

## BB512 - Instructor Resources

Owen R. Jones (Course Coordinator)

2024-11-10



# Contents

<b>1</b>	<b>This website and other course materials</b>	<b>9</b>
1.1	Software . . . . .	9
<b>I</b>	<b>Evolution by Natural Selection</b>	<b>11</b>
<b>2</b>	<b>The Blind Watchmaker</b>	<b>13</b>
2.1	Introduction . . . . .	13
2.2	Key concepts . . . . .	13
2.3	Learning outcomes . . . . .	13
2.4	Activity Overview . . . . .	14
2.5	Instructions for facilitating . . . . .	14
2.6	Questions and model answers . . . . .	14
2.7	Teaching Tips . . . . .	15
2.8	Common Pitfalls to Watch For . . . . .	15
<b>3</b>	<b>Bug Hunt Camouflage (NetLogo)</b>	<b>17</b>
3.1	Introduction . . . . .	17
3.2	Key Concepts . . . . .	17
3.3	Learning Outcomes . . . . .	17
3.4	Activity Overview . . . . .	18
3.5	Instructions for Facilitating . . . . .	18
3.6	Questions & Model Answers . . . . .	19
3.7	Teaching Tips . . . . .	20
3.8	Common Pitfalls . . . . .	20
3.9	Additional Resources . . . . .	20

<b>II</b>	<b>Population Growth Models</b>	<b>21</b>
<b>4</b>	<b>Geometric growth</b>	<b>23</b>
4.1	Introduction . . . . .	23
4.2	Key Concepts . . . . .	23
4.3	Learning outcomes . . . . .	23
4.4	Activity Overview . . . . .	24
4.5	Instructions for Facilitating . . . . .	24
4.6	Questions & Model Answers . . . . .	25
4.7	Teaching Tips: . . . . .	26
4.8	Additional Resources . . . . .	26
<b>5</b>	<b>Estimating Population Growth Rate</b>	<b>27</b>
5.1	Introduction . . . . .	27
5.2	Key Concepts . . . . .	27
5.3	Learning outcomes . . . . .	27
5.4	Activity Overview . . . . .	28
5.5	Instructions for Facilitating . . . . .	28
5.6	Questions & Model Answers . . . . .	29
5.7	Teaching Tips: . . . . .	30
5.8	Common Pitfalls . . . . .	30
<b>6</b>	<b>Stochastic population growth</b>	<b>31</b>
6.1	Introduction . . . . .	31
6.2	Key Concepts . . . . .	31
6.3	Learning Outcomes . . . . .	32
6.4	Activity Overview . . . . .	32
6.5	Instructions for Facilitating . . . . .	32
6.6	Questions & Model Answers . . . . .	33
6.7	Teaching Tips . . . . .	33
6.8	Common Pitfalls . . . . .	34

<i>CONTENTS</i>	5
<b>7 Basic logistic population growth</b>	<b>35</b>
7.1 Introduction . . . . .	35
7.2 Key Concepts . . . . .	35
7.3 Learning Outcomes . . . . .	36
7.4 Activity Overview . . . . .	36
7.5 Instructions for Facilitating . . . . .	36
7.6 Questions & Model Answers . . . . .	37
7.7 Teaching Tips . . . . .	37
7.8 Common Pitfalls . . . . .	37
7.9 Concrete Real-World Examples . . . . .	38
<b>8 Deeper into logistic growth</b>	<b>39</b>
8.1 Key Concepts . . . . .	39
8.2 Learning Outcomes . . . . .	40
8.3 Activity Overview . . . . .	40
8.4 Instructions for Facilitating . . . . .	40
8.5 Questions & Model Answers . . . . .	41
8.6 Teaching Tips . . . . .	41
8.7 Common Pitfalls . . . . .	42
8.8 Concrete Real-World Examples . . . . .	42
<b>9 Life Tables and Survivorship Types</b>	<b>45</b>
9.1 Introduction . . . . .	45
9.2 Key Concepts . . . . .	45
9.3 Learning Outcomes . . . . .	46
9.4 Activity Overview . . . . .	46
9.5 Instructions for Facilitating . . . . .	46
9.6 Questions & Model Answers . . . . .	47
9.7 Teaching Tips . . . . .	48
9.8 Common Pitfalls . . . . .	48

<b>10 Matrix population modelling</b>	<b>49</b>
10.1 Introduction . . . . .	49
10.2 Key Concepts . . . . .	49
10.3 Learning Outcomes . . . . .	50
10.4 Activity Overview . . . . .	50
10.5 Instructions for Facilitating . . . . .	50
10.6 Questions & Model Answers . . . . .	50
10.7 Teaching Tips . . . . .	51
10.8 Common Pitfalls . . . . .	51
<b>11 Pre- and Post-reproduction census</b>	<b>53</b>
<b>12 Life Table Response Experiments</b>	<b>55</b>
<b>13 How many eggs should a bird lay?</b>	<b>57</b>
13.1 Introduction . . . . .	57
13.2 Key Concepts . . . . .	57
13.3 Learning Outcomes . . . . .	58
13.4 Activity Overview . . . . .	58
13.5 Instructions for Facilitating . . . . .	58
13.6 Questions & Model Answers . . . . .	58
13.7 Teaching Tips . . . . .	59
13.8 Common Pitfalls . . . . .	59
<b>14 Trade-offs and the Declining Force of Selection</b>	<b>61</b>
14.1 Introduction . . . . .	61
14.2 Key Concepts . . . . .	61
14.3 Learning Outcomes . . . . .	61
14.4 Activity Overview . . . . .	62
<b>III Population Genetics and Evolution</b>	<b>65</b>
<b>15 Hardy-Weinberg equilibrium</b>	<b>67</b>
15.1 Introduction . . . . .	67
15.2 Key Concepts . . . . .	67
15.3 Learning Outcomes . . . . .	67

<i>CONTENTS</i>	<b>7</b>
15.4 Activity Overview . . . . .	68
15.5 Instructions for Facilitating . . . . .	68
<b>16 The Gene Pool Model</b>	<b>71</b>
16.1 Introduction . . . . .	71
16.2 Key Concepts . . . . .	71
16.3 Learning Outcomes . . . . .	71
16.4 Activity Overview . . . . .	72
16.5 Instructions for Facilitating . . . . .	72
16.6 Questions & Model Answers . . . . .	72
16.7 Teaching Tips . . . . .	73
16.8 Common Pitfalls . . . . .	73
<b>17 Neutral or Adaptive Evolution in Humans: What Drives Evolution of Our Traits?</b>	<b>75</b>
17.1 Introduction . . . . .	75
17.2 Key Concepts . . . . .	75
17.3 Learning Outcomes . . . . .	76
17.4 Activity Overview . . . . .	76
17.5 Instructions for Facilitating . . . . .	76
17.6 Questions & Model Answers . . . . .	77
17.7 Teaching Tips . . . . .	79
17.8 Common Pitfalls . . . . .	79
<b>18 Heritability from a linear regression</b>	<b>81</b>
18.1 Introduction** . . . . .	81
18.2 Key Concepts . . . . .	81
18.3 Learning Outcomes . . . . .	81
18.4 Activity Overview . . . . .	82
18.5 Instructions for Facilitating . . . . .	82
18.6 Questions & Model Answers . . . . .	82
18.7 Teaching Tips . . . . .	83
18.8 Common Pitfalls . . . . .	84

<b>IV Interactions Between Species and Community Structure</b>	<b>85</b>
<b>19 Lotka-Volterra competition</b>	<b>87</b>
19.1 Introduction . . . . .	87
19.2 Key Concepts . . . . .	87
19.3 Learning Outcomes . . . . .	88
19.4 Activity Overview . . . . .	88
<b>20 Lotka-Volterra predator-prey dynamics</b>	<b>91</b>
20.1 Introduction . . . . .	91
20.2 Key Concepts . . . . .	91
20.3 Learning Outcomes . . . . .	91
20.4 Activity Overview . . . . .	92
20.5 Instructions for Facilitating . . . . .	92
20.6 Questions & Model Answers . . . . .	93
20.7 Teaching Tips . . . . .	94
20.8 Common Pitfalls . . . . .	94
<b>V Animal behaviour, altruism and sexual selection</b>	<b>95</b>
<b>21 Game theory: Hawks and doves</b>	<b>97</b>
<b>VI Appendix - extras</b>	<b>99</b>
<b>22 Exponential growth in detail</b>	<b>101</b>
<b>23 The legend of Ambalapuzha</b>	<b>103</b>
<b>24 From population biology to fitness</b>	<b>105</b>



# Chapter 1

## This website and other course materials

This website contains resources for instructors in BB512.

