call the Leslie matrix irreducible if its Leslie graph is strongly connected, which means that there is a directed path between any two nodes. We call the Leslie matrix primitive if the greatest common divisor of the lengths of all circuits in the Leslie graph is 1. The following theorem is then true:

Theorem 4.1. *If the Leslie matrix is irreducible and primitive, then it has a unique dominant eigenvalue that is real and positive. The corresponding right eigenvector is real and strictly positive.*

This is a special case of the Perron-Frobenius theorem, which is a general theorem about non-negative matrices, and is used extensively in the theory of Markov chains. The above theorem is exactly what we need, because it tells us when the Leslie matrix has a unique dominant eigenvalue and a corresponding eigenvector that gives the stable age distribution.

4.3 Exercises

4.3.0.1 * Age-independent rates

Exercise 4.1. In the continuous-time age-structured population model consider the case where $b(a) = b$ and $\mu(a) = \mu$ are both constant. Repeat all steps of the analysis but simplifying the expressions at each step by using the constant values for birth and death rates.

1. Solve the partial differential equation of the age-structured model by making the Ansatz $n(t, a) = f(t)r(a)$ and introducing the separation constant γ.
2. Use the boundary condition at $a = 0$ to determine the value of γ.
3. Give the condition under which the population goes extinct and compare it to the condition in the exponential model from chapter 1.

4.3.0.2 o Harvestings an age-structured population

Exercise 4.2. Consider an age-structured fish population in which all individuals above the maturity age a_m are reproducing, at a fixed rate, so that

$$b(a) = \begin{cases} 0 & \text{if } a < a_m, \\ b & \text{if } a \geq a_m. \end{cases} \tag{4.46}$$

All fish at all ages experience a natural death rate μ_0. In addition, fish above the maturity size are harvested at a constant rate μ_F, so that

$$\mu(a) = \begin{cases} \mu_0 & \text{if } a < a_m, \\ \mu_0 + \mu_F & \text{if } a \geq a_m. \end{cases} \tag{4.47}$$

By calculating the expected number of offspring per individual, determine the limit on the harvesting rate μ_F that allows the population to be sustainable.

A Solutions

This appendix holds the solutions to selected exercises in the book. Please look at these solutions only after having made a serious attempt at solving the exercises and knowing exactly where you got stuck.

A.1 Continuous-time population models

Exercise 1.2

Von Bertalanffy growth

i) Seeking a steady state we find $\alpha w^{2/3} - \beta w = 0 \implies w^{2/3}(\alpha - \beta w^{1/3}) = 0 \implies w = 0$ or $w^{1/3} = \alpha/\beta$. With the graphical approach in Figure A.1 we see that the non-zero steady state is stable. Hence,

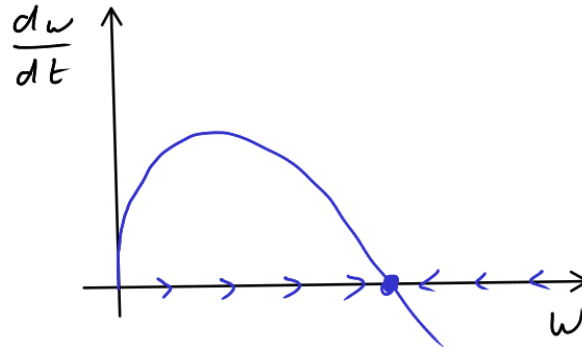$$\lim_{t\to\infty} w(t) = \left(\frac{\alpha}{\beta}\right)^3.$$

Figure A.1: dw/dt versus w for the von Bertalanffy growth model.

ii) For the time derivative of $u = w^{1/3}$ we find by the chain rule that

$$\frac{du}{dt} = \frac{1}{3}w^{-2/3}\frac{dw}{dt} = \frac{1}{3u^2}\left(\alpha w^{2/3} - \beta w\right).$$

Hence
$$3\frac{du}{dt} = \frac{1}{u^2}\left(\alpha u^2 - \beta u^3\right) = \alpha - \beta u.$$

