

Mathematical Ecology and Epidemiology

Lecture notes for Spring 2025

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Welcome

This site will contain the lecture notes for the Ecology and Epidemiology part of the “Mathematical Ecology, Epidemiology and Evolution” module taught at the University of York in the Spring of 2025. 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 and one examples class. Between each block there will be a two-week block of Mathematical Evolution.

These days it is no longer necessary to explain why it is important to apply mathematics to ecology or to epidemiology. We are causing global warming and the only way to predict and hence mitigate the ecological consequences is to employ mathematical models. During the Covid epidemic the public was informed daily about the latest prediction about the state of the epidemic derived from mathematical models, often summarised in terms of the R_0 value. People with skills in mathematical modelling are clearly crucial in these fields and will have a great impact. Furthermore, the techniques of mathematical modelling are transferable to other domains. The skills you acquire in this module will also be useful if you want to model the economy or the climate, to mention just two.

In this module we will concentrate on mathematical models that capture the essence of the real-world phenomena and strip away most of the details. Our models will be simple enough to allow for an analytical understanding of the model predictions. In practice, more complicated models are also employed, which need to be solved numerically. Only if you are taking this module as an M-level module will you be expected to perform numerical calculations. It is very wise to first start with a simple model for which you can obtain exact results before adding complications that force you to turn to numerics. That way you can test your numerics against the exact results in the regime where they are available. Also the insight from the simple models will allow you to better interpret the output from numerical models. This deeper understanding will give you a big advantage when you continue into applied research. But this understanding is also beneficial to you as a citizen who wants to take part in discussions about ecological preservation or of vaccination or similar questions of societal importance.

The notes will be released 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.

Exercises are scattered throughout the notes. 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. Exercises marked with an o are likely to be covered in a problems class.

Your solutions to the essential exercises covered throughout each 2 week block are due on Monday at 9:00 in the week following that block, i.e., in weeks 3, 5, 7, 9 and 11. The exercises will then be discussed at a seminar in that week. You will then be very well prepared for the summative Moodle Quizzes that will be released at 14:00 on Thursdays in Weeks 3, 5, 7, 9 and 11 and are due 24 hours later (14:00 on Fridays of Weeks 3, 5, 7, 9 and 11). These quizzes should not take you long to complete because they are based on the exercises that have already been discussed at the seminar.

For details of how this module will be assessed, see the assessment information on the [VLE](#).

In this part of the module you are allowed (and encouraged) to get as much help from AIs (like Gemini) and CASs (Computer Algebra Systems like Wolfram Alpha) as you like. Just be aware that you won't have access to an AI or to a CAS in the final exam, so make sure that you use the AI to learn things, not to let the AI do the work for you.

1 Continuous-time population models

Population dynamics is the study of how populations change over time. A population can be any group of individuals of the same species in a particular area, such as a population of bacteria in a petri dish, a herd of deer in a forest, the Cod stock in the Baltic Sea, or the human population of a country. Understanding how population size evolves is important in many fields, including ecology, conservation biology, epidemiology, and resource management.

To model a population mathematically, we introduce a function $N(t)$ that represents the number of individuals in the population at time t . We assume that at the starting time, which we take to be $t = 0$, the population has some initial size $N(0) = N_0$.

Since the population size changes over time, we are interested in its rate of change, which describes how quickly individuals are added or removed from the population. There are several fundamental processes that affect population size:

- Births: New individuals are born into the population, increasing its size.
- Deaths: Individuals die, decreasing the population.
- Immigration: Individuals arrive from outside the population, increasing its size.
- Emigration: Individuals leave the population to settle elsewhere, decreasing its size.

These processes together determine the overall rate of change of the population, which we can express mathematically as:

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

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 how these rates depend on the population size (or possibly other factors such as available resources or competition) lead to different population models. In the following sections, we will examine some influential models that help us understand different population growth scenarios.

Learning Objectives

After completing this chapter, you should be able to:

1. Mathematical Modeling

- Write down differential equations for population dynamics
- Identify and interpret key parameters in population models
- Solve basic population models analytically

2. Model Analysis

- Sketch solutions of population models
- Find steady states of population models
- Determine stability of steady states
- Interpret phase line diagrams
- Predict long-term behavior of populations

3. Applications

- Compare and contrast different population growth models
 - Understand how density dependence affects population growth
 - Analyze the effects of different harvesting strategies
-

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

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

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

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

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.

You may note that in this model $N(t)$ can take on non-integer values, so strictly speaking it can not describe the number of individuals. When the population is large, this is not a big problem. You can simply round $N(t)$ to the nearest integer without making much of a change. However if one wants to describe small populations correctly, one would have to switch from the deterministic differential equation to a stochastic process that models each birth and death individually. In these notes we will restrict ourselves to deterministic models.

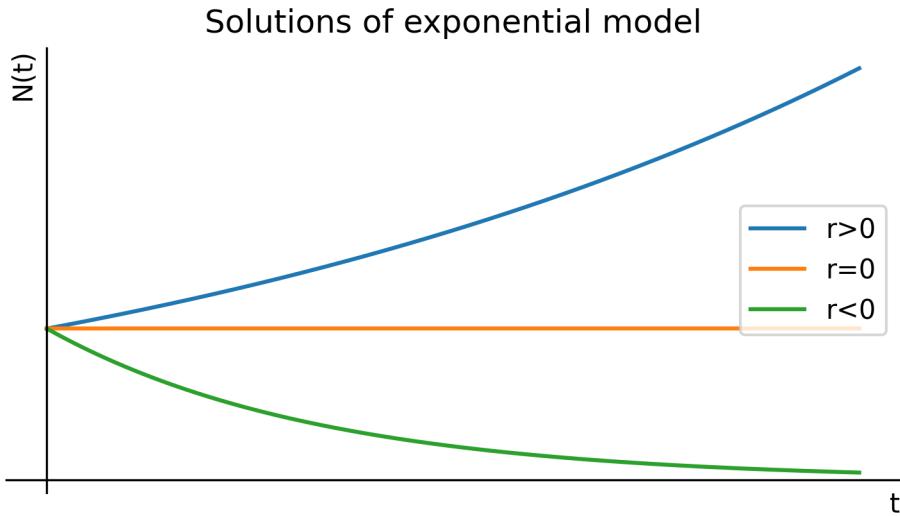


Figure 1.1: Solutions to the exponential model.

Exercise 1.1 (* Immigration). Let us try to model the population of a country with currently $N_0 = 70$ million inhabitants. Let us assume that the per-capita death rate is $d = 0.015$ deaths per year and the per-capita birth rate is $b = 0.01$ births per year. In addition there is a constant rate of immigration of $a = 300,000$ individuals per year.

- Write down the ODE for the population number $N(t)$. At this point, do not use the numerical values yet but the symbols.
 - Solve the ODE for $N(t)$ with the given initial condition. You may not have solved an ODE for some while so may need to look back at your Calculus notes. But don't panic: the equation from part (i) should be a linear, non-homogeneous, first-order ODE with constant coefficients, so you definitely know how to solve it. The easiest way to go about it is to first convert it into a homogeneous ODE by shifting the dependent variable.
 - Substitute the numerical values to obtain the projected population after 10 years.
-

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

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

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 we 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 $N = K$.

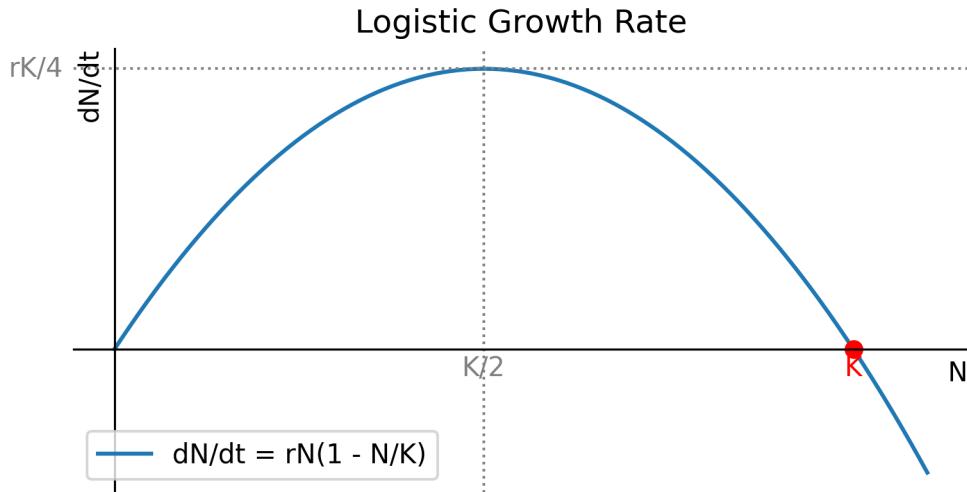


Figure 1.2: The logistic growth rate as a function of the population number.

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

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

Solutions of logistic model

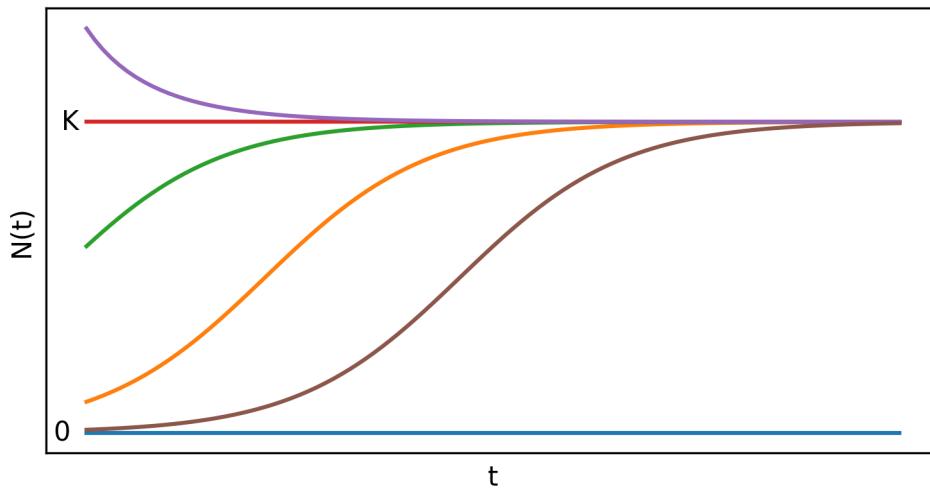


Figure 1.3: Solutions to the logistic equation.

Exercise 1.2 (Solving logistic equation). By using separation of variables and partial fractions, solve the logistic model Eq. 1.4 with initial condition $N(0) = N_0$ to derive Eq. 1.5.

This exercise is for you if you like practising your skills at solving ODEs. The logistic model is one of the few non-linear models that can be solved relatively easily

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 is not captured by the logistic model because there the per-capita growth rate decreases linearly with population size.

There can be several causes for an Allee effect. For example:

- In many plant species, pollination becomes less effective at low densities because pollinators are less likely to visit sparse populations
- Social animals like wolves hunt more successfully in packs, so individuals in larger groups have higher survival rates
- Colonial seabirds like puffins rely on large colony sizes for protection from predators

- Many marine broadcast spawners (like sea urchins or abalone) require sufficient population density for successful fertilization
- Small populations of endangered species may suffer from genetic inbreeding, reducing reproductive success

But even in the case of an Allee effect, eventually the population growth has to slow again as the population reaches the carrying capacity of the ecosystem.

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.

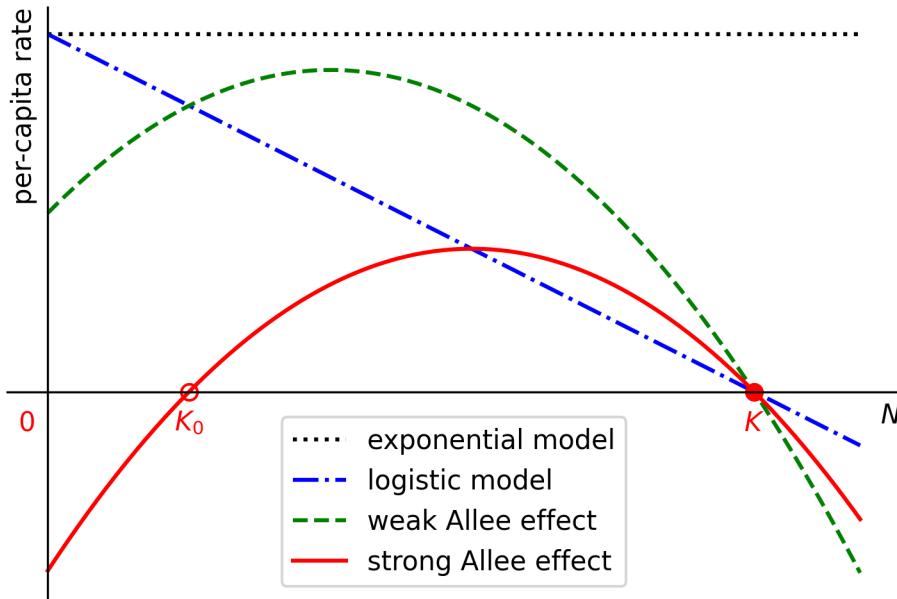


Figure 1.4: The per-capita growth rate as a function of the population number.

The green curve in Figure 1.4 shows a weak Allee effect, where the per-capita rate is small but positive 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 :

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

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.

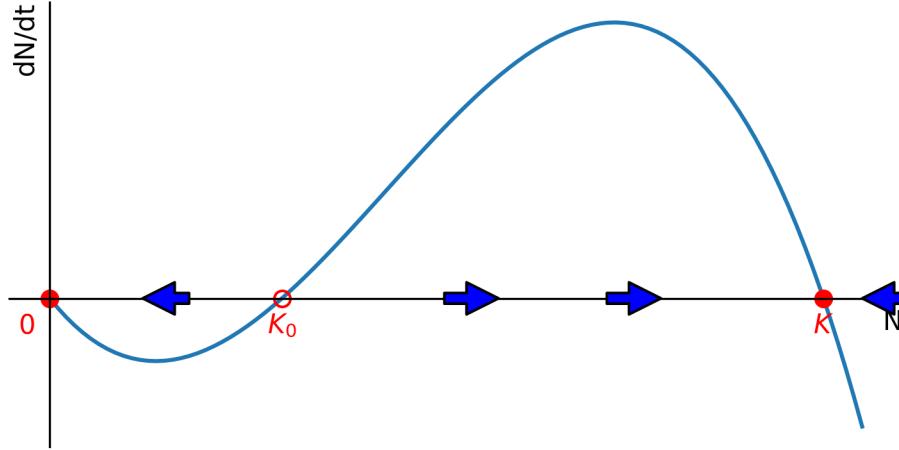


Figure 1.5: The Allee growth rate as a function of the population number.

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.

Exercise 1.3 (*Sketching solutions). Consider the population model with carrying capacity and Allee effect given by Eq. 1.6 with $r > 0$ and $K > K_0 > 0$. 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. You are explicitly asked not to make the plot with a computer as in Figure 1.3.

1.4 General autonomous ODE model

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

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

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

$$f(N) = rN \left(1 - \frac{N}{K}\right). \quad (1.8)$$

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

$$\frac{dN}{dt} = \frac{dN^*}{dt} + \frac{dn}{dt} = f(N^* + n(t)) \approx f(N^*) + f'(N^*) n(t). \quad (1.9)$$

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

$$\frac{dn}{dt} \approx f'(N^*) n(t). \quad (1.10)$$

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

$$n(t) = n(0)e^{f'(N^*)t} \quad (1.11)$$

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

$$f'(N) = r \left(1 - \frac{2N}{K}\right). \quad (1.12)$$

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.

For a more detailed discussion of one-dimensional autonomous dynamical systems I recommend the first 50 pages of (Strogatz 2000).