**We may not do ALL of these exercises, but you are welcome to do ones we miss in your own time.**

### 1.1 Software

We will use Excel and R/RStudio during this course.

#### 1.1.1 Excel

I expect you will already have Excel installed, so there is not much to say here.

Be aware that Excel differs depending on the language it is localised in. For example, Danish vs. English. This means that some of the commands might differ between version. See [here](#) for examples.

#### 1.1.2 R and RStudio

R and RStudio are two separate pieces of software. RStudio is a user-friendly interface to talk to R, it cannot work if you have not got R installed. So, when you install these two programs, install R first, then RStudio.

Already have them installed? I strongly recommend to update to the latest versions of R, which you can download [here](#) and RStudio Desktop, which you can find [here](#).



Part I

**Evolution by Natural  
Selection**



## Chapter 2

# The Blind Watchmaker

### 2.1 Introduction

This exercise simulates evolutionary processes using an algorithm inspired by *The Blind Watchmaker*. Students will observe how random mutations and selection pressure shape the evolution of a target phrase from an initial random string. By altering parameters of selection and phrase length, students will explore the balance between randomness (mutation) and determinism (selection) in evolutionary processes. This exercise provides insight into natural selection and highlights the filtering nature of natural selection.

### 2.2 Key concepts

- **Random Mutation:** Each generation introduces random changes (mutations) in the string.
- **Selection Pressure:** When active, selection favours letters that match the target phrase, simulating the process of natural selection.
- **Stochasticity vs Determinism:** Evolution combines random mutations and deterministic selection, resulting in gradual adaptation toward a specific goal (in this case, a predefined phrase).

### 2.3 Learning outcomes

- Greater understanding of adaptive evolution via natural selection.
- Understanding that random change does NOT result in disorder, if paired with selection.
- Use of R for exploring biological phenomenon.

## 2.4 Activity Overview

### 2.4.1 Time: 30 minutes

1. **Introduction (5-10 min):** Explain the activity, including the basic concepts of natural selection.
2. **Loading RStudio, Script setup (5 min):** Students load RStudio, create a new script and paste the exercise script into it.
3. **Main Activity (15 min):** Students may use their own phrase, they should use the script and then answer the questions.
4. **Discussion and Wrap-Up (5-10 min):** Run through the questions and answers. Reflect on how the simulation demonstrates key concepts of selection, adaptation, and evolution.

## 2.5 Instructions for facilitating

### 2.5.1 Code Setup

1. **Preparation:** Ensure students have R and RStudio installed. If needed, provide assistance with installation or setting up the R environment.
2. **Running the Code:** Students open a new R script, paste the provided code, and save it.
  - Explain that the simulation uses random letter generation to mimic mutations, and selection fixes correct letters over time, just as beneficial traits are selected in nature.
3. **Modifying Parameters:** Have students edit parameters like `phrase`, `nGenerations`, and `selection`, observing the effects.

### 2.5.2 Key Observation

- When **selection is ON**, the phrase gradually becomes more similar to the target, showing how selection can direct random mutations toward a specific outcome.
- When **selection is OFF**, the output remains random, illustrating that random changes without selection do not lead to order or meaningful results.

## 2.6 Questions and model answers

**Question 1: What happens if selection is turned OFF?** - Without selection, mutations accumulate randomly without any guidance, resulting in no directional progress toward the target phrase.

**Question 2: Does the number of generations affect whether the target phrase is reached?** - Yes, more generations allow more opportunities for

mutations and selection to work, increasing the chances of reaching the target phrase, but there is no absolute guarantee.

**Question 3: Does the speed of reaching the target phrase depend on the length of the phrase?** - Yes, longer phrases require more steps to match each letter, meaning the process takes more time and generations due to the greater complexity.

**Question 4: How does this simulation differ from real natural selection?** - Real natural selection is not driven by a specific goal. It is shaped by environmental pressures and the organisms' fitness relative to their surroundings, rather than aiming for a specific outcome like in this simulation.

## 2.7 Teaching Tips

1. **Clarify the Role of Selection:** Emphasise that selection drives the evolutionary process toward the target, while random mutations provide the variation necessary for evolution.
2. **R Programming Guidance:** Assist students in modifying parameters like mutation rate, number of generations, and selection to observe different outcomes.
3. **Link to Real Evolution:** Discuss how real-world evolution is more complex and involves multiple factors such as genetic drift, environmental changes, and does not have a predetermined goal like the target phrase.

## 2.8 Common Pitfalls to Watch For

- **Misunderstanding Selection:** Students might think that selection always chooses perfect sequences. Clarify that selection favours the closest match, not necessarily perfection.
- **R Script Issues:** Ensure students accurately modify the code to adjust parameters like the mutation rate and number of generations.
- **Misinterpretation of the Target Concept:** Make sure students understand that real natural selection does not work toward a fixed outcome like in this simulation.





## Chapter 3

# Bug Hunt Camouflage (NetLogo)

### 3.1 Introduction

This exercise demonstrates adaptive evolution and natural selection using a predator-prey simulation in NetLogo. Students take on the role of a predator (a bird) and hunt bugs to observe how the bug population evolves in response to selective pressures. The key concept is the relationship between camouflage and predator efficiency, mirroring real-world natural selection.

### 3.2 Key Concepts

- **Natural Selection:** The process where individuals with traits better suited to the environment survive and reproduce, passing those traits to the next generation.
- **Adaptive Evolution:** Changes in populations over time that enhance survival and reproduction in a given environment.
- **Selection Pressure:** The environmental factors that influence which individuals survive and reproduce.
- **Heritability:** A measure of the fraction of phenotype that can be attributed to genetic variation.

### 3.3 Learning Outcomes

- Understanding adaptive evolution via natural selection.
- Understanding how fitness depends on the environment.
- Understanding the terms adaptation, selection, selection pressure, heritability.

## 3.4 Activity Overview

### 3.4.1 Time: 45 minutes

1. **Introduction (5 min):** Explain the activity, including the basic concepts of natural selection and camouflage.
2. **Simulation Setup (5-10 min):** Students log into NetLogo and load the Bug Hunt Camouflage model.
3. **Main Activity (25 min):** Students play the role of a predator, hunting bugs and observing how the bug population evolves over time. Students pause and analyse the graphs to assess hunting efficiency and bug color evolution.
4. **Discussion and Wrap-Up (5-10 min):** Reflect on how the simulation demonstrates key concepts of selection, adaptation, and evolution.

## 3.5 Instructions for Facilitating

### 3.5.1 Simulation Setup

1. Guide students to open NetLogo and find the “Bug Hunt Camouflage” model.
  - **Tip:** If using UCloud, ensure students are familiar with the platform steps outlined in the task description.
2. Explain the interface: sliders control population and mutation rates, while the graphs provide real-time feedback on bug traits and hunting efficiency.