So this change of variables has yielded a first-order ODE with linear coefficients, which is easy for us to solve:
$$u(t) = \frac{1}{\beta}\left(\alpha - Ae^{-\beta t/3}\right)$$

for some integration constant A. If $u(0) = u_0$ then $A = \alpha - \beta u_0$.

iii) Translating back to w with $w_0 = u_0^3$ we finally have
$$w(t) = u(t)^3 = \frac{1}{\beta^3}\left(\alpha - \left(\alpha - \beta w_0^{1/3}\right)e^{-\beta t/3}\right)^3.$$

Exercise A.1

Solving logistic equation

We separate the variables by dividing both sides of the ODE by $N(1 - N/K)$ and multiplying by dt, and then integrate to get
$$\int_{N_0}^{N(t)} \frac{dN}{N\left(1 - \frac{N}{K}\right)} = \int_0^t r\, dt.$$

The right hand side is trivial to integrate, but for the integral on the left-hand side we need to employ the method of partial fractions, using that
$$\frac{dN}{N\left(1 - \frac{N}{K}\right)} = \frac{1}{N} + \frac{1}{K - N}.$$

The left-hand side then gives
$$\int_{N_0}^{N(t)} \left(\frac{1}{N} + \frac{1}{K - N(t)}\right) dN = \log N(t) - \log N_0 - \log(K - N(t)) + \log(K - N_0).$$

We exponentiate both sides to get
$$\frac{N(t)}{N_0}\frac{K - N_0}{K - N(t)} = e^{rt}.$$

Now we just need to solve for $N(t)$:
$$N(t) = \frac{N_0 K e^{rt}}{K + N_0(e^{rt} - 1)}.$$

Exercise A.1

Harvesting with fixed quota

If we harvest with a fixed quota Q, the population is described by the equation

$$\frac{dN}{dt} = \alpha N \log \frac{K}{N} - Q.$$

The subtraction of Q shifts the graph of the right-hand side down by a distance Q. This brings the non-zero fixed points closer together until Q is equal to the maximum of the growth rate of the unfished population. If Q is increased beyond this value the non-zero fixed points disappear and the population will go extinct. is because we are removing Q individuals from the population at a constant rate. Thus the maximum sustainable yield occurs when Q equals the maximum replenishment rate of the unfished population. To find that maximum we first solve

$$0 = \frac{d}{dN}\left(\alpha N \log \frac{K}{N}\right) = \alpha\left(\log \frac{K}{N} - 1\right).$$

This tells us that the maximum is at

$$N_{max} = K\,e^{-1}.$$

Hence the value at the maximum is

$$MSY = Q_{max} = \alpha N_{max} \log \frac{K}{N_{max}} = \alpha\,K\,e^{-1}.$$

Fishing at this quota is not wise, as this reduces the population to the threshold level below which the population will go extinct.

Exercise 1.6

Wasps

For $0 \le t \le t_c$ the number of workers satisfies

$$\frac{dn}{dt} = r\,n.$$

Therefore

$$n(t) = n_0 e^{r\,t}.$$

For $t_c \le t \le T$ the number of reproducers satisfies

$$\frac{dN}{dt} = Rn(t_c) = R\,n_0\,e^{r\,t_c},$$

so that
$$N(T) = (T - t_c) R e^{r t_c}.$$

To find the value of t_c that maximises $N(T)$ we set the derivative of $N(T)$ with respect to t_c to zero:
$$0 = \frac{d}{dt_c} N(T) = \frac{d}{dt_c} (T - t_c) R e^{r t_c} = -R e^{r t_c} + (T - t_c) R r e^{r t_c} = R e^{r t_c} (r T - r t_c - 1).$$

This implies that
$$t_c = T - \frac{1}{r}.$$

Exercise A.1

Wasp with death

For $0 \le t \le t_c$ the number of workers satisfies
$$\frac{dn}{dt} = (r - d)n.$$

Therefore
$$n(t) = e^{(r-d)t}.$$

For $t_c \le t \le T$ we have
$$\frac{dn}{dt} = -dn$$

so that
$$n(t) = n(t_c) e^{-d(t-t_c)} = e^{(r-d)t_c} e^{-d(t-t_c)} = e^{r t_c} e^{-d t}.$$