Exercise 1.4 (+Von Bertalanffy growth). Assume the weight $w(t)$ of an individual fish at time t is governed by the differential equation

$$\frac{dw}{dt} = \alpha w^{2/3} - \beta w \quad (1.13)$$

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 $\lim_{t \rightarrow \infty} w(t)$.
 - 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 .
-

1.5 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 to harvest fish from the sea, to hunt deer in the forest, and to cut down trees in the jungle. These days 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 Fixed fishing 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

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right) - EN = f(N). \quad (1.14)$$

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

$$\frac{dN}{dt} = rN \left(\left(1 - \frac{E}{r}\right) - \frac{N}{K} \right) = (r - E)N \left(1 - \frac{N}{K(1 - \frac{E}{r})} \right). \quad (1.15)$$

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

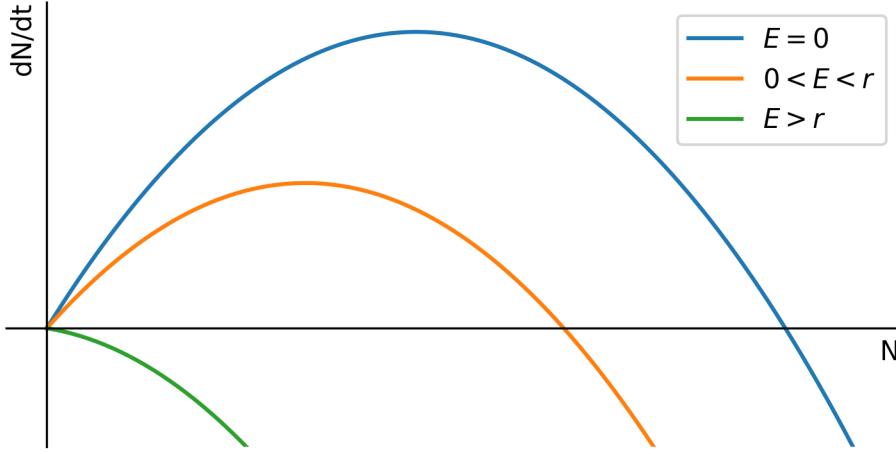


Figure 1.6: Growth rate when harvesting with fixed effort.

We are now interested in finding out at what level we should fish in order to achieve 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 $N^* = K(1 - \frac{E}{r})$. The yield is the amount of fish that can be harvested per unit time, and it is given at the fixed point by

$$Y^*(E) = EN^* = EK \left(1 - \frac{E}{r} \right). \quad (1.16)$$

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

$$\frac{dY^*}{dE} = K \left(1 - \frac{2E}{r} \right) = 0. \quad (1.17)$$

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

$$E^* = \frac{r}{2}. \quad (1.18)$$

The resulting maximum sustainable yield is

$$MSY = Y^*(E^*) = \frac{r}{2}K \left(1 - \frac{r}{2r} \right) = \frac{rK}{4}. \quad (1.19)$$

Exercise 1.5 (* Harvesting in Gompertz model). Consider a population $N(t)$ that is described by the Gompertz model

$$\frac{dN}{dt} = \alpha N \log \frac{K}{N}, \quad (1.20)$$

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.

1.5.2 Fixed fishing quota

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 :

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right) - Q. \quad (1.21)$$

This is visualised in Figure 1.7.

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.

Exercise 1.6 (Harvesting with fixed quota in Gompertz model). As in Exercise 1.5, 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

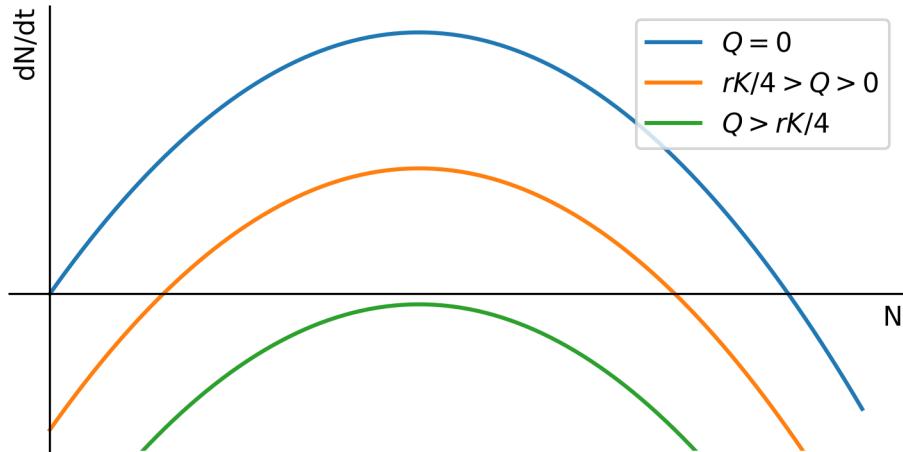


Figure 1.7: Growth rate when harvesting with fixed quota.

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?

Summary

This chapter introduced several key models for population dynamics in continuous time:

1. Exponential Model

- Simplest model with constant per-capita birth and death rates
- Solution: $N(t) = N_0 e^{rt}$ where $r = b - d$
- Predicts unlimited growth ($r > 0$) or decay ($r < 0$)
- Main limitation: Ignores environmental constraints

2. Logistic Model

- Incorporates carrying capacity K
- Growth rate decreases as population approaches K
- Equation: $\frac{dN}{dt} = rN(1 - \frac{N}{K})$
- Has stable equilibrium at $N = K$ and unstable equilibrium at $N = 0$

3. Allee Effect Model

- Captures reduced growth at low population densities
- Strong Allee effect has critical population threshold K_0
 - Below K_0 : population declines to extinction
 - Above K_0 : population grows to carrying capacity

4. Harvesting Models

- Fixed effort (E): $\frac{dN}{dt} = rN(1 - \frac{N}{K}) - EN$
 - Maximum sustainable yield at $E = \frac{r}{2}$
- Fixed quota (Q): $\frac{dN}{dt} = rN(1 - \frac{N}{K}) - Q$
 - Introduces critical depensation
 - More risky management approach

Key concepts:

- Population dynamics can be modelled by specifying the rates of change coming from processes such as birth, death, immigration, emigration, harvesting, etc.
 - For autonomous models, one can make qualitative sketches of the solutions
 - Steady states and their stability determine long-term behavior
 - More realistic models incorporate density dependence
 - Conservation and management strategies must consider population thresholds
 - Choice of harvesting strategy has important implications for sustainability
-

Further exercises

Exercise 1.7 (Wasp model). 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.

Exercise 1.8 (Wasp model with death). In the wasp example from Exercise 1.7, 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 1.7. 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 switch-over time t_c .

Exercise 1.9 (Conceptual Questions).

1. How does the logistic model address the limitations of the exponential model?
 2. Why might a population exhibit an Allee effect? Give two biological examples.
 3. Compare and contrast harvesting with fixed effort versus fixed quota. What are the management implications of each approach?
 4. Under what conditions might the exponential model be appropriate, despite its limitations?
-

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

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

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 : $N_1 = f(N_0)$, $N_2 = f(N_1) = f(f(N_0))$, ... $N_t = f(f(\dots f(N_0) \dots))$.

Learning Objectives

After completing this chapter, you should be able to:

1. Mathematical Modeling

- Write down difference equations for population dynamics
- Identify and interpret key parameters in discrete-time models
- Solve basic discrete-time population models

2. Model Analysis

- Find fixed points of discrete-time models
- Determine stability using linear analysis and cobweb diagrams
- Interpret cobweb diagrams
- Predict long-term behavior of populations

3. Bifurcations

- Identify different types of bifurcations in discrete-time models
- Analyze how model behavior changes at bifurcation points
- Understand period-doubling bifurcations unique to discrete systems

4. Applications

- Compare and contrast different discrete-time population models
- Analyze harvesting strategies in discrete-time models
- Understand critical depensation in discrete systems

Key Ecological Concepts

Before diving into the mathematical models, let's clarify some ecological terminology:

- **Population:** A group of individuals of the same species living in a particular area
- **Carrying capacity:** The maximum sustainable population size in a given environment
- **Critical depensation:** A threshold effect where populations below a certain size tend to decline to extinction
- **Density dependence:** How population growth rates change with population size
- **Seasonal reproduction:** When breeding occurs at specific times of year rather than continuously

These concepts will help explain why we choose particular mathematical forms for our models.

2.1 Exponential model

Just as we started with the exponential model in Chapter 1, we begin here with the simplest discrete-time model

$$N_{t+1} = RN_t \quad (2.2)$$

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

$$N_t = N_0 R^t. \quad (2.3)$$

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

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

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.

Exercise 2.1 (AER). You may be familiar with the distinction between the instantaneous rate r in a continuous-time model and the annual equivalent rate R in the corresponding discrete-time model from your savings account. Assuming that the bank pays interest into your account but you do not withdraw any money, what interest rate r do you need so that the money has increased by 5% after one year, i.e., so that the yearly growth factor is $R = 1.05$?

2.2 Logistic model

Recall how we introduced the continuous-time 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

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

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

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

We have written the model in two alternative forms, with $R = R_0 + 1$ and $\tilde{K} = K(R_0 + 1)/R_0$, because the first form makes it easier to read off the fixed point, while the second form makes the analogy with the continuous-time logistic model more obvious. Eq. 2.6 is also often referred to as the logistic map and is a famous example of a chaotic system.

Again it is important to stress that R_0 is not a growth *rate* but a dimensionless growth factor. We are interested in the case where $R_0 > 0$ and $K > 0$.

A 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.

2.3 Linear stability analysis

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

$$N_{t+1} = N^* + n_{t+1} = f(N_t) = f(N^* + n_t) = f(N^*) + f'(N^*)n_t + \dots \quad (2.7)$$

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

$$n_{t+1} \approx f'(N^*)n_t \quad (2.8)$$

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:

$$n_t = n_0(f'(N^*))^t. \quad (2.9)$$

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.

Exercise 2.2 (+ Stability in Verhulst model). Use the stability criterion that we just derived to derive a condition on the parameter R_0 of the Verhulst model that makes the non-zero fixed point $N^* = K$ a stable fixed point.

2.4 Cobweb diagrams

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.

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Figure 2.1: Cobweb diagram for a stable fixed point.

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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. Ecologically, what is happening as the growth factor increases through $R = 3$ is that in a single year the population grows so much that it exceeds its carrying capacity. That then leads to unfavourable conditions in the following year, leading to a decrease below carrying capacity. Such oscillations in population numbers are not possible in a continuous-time model for a single un-structured population.

In Figure 2.1 the oscillations get damped over time and the system evolves towards a steady state. In Figure 2.1 the system evolves towards a state where the population number oscillates between two values. This is called a period-two orbit. We will have more to say about this in Section 2.7.

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 because the system will not be oscillating around the fixed point but will be evolving towards it. Figure 2.3 shows the cobweb for a stable fixed point with positive slope $0 < f'(N^*) < 1$ and Figure 2.4 shows the cobweb for an unstable fixed point with positive slope $f'(N^*) > 1$.

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

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Figure 2.4: Cobweb diagram for an unstable fixed point with positive slope.

Exercise 2.3 (+ Verhulst model). For some choices of the parameters, the Verhulst model

$$N_{t+1} = RN_t \left(1 - \frac{N_t}{\tilde{K}}\right) \quad (2.10)$$

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.

2.5 Other models with limited carrying capacity

You showed in Exercise 2.3 that the Verhulst model has the disadvantage that it can give negative population numbers. There are several other models that are discrete-time versions of the logistic model and do not have this problem. We will now look at the two most important of them.

2.5.1 Ricker model

Many fish species, like salmon, have distinct breeding seasons and their reproduction shows strong density dependence - when population density is too high, fewer offspring survive due to competition for spawning sites. The Ricker model captures this behavior through the equation:

$$N_{t+1} = N_t e^{R_0 \left(1 - \frac{N_t}{K}\right)}. \quad (2.11)$$

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.

Exercise 2.4 (* Ricker model). Find the fixed points in the Ricker model

$$N_{t+1} = N_t e^{R_0(1 - \frac{N_t}{K})}. \quad (2.12)$$

and investigate their stability. Do this both analytically and by drawing cobweb diagrams. Allow also negative values of R_0 in your analysis, even though this is not ecologically realistic. Note that you will then need at least three cobweb diagrams because there are then two bifurcations.

2.5.2 Beverton-Holt model

The Beverton-Holt model, introduced by Ray Beverton and Sidney Holt in 1957, was developed to understand fish population dynamics. The model arose from their groundbreaking work on sustainable fisheries management while working at the Fisheries Laboratory in Lowestoft, UK. They were particularly interested in how the number of young fish (recruits) entering a population depends on the number of parent fish (spawning stock).

They proposed the model

$$N_{t+1} = \frac{RN_t}{1 + \frac{R-1}{K}N_t}. \quad (2.13)$$

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 trick is to make a change of variables from N_t to $u_t = 1/N_t$. Then we have

$$u_{t+1} = \frac{1}{N_{t+1}} = \frac{1 + \frac{R-1}{K}N_t}{RN_t} = \frac{u_t}{R} + \frac{R-1}{RK}. \quad (2.14)$$

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

$$\begin{aligned} u_1 &= \frac{u_0}{R} + \frac{R-1}{RK}, \\ u_2 &= \frac{u_0}{R^2} + \frac{R-1}{RK} \left(1 + \frac{1}{R}\right), \\ u_3 &= \frac{u_0}{R^3} + \frac{R-1}{RK} \left(1 + \frac{1}{R} + \frac{1}{R^2}\right), \\ &\vdots \\ u_t &= \frac{u_0}{R^t} + \frac{R-1}{RK} \left(1 + \frac{1}{R} + \frac{1}{R^2} + \dots + \frac{1}{R^{t-1}}\right). \end{aligned} \quad (2.15)$$

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

$$1 + x + x^2 + \dots + x^{t-1} = \frac{1 - x^t}{1 - x}. \quad (2.16)$$

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.

$$u_t = \frac{u_0}{R^t} - \frac{(1/R)^t - 1}{K} = \frac{Ku_0 - 1 + R^t}{KR^t}. \quad (2.17)$$

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

$$\begin{aligned} N_t &= \frac{1}{u_t} = \frac{KR^t}{Ku_0 - 1 + R^t} \\ &= \frac{K/u_0}{KR^{-t} - R^{-t}/u_0 + 1/u_0} \\ &= \frac{KN_0}{N_0 + (K - N_0)R^{-t}}. \end{aligned} \quad (2.18)$$

This is the solution to the Beverton-Holt model. Comparing this to the solution of the continuous-time logistic model from Eq. 1.5,

$$N(t) = \frac{KN_0}{N_0 + (K - N_0)\exp(-rt)}, \quad (2.19)$$

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

Exercise 2.5 (Beverton-Holt model). Find the fixed points in the Beverton-Holt model

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

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

2.6 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 conventional 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.

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 2.5.