### 3.5.2 Running the Simulation

- Students begin by adjusting the population size to 30 bugs using the “carrying-capacity” slider.
- Students click “set up”, then start the simulation with “Go”. They then hunt bugs by clicking on them. Encourage them to hunt quickly to avoid bias in their selection process.
- Students observe how their hunting impacts the bug population, paying attention to changes in color traits (hue, saturation, brightness) and hunting efficiency (the slope of the graph showing number of bugs caught) over time.
- After 5 minutes of hunting, students should pause the simulation and examine the graphs.
  1. **Bugs Caught vs. Time:** Steep slopes indicate high hunting efficiency.
  2. **Color Distribution:** This will show the shift in color traits due to selective pressures from hunting.
- Encourage students to reflect on how the bug population becomes better adapted to their environment over successive generations.

- After about 10 minutes, get them to pause (by pressing “Go”) and change the background picture.

## 3.6 Questions & Model Answers

### 1. What happens to the average color of the bug population with time as you hunt?

Over time, the average color of the bug population tends to shift towards colors that blend in better with the environment. As you hunt, bugs with less effective camouflage are caught more easily, while those that are harder to spot survive and pass on their traits to their offspring. This results in a gradual change in the population’s average color.

### 2. What happens to your hunting efficiency?

Initially, hunting efficiency is high, as the bugs are easy to spot. However, as the population evolves and the bugs’ colors become better camouflaged with the environment, hunting efficiency decreases. This reflects natural selection, where better-adapted individuals (bugs) are harder to catch.

### 3. Would you say that the bug population becomes worse or better adapted to their environment?

The bug population becomes better adapted to their environment. As selective pressure is applied (through predation), bugs with colors that offer better camouflage survive and reproduce, increasing the frequency of these adaptive traits in the population.

### 4. Can you explain how this happens?

This is a result of natural selection. Bugs with colors that provide better camouflage have a higher chance of survival because they are harder to detect by predators. These surviving bugs reproduce, passing on their coloration traits to their offspring. Over generations, the population’s coloration shifts to match the environment better, increasing the population’s overall fitness in that habitat.

### 5. After simulating in one environment (e.g. poppy field) for a few minutes, pause then switch to another environment. Are the bugs now well- or poorly-adapted to their new environment?

When the environment is changed, the bugs are usually poorly adapted to the new environment initially. The traits that made them well-camouflaged in the previous environment may now stand out, making them more visible to predators. This change highlights the importance of the environment in determining what traits are beneficial for survival.

### 6. Do the genotypes of individuals change (e.g., with individual age)?

No, the genotypes of individual bugs do not change as they age. The genotypes are fixed at birth and are inherited from their parents. However, the population’s genotype distribution can change over time due to natural selection favoring certain traits (such as better camouflage) and through mutations in the offspring.

### 7. Increasing the “max-mutation-step” makes bug offspring less like their parents. How do you think this will influence the speed of adaptation of the bugs?

Increasing the mutation step introduces greater genetic variability into the population. This can speed up adaptation by providing more opportunities for new beneficial traits to arise. However, it can also produce non-adaptive traits that may decrease the fitness of individuals. The overall effect on adaptation speed will depend on how many of the mutations are beneficial in the given environment.

### 3.7 Teaching Tips

- **Concept Reinforcement:** Frequently remind students of the evolutionary principles at play. Point out how the simulation reflects real-world dynamics, such as how organisms evolve to evade predators or increase predation efficiency.
- **Model Flexibility:** Depending on student progress, you may encourage them to modify other sliders (e.g., mutation rate) to explore more complex evolutionary dynamics.
- **Connecting Theory to Simulation:** Help students relate their observations in the simulation to theoretical principles, such as the definition of evolution as “change in heritable traits over generations.”

### 3.8 Common Pitfalls

- **Misinterpreting Graphs:** Students may struggle to understand the relationship between color changes and hunting efficiency. Emphasise that selection pressure favors bugs that are harder to see, and this trait is passed on to future generations.
- **Technical Issues with NetLogo:** Ensure students are comfortable with the UCloud setup or have downloaded NetLogo in advance.

### 3.9 Additional Resources

- Read more about the model here: [NetLogo Bug Hunt Camouflage](#).

## Part II

# Population Growth Models



## Chapter 4

# Geometric growth

### 4.1 Introduction

This exercise explores the geometric growth model in discrete time steps, focusing on how different values of  $\lambda$  affect population dynamics. It aims to develop students' understanding of growth models, the effects of log transformations, and the limitations of simple models.

### 4.2 Key Concepts

- Geometric growth assumes constant  $\lambda$ , leading to exponential growth or decline.
- Plotting log-transformed population sizes allows easier visualisation of trends.
- Limitations of the model include the assumption of infinite resources and lack of environmental constraints.

### 4.3 Learning outcomes

- Competence in using Excel formulae for mathematical modeling.
- Understanding the parameters of exponential/geometric growth.
- Competence in using mathematical models in Excel to strengthen own understanding of biological processes.
- Awareness of rearranging of mathematical formulae to produce different forms of models.
- Knowing that the slope of the  $\ln(N_t)$  vs.  $t$  relationship can tell you about population growth rate (it is  $\ln(\lambda)$ ).

## 4.4 Activity Overview

### 4.4.1 Time: 40-45 minutes

1. **Introduction (5 min):** Explain the activity, including the basic concepts of geometric growth
2. **Main Activity (25 min):** Students complete the Excel sheet and answer the questions provided.
3. **Discussion and Wrap-Up (5-10 min):** Run through the questions and discuss answers.

## 4.5 Instructions for Facilitating

### 4.5.1 Excel Setup

1. **Download File:** Ensure students have downloaded the provided Excel file `GeometricGrowth.xlsx`.
2. **Initial Setup:**
  - Start with an initial population size ( $N_0$ ) of 10 and a growth rate ( $\lambda$ ) of 1.1.
  - Use Excel formulas to calculate population size at each time step from  $t = 1$  to  $t = 20$ .
  - Example formula: `=B8*$F$8`, where B8 is the population at time  $t$  and `$F$8` is the growth rate  $\lambda$ .
3. **Creating Charts:**
  - Plot the population size against time using an x-y scatterplot.
  - Create a second plot using the natural logarithm of population size ( $\ln()$ ) on the y-axis.

### 4.5.2 Key Observations

- **Plot Comparison:** The linear plot will show exponential (curved) growth, while the log-transformed plot should display a straight line, where the slope represents  $\ln(\lambda)$ .
- **Altering  $\lambda$ :** As students experiment with different values for  $\lambda$  (e.g., 0.8, 1, 1.2), they will observe changes in the steepness of the population growth curve. A  $\lambda$  of 1 results in no population growth, while  $\lambda$  values below 1 indicate population decline.
- **Trendline Slope:** Adding a trendline to the log-transformed graph and determining its slope will give  $\ln(\lambda)$ . Students can use this slope to compute  $\lambda$  using the Excel function `EXP()`.



### 4.5.3 Geometric Series Calculation

- **Geometric Series Formula:** Introduce students to the geometric series formula,  $N_t = N_0\lambda^t$ . This formula provides a shortcut to calculate population size at any given time without stepping through each time point manually.
- **Application:** Use this formula to calculate population size for  $t = 5$  and compare it to earlier manual calculations. Then extend it to predict population size after a large number of generations (e.g.,  $t = 900$ ).
- **Where does that equation come from?**

As a starting point, consider this equation:  $N_{t+1} = \lambda N_t$ .

If we want to calculate  $N_{t+2}$ , we would need to plug in  $N_{t+1}$  instead of  $N_t$ :  $N_{t+2} = \lambda N_{t+1}$ ,

and, since we know that  $N_{t+1} = \lambda N_t$ ,  $N_{t+2} = \lambda\lambda N_t$ .

Similarly, if we wanted to calculate  $N_{t+3}$ , we'd end up with:  $N_{t+3} = \lambda\lambda\lambda N_t$ .