Also for $t_c \le t \le T$ the number of reproducers satisfies
$$\frac{dN}{dt} = Rn(t) = R e^{r t_c} e^{-d t},$$

so that
$$N(T) = \int_{t_c}^{T} R e^{r t_c} e^{-d t} dt = \frac{R}{d} e^{r t_c} \left(e^{-d t_c} - e^{-d T} \right).$$

To find the value of t_c that maximises $N(T)$ we set the derivative of $N(T)$ with respect to t_c to zero:
$$0 = \frac{d}{dt_c} N(T) = \frac{d}{dt_c} \left(\frac{R}{d} e^{r t_c} \left(e^{-d t_c} - e^{-d T} \right) \right) = R e^{r t_c} \left(\left(\frac{r}{d} - 1 \right) e^{-d t_c} - \frac{r}{d} e^{-d T} \right)$$

This is equivalent to
$$e^{-d t_c} = \frac{1}{1 - d/r} e^{-d T}$$

and thus
$$t_c = T + \frac{1}{d} \ln \left(1 - \frac{d}{r} \right).$$

A.2 Discrete-time population models

Exercise A.2

Verhulst model

Let's write the equation as $N_{t+1} = f(N_t)$ with

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

Because $f(N)$ is positive for all $N < K$, the only way for N_{t+1} to be negative is for N_t to be greater than K. This in turn is only possible if $f(N_{t-1}) > K$. So the function f at its maximum needs to be larger than K. Because the function describes an upside-down parabola with zeros at 0 and K, its maximum is in the middle at $N = K/2$, where $f(K/2) = rK/4$. Thus the population can get negative iff $rK/4 > K$, which is equivalent to $r > 4$.

A.3 Age-structured population models

Exercise A.3

Harvestings an age-structured population

We can start from Eq. 4.14 that gives the expected number of offspring produced by an individual within their lifetime:

$$\phi(0) = \int_0^\infty b(a)\exp\left(-\int_0^a \mu(a')\,da'\right)\,da.$$

This will now simplify when we use the given expressions Eq. 4.46 and Eq. 4.47 for the rates. Because $b(a)$ is non-zero only for $a > a_m$, the outer integral only has to run from a_m to ∞. The inner integral from 0 to a we need to split into two integrals because of the piece-wise nature of $\mu(a)$. Hence

$$\phi(0) = \int_{a_m}^\infty b(a)\exp\left(-\int_0^{a_m} \mu(a')\,da' - \int_{a_m}^a \mu(a')\,da'\right)\,da.$$

We can now substitute the appropriate constants for the rates:

$$\phi(0) = \int_{a_m}^{\infty} b \, \exp\left(-\int_0^{a_m} \mu_0 \, da' - \int_{a_m}^{a} (\mu_0 + \mu_F) \, da'\right) \, da$$

$$= \int_{a_m}^{\infty} b \, \exp\left(-\mu_0 a_m - (\mu_0 + \mu_F)(a - a_m)\right) \, da$$

$$= b \, \exp(-\mu_F a_m) \int_{a_m}^{\infty} \exp\left(-(\mu_0 + \mu_F)a\right) \, da$$

$$= b \, \exp(-\mu_F a_m) \left[-\frac{1}{\mu_0 + \mu_F} \exp\left(-(\mu_0 + \mu_F)a\right)\right]_{a_m}^{\infty}$$

$$= b \, \exp(-\mu_F a_m) \frac{1}{\mu_0 + \mu_F} \exp\left(-(\mu_0 + \mu_F)a_m\right)$$

$$= \frac{b}{\mu_0 + \mu_F} \exp\left(-\mu_0 a_m\right).$$

This expected number of offspring produced by an individual within their lifetime must be greater or equal to 1 for the population to sustain itself. Hence the upper limit on the harvesting rate μ_F is given by

$$\mu_F \leq b \exp\left(-\mu_0 a_m\right) - \mu_0.$$