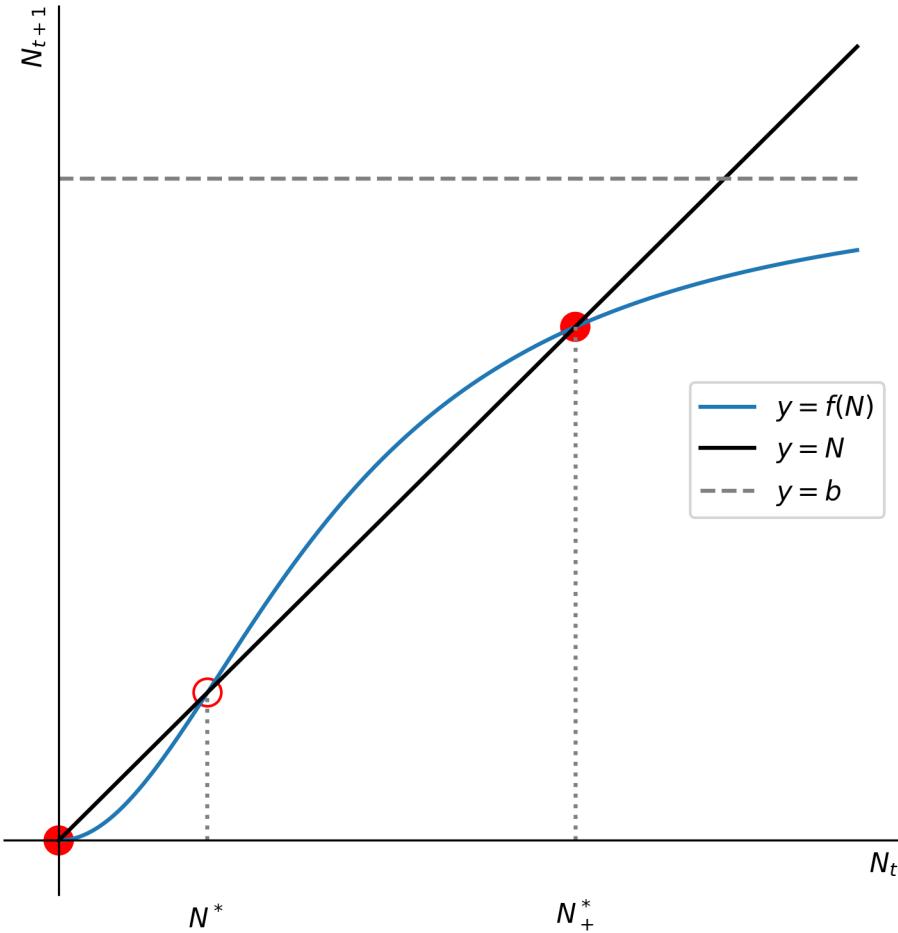


Figure 2.5: Graph of the function $f(N) = \frac{bN^2}{1+N^2}$.

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 2.5 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 2.6.

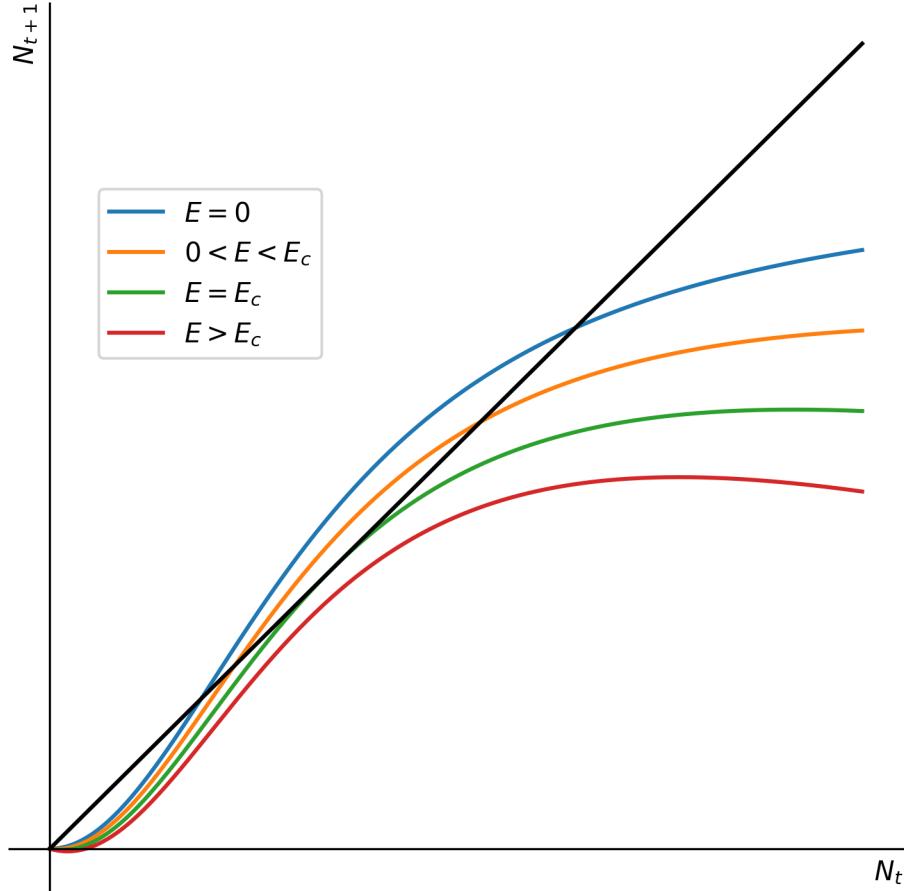


Figure 2.6: Graph of the function $f(N) = \frac{bN^2}{1+N^2} - EN$.

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

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

Again this has a 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

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

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.

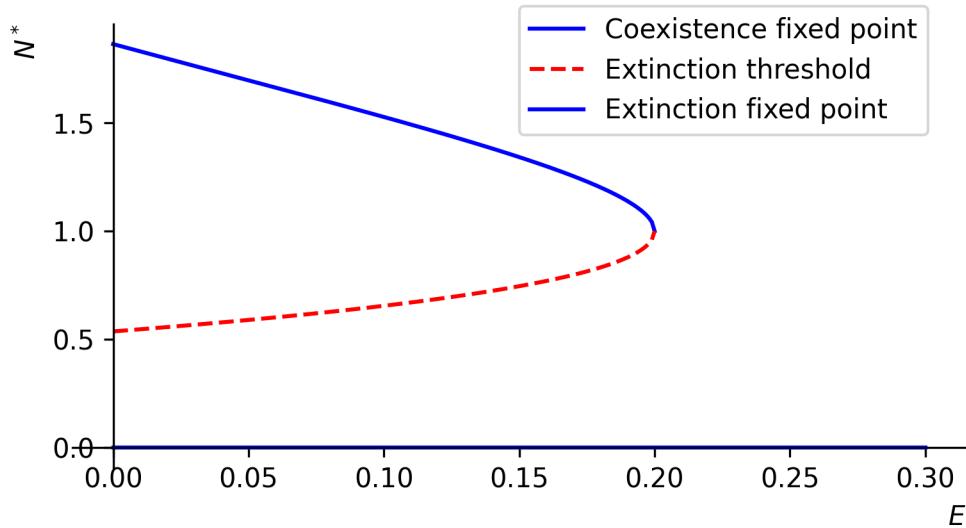


Figure 2.7: Bifurcation diagram for the discrete-time harvesting model.

2.7 Period-doubling route to chaos

Take another look at Figure 2.1 and Figure 2.2. Just a little change in the function $f(N)$ changed the nature of the fixed point. Such a change can be the consequence of a small change in a model parameter, for example the intrinsic growth rate.

We will use the logistic map to illustrate the period-doubling route to chaos, although the phenomenon is more general. The logistic map is a simple discrete-time model for population growth that exhibits a period-doubling route to chaos. It is defined as

$$X_{t+1} = R X_t (1 - X_t) =: f(X_t).$$

It is the same as the Verhulst model Eq. 2.6, just written in terms of $X_t = N_t/\tilde{K}$. Figure 2.8 shows the graph of $f(X)$ of the Verhulst model at three different values of the intrinsic growth factor R . For $R = 2.8$ the slope of f at the fixed point is less steep than -1 and thus the fixed point is stable, as in Figure 2.1. For $R = 3.2$ the slope of f at the fixed point is steeper than -1 and thus the fixed point is unstable and the population number starts to oscillate, as in Figure 2.2. At $R = 3$ the system switches from one behaviour to the other. That is the bifurcation point.

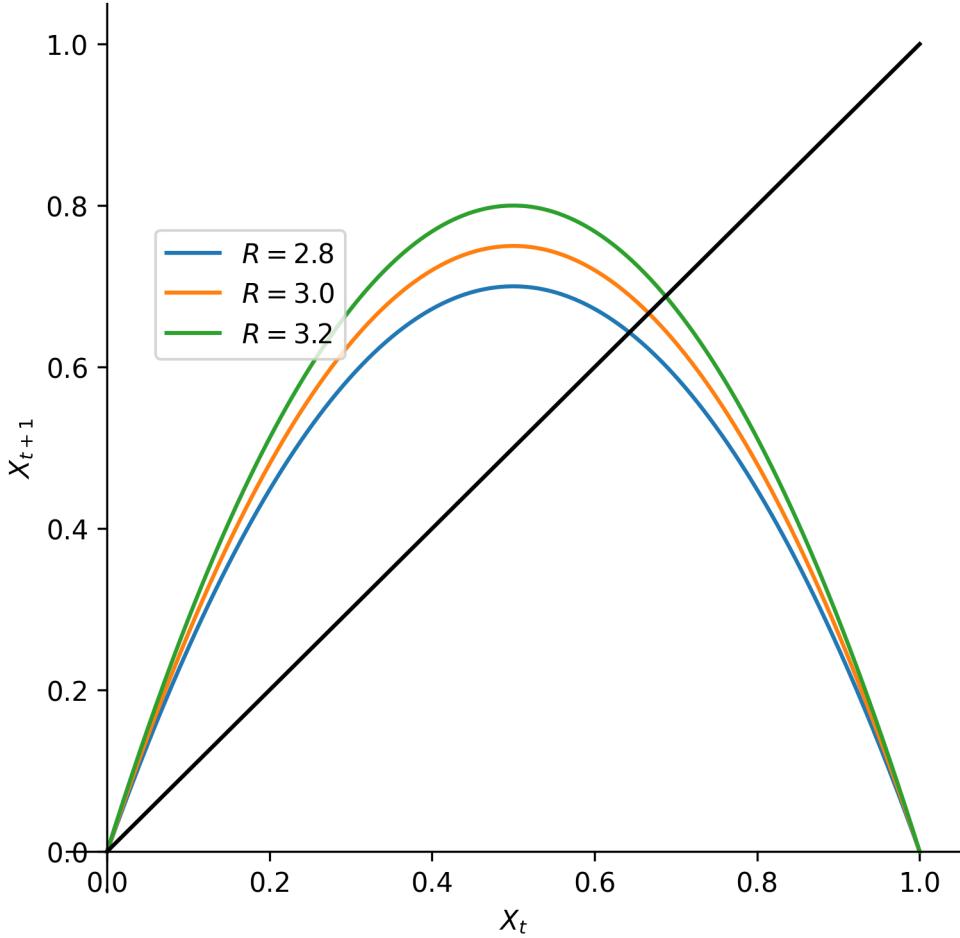


Figure 2.8: Plot showing a period-doubling bifurcation in the Verhulst model.

Figure 2.9 shows a simplified bifurcation diagram for the Verhulst model. A bifurcation diagram shows the location of fixed points or periodic orbits, with stable fixed points or stable periodic orbits represented by solid lines and unstable fixed points or unstable periodic orbits represented by dashed lines. Reading the diagram from left to right, which corresponds to increasing growth factor R in the Verhulst model, we see how at first the stable fixed point (which is located at the carrying capacity K) moves towards larger population sizes. At $R = 3$

it becomes unstable and spawns a stable periodic orbit whose amplitude grows until that periodic orbit itself becomes unstable, in another period-doubling bifurcation.

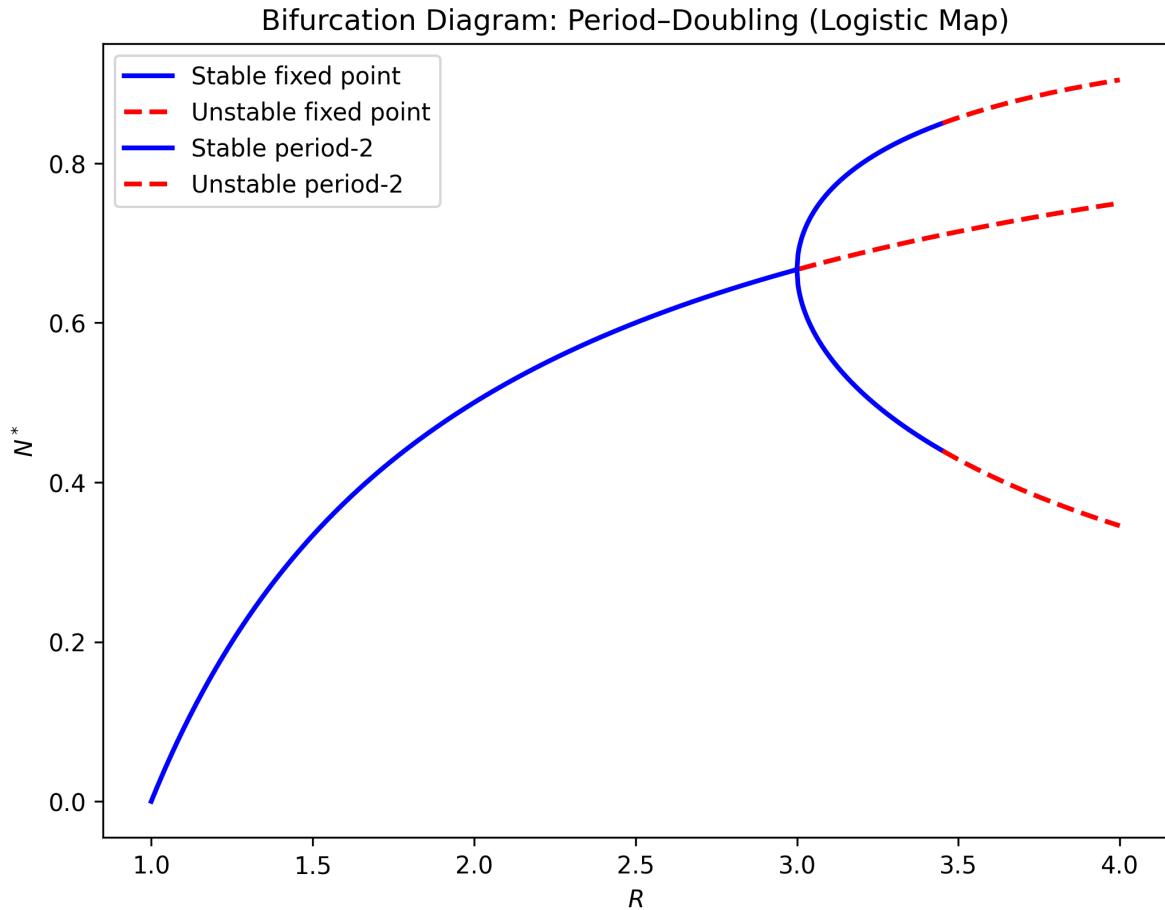


Figure 2.9: Bifurcation diagram for the period-doubling bifurcation.

Figure 2.9 does not show the period 4 orbit that emerges when the period 2 orbit becomes unstable. The full diagram quickly becomes very messy as R increases, as shown in Figure 2.10. Period-doubling cascades continue until the system enters a chaotic regime for $R > 3.56995$.

In the chaotic regime the system displays highly sensitive dependence on initial conditions, where small differences in the starting population can result in vastly different outcomes over time. The period-doubling route to chaos, as seen in the logistic map, is a classic example of how simple nonlinear equations can produce complex and unpredictable behavior. How important chaos is for ecological systems is a subject of ongoing debate.