This can be simplified by raising  $\lambda$  to a suitable power, and using the starting population at time = 0,  $N_0$ :

**eqn. 9.**  $N_t = \lambda^t N_0$ .

This should be familiar to those of you that did (or remember!) the concept of geometric series which you have likely covered in earlier maths classes.

## 4.6 Questions & Model Answers

### 1. How does the population size change with time for different values of $\lambda$ ?

The growth rate  $\lambda$  drives the population's exponential increase or decrease.

- For  $\lambda > 1$ , the population size increases exponentially.
- For  $\lambda = 1$ , the population size remains constant.
- For  $\lambda < 1$ , the population size decreases exponentially.

### 2. Why is it useful to plot log-transformed population size?

Log-transformations linearise exponential relationships. Therefore, the transformation converts the exponential growth trajectory into a straight line allowing for easier interpretation of the growth rate, as the slope corresponds to  $\log(\lambda)$ . You can get the  $\lambda$  value by taking the exponential of  $\log(\lambda)$  (in Excel =EXP()).

**3. What are the limitations of the geometric growth model?** - The model assumes infinite resources, no competition, or environmental constraints, making it unrealistic for real-world populations. Real-world populations face density-dependent factors and environmental stochasticity, which the geometric model does not account for.

**4. What would happen if we introduced a carrying capacity to this model?** - The population would follow a logistic growth model, where growth slows as the population nears the carrying capacity.

## 4.7 Teaching Tips:

- **Reinforce Mathematical Understanding:** Emphasize how rearranging and transforming formulas, such as logarithmic transformations, are useful tools for interpreting population growth models.
- **Visual Learning:** Encourage students to compare the linear and log-transformed plots side by side to see how exponential growth behaves differently in each case.
- **Connect to Ecology:** When discussing real-world applications, introduce concepts like carrying capacity and logistic growth to contrast with geometric growth. -. **Model limitations:** Engage students in discussions about how the model could be adapted to account for real-world variables like environmental factors or density dependence.

## 4.8 Additional Resources

- **Excel Tutorial:** If students are unfamiliar with Excel's log transformation and trendline features, provide a walkthrough. They should use natural log (=LN).

## Chapter 5

# Estimating Population Growth Rate

### 5.1 Introduction

This exercise allows students to work with real population data to estimate the population growth rate ( $\lambda$ ) by applying log transformation and linear regression in Excel. It reinforces concepts of geometric growth, exponential growth, and practical skills in data analysis using Excel. Students will learn how to interpret log-transformed data, calculate the growth rate, and understand model assumptions and real-world factors that may affect population growth.

### 5.2 Key Concepts

- **Exponential Growth:** Populations grow by a constant rate ( $\lambda$ ) each time step, leading to exponential growth. Log-transforming the data linearizes this relationship.
- **Log Transformation:** Applying  $\log_e$  to population size makes it possible to fit a linear model to exponential growth data. The slope of this line gives  $\log(\lambda)$ , and exponentiating this value yields  $\lambda$ , the population growth rate.
- **Limitations of the Model:** The exercise uses a geometric growth model, which assumes a constant growth rate. Real-world populations often deviate from this due to environmental variability, competition, and other factors.

### 5.3 Learning outcomes

- Competence in using Excel formulae for data transformation and regression analysis.

- Understanding the role of  $\lambda$  in population growth and its estimation through log-transformed data.
- Competence in applying mathematical models in Excel to analyse real biological data.
- Awareness of how log transformations can linearise exponential growth data for easier interpretation.
- Knowing that the slope of the  $\ln(N)$  vs. time relationship represents  $\ln(\lambda)$  and can be used to estimate population growth rate.

## 5.4 Activity Overview

### 5.4.1 Time: 20 minutes

- 1-2 minutes: Introduce the exercise
- 2-3 minutes: Students read the exercise introduction and instructions.
- 10 minutes: Students do the exercise. Check on them as you walk around the class.
- 5 minutes: Wrap up and go through answers to questions.

## 5.5 Instructions for Facilitating

### 5.5.1 Step 1: Download and Open the Data

1. Ensure students download the provided Excel file **EstimatingGrowth.xlsx**.
2. Once students open the file, explain that the dataset contains population sizes recorded annually over 25 years.

### 5.5.2 Step 2: Plot the Population Size Over Time

- In Excel, have students create an x-y scatter plot of **population size**  $N_t$  against **time** (Year).
- Ensure students correctly label the axes and choose an appropriate chart type.

### 5.5.3 Step 3: Log-Transform the Population Size

1. Guide students to create a new column for the **natural logarithm** of the population size by using the Excel formula `=LN(cell)` where `cell` refers to the population size at a specific time step.
2. Students should then create a second scatter plot using the **log-transformed population size** on the y-axis and **time** on the x-axis.

### 5.5.4 Step 4: Fit a Linear Regression Model

1. In the log-transformed scatter plot, students will add a **linear trendline**.
  - Right-click on the data points and select “Add Trendline.”
  - Choose “Linear” and check the box for “Display Equation on Chart.”
2. Explain that the **slope** of the trendline represents  $\log(\lambda)$ .

### 5.5.5 Step 5: Calculate $\lambda$

- Once students have the slope from the trendline, they will calculate  $\lambda$  using the formula  $\lambda = e^{\text{slope}}$ , which can be done in Excel with the formula `=EXP(cell)`.

## 5.6 Questions & Model Answers

**1. Interpret the Plot: What does the log-transformed plot of population size over time tell you about the population’s growth trend? Does the population appear to grow exponentially?**

- The log-transformed plot should show a straight line if the population is growing exponentially, because the natural logarithm of an exponentially growing population will linearize the exponential curve. A positively sloped line indicates growth, a flat line suggests stability, and a negatively sloped line indicates population decline.

**Estimate Growth Rate: What is the estimated population growth rate ( $\lambda$ ) based on your linear regression analysis?**

- The slope of the regression line from the log-transformed plot corresponds to  $\log(\lambda)$ . To find  $\lambda$ , students one can exponentiate the slope:  $\lambda = e^{\text{slope}}$ .
- Example: If the slope of the regression line is 0.086, then  $\lambda = e^{0.086} \approx 1.09$ , meaning the population grows by approximately 9% per year.

**Model Assumptions: What assumptions does this model make about population growth? Discuss any potential real-world factors that might affect the accuracy of your estimate for  $\lambda$ .**

- The model assumes that population growth follows a constant rate ( $\lambda$ ) over time, without any external influences such as migration, resource limitations, or environmental changes. In the real world, population growth rates can fluctuate due to factors such as weather, food availability, disease, or human intervention.
- Other factors, like density dependence (competition for resources), may also affect the accuracy of the model. The geometric model does not account for a carrying capacity, which limits population growth in real ecosystems.

## 5.7 Teaching Tips:

1. **Ensure Students Understand Log Transformations:** Emphasize why log transformation linearises the exponential growth model, making it easier to interpret the population's growth trend. A short explanation of the mathematics behind this is helpful. Explain that exponential growth is linear in log space because  $\log(N_t) = \log(N_0) + t \log(\lambda)$ , which is analogous to the standard equation for a straight line  $y = ax + b$ .
2. **Excel Skills:** Ensure students know how to use Excel for log transformations (LN function), plot data, add trendlines, and display the regression equation on their charts. Consider providing a walkthrough if they are not familiar with Excel's plotting tools.
3. **Discuss Model Assumptions:** Encourage students to critically think about the assumptions behind geometric growth models. A good discussion could involve real-world examples where the assumptions break down, such as predator-prey dynamics, food shortages, or disease outbreaks.
4. **Data Quality and Measurement Error:** Highlight how measurement error or random fluctuations can influence data analysis. If measurement noise was introduced in the exercise, this can be a good opportunity to discuss the impact of imperfect data on the accuracy of the estimated growth rate.
5. **Comparing to Year-over-Year Estimates:** Have students compare the growth rate they estimate from the regression model to a simple year-over-year ratio estimate of population growth. Discuss why these values might differ, particularly in the presence of noise or irregularities in the data.

## 5.8 Common Pitfalls

- **Confusion with Log Transformation:** Students may not understand why log transformation creates a straight line from exponential data.
- **Exponentiating the Slope:** Remind students that the slope of the regression line represents  $\log(\lambda)$ , and they need to calculate  $\lambda = e^{\text{slope}}$  to find the actual growth rate.
- **Interpreting  $\lambda$ :** Make sure students understand that  $\lambda > 1$  indicates growth,  $\lambda = 1$  indicates a stable population, and  $\lambda < 1$  indicates population decline.

## Chapter 6

# Stochastic population growth

### 6.1 Introduction

This exercise introduces students to the stochastic version of population growth models, focusing on how randomness and variability can influence population dynamics over time. By working with both Excel and R, students will explore the differences between deterministic and stochastic population models, specifically applying them to geometric (discrete) growth models. The exercise allows students to build skills in mathematical modeling, data analysis, and stochastic simulation, all of which are essential for understanding real-world ecological systems and predicting population trajectories under uncertainty.

### 6.2 Key Concepts

- **Deterministic vs. Stochastic Models:**  
Deterministic models assume a fixed growth rate, while stochastic models incorporate randomness, leading to more realistic projections.
- **Geometric Growth Model:**  
The model is expressed as  $N_{t+1} = \lambda N_t$ , where  $\lambda = e^{r_m}$  and  $r_m = \ln(\lambda)$ . It is used to predict population size in the next generation.
- **Stochasticity:**  
Variability in growth rates, often modeled by drawing random values from a normal distribution for  $r_m$ . This randomness reflects environmental fluctuations and individual-level variation.
- **Extinction Risk:**  
As stochasticity increases, populations are more likely to decline or go extinct. Extinction risk depends on factors such as variance in  $r_m$ , initial population size, and mean growth rate.

### 6.3 Learning Outcomes

- Understand and apply stochastic models to population dynamics.
  - Build competence in using Excel for mathematical modeling and simulations.
  - Grasp the relationship between stochasticity, extinction risk, and environmental variability.
  - Use R to simulate population growth and estimate extinction risk.
- 

### 6.4 Activity Overview

**Suggested Timings:**

- **5 minutes:** Introduce the concept of stochastic population growth.
  - **5 minutes:** Students read through the background and instructions.
  - **20 minutes:** Students work on Excel-based deterministic and stochastic population growth modeling. Students with R experience may also explore stochastic simulations using R.
  - **10 minutes:** Wrap up discussion and review key takeaways.
- 

### 6.5 Instructions for Facilitating

**1. Introduction:**

Briefly explain the difference between deterministic and stochastic models, focusing on why stochasticity is more reflective of real-world populations. Emphasize how the exercise will involve building models in Excel (and optionally R).

**2. Excel Modeling:**

Guide students through calculating deterministic population growth first, then introduce stochastic variation in growth rates by using the provided formula [English Excel: `=NORMINV(RAND(),$F$10,SQRT($F$11))` / Danish Excel: `=NORMINV(SLUMP();$F$10;KVR0D($F$11))`]. If you get errors, check whether Excel is expecting commas or semi-colons].

**3. R Simulation:**

For the R component, ensure students understand the basic structure of the code and how the simulation works. Encourage them to modify parameters like `mean.r` and `var.r` to observe different outcomes.



**4. Discussion:**

Facilitate a discussion on extinction risk, the impact of variability, and how different levels of stochasticity affect population trajectories.

---

## 6.6 Questions & Model Answers

**1. What is the main difference between deterministic and stochastic population growth models?** - Deterministic models use fixed growth rates, while stochastic models incorporate random variability, making them more realistic for representing natural populations.

**2. Describe how incorporating randomness into the stochastic model makes it more realistic for understanding real-world populations.** - Real-world populations face unpredictable environmental conditions and other factors that influence growth. Stochastic models account for these fluctuations, better mimicking actual population dynamics.

**3. Simulate a scenario where two populations with identical growth rates experience different outcomes due to stochastic factors. Explain the implications of these findings.** - Due to randomness, populations with the same initial conditions can diverge significantly over time. This demonstrates how chance events can lead to different outcomes, including extinction for one population and growth for another.

**4. What can this stochastic model tell us about extinction risk and population size?** - Smaller populations are more vulnerable to extinction in stochastic models because random negative growth events can have a greater impact.

**5. What can this stochastic model tell us about extinction risk and environmental variation?** - As environmental variability (represented by increased stochasticity) increases, populations face a higher risk of extinction due to more frequent poor years.

---

## 6.7 Teaching Tips

- **Stochasticity:**

Ensure students understand that stochasticity represents environmental and biological variability. Highlight how the normal distribution used to model  $r_m$  generates different growth rates across generations.

- **Excel Formulae:**

Some students may struggle with Excel formula syntax, particularly in different language settings. Double-check that students are using the correct formula (e.g., commas vs. semicolons).

- **R Simulations:**

Not all students may be familiar with R, so you may need to provide extra guidance on running the simulations and interpreting results.

- **Comparing Models:**

Emphasize the importance of comparing deterministic and stochastic models using visual charts. This comparison helps students see how randomness impacts long-term population trends.

---

## 6.8 Common Pitfalls

- **Formula Errors in Excel:**

Ensure students understand how to use the Excel function to generate stochastic  $r_m$  values. Remind them that Excel might expect different delimiters (commas or semicolons).

- **Misinterpreting Stochasticity:**

Students may confuse the effects of stochasticity with systematic trends. Clarify that stochasticity introduces random fluctuations that are just as likely to be negative as positive, not directional trends.

- **R Familiarity:**

If students are unfamiliar with R, they may find the simulation code challenging. Ensure they don't modify critical parts of the script unnecessarily.

““

## Chapter 7

# Basic logistic population growth

### 7.1 Introduction

This exercise allows students to explore the logistic population growth model by manipulating parameters in an Excel spreadsheet and analyzing the resulting population dynamics. Students will apply the model to observe how population growth behaves under different conditions, deepening their understanding of ecological processes such as carrying capacity, population regulation, and deterministic chaos. The exercise will strengthen their ability to use Excel for modeling and analysis, while also helping them to grasp the mathematical principles behind population ecology and biological conservation.

### 7.2 Key Concepts

The exercise involves the following key concepts:

- **Logistic Growth Model:** A population growth model that accounts for environmental limitations, leading to a stabilization at the carrying capacity ( $K$ ).
- **Carrying Capacity ( $K$ ):** The maximum population size that an environment can support long-term, based on resources and other limiting factors.
- **Intrinsic Rate of Increase ( $r_m$ ):** The maximum per capita growth rate under ideal conditions, which determines how fast a population grows.
- **Deterministic Chaos:** A concept where slight changes in initial conditions can lead to drastically different outcomes, making long-term predictions challenging.

Mathematically, the logistic growth equation is given by:

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

This equation shows that as population size approaches the carrying capacity, the growth rate decreases until the population stabilizes at  $K$ .

### 7.3 Learning Outcomes

Students will achieve the following learning outcomes:

- Increased competence in using Excel for mathematical modeling of biological processes.
- Understanding the parameters of the logistic population growth model, particularly how  $r_m$  and  $K$  affect population dynamics.
- Ability to explain how population dynamics vary with changes in the population growth rate, from stable to chaotic dynamics.
- Understanding the concept of deterministic chaos and its difference from randomness.
- Practical experience using mathematical models in ecology and conservation.

### 7.4 Activity Overview

Suggested timings: - **5 minutes**: Introduce the exercise and demonstrate how to use the Excel spreadsheet. - **5 minutes**: Students familiarize themselves with the Excel sheet and instructions. - **20-30 minutes**: Students complete the exercise by experimenting with different parameter values and analyzing the graphs. - **5 minutes**: Wrap up by discussing the key findings and concepts.