Bifurcation Diagram: Period-Doubling Route to Chaos in the Logistic Map

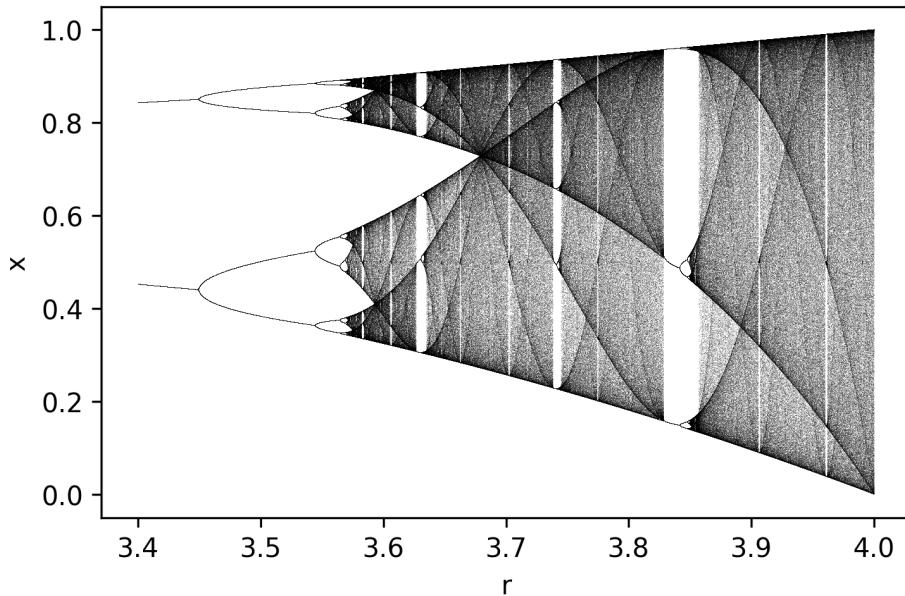


Figure 2.10: Bifurcation diagram for the period-doubling bifurcation.

2.8 Transcritical and pitchfork bifurcations

As mentioned before, a bifurcation is a change in the existence and stability of fixed points or periodic orbits as the parameters of the model are varied. You have met bifurcations in continuous-time models already in your Classical Dynamics 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 and we will discuss and visualise each of these bifurcation types below. These bifurcations happen if there is a fixed point with $f'(N^*) = 1$. Then there is also one more type: the period-doubling bifurcation, which happens when $f'(N^*) = -1$, and which we have met in Section 2.7.

2.8.1 Saddle-node bifurcation

We have already seen a saddle-node bifurcation in the discrete-time harvesting mode, where two fixed points merge and disappear as the parameter is varied. This is also sometimes referred to as a tangent bifurcation. Figure 2.11 shows an example of a function $f(N)$ that depends on a parameter r in such a way that for $r > 0$ the graph of $f(N)$ crosses the diagonal twice, which means that there are two fixed points. Then at exactly $r = 0$ the function is

tangent to the diagonal, i.e., there is only a single fixed point. Then for $r < 0$ the function does not touch the diagonal so that there are no fixed points left.

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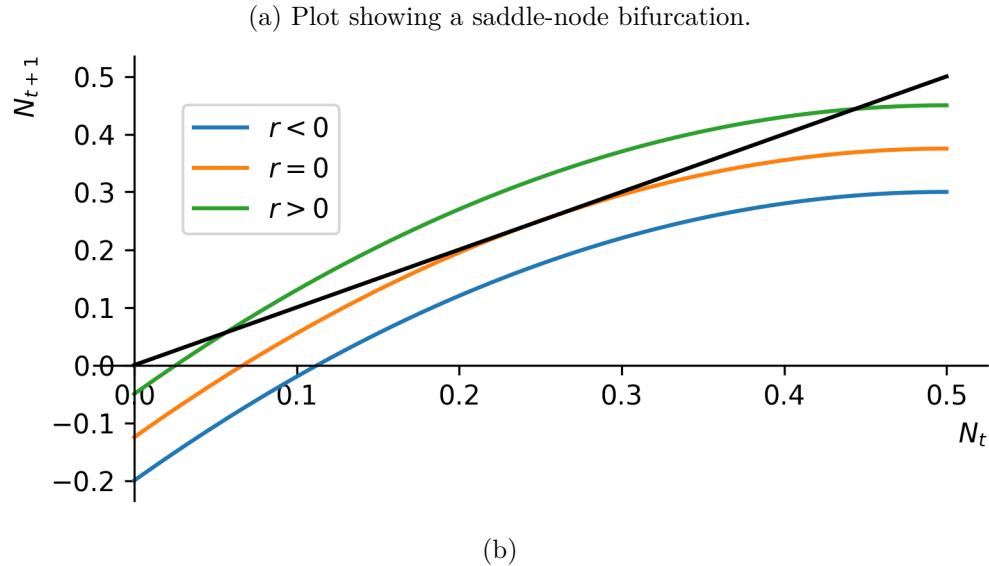


Figure 2.11

Figure 2.12 shows the corresponding bifurcation diagram.

2.8.2 Transcritical bifurcation

2.8.3 Pitchfork bifurcation

Exercise 2.6 (o House finches). [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.

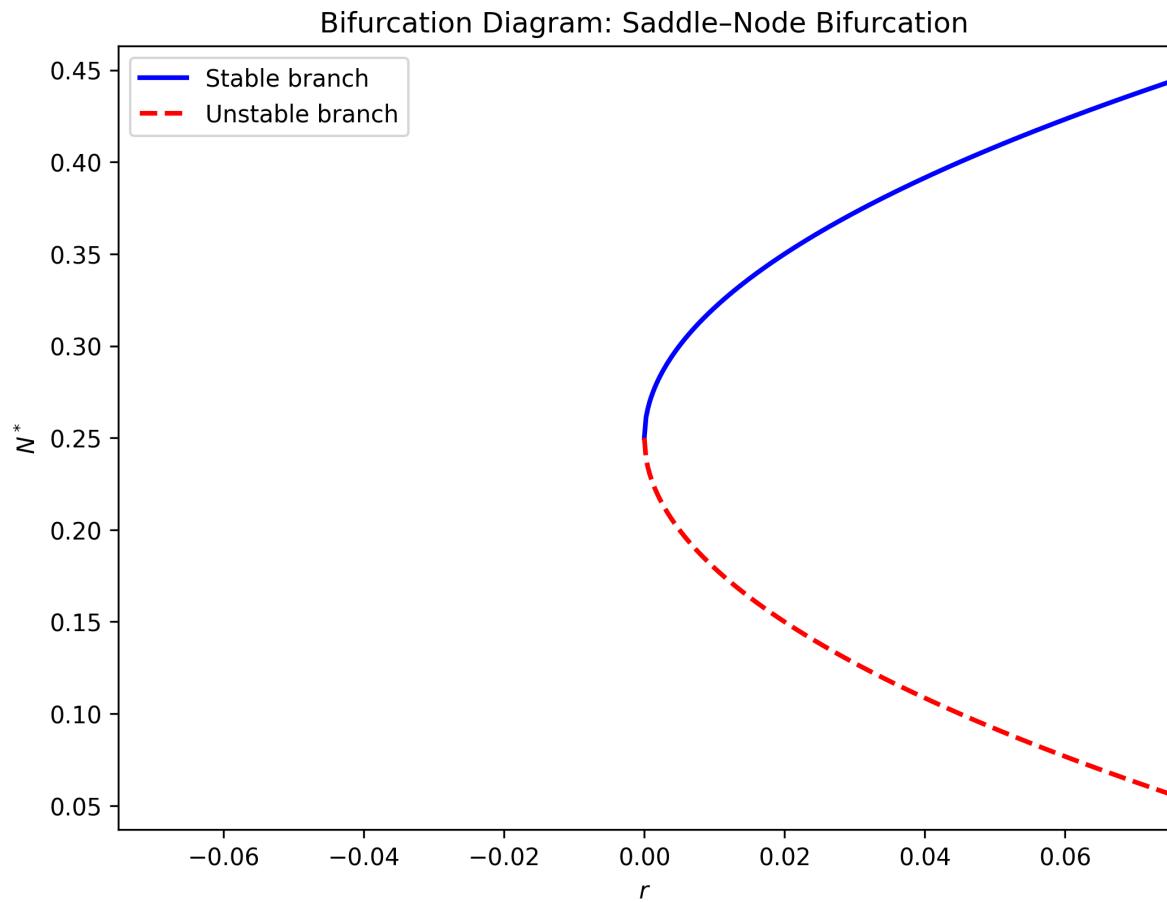


Figure 2.12: Bifurcation diagram for a saddle-node bifurcation.

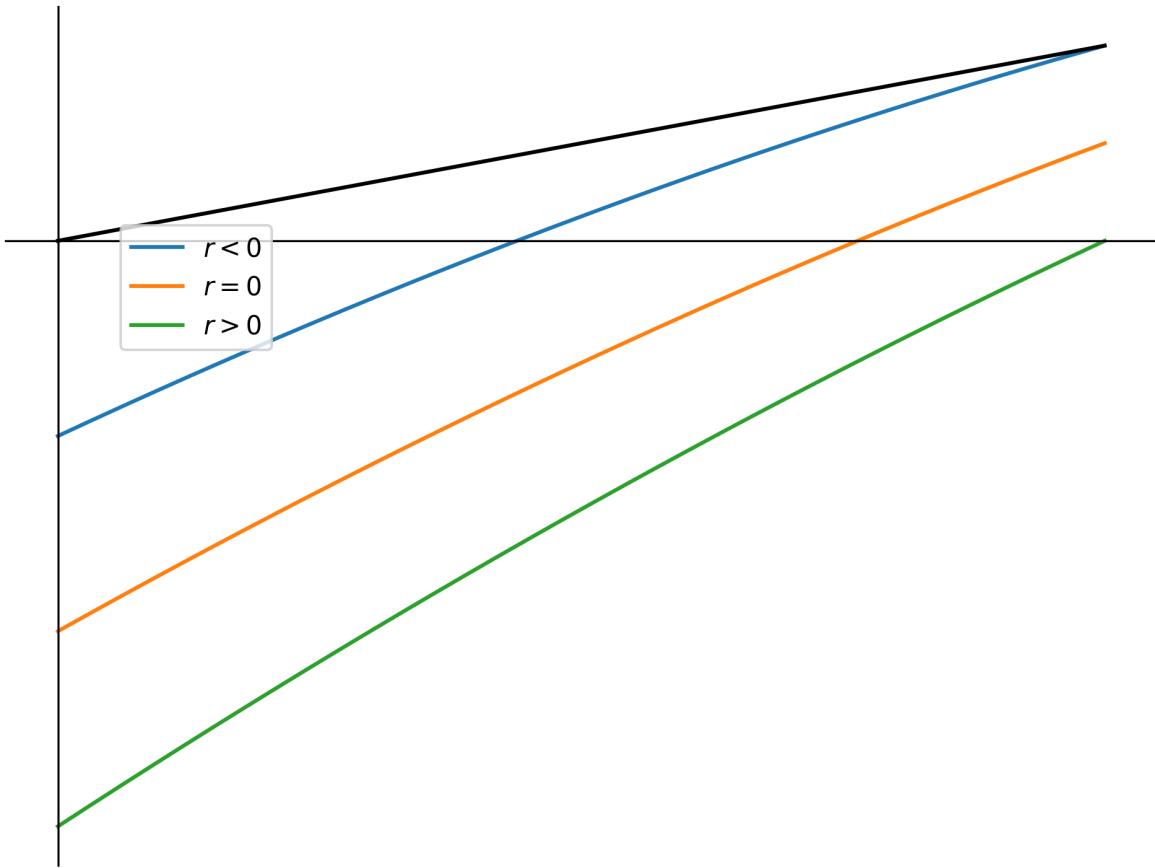


Figure 2.13: Plot showing a transcritical bifurcation.

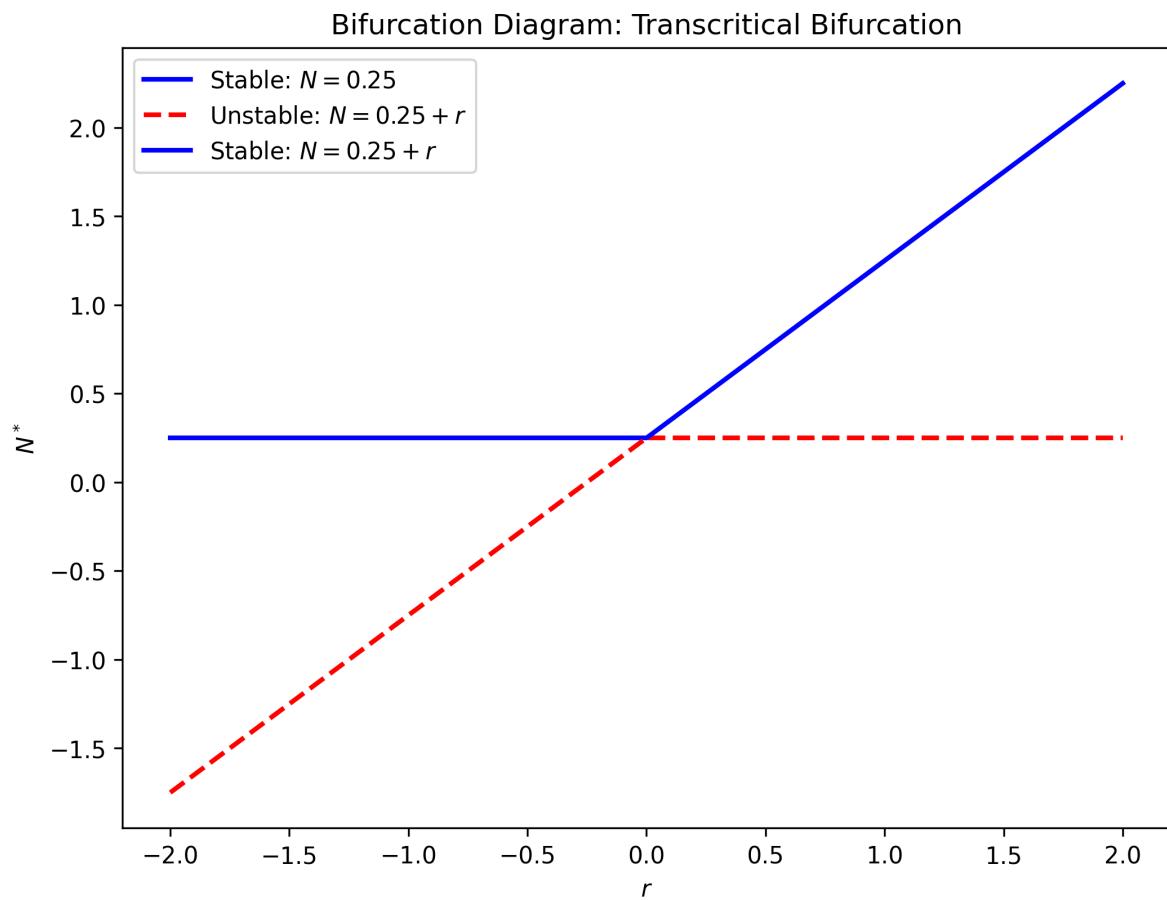


Figure 2.14: Bifurcation diagram for a transcritical bifurcation.