### 7.5 Instructions for Facilitating

1. Begin by introducing the logistic growth model and its relevance in ecology.
2. Walk students through the Excel spreadsheet, highlighting the areas they will interact with (the pink block) and the three graphs.
3. Encourage students to change the initial population size, growth rate ( $r_m$ ), and carrying capacity ( $K$ ) and observe the results on the graphs.
4. Ask students to predict outcomes before modifying parameters, fostering engagement with the model's underlying logic.
5. Guide students through the additional questions to reinforce theoretical understanding.

## 7.6 Questions & Model Answers

Students will answer the following questions:

1. **What is the maximum population size?**
  - Focus on comparing the maximum population size with the carrying capacity ( $K$ ). Students should observe that when  $r_m$  is around 1 or lower, the maximum population size matches  $K$ . For higher values of  $r_m$  the population size can overshoot carrying capacity.
2. **What do you predict will happen if you increase  $K$  to 300?**
  - The population will adjust, and the new maximum population size will equal the increased  $K$ .
3. **What happens if you reduce  $r_m$  to 0.4?**
  - The time to reach the maximum population size will increase, as a lower growth rate slows down the population's approach to  $K$ .
4. **What happens if you set  $r_m$  to 1.8?**
  - The population will overshoot  $K$  and oscillate around it with damped oscillations. The dynamics will show a period of fluctuation before stabilizing.
5. **What do you observe when you set  $r_m$  to 2.8 or higher?**
  - The population will display chaotic dynamics, with irregular fluctuations around  $K$ . The system becomes harder to predict as  $r_m$  increases beyond 2.57.

## 7.7 Teaching Tips

- **Clarify the Concept of Carrying Capacity ( $K$ ):** Students may confuse carrying capacity with a fixed limit on growth rather than an equilibrium point.
- **Demonstrate the Importance of  $r_m$ :** Encourage students to try different values of  $r_m$  to understand the transition from stable growth to chaotic behavior.
- **Excel Skills:** Some students may need assistance with basic Excel functions, particularly using formulas and interpreting graph outputs.
- **Connect to Real-World Applications:** Relate the logistic model to real-world population management scenarios, such as pest control or endangered species conservation.

## 7.8 Common Pitfalls

- **Misunderstanding Population Oscillations:** Students may assume that overshooting  $K$  means the model is broken. Explain that oscillations are a natural result of high growth rates and density dependence.

- **Confusion Between Chaos and Randomness:** Students might think chaotic dynamics are purely random. Emphasize that chaotic systems are deterministic but highly sensitive to initial conditions.
- **Excel Formula Errors:** Watch for common Excel mistakes, such as incorrect cell references when entering formulas in the pink block.

## 7.9 Concrete Real-World Examples

### 7.9.1 1. Pest Control (e.g., Locusts)

- **Scenario:** Locusts have a high growth rate and can quickly overrun an area during favorable conditions.
- **Logistic Model:** Locusts overshoot the carrying capacity, leading to resource depletion and population crashes. The model helps predict outbreaks and plan timely interventions.

### 7.9.2 2. Endangered Species Conservation (e.g., California Condor)

- **Scenario:** Conservation efforts focus on increasing populations without exceeding  $K$ .
- **Logistic Model:** The model helps determine sustainable population levels, ensuring growth without resource depletion.

### 7.9.3 3. Fisheries Management (e.g., Atlantic Cod)

- **Scenario:** Overfishing can drive populations below the sustainable level.
- **Logistic Model:** Managers use the model to balance fish harvest with population growth, ensuring long-term viability.

### 7.9.4 4. Invasive Species Management (e.g., Cane Toads in Australia)

- **Scenario:** Cane toads expand rapidly without natural predators, surpassing  $K$  and impacting ecosystems.
- **Logistic Model:** Predicts rapid expansion and highlights the need for quick control measures to manage invasive populations.

By using these real-world examples, students can see how the logistic growth model is a practical tool for predicting and managing population dynamics in various environmental and conservation contexts.

## Chapter 8

# Deeper into logistic growth

This exercise helps students dive deeper into understanding the relationship between exponential (or geometric) and logistic growth models and how mathematical models can be explored from different perspectives. By experimenting with the Excel worksheet, students will observe how the logistic growth model can be modified and visualized in various ways. The exercise is designed to strengthen students' competence in using Excel for mathematical modeling and to enhance their understanding of population dynamics.

### 8.1 Key Concepts

This exercise covers the following key concepts:

- **Exponential Growth Model:** A simple population growth model where the population grows continuously without any limiting factors.
- **Logistic Growth Model:** A model that accounts for environmental constraints, introducing a carrying capacity ( $K$ ) that limits population growth.
- **Carrying Capacity ( $K$ ):** The maximum population size that an environment can sustain long-term.
- **Intrinsic Rate of Increase ( $r_m$ ):** The maximum per capita population growth rate under ideal conditions.
- **Time Lag in Population Growth:** A delay in how population size at a previous time step influences current growth dynamics, which can lead to cyclic behavior.
- **Per Capita Growth Rate ( $r$ ):** The rate of population growth per individual as a function of population size.

Mathematically, the logistic growth equation is:

$$\frac{\delta N}{\delta t} = r_m N \left( 1 - \frac{N}{K} \right)$$

If  $K$  is set to infinity, the logistic model reduces to the exponential growth model:

$$\frac{\delta N}{\delta t} = r_m N$$

## 8.2 Learning Outcomes

- Increased competence in using Excel formulae for mathematical modeling.
- Understanding the relationship between exponential and logistic growth models.
- Ability to modify mathematical models to explore different phenomena, such as time lags.
- Understanding how and why model outputs can be explored from different perspectives.
- Practical skills in using Excel to strengthen their understanding of biological processes, specifically population dynamics.

## 8.3 Activity Overview

Suggested timings:

- **5 minutes:** Introduce the exercise and explain the relationship between exponential and logistic growth models.
- **10 minutes:** Students explore different views of the logistic growth model in Excel.
- **20-30 minutes:** Students experiment with  $r_m$ ,  $K$ , and the time lag in the Excel worksheet to observe changes in the population dynamics.
- **5 minutes:** Wrap up by discussing how exponential growth differs from logistic growth and how time lags affect population dynamics.

## 8.4 Instructions for Facilitating

1. Start by explaining the connection between exponential and logistic growth models, using the example of  $K$  approaching infinity to show how the logistic model reduces to the geometric growth equation.
2. Walk students through the Excel worksheet, particularly focusing on the **BasicLogistic** tab where they can manipulate  $r_m$  and  $K$  values.
3. Guide students through the analysis of **Figure 1** (population size over time), **Figure 2** (per capita growth rate vs. population size), and **Figure 3** (population growth rate vs. population size).
4. Encourage students to predict population dynamics as they adjust parameters, such as  $r_m$  and  $K$ .
5. Introduce the concept of time lags and direct students to the **TimeLag** tab to observe how introducing a delay in population feedback influences the system's dynamics.



## 8.5 Questions & Model Answers

Students will answer the following questions:

1. **What dynamics do you observe in Figure 1 as you change  $r_m$ ?**
  - With small  $r_m$  values, the population grows smoothly and stabilizes at  $K$ . As  $r_m$  increases, the system shows oscillations, damped oscillations, and eventually chaotic or unpredictable behavior.
2. **What do you notice about the intercepts in Figure 2?**
  - The intercept on the x-axis occurs at  $K$ , while the intercept on the y-axis is  $r_m$ . Therefore, a plot of  $N$  vs. per capita growth rate can tell us what  $K$  and  $r_m$  are.
3. **How does adding a time lag affect the population dynamics?**
  - Adding a time lag can introduce cycling into the system, even when the intrinsic growth rate ( $r_m$ ) is small. This shows that delayed responses in population feedback can lead to fluctuations in population size, despite stable conditions.
4. **How do the figures for exponential growth differ from those for logistic growth?**

**Figure 1: Population Size Through Time - Exponential Growth:** The population shows a **J-shaped curve**, growing rapidly without limit, suggesting **unlimited resources**. - **Logistic Growth:** The population typically follows an S-shaped curve, with growth slowing as it approaches carrying capacity ( $K$ ). However, at higher population growth rates, the dynamics can become more complex, including oscillations or chaotic behaviour, rather than simply leveling off. The exact trajectory depends on the growth rate and can lead to unpredictable, fluctuating patterns around  $K$ .