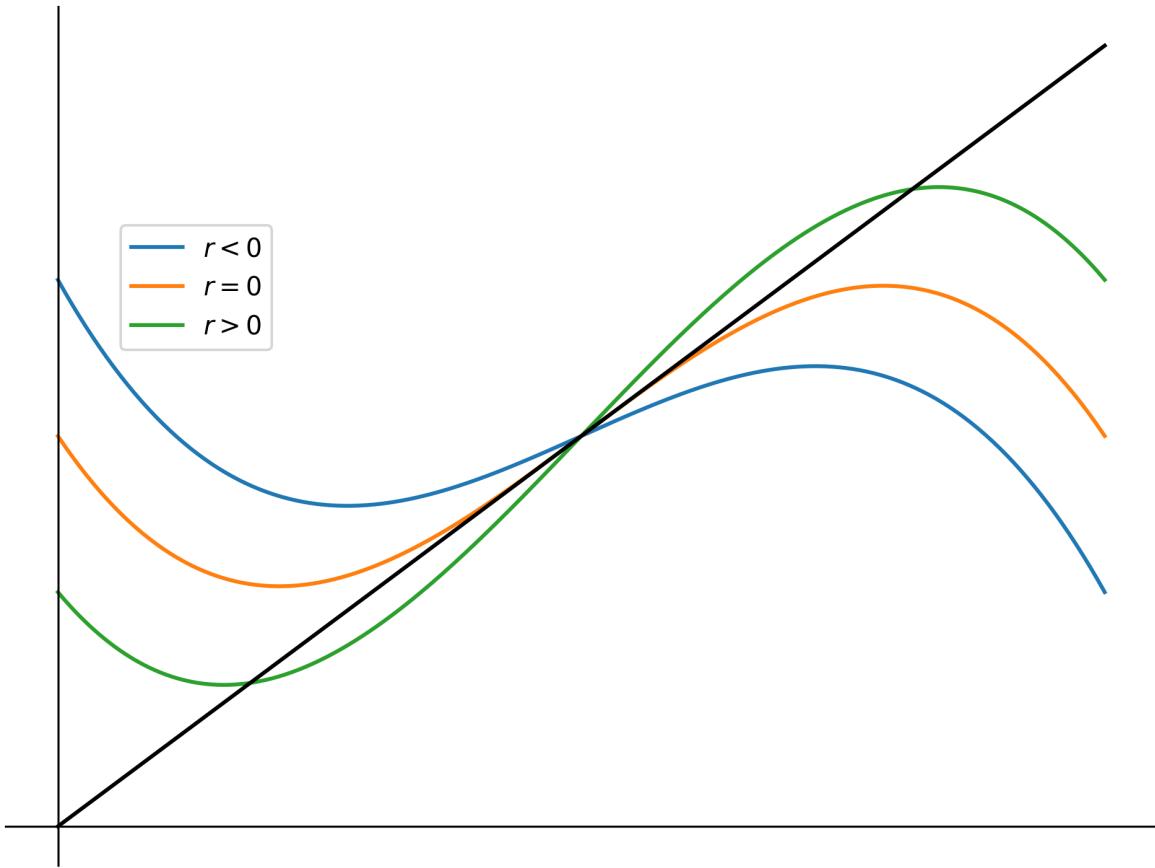


Figure 2.15: Plot showing a pitchfork bifurcation.

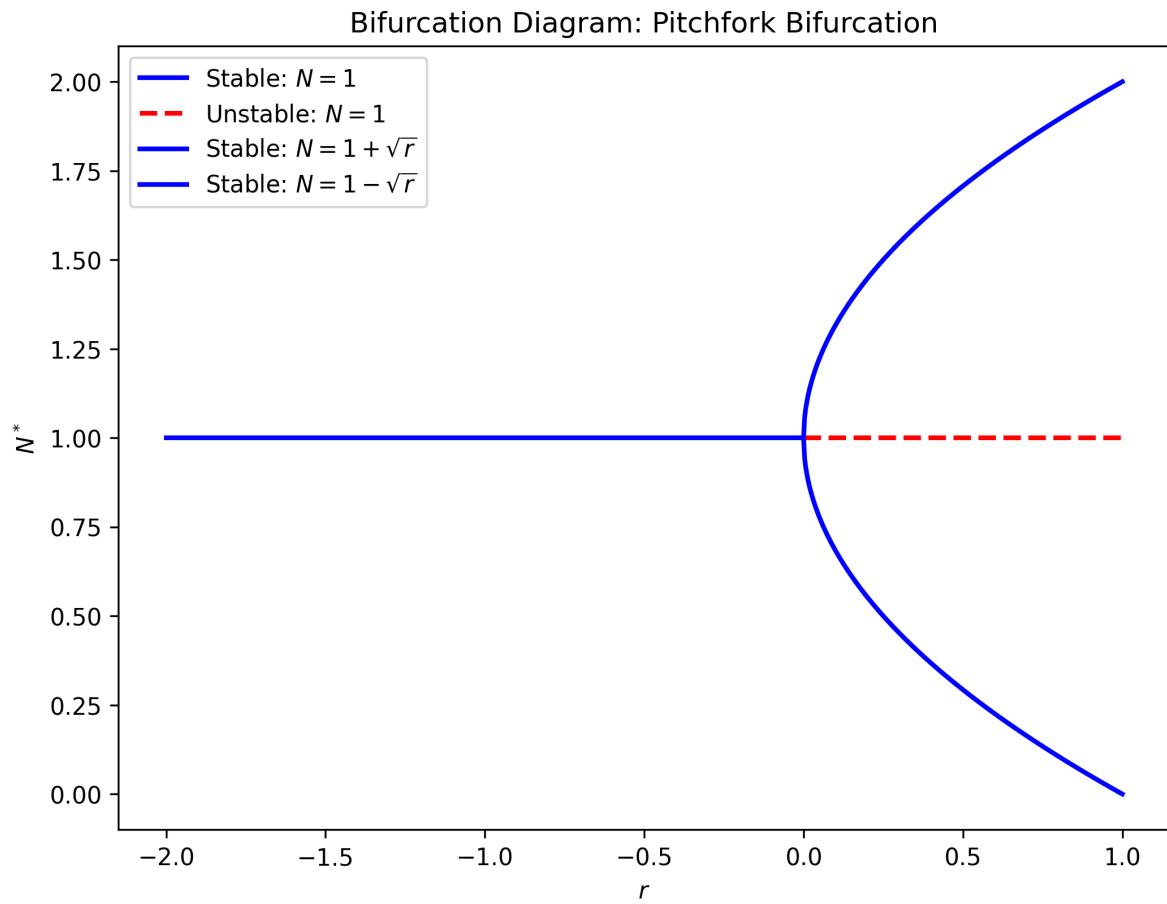


Figure 2.16: Bifurcation diagram for a pitchfork bifurcation.

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

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

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)?

Exercise 2.7 (Period-doubling and tangent bifurcations). Consider the discrete time model

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

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 $r = 1$.

Summary

This chapter introduced several key concepts in discrete-time population dynamics:

1. Discrete vs Continuous Time

- Discrete models track populations at fixed time intervals
- Useful for populations with seasonal reproduction
- Can exhibit more complex dynamics than continuous models

2. Key Models

- Discrete exponential: $N_{t+1} = RN_t$
- Verhulst model: Shows logistic-type growth but can give negative populations

- Ricker model: Prevents negative populations, used for salmon populations
- Beverton-Holt model: Important in fisheries science

3. Analysis Tools

- Fixed points found by solving $N^* = f(N^*)$
- Linear analysis near fixed points: Stability when $|f'(N^*)| < 1$
- Cobweb diagrams visualize iteration dynamics

4. Bifurcations

- Four types possible in discrete-time models:
 - Saddle-node (tangent)
 - Transcritical
 - Pitchfork
 - Period-doubling (unique to discrete-time models)
- Period-doubling leads to oscillatory behavior

5. Harvesting

- Can introduce critical depensation
- Critical harvesting thresholds exist
- Risk of population collapse near thresholds

Key differences from continuous models:

- Can exhibit more complex dynamics
- Period-doubling bifurcations possible
- Cobweb diagrams replace phase lines
- Solutions can oscillate or become chaotic

3 Interacting populations

Ecological systems are complex networks of interactions involving multiple species, which can be categorized into different trophic levels based on their roles in the ecosystem. Understanding these interactions is crucial for studying ecosystem dynamics, population control, and biodiversity. While the study of multiple interacting species can become quite intricate, analysing the interactions between two species offers a more manageable framework while still providing significant insights into the dynamics of ecological relationships. This chapter focuses on two-species interactions, offering a foundational understanding that can be applied or extended to more complex scenarios.

Mathematical Framework for Two-Species Interactions

To model the interactions between two species, we employ a system of two autonomous coupled ordinary differential equations (ODEs). These equations describe the rate of change of the population sizes over time, capturing the essence of their interaction. The general form of these equations is given by:

$$\frac{dX}{dt} = f(X, Y), \quad \frac{dY}{dt} = g(X, Y). \quad (3.1)$$

where X and Y represent the population sizes of the two species, and $f(X, Y)$ and $g(X, Y)$ are functions that describe how the populations influence each other. These functions are crafted based on the nature of the interaction between the species, reflecting the underlying biological processes.

Types of Two-Species Interactions

The dynamics of two interacting species are generally categorized into three primary types, each with its unique characteristics and implications for the populations involved:

- **Predator-Prey Interactions:** In this type of interaction, one species (the predator) feeds on the other (the prey). The population growth of the predator increases with increased availability of the prey, while the prey population is negatively affected by the presence of the predator. Mathematically, this interaction often leads to oscillatory dynamics, exemplified by the classic Lotka-Volterra model.
- **Competition:** When two species compete for the same resources, their growth rates are adversely affected by their interaction. This situation is characterized by negative impacts on both species' growth rates, potentially leading to the exclusion of one species or to a stable coexistence, depending on the specific conditions and competition coefficients.

- **Mutualism:** This positive interaction benefits both species, leading to an increase in their growth rates. The mutualistic relationship is such that each species provides some benefit to the other, which could be in the form of nutrients, shelter, or any other factor that enhances growth or survival.

While this chapter focuses on these primary interaction types, it's important to recognize the spectrum of interactions in nature, including parasitism, amensalism, and others. Moreover, the real-world ecological systems often exhibit a mix of these interactions, adding layers of complexity. By starting with the analysis of two-species systems, we lay the groundwork for understanding more intricate interactions and the overall dynamics of ecosystems.

3.1 Lotka-Volterra Model

The Lotka-Volterra model, developed independently by Alfred Lotka in 1925 and Vito Volterra in 1926, serves as a foundational mathematical model for understanding the dynamic interplay between a prey population (denoted by N) and a predator population (denoted by P).

Model Formulation

The model assumes that the prey population, in the absence of predators, grows exponentially with a per capita growth rate $a > 0$. However, the prey die due to being eaten by predators, and we assume that the per-capita mortality rate grows in proportion to the abundance of predators, with some proportionality constant $b \geq 0$. This leads to the equation

$$\frac{dN}{dt} = N(a - bP). \quad (3.2)$$

Conversely, the predators benefit from the abundance of prey and we encode that by giving them a per-capita growth cN , where $c \geq 0$. We assume that the per capita mortality rate is a constant d . This yields the following equation for the predator dynamics:

$$\frac{dP}{dt} = P(cN - d). \quad (3.3)$$

The two plots in Figure 3.1 generated from the Lotka-Volterra model provide a visual representation of the dynamics between a predator and prey population over time. The phase plane plot illustrates the cyclic nature of the interaction between the prey (N) and predator (P) populations, depicting a closed trajectory that indicates the continuous oscillation of both populations in relation to each other: as the prey population increases, it provides more food for the predators, which then also increase in number. However, as the predator population grows, it puts more pressure on the prey, leading to a decline in the prey population, which eventually causes the predator population to decrease due to lack of food.

The plot at the bottom shows the prey and predator populations over time. It highlights the periodic rises and falls of each population, showing how the increase in the prey population precedes the increase in the predator population, followed by a subsequent decline in the prey and then the predator population. The time series plot complements the phase plane by showing how the dynamics unfold over time.

Non-dimensionalization of the Model

Non-dimensionalization is a crucial step to reduce the complexity of the model by decreasing the number of parameters, thereby simplifying the analysis. By introducing the non-dimensional variables $u = \frac{cN}{d}$, $v = \frac{bP}{a}$, and the non-dimensional time $\tau = at$, along with the parameter $\alpha = \frac{d}{a}$, we can transform the Lotka-Volterra equations into a more tractable form:

$$\frac{du}{d\tau} = u(1 - v), \quad \frac{dv}{d\tau} = \alpha v(u - 1). \quad (3.4)$$

Phase plane paths

To determine the phase plane paths we consider v as a function of u which satisfies the equation

$$\frac{dv}{du} = \frac{\frac{dv}{d\tau}}{\frac{du}{d\tau}} = \frac{\alpha v(u - 1)}{u(1 - v)}. \quad (3.5)$$

We rewrite this by separating the variable and integrate:

$$\int \frac{1 - v}{v} dv = \alpha \int \frac{u - 1}{u} du. \quad (3.6)$$

This gives

$$\log v - v - \alpha(u - \log u) = \text{constant}. \quad (3.7)$$

So even though u and v are changing with time, this particular combination stays constant. This is a conserved quantity. Let us suggestively call the constant of the motion H for Hamiltonian and write it in terms of new variables $p = \log u$ and $q = \log v$:

$$H(q, p) = v - \log v + \alpha(u - \log u) = e^q - q + \alpha(e^p - p). \quad (3.8)$$

Hamilton's equations

$$\dot{q} = \frac{dH}{dp}, \quad \dot{p} = -\frac{dH}{dq} \quad (3.9)$$

then reproduce our equations of motion.

This formulation underscores the conservative nature of the model, where the energy-like quantity H is conserved, leading to neutrally stable periodic orbits. This Hamiltonian nature is a rather special feature of the Lotka-Volterra model. Any slight modification of the model will destroy the conserved quantity and the periodic orbits. Thus we should not expect to see such perfect periodic predator-prey cycles in nature. We will discuss more realistic predator-prey models later.

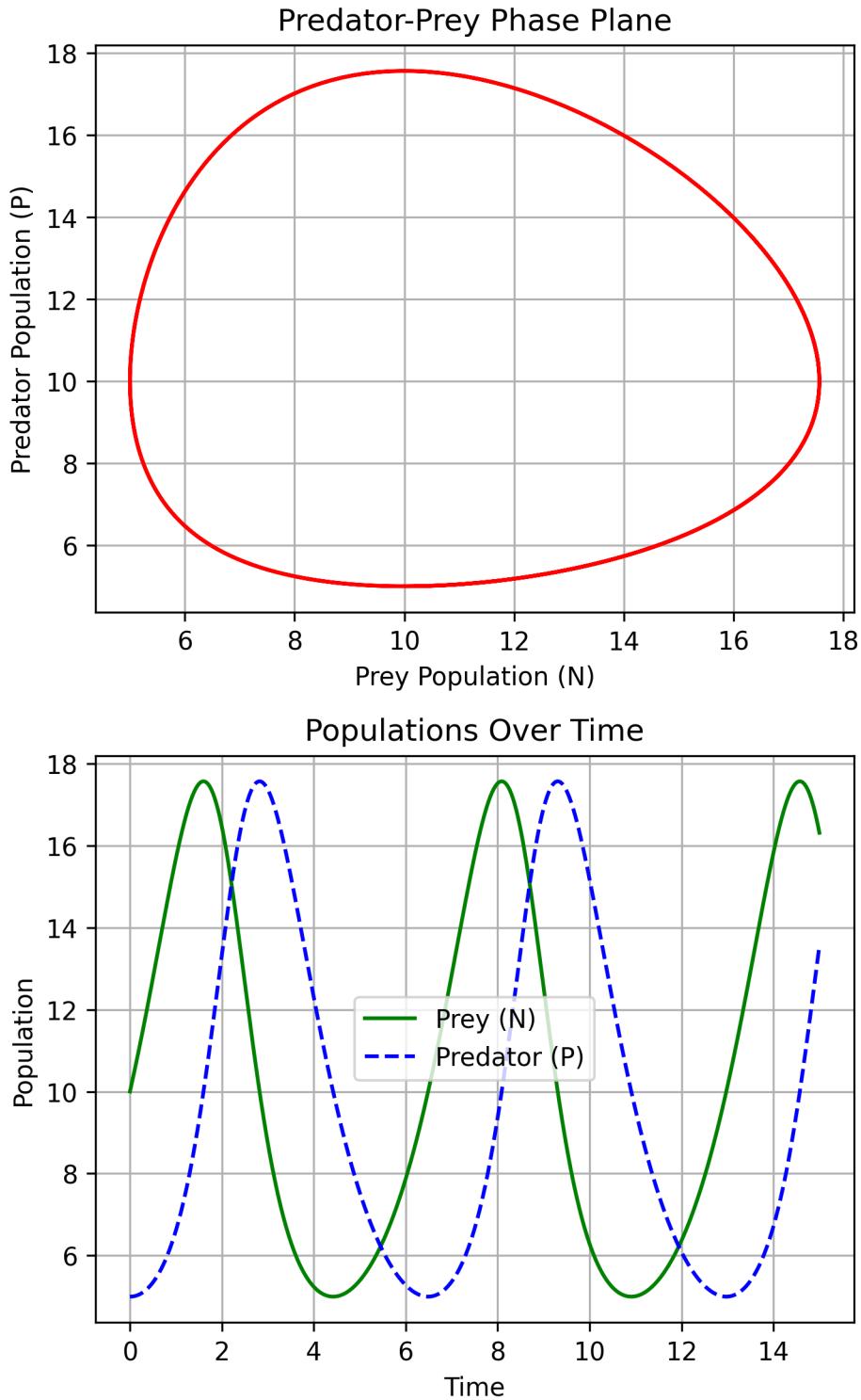


Figure 3.1: Solutions to the Lotka-Volterra model with parameters $a = 1.0$, $b = 0.1$, $c = 0.1$, and $d = 1.0$ and initial conditions $N_0 = 10$ and $P_0 = 5$.