**Figure 2: Per Capita Growth Rate vs.  $N$  - Exponential Growth:** The per capita growth rate is **constant**, unaffected by population size, indicating no resource constraints. - **Logistic Growth:** The per capita growth rate **declines linearly** as population increases, reflecting **density dependence** and resource limitation as  $N$  approaches  $K$ .

**Figure 3: Relationship Between  $dN/dt$  and  $N$  - Exponential Growth:** The relationship is **linear**, with  $dN/dt$  increasing proportionally as population size grows. - **Logistic Growth:**  $dN/dt$  forms a **parabolic curve**, increasing initially but declining as  $N$  approaches  $K$ , reaching zero at carrying capacity.

## 8.6 Teaching Tips

- **Clarify the Relationship Between Exponential and Logistic Growth:** Make sure students understand how the logistic model becomes the exponential model when  $K$  is removed (i.e. when it is infinity).

- **Highlight the Role of  $r_m$ :** Encourage students to experiment with different  $r_m$  values to understand the transition from stable growth to chaotic dynamics.
- **Time Lags and Cyclic Behavior:** Some students may struggle to grasp how time lags cause population cycles. Show them step-by-step how changing the reference population size (e.g.,  $N_{t-1}$ ) affects the dynamics.
- **Connect to Real-World Applications:** Discuss how these models apply to real-world populations, such as predator-prey systems or species with delayed reproductive responses.

## 8.7 Common Pitfalls

- **Overlooking the Impact of Time Lags:** Students might expect that small changes in the model have minimal effects. Emphasize that even slight time delays can drastically alter population dynamics.
- **Misinterpreting Figure 2:** Some students may find it confusing that the per capita growth rate decreases as population size approaches  $K$ . Reinforce the concept that as resources become limited, growth slows.
- **Excel Formula Errors:** Students may struggle with modifying Excel formulas, especially when introducing time lags. Ensure they understand how to correctly reference previous population sizes.

## 8.8 Concrete Real-World Examples

### 8.8.1 1. Insect Population Control (e.g., Mosquitoes)

- **Scenario:** Mosquito populations often experience delayed responses to environmental changes, such as seasonal rainfall.
- **Time Lag:** Adding a time lag to the logistic growth model demonstrates how insect populations might cyclically fluctuate before stabilizing, helping to predict pest outbreaks.

### 8.8.2 2. Conservation of Slow-Reproducing Species (e.g., Elephants)

- **Scenario:** For species with long gestation periods, the impact of population growth may be delayed.
- **Application of Time Lag:** Introducing time lags helps model how long-term population growth might respond to conservation efforts, showing periods of slow recovery followed by more rapid growth.

### 8.8.3 3. Fisheries Management

- **Scenario:** Fish stocks often experience delayed population responses to overfishing or recovery efforts.

- **Time Lag in Growth Models:** Managers use time-lagged models to account for the slow recovery of fish populations, ensuring sustainable harvest rates.

These examples help students understand how the logistic growth model, with or without time lags, can be applied to real-world population management and conservation challenges.



## Chapter 9

# Life Tables and Survivorship Types

### 9.1 Introduction

This exercise allows students to **work with life tables** and **explore survivorship curves** by applying **Excel-based modeling techniques**. It reinforces concepts of **life expectancy**, **mortality patterns**, and **population dynamics**. Students will learn how to calculate **survivorship ( $l_x$ )**, **survival probabilities ( $g_x$ )**, and other critical life table metrics, as well as how to construct and interpret **survivorship curves (Type I, II, III)**. These skills are relevant for understanding population biology, demography, and ecology, with applications in **conservation biology**, **public health**, and **policy-making**.

### 9.2 Key Concepts

The exercise covers the following key concepts:

- **Life Table Calculations:** Life tables provide a systematic approach to tracking the survival and reproduction of individuals within a cohort, revealing age-specific risks, life expectancy, and population growth rates.
- **Survivorship ( $l_x$ ):** The probability of surviving to a particular age, calculated from the proportion of individuals still alive.
- **Survivorship Types:**
  - **Type I:** Low early-life mortality, high mortality later (e.g., humans).
  - **Type II:** Constant mortality rate across all ages (e.g., birds).
  - **Type III:** High early-life mortality, low mortality later (e.g., fish, plants).
- **Survival Probability ( $g_x$ ):** The probability of surviving the current age class, calculated as  $g_x = l_{x+1}/l_x$ .

- **Force of Selection:** The concept that events earlier in life (reproduction, mortality) have a larger effect on population growth ( $R_0$ ,  $r$ ) than later-life events.

### 9.3 Learning Outcomes

Students will achieve the following learning outcomes:

- Increased competence in using Excel formulae for mathematical modeling.
- Competence in using mathematical models in Excel to strengthen understanding of biological processes.
- Understanding how life tables are calculated.
- Understanding the three types of survivorship curves and how they relate to mortality and survival probabilities.
- Understanding the decline in the “force of selection” and how it impacts population growth.

### 9.4 Activity Overview

Suggested timings:

- **5 minutes:** Introduce the exercise and background concepts.
- **10 minutes:** Students read instructions and download Excel file.
- **20-30 minutes:** Students complete the life table and survivorship curve tasks.
- **5 minutes:** Wrap up and discuss key findings.

### 9.5 Instructions for Facilitating

1. Introduce life tables, explaining their relevance in population biology and mortality studies.
2. Guide students through downloading the Excel file and briefly explain the worksheets: **Life table**, **Survivorship Curves**, and **Gotelli Table 3.1 example**.
3. Explain survivorship ( $l_x$ ), survival probability ( $g_x$ ), and probability of death ( $q_x$ ), emphasizing their importance in understanding population dynamics.
4. Encourage students to experiment with altering reproduction rates to observe the **force of selection**.
5. Facilitate discussions on survivorship curves, ensuring students understand the differences between Types I, II, and III.

## 9.6 Questions & Model Answers

1. **What are the three main types of survivorship curves, and which organisms typically exhibit each type?**

Type I curves indicate high survival in early life and high mortality at older ages (e.g., humans and other long-lived mammals). Type II curves show constant mortality throughout life (e.g., many birds). Type III curves represent high juvenile mortality with survivors living long lives (e.g., marine fish, plants).

2. **What does a net reproductive rate ( $R_0$ ) of less than 1 signify for a population?**

An  $R_0$  of less than 1 indicates that, on average, each individual in the population is replaced by fewer than one offspring, suggesting that the population is declining over time.

3. **How does the shape of a survivorship curve reflect trade-offs in life history strategies, typically?**

Type I curves suggest investment in offspring with low juvenile mortality, typical in species with fewer offspring and greater parental care. Type III curves reflect species that produce many offspring but provide little care, leading to high early mortality.

4. **How is survivorship ( $l_x$ ) different from survival probability ( $g_x$ )?**

Survivorship ( $l_x$ ) and survival probability ( $g_x$ ) are related concepts in life tables, but they measure different aspects of survival in a population.