3.2 Linear Stability Analysis

Before we study more realistic models, we revisit the concept of linear stability analysis, an essential tool in understanding the dynamics near the fixed points of systems described by autonomous coupled ordinary differential equations (ODEs) of the form

$$\frac{dX}{dt} = f(X, Y), \quad \frac{dY}{dt} = g(X, Y). \quad (3.10)$$

Let us denote the fixed points (stable states) of the system as (x^*, y^*) . They satisfy $f(x^*, y^*) = 0$ and $g(x^*, y^*) = 0$.

Linearisation around the Fixed Points

To analyse the stability of these fixed points, we introduce small perturbations x and y around them, setting $X = x^* + x$ and $Y = y^* + y$. By applying a Taylor expansion and retaining only the linear terms, we obtain a linearised system:

$$\frac{d}{dt} \begin{pmatrix} x \\ y \end{pmatrix} = \mathbf{A}(x^*, y^*) \begin{pmatrix} x \\ y \end{pmatrix}, \quad (3.11)$$

where the Jacobian matrix \mathbf{A} is defined as:

$$\mathbf{A} = \begin{pmatrix} f_X & f_Y \\ g_X & g_Y \end{pmatrix}_{(x^*, y^*)}. \quad (3.12)$$

Eigenvalue Analysis for Stability

The solution to the linearised system takes the form $(x, y) = \mathbf{v}e^{\lambda t}$, where \mathbf{v} is an eigenvector of \mathbf{A} , and λ is the corresponding eigenvalue. By setting the determinant of $\mathbf{A} - \lambda\mathbf{I}$ to zero, we obtain the characteristic equation:

$$\det(\mathbf{A} - \lambda\mathbf{I}) = \begin{vmatrix} f_X - \lambda & f_Y \\ g_X & g_Y - \lambda \end{vmatrix}_{(x^*, y^*)} = 0, \quad (3.13)$$

which leads to the eigenvalues:

$$\lambda = \frac{\text{Tr}\mathbf{A} \pm \sqrt{(\text{Tr}\mathbf{A})^2 - 4 \det \mathbf{A}}}{2}. \quad (3.14)$$

The stability of the fixed point is determined by the sign of the real parts of the eigenvalues:

- If both eigenvalues have negative real parts, the fixed point is stable (attracting).
- If both eigenvalues have positive real parts, the fixed point is unstable (repelling).

- If the eigenvalues have real parts of opposite signs, the fixed point is a saddle point, which is unstable.
- For a complex conjugate pair of eigenvalues, if the real part is positive, the system exhibits an unstable spiral; if the real part is negative, the system exhibits a stable spiral.

This analysis is pivotal for understanding how small deviations from equilibrium evolve over time, providing insights into the system's long-term behaviour near the fixed points. For instance, in the context of the predator-prey dynamics, such analysis helps elucidate under what conditions the populations will return to equilibrium after a disturbance or potentially diverge away from it.

We can reformulate the stability conditions of a fixed point in terms of the determinant and trace of the Jacobian matrix. We need to recall how these two characteristics of the Jacobian relate to the eigenvalues. For a 2×2 matrix A with eigenvalues λ_1 and λ_2 , the trace $\text{Tr}(A)$ is the sum of the eigenvalues, and the determinant $\text{Det}(A)$ is the product of the eigenvalues:

- $\text{Tr}(A) = \lambda_1 + \lambda_2$
- $\text{Det}(A) = \lambda_1 \lambda_2$

Using these relationships, we can express the conditions for the stability of fixed points as follows:

1. **Stable (Attracting) Fixed Point:** If both eigenvalues have negative real parts, their sum (the trace) is negative, and their product (the determinant) is positive because the product of two negative numbers is positive. Therefore, for stability, $\text{Tr}(A) < 0$ and $\text{Det}(A) > 0$. Additionally, to ensure that both eigenvalues are real and negative, we require that $\text{Tr}(A)^2 - 4\text{Det}(A) \geq 0$ to avoid complex eigenvalues.
2. **Unstable (Repelling) Fixed Point:** If both eigenvalues have positive real parts, the trace is positive, and the determinant is positive (the product of two positive numbers is positive). Thus, for instability, $\text{Tr}(A) > 0$ and $\text{Det}(A) > 0$.
3. **Saddle Point (Unstable):** If the eigenvalues have real parts of opposite signs, the determinant (the product of the eigenvalues) is negative. So, for a saddle point, $\text{Det}(A) < 0$, regardless of the trace.
4. **Spiral Points:** For a complex conjugate pair of eigenvalues, the determinant will be positive (since the product of complex conjugates is positive), but the stability depends on the sign of the real part of the eigenvalues, which is represented by the trace. Here, we also need to ensure that $\text{Tr}(A)^2 - 4\text{Det}(A) < 0$ to confirm that the eigenvalues are complex.
 - **Unstable Spiral:** If the real part is positive, $\text{Tr}(A) > 0$ and $\text{Det}(A) > 0$.
 - **Stable Spiral:** If the real part is negative, $\text{Tr}(A) < 0$ and $\text{Det}(A) > 0$.

These conditions provide a concise way to determine the stability of fixed points using only the determinant and trace of the Jacobian matrix, without explicitly computing the eigenvalues.

Example 3.1 (Linear Stability Analysis of the Lotka-Volterra Model). To explore the stability of steady states in the Lotka-Volterra model, we analyse the system near its fixed points using the Jacobian matrix \mathbf{A} . For the non-dimensionalized Lotka-Volterra system, the Jacobian matrix is given by

$$\mathbf{A} = \begin{pmatrix} 1-v & -u \\ \alpha v & \alpha(u-1) \end{pmatrix}. \quad (3.15)$$

Steady State at $(u, v) = (0, 0)$

For the fixed point $(u, v) = (0, 0)$, we substitute these values into the Jacobian matrix and find the eigenvalues:

$$\mathbf{A} = \begin{pmatrix} 1 & 0 \\ 0 & -\alpha \end{pmatrix}. \quad (3.16)$$

The eigenvalues are $\lambda_1 = 1$ and $\lambda_2 = -\alpha$, indicating that this fixed point is a saddle point due to the eigenvalues having opposite signs. This configuration is inherently unstable as trajectories near the point will diverge away along the direction associated with the positive eigenvalue.

Steady State at $(u, v) = (1, 1)$

At the fixed point $(u, v) = (1, 1)$, the Jacobian matrix becomes:

$$\mathbf{A} = \begin{pmatrix} 0 & -1 \\ \alpha & 0 \end{pmatrix}. \quad (3.17)$$

The characteristic equation for the eigenvalues λ is $\lambda^2 + \alpha = 0$, leading to complex eigenvalues $\lambda = \pm i\sqrt{\alpha}$. The real part of these eigenvalues is zero, indicating that this fixed point is a centre. Trajectories around this point are closed loops, implying that the system exhibits neutrally stable periodic behaviour around the $(1, 1)$ steady state.

The period T of the oscillations can be determined from the imaginary part of the eigenvalues, which is $\sqrt{\alpha}$, so the period $T = \frac{2\pi}{\sqrt{\alpha}}$.

3.3 More Realistic Predator-Prey Models

While the basic Lotka-Volterra model provides a fundamental understanding of predator-prey interactions, more nuanced models incorporate additional biological realism. These models may account for factors like limited resources, satiation, prey switching, predator avoidance, and many others.

3.3.1 Generalized Predator-Prey Model

The generalized model introduces a function $F(N, P)$ representing the prey population's per-capita growth and a function $G(N, P)$ for the predator's per-capita growth rate, so that the dynamics are:

$$\frac{dN}{dt} = NF(N, P), \quad \frac{dP}{dt} = PG(N, P). \quad (3.18)$$

The prey might exhibit logistic growth in the absence of predators. To model this we could choose

$$F(N, P) = r \left(1 - \frac{N}{K}\right) - R(N)P, \quad (3.19)$$

where r is the intrinsic growth rate, K is the carrying capacity, and $R(N)$ models how the predation rate of a predator changes with the prey population size. $NR(N)$ is the rate at which each individual predator consumes prey. The dependence of this rate on the prey population size N is often referred to as "functional response" in the ecological literature. Holling introduced three types of functional responses, which are widely used in predator-prey models:

3.3.1.1 Holling Type functional responses

1. **Type I** $NR(N) = bN$, which corresponds to the standard Lotka-Volterra model. This simplification lacks realism as it assumes an unlimited predator appetite regardless of prey population size.
2. **Type II** $NR(N) = \frac{AN}{N+B}$, with A and B being positive constants. In this model, the rate approaches a saturation level A for large N , reflecting a limit to the predator's consumption rate. This model is more realistic as it accounts for the predator's limited appetite, which might be because there is a minimum handling time, the time the predator needs to consume a prey item.
3. **Type III** $NR(N) = \frac{AN^2}{N^2+B^2}$. This response includes a saturation effect like the previous example but also models that if the prey is rare the predator may not be able to find it. This model is more complex and captures the idea that predators may switch to alternative prey when the primary prey is scarce. It may also encode a learning effect, where the predator's efficiency in capturing prey increases with experience so that initially the predator's consumption rate increases with prey density.

3.3.2 Example

Consider a model where the prey growth rate follows logistic dynamics in the absence of prey and predation mortality is described by a Holling type II function encoding satiation effects. The predator's growth rate goes down as the prey population decreases. The model equations are:

$$\frac{dN}{dt} = N \left[r \left(1 - \frac{N}{K} \right) - \frac{A}{N+B} P \right], \quad \frac{dP}{dt} = Ps \left(1 - \frac{hP}{N} \right), \quad (3.20)$$

where r , K , A , B , s , and h are positive constants.

Nondimensionalization

To reduce the complexity, we nondimensionalize the system with $\tau = tr$, $u = \frac{N}{K}$, $v = \frac{hP}{K}$, $a = \frac{A}{hr}$, $b = \frac{B}{K}$, and $c = \frac{s}{r}$, leading to:

$$\frac{du}{d\tau} = u(1-u) - a \frac{uv}{u+b}, \quad \frac{dv}{d\tau} = cv \left(1 - \frac{v}{u} \right). \quad (3.21)$$

Stability Analysis of Steady States

The steady states (u^*, v^*) include $(1, 0)$ and a coexistence steady state (u_+^*, u_+^*) , where

$$u_+^* = \frac{1 - a - b + \sqrt{(1-a-b)^2 + 4b}}{2}. \quad (3.22)$$

The community matrix $\mathbf{A}(u, v)$ at these points helps determine their stability. For the fixed point $(1, 0)$, where the prey population is at carrying capacity and there are no predators, we have find

$$\mathbf{A}(1, 0) = \begin{pmatrix} -1 & -\frac{a}{1+b} \\ 0 & c \end{pmatrix}. \quad (3.23)$$

The eigenvalues -1 and c have opposite sign, indicating that the fixed point is a saddle point.

At the coexistence fixed point (u_+^*, u_+^*) the Jacobian is more complex and we will skip the analysis here.

3.4 Competition Models

In ecological systems, species often compete for limited resources, such as food or territory. This competition influences their growth rates and can determine their survival and dominance within an ecosystem. The Lotka-Volterra competition model provides a framework to study these dynamics, extending the principles of logistic growth to account for interspecies interactions.

3.4.1 Lotka-Volterra Competition Dynamics

The model is formulated as follows for two competing species N_1 and N_2 :

$$\begin{aligned}\frac{dN_1}{dt} &= r_1 N_1 \left(1 - \frac{N_1 + b_{12}N_2}{K_1}\right), \\ \frac{dN_2}{dt} &= r_2 N_2 \left(1 - \frac{N_2 + b_{21}N_1}{K_2}\right),\end{aligned}\tag{3.24}$$

where r_i is the intrinsic growth rate and K_i is the carrying capacity of species i . The coefficients b_{ij} represent the competitive effect of species j on species i , effectively reducing the carrying capacity for species i due to the presence of species j .

3.4.2 Nondimensionalization of the Model

To simplify the analysis, we nondimensionalize the system using:

$$u_i = \frac{N_i}{K_i}, \quad a_{ij} = \frac{b_{ij}K_j}{K_i}, \quad \tau = r_1 t, \quad \rho = \frac{r_2}{r_1},\tag{3.25}$$

leading to:

$$\frac{du_1}{d\tau} = u_1(1 - u_1 - a_{12}u_2), \quad \frac{du_2}{d\tau} = \rho u_2(1 - u_2 - a_{21}u_1).\tag{3.26}$$

3.4.3 Analysis of Steady States

The system has four potential steady states: $(0, 0)$, $(0, 1)$, $(1, 0)$, and a coexistence steady state $\left(\frac{1-a_{12}}{1-a_{12}a_{21}}, \frac{1-a_{21}}{1-a_{12}a_{21}}\right)$.

To determine the stability of these points, we evaluate the Jacobian matrix $\mathbf{A}(u_1, u_2)$ at each steady state and analyse its eigenvalues:

1. **At $(0, 0)$:** The eigenvalues are 1 and ρ , indicating an unstable node as both are positive.
2. **At $(1, 0)$:** The eigenvalues are -1 and $\rho(1 - a_{21})$. This point is a saddle if $a_{21} < 1$ and a stable node if $a_{21} > 1$.
3. **At $(0, 1)$:** By symmetry, this point behaves like $(1, 0)$ with roles reversed between species.
4. **Coexistence point $\left(\frac{1-a_{12}}{1-a_{12}a_{21}}, \frac{1-a_{21}}{1-a_{12}a_{21}}\right)$:** The stability is determined by the sign of the trace and the determinant of \mathbf{A} . The system's behaviour at this point depends on the specific values of a_{12} and a_{21} , indicating potential scenarios where both species can coexist or one outcompetes the other.

3.4.4 Nullclines and Phase Portraits

Nullclines, where the growth rate of one of the species are zero, are a very useful aid when drawing phase plane diagrams, also known as phase portraits. The nullclines for the Lotka-Volterra competition model are:

- u_1 nullclines: $du_1/d\tau = 0$ when $u_1 = 0$ or $u_2 = \frac{1-u_1}{a_{12}}$.
- u_2 nullclines: $du_2/d\tau = 0$ when $u_2 = 0$ or $u_2 = 1 - a_{21}u_1$.

Along the u_1 nullclines the flow is purely vertical and along the u_2 nullclines the flow is purely horizontal. The intersection of the nullclines gives the steady states of the system. We can now draw the phase portrait to visualize the dynamics of the system. Very rough sketches are enough to understand the dynamics.

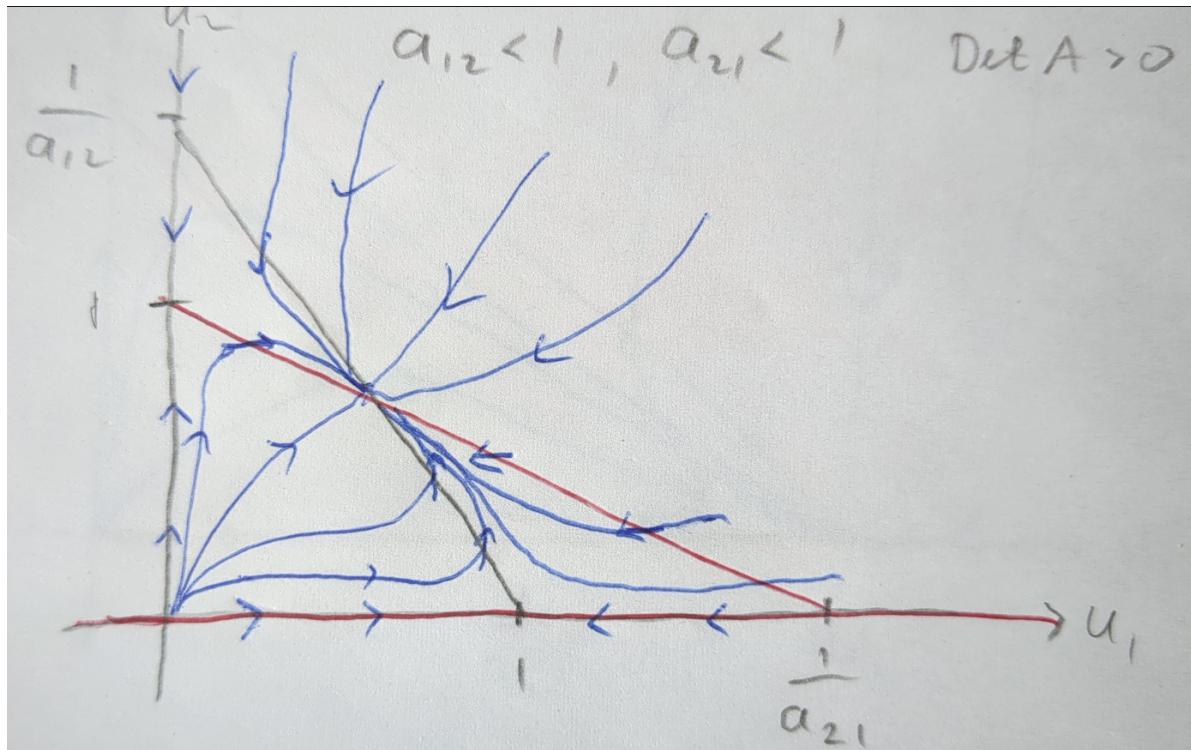


Figure 3.2: Phase portrait of competition model when $a_{12} < 1$ and $a_{21} < 1$.

Figure 3.2 shows the phase portrait of the competition model when $a_{12} < 1$ and $a_{21} < 1$. The nullclines are shown in grey and red, the flow lines in blue, with the arrows indicating the direction of the flow. The system exhibits a stable coexistence steady state, where both species persist in the ecosystem.

$$a_{12} > 1, \quad a_{21} > 1 \quad \text{Det } A < 0$$

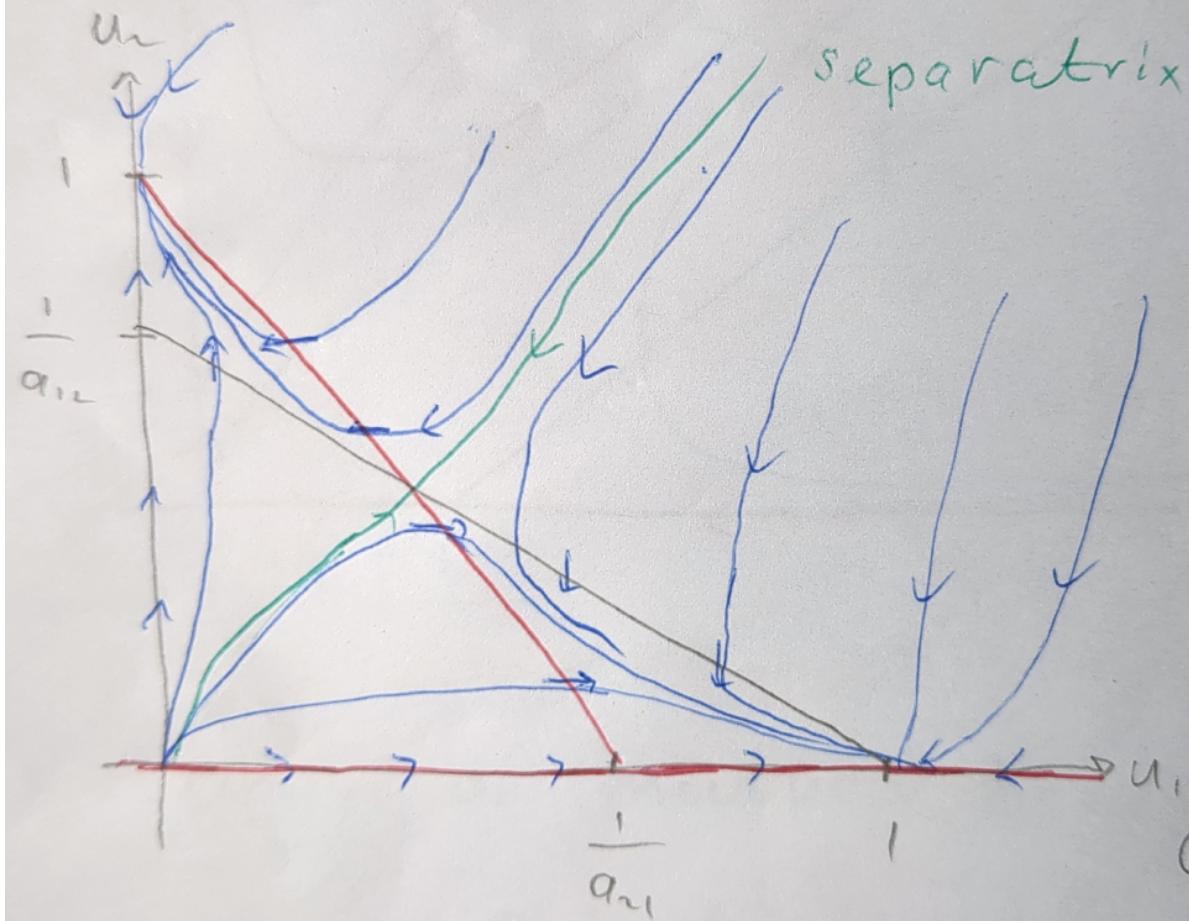


Figure 3.3: Phase portrait of competition model when $a_{12} > 1$ and $a_{21} > 1$.

Figure 3.3 illustrates the phase portrait of the competition model when $a_{12} > 1$ and $a_{21} > 1$. In this scenario, the coexistence steady state is a saddle, leading to the exclusion of one species. Which species dominates depends on the initial conditions. If the initial condition is below the separatrix, species 1 will dominate, and if it is above, species 2 will dominate.

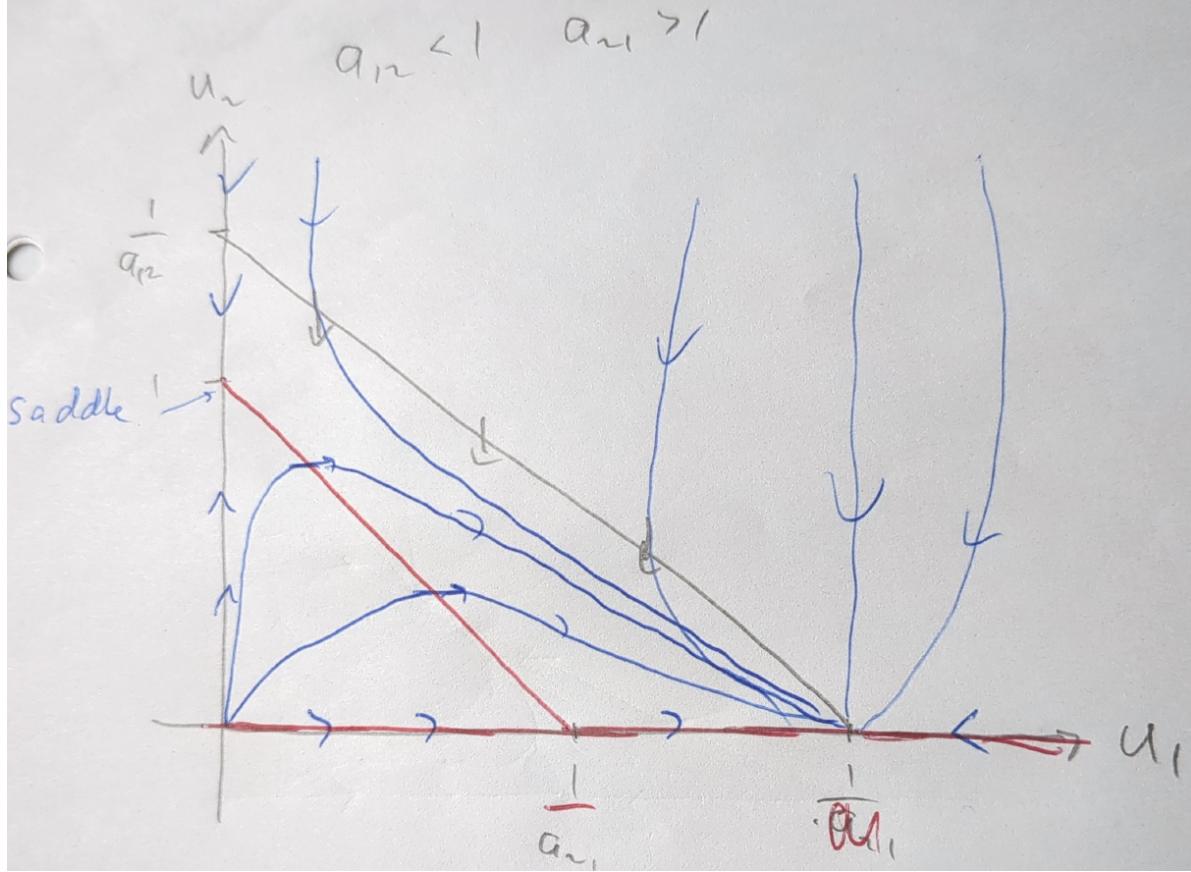


Figure 3.4: Phase portrait of competition model when $a_{12} < 1$ and $a_{21} > 1$.

Figure 3.4 depicts the phase portrait of the competition model when $a_{12} < 1$ and $a_{21} > 1$. In this case, the coexistence steady state has disappeared (it has moved into a region with negative population numbers that is not ecologically relevant). Irrespective of initial conditions, the system will evolve towards the state where only species 1 exists. Species 2 is driven to extinction.

We are not drawing the case $a_{12} > 1$ and $a_{21} < 1$ as it is similar to the case $a_{12} < 1$ and $a_{21} > 1$ just with the role of species 1 and 2 reversed. In this case species 2 will dominate and species 1 will go extinct.

3.4.5 Competitive Exclusion Principle

The competitive exclusion principle, proposed by Gause in the 1930s, states that two species competing for the same resources cannot coexist indefinitely, with one species eventually out-competing the other.

In the model we studied the two species shared resources but each also had its own resources, hence we observed a weaker form of the competitive exclusion principle. The coexistence steady state was stable when the competition was weak enough, allowing both species to persist in the ecosystem. This highlights the delicate balance between competition and coexistence in ecological systems, where the strength of interspecies interactions plays a crucial role in determining the long-term dynamics of species populations.

3.5 Mutualism Models

In ecological systems, mutualism refers to interactions where all participating species benefit, leading to increased growth rates. An example is the relationship between plants and their seed dispersers, such as insects, where both parties gain advantages from their association.

3.5.1 Example

This model incorporates logistic growth, akin to the competition model, but with a twist to account for the mutualistic interaction:

$$\frac{dN_1}{dt} = r_1 N_1 \left[1 - \frac{N_1}{K_1} + b_{12} \frac{N_2}{K_1} \right], \quad \frac{dN_2}{dt} = r_2 N_2 \left[1 - \frac{N_2}{K_2} + b_{21} \frac{N_1}{K_2} \right], \quad (3.27)$$

where r_i , K_i , and b_{ij} are all positive constants, with b_{ij} representing the mutualistic benefit to species i from species j . Notice that we simply changed the sign of the competition terms in the competition model to turn them into mutualistic terms

3.5.2 Nondimensionalization of the Model

Using nondimensional variables $u_i = N_i/K_i$, $a_{ij} = b_{ij}K_j/K_i$, $\tau = r_1 t$, and $\rho = r_2/r_1$, the equations transform to:

$$\frac{du_1}{d\tau} = u_1(1 - u_1 + a_{12}u_2), \quad \frac{du_2}{d\tau} = \rho u_2(1 - u_2 + a_{21}u_1). \quad (3.28)$$

This is as in the competition model but with the signs in front of a_{12} and a_{21} reversed.

3.5.3 Steady States and Stability

The system has the steady states $(0, 0)$, $(0, 1)$, $(1, 0)$, and $\left(\frac{1+a_{12}}{\delta}, \frac{1+a_{21}}{\delta}\right)$, where $\delta = 1 - a_{12}a_{21}$. The coexistence steady state is ecologically relevant only if $\delta > 0$.

- **At $(0, 0)$:** The eigenvalues are 1 and ρ , indicating an unstable node.
- **At $(0, 1)$ and $(1, 0)$:** These points are saddles, with eigenvalues showing a mix of positive and negative signs.
- **At the mutualistic steady state:** The trace and determinant of the community matrix \mathbf{A} suggest that this point is stable if $\delta > 0$.

3.5.4 Nullclines and Phase Portraits

The equations for the nullclines for this model are similar to those in the competition model, but now with positive slope rather than negative slope.

- u_1 nullclines: $du_1/d\tau = 0$ when $u_1 = 0$ or $u_2 = \frac{u_1 - 1}{a_{12}}$.
- u_2 nullclines: $du_2/d\tau = 0$ when $u_2 = 0$ or $u_2 = 1 + a_{21}u_1$.

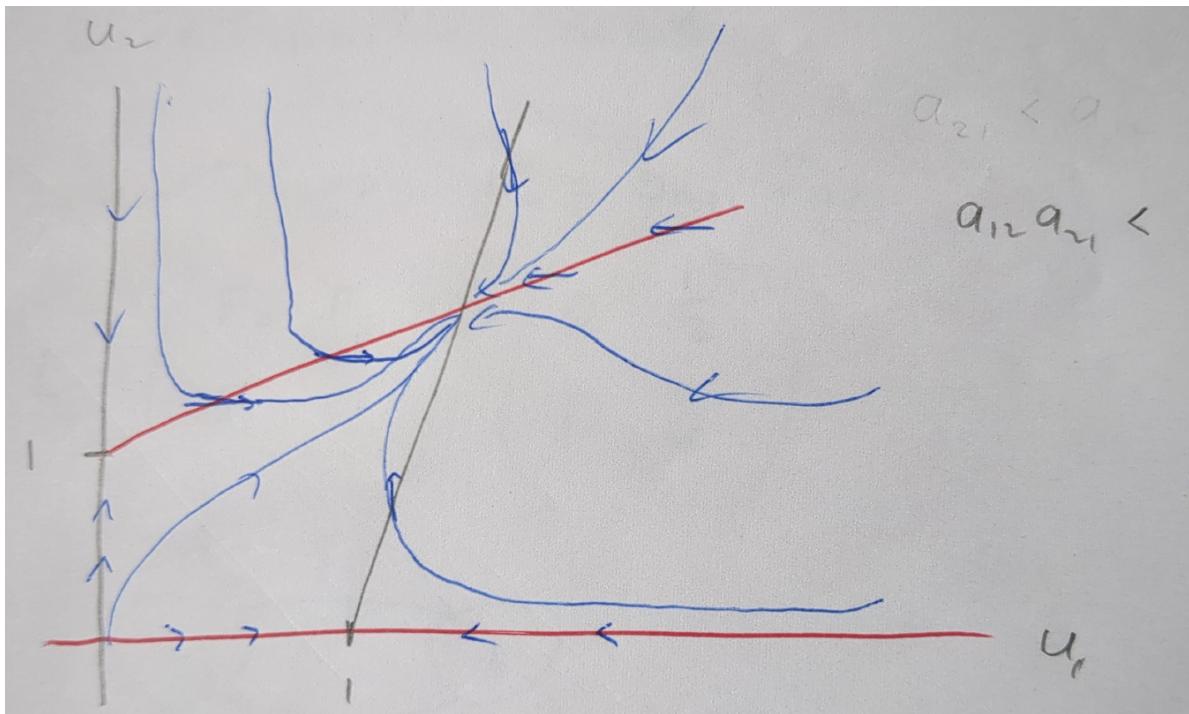


Figure 3.5: Phase portrait of mutualistic model when $a_{12}a_{21} < 1$.

Figure 3.5 illustrates the phase portrait of the mutualism model when $a_{12}a_{21} < 1$. The nullclines are shown in grey and red, with the flow lines in blue. The system exhibits a stable coexistence steady state, where both species benefit from the mutualistic interaction.

3.5.5 Limitations and Unbounded Growth

A cautionary note is that if the mutualistic coefficients $a_{12}a_{21}$ are too large, leading to $\delta < 0$, the model predicts unbounded growth, which is unrealistic. This phenomenon, known as May's "orgy of mutual benefaction," highlights the need for constraints in mutualism models to avoid predicting ecological impossibilities.

Through this mutualism model, we gain insights into how species interactions can foster increased growth and stability, contrasting with competitive dynamics. It underscores the diversity of ecological interactions and their varying implications for species survival and community structure.

3.6 Exercises

3.6.0.1 * Two-species model 1

Exercise 3.1.

Consider a model for the interaction of two species with populations N_1 and N_2

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1} - b_{12} \frac{N_2}{K_1} \right), \quad (3.29)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - b_{21} \frac{N_1}{K_2} \right), \quad (3.30)$$

where all the parameters are positive.

- What type of interaction exists between N_1 and N_2 ?
- Non-dimensionalize the system by introducing $u = N_1/K_1$ and $v = N_2/K_2$ as well as a non-dimensional time variable. What are the resulting non-dimensional parameters? Give the equations of motion for u and v in terms of these parameters.
- Determine the steady states in the non-dimensionalised system. Investigate their stability. At what values of the parameters do bifurcations take place?
- Determine the nullclines and use these to make rough phase-plane sketches (You will need two sketches).

- e) Describe under what ecological circumstances N_2 becomes extinct.
 Do the same for N_1 . Show that the principle of competitive exclusion holds irrespective of the size of the parameters.
-

3.6.0.2 Two-species model 2

Exercise 3.2.

A model for the interaction between two species with populations N_1 and N_2 is determined to be

$$\begin{aligned}\frac{dN_1}{dt} &= rN_1 \left(1 - \frac{N_1}{K}\right) - aN_1 N_2 (1 - \exp(-bN_1)), \\ \frac{dN_2}{dt} &= -dN_2 + cN_2 (1 - \exp(-bN_1)),\end{aligned}\tag{3.31}$$

where a, b, c, d, r and K are positive constants.

- a) Introducing the dimensionless variables and parameters

$$u = \frac{N_1}{K}, \quad v = \frac{aN_2}{r}, \quad \tau = rt, \quad \beta = bK,\tag{3.32}$$

show that

$$\begin{aligned}\frac{du}{d\tau} &= u(1-u) - uv(1-e^{-\beta u}), \\ \frac{dv}{d\tau} &= -\delta v + \alpha v(1-e^{-\beta u}),\end{aligned}\tag{3.33}$$

giving the positive constants α and δ in terms of c, d and r .

- b) Describe the relevance of each term and, hence, determine the type of interaction between the two populations.
- c) Show that the non-negative fixed points are given by $(u^*, v^*) = (0, 0), (1, 0)$ and $(u_1, (1-u_1)\alpha/\delta)$, where $u_1 = -\ln(1-\delta/\alpha)/\beta$, and that the steady state where u^* and v^* are both non-zero can only exist if $\alpha > \delta$ and $\beta > \beta_c = -\ln(1-\delta/\alpha)$.
- d) Show that the community matrix, A , is given by

$$A = \begin{pmatrix} 1 - 2u - v(1 - e^{-\beta u}) - \beta u v e^{-\beta u} & -u(1 - e^{-\beta u}) \\ \alpha v \beta e^{-\beta u} & -\delta + \alpha(1 - e^{-\beta u}) \end{pmatrix}.\tag{3.34}$$

- e) Assuming henceforth that $\delta/\alpha < 1$, determine the linear stability of each of the fixed points.

- f) Sketch the (u, v) phase portrait to indicate the stability of each steady state for the two cases $\beta > \beta_c$ and $0 < \beta < \beta_c$ (remember $\alpha > \delta$).
-

3.6.0.3 Predator-prey model with Allee effect

Exercise 3.3.

Consider the predator-prey model with Allee effect in the prey:

$$\begin{aligned}\frac{dN}{dT} &= rN \left(\frac{N}{K_0} - 1 \right) \left(1 - \frac{N}{K} \right) - cNP, \\ \frac{dP}{dT} &= bNP - mP,\end{aligned}\tag{3.35}$$

where $N(T)$ is the number of prey and $P(T)$ is the number of predators at time T , and r, K, c, b, m are positive constants with $0 < K_0 < K$. The populations $N(T), P(T)$ are non-negative quantities.

- (a) Provide brief biological interpretations for r, K, K_0, c, b, m for the above predator-prey model. What is the biological role of K_0 in the modified prey growth rate?
- (b) Introduce the dimensionless variables $\frac{N}{K} = x$, $\frac{cP}{r} = y$, $rT = t$ and show that the above system can be reduced to

$$\begin{aligned}\frac{dx}{dt} &= x \left(\left(\frac{x}{\gamma} - 1 \right) (1 - x) - y \right) = x[g(x) - y], \\ \frac{dy}{dt} &= \beta(x - \alpha)y.\end{aligned}\tag{3.36}$$

How are the new dimensionless constants α, β and γ expressed in terms of the original parameters?

- (c) For the dimensionless system:
 - i) Calculate the nullclines, clearly stating any conditions for their existence.
 - ii) Use your answer from (i) to sketch nullclines, depicting their intersections and the vector field direction along each isocline in the phase plane.
 - iii) Find the fixed points.
- (d) For the non-trivial fixed point, where both predators and preys may coexist:

- i) Calculate the Jacobian at this point in terms of the function $g(x), g'(x)$, where ' denotes derivative in respect with x .
- ii) Evaluate the characteristic equation and study the stability of this fixed point as the parameter varies within the range $\gamma < \alpha < 1$, classifying the non-trivial fixed point accordingly (i.e. node, spiral, centre or saddle point).

4 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.

$$\begin{aligned}\frac{dF}{dt} &= -\mu_F F + b_F \varphi(F, M) \\ \frac{dM}{dt} &= -\mu_M M + b_M \varphi(F, M).\end{aligned}\tag{4.1}$$

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.

4.1 Symmetric model

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

$$\mu_F = \mu_M = \mu, \quad b_F = b_M = b.\tag{4.2}$$

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

$$\frac{d(F - M)}{dt} = -\mu(F - M).\tag{4.3}$$

This equation has the solution

$$F(t) - M(t) = (F(0) - M(0))e^{-\mu t}. \quad (4.4)$$

This means that the difference decreases exponentially over time. In particular, if we start with equal number females and males then 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 choice

$$\varphi(F, M) = F M. \quad (4.5)$$

This choice is motivated by the fact that both a male and a female is needed to produce offspring. Also the rate of births should increase if there are more females but also when there are more males.

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

$$\frac{dF}{dt} = -\mu F. \quad (4.6)$$

This has the solution

$$F(t) = F(0)e^{-\mu t}. \quad (4.7)$$

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

$$\frac{dF}{dt} = -\mu F + bF^2. \quad (4.8)$$

This is illustrated in Figure 4.1.

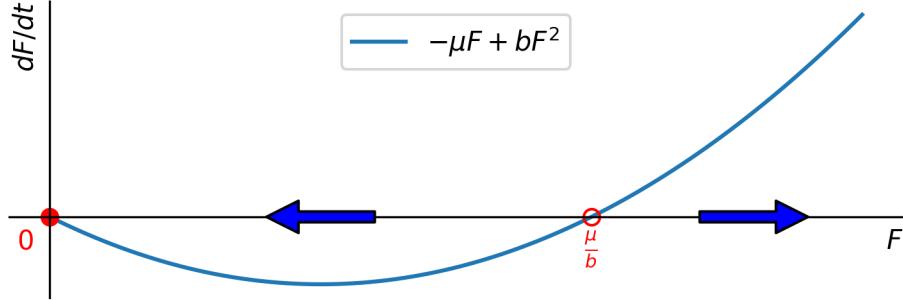


Figure 4.1: Quadratically increasing growth rate.

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. 4.8 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

$$F(t) = \frac{1}{1/F(0) - bt}. \quad (4.9)$$

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

4.2 Female-limited reproduction

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

$$\varphi(F, M) = F. \quad (4.10)$$

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

$$\frac{dF}{dt} = -\mu_F F + b_F F = (-\mu_F + b_F)F. \quad (4.11)$$

This has the solution

$$F(t) = F(0)e^{(-\mu_F + b_F)t}. \quad (4.12)$$

We can now use this in the equation for M :

$$\frac{dM}{dt} = -\mu_M M + b_M F = -\mu_M M + b_M F_0 e^{(-\mu_F + b_F)t}. \quad (4.13)$$

(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

$$\frac{dM}{dt} + \mu_M M = b_M F_0 e^{(-\mu_F + b_F)t} \quad (4.14)$$

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

$$\frac{dM}{dt} + \mu_M M = \frac{d}{dt}(e^{\mu_M t} M) e^{-\mu_M t} \quad (4.15)$$

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

$$\frac{d}{dt}(e^{\mu_M t} M) = b_M F_0 e^{(\mu_M - \mu_F + b_F)t}. \quad (4.16)$$

We can now integrate both sides to get

$$e^{\mu_M t} M(t) - e^{\mu_M t} M_0 = \frac{b_M F_0}{\mu_M - \mu_F + b_F} (e^{(\mu_M - \mu_F + b_F)t} - 1). \quad (4.17)$$

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

$$M(t) = M_0 + \frac{b_M F_0}{\mu_M - \mu_F + b_F} (e^{(-\mu_F + b_F)t} - e^{-\mu_M t}). \quad (4.18)$$

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 $t \rightarrow \infty$. Of course this only makes sense in the case where $b_F \geq \mu + F$ because otherwise, according to Eq. 4.12, the females go extinct and then so do the males. With $b_F \geq \mu + F$ we find

$$\begin{aligned} s &= \lim_{t \rightarrow \infty} \frac{M(t)}{F(t)} = \lim_{t \rightarrow \infty} \frac{M_0 + \frac{b_M F_0}{\mu_M - \mu_F + b_F} (e^{(-\mu_F + b_F)t} - e^{-\mu_M t})}{F_0 e^{(-\mu_F + b_F)t}} \\ &= \frac{b_M}{b_F - \mu_F + \mu_M}. \end{aligned} \quad (4.19)$$

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.

$$\begin{aligned} \mu_F &= 807/100,000/\text{year}, & \mu_M &= 902/100,000/\text{year}, \\ b_F &= 1480/100,000/\text{year}, & b_M &= 1550/100,000/\text{year}. \end{aligned} \quad (4.20)$$

Substituting these values into Eq. 4.19 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.

4.3 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 :

$$\varphi(F, M) = D M + (1 - D)F \quad (4.21)$$

with some suitably chosen weighting factor D . We want to keep the feature that when there is an over-abundance 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

$$\varphi(F, M) = \frac{M}{F+M}F + \frac{F}{F+M}M = \frac{2FM}{F+M}. \quad (4.22)$$

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

$$\begin{aligned} \frac{dF}{dt} &= -\mu_F F + b_F \frac{2FM}{F+M}, \\ \frac{dM}{dt} &= -\mu_M M + b_M \frac{2FM}{F+M}. \end{aligned} \quad (4.23)$$

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

$$\frac{d}{dt} \frac{M}{F} = \frac{\frac{dM}{dt}F - M \frac{dF}{dt}}{F^2}. \quad (4.24)$$

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

$$\frac{dM}{dt}F - M \frac{dF}{dt} = 0. \quad (4.25)$$

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

$$\begin{aligned} \frac{dM}{dt}F - M \frac{dF}{dt} &= \left(-\mu_M M + b_M \frac{2FM}{F+M} \right) F \\ &\quad - M \left(-\mu_F F + b_F \frac{2FM}{F+M} \right) = 0. \end{aligned} \quad (4.26)$$

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

$$-\mu_M(F+M) + 2b_MF + \mu_F(F+M) - 2b_FM = 0. \quad (4.27)$$

Collecting terms proportional to F and M we get

$$(-\mu_M + 2b_M + \mu_F)F = (\mu_M - \mu_F + 2b_F)M. \quad (4.28)$$

We can now solve this equation for the asymptotic sex ratio

$$s = \lim_{t \rightarrow \infty} \frac{M(t)}{F(t)} = \frac{\mu_M - \mu_F + 2b_F}{-\mu_M + 2b_M + \mu_F}. \quad (4.29)$$

Even though the sex ratio approaches a fixed point as $t \rightarrow \infty$, 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 :

$$\begin{aligned} \frac{dF}{dt} &= -\mu_F F + b_F \frac{2MF}{F+M} \\ &= -\mu_F F + \frac{2s}{s+1} b_F F. \end{aligned} \quad (4.30)$$

This is a linear equation and has the solution

$$F(t) = F_0 e^{(-\mu_F + \frac{2s}{s+1} b_F)t}. \quad (4.31)$$

Similarly we obtain

$$M(t) = M_0 e^{(-\mu_M + \frac{2s}{s+1} b_M)t}. \quad (4.32)$$

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.

4.4 Exercises

4.4.0.1 * Geometric mean sex-structured model

Exercise 4.1. 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

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

Determine the asymptotic sex ratio

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

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

4.4.0.2 Dominance structure

Exercise 4.2. We consider a population of primates and split this into three components:

M : dominant (alpha) males,

F : dominant (alpha) females,

Q : subordinate males or females.

Only alpha males and alpha females mate to reproduce offspring. The subordinate individuals are prevented from mating. The alpha females are too engaged with looking after their young to gather food and instead rely on the food gathered by the subordinate individuals. We propose to model this with the equations

$$\begin{aligned}\frac{dF}{dt} &= b_F F - \frac{\mu_F F}{Q} F, \\ \frac{dM}{dt} &= b_M F - \mu_M M, \\ \frac{dQ}{dt} &= b_Q F - \mu_Q Q,\end{aligned}$$

where $b_F > \mu_F$, $b_M > \mu_M$ and $b_Q > \mu_Q$ are all positive constants.

- (a) One of the terms incorporates a ratio of different components. Describe what this might be intended to model.
- (b) Derive an ODE for the ratio F/Q . Either by recognising the ODE for F/Q as equivalent to one for which the solution was given in the lecture notes, or by integrating the ODE, give the solution for F/Q as a function of time, with initial condition $F(0) = F_0$, $Q(0) = Q_0$.
- (c) By using your solution from the previous part or by other means, show that as $t \rightarrow \infty$ the ratio between alpha females and subordinate individuals goes to

$$\frac{b_F + \mu_Q}{b_Q + \mu_F}.$$

- (d) Derive an expression for the long-term alpha female to alpha male ratio $R = \lim_{t \rightarrow \infty} F/M$ in terms of the model parameters and show that it is positive.
- (e) Describe a limitation of the birth terms in the model and suggest improved expressions.

Strogatz, Steven H. 2000. *Nonlinear Dynamics and Chaos: With Applications to Physics, Biology, Chemistry and Engineering*. Perseus Books, U.S.