- **Survivorship ( $l_x$ ):** This is the proportion of individuals that survive from birth (or the start of an age class) to a specific age class  $x$ . It provides a cumulative measure of survival across multiple age classes. For example, if  $l_0 = 1$  (all individuals alive at birth), then  $l_1$  might be 0.8 (indicating that 80% of individuals survive to the first age class).  $l_x$  declines with increasing age as more individuals die.
- **Survival Probability ( $g_x$ ):** This is the probability that an individual who is alive at age class  $x$  will survive to age class  $x + 1$ . It measures survival over a single time step, unlike survivorship, which is cumulative. For example, if 80% of individuals survive from age 1 to age 2, then  $g_1 = 0.8$ .

In short, **survivorship** tracks the cumulative proportion of individuals surviving to a given age class, while **survival probability** reflects the likelihood of surviving just one more time step.

5. **How does altering reproduction or survival/mortality at different ages affect  $R_0$  and population growth rate**

Changes early in life have a larger impact on  $R_0$  and population growth rate than changes later in life, due to the declining force of selection.

## 9.7 Teaching Tips

To help students successfully complete the exercise, consider these teaching tips:

- **Excel Skills:** Ensure students understand the use of the \$ symbol for absolute references in Excel formulae. Demonstrate how to drag formulas to fill columns efficiently.
- **Understanding Survivorship Curves:** Explain the importance of log-transforming survivorship data ( $\ln(l_x)$ ) to reveal the distinct shapes of Type I, II, and III curves. Encourage students to relate survivorship curves to real-life biological strategies (e.g., high parental care vs. high offspring production).
- **Force of Selection Experiment:** Emphasize the biological significance of reproductive changes at different life stages. Guide students in interpreting graphs of age vs. change in  $R_0$  to observe how early-life events have more impact on population growth.

## 9.8 Common Pitfalls

Watch out for these common pitfalls:

- **Confusing  $l_x$  and  $g_x$ :** Students may confuse **survivorship** ( $l_x$ ) with **age-specific survival probability** ( $g_x$ ). Reinforce that  $l_x$  refers to survival up to an age, while  $g_x$  is the probability of surviving from one age to the next.
- **Excel Formula Errors:** Students may forget to lock cells when copying formulas (using \$ in Excel). Remind them to check their formulas carefully.
- **Misinterpreting Survivorship Curves:** Students might struggle to distinguish between the three survivorship types. Ensure they understand that Type I has a convex curve, Type II a straight line, and Type III a concave curve on a log scale.



## Chapter 10

# Matrix population modelling

### 10.1 Introduction

This exercise introduces students to **matrix population models**, which are vital in population ecology for studying structured populations. Unlike simple models, these account for variation in life stages (e.g., seedling, juvenile, adult) by using transition matrices to represent relationships between life stages and transitions over time. The practical involves building life-cycle diagrams, converting them into matrix models, and using **R** to simulate population projections, calculate population growth rates ( $\lambda$ ), and explore **elasticity** and **LTRE** (life table response experiments).

This exercise equips students with the ability to construct and analyze matrix population models, understand demographic impacts on populations, and perform simulations to address management and conservation questions.

### 10.2 Key Concepts

- **Matrix Population Models:** Frameworks for studying populations with distinct life stages, using transition matrices for survival and fecundity.
- **Population Growth Rate ( $\lambda$ ):** The dominant eigenvalue of the matrix, representing long-term population growth or decline.
- **Elasticity Analysis:** Measures the sensitivity of population growth to changes in vital rates, helping identify key transitions in a species' life cycle for conservation or management.
- **Life Table Response Experiment (LTRE):** A method of running “in silico” experiments by modifying matrix elements to predict effects on population dynamics.

### 10.3 Learning Outcomes

By the end of this exercise, students will: - Construct life cycle diagrams representing life stages of organisms. - Parameterize life-cycle diagrams and convert them into matrix population models. - Use R to calculate population growth rates and project population sizes. - Link population projections to biological and management questions. - Perform *in silico* experiments to explore the effects of demographic changes on population dynamics.

### 10.4 Activity Overview

**Suggested Timings:** - 5 minutes: Introduce matrix population models and provide background. - 10 minutes: Students think about an organism and design a life cycle diagram. - 20-30 minutes: Create and analyze matrix models, calculate population growth, and run elasticity and LTRE analyses. - 5 minutes: Wrap-up and discuss answers.

### 10.5 Instructions for Facilitating

1. Introduce matrix population models, emphasizing their application in ecology and conservation.
2. Guide students in selecting an organism and drawing a simplified life cycle diagram.
3. Ensure students assign plausible survival and fecundity rates to the life stages.
4. Assist students in translating their life cycle diagram into a matrix model.
5. Walk through how to use **R** for projecting population growth and analyzing  $\lambda$  and elasticity.
6. Encourage students to perform LTRE by modifying vital rates and interpreting the results.

### 10.6 Questions & Model Answers

1. **In the graph showing log-transformed population size through time, what is the significance of the lines being straight after the transient phase?**
  - A straight line in the log-transformed population size graph indicates exponential population growth, meaning the population growth rate has stabilized.
2. **Explain how an elasticity analysis of a matrix model can be used to inform the management of a threatened species.**
  - Elasticity analysis highlights which life stages have the greatest effect on population growth. Managers can focus conservation efforts on

stages with the highest elasticity, such as enhancing survival rates of critical stages.

### 3. What are some of the assumptions of a matrix population model?

- Constant vital rates, stable environments, closed populations (no immigration or emigration), and absence of density dependence, similar to assumptions in exponential growth models.

## 10.7 Teaching Tips

- **Ensure familiarity with matrix population models:** Many students may need a refresher on basic matrix operations and their role in population dynamics.
- **R skills:** Some students may struggle with R coding. Encourage them to ask questions if they face difficulties with syntax or package installations.
- **Connecting models to management:** Help students understand how matrix models inform real-world conservation efforts, such as targeted interventions based on elasticity results.

## 10.8 Common Pitfalls

- **Incorrect matrix dimensions:** Students may input matrices with the wrong number of rows and columns. Remind them that the matrix must have dimensions matching the number of life stages.
- **Misinterpreting eigenvalues:** Ensure students understand that  $\lambda$  represents the long-term population growth rate and that it's the dominant eigenvalue. Emphasize the significance of elasticity results for identifying key transitions.
- **Rounding errors:** When assigning survival and fecundity rates, students may enter values that lead to rounding mistakes in the matrix, particularly when dealing with small decimal values. Encourage students to double-check their values before running projections.
- **Mathematically infeasible models:**
  - **Sum of transition probabilities >1:** Students may assign transition values that, when summed, exceed 1 for a given stage. For example, if an organism can transition from **Stage A** to **Stage B** and **Stage A** to **Stage C**, the sum of these transitions cannot exceed 1, since survival rates and transitions are probabilities. Ensure students understand that the total probability of transitioning out of any stage cannot be greater than 1.
  - **Non-ergodic models:** Sometimes students may create non-ergodic matrices, where certain stages are isolated or disconnected from others. Instruct students to verify that all stages are reachable either directly or indirectly from any other stage to ensure the matrix is realistic.

Emphasize that matrix elements, as well as their sums, must adhere to biological and mathematical constraints, helping students build feasible models that accurately represent population dynamics.

## Chapter 11

# Pre- and Post-reproduction census

Coming soon. . .



## Chapter 12

# Life Table Response Experiments

Coming soon. . .





## Chapter 13

# How many eggs should a bird lay?

### 13.1 Introduction

This exercise introduces students to life-history trade-offs, a key concept in evolutionary ecology. By analyzing data on the *Bigus canarius*, students will explore how birds balance clutch size and chick survival, reinforcing the idea that biological trade-offs often result in intermediate trait values. Specifically, students will model how increasing the number of eggs affects the survival probability of offspring and identify the optimal clutch size to maximize reproductive success.

Through this activity, students will learn to:

- Understand life-history trade-offs, specifically clutch size versus offspring survival.
- Use data analysis in Excel to generate graphs and calculate expected values for survival.
- Evaluate and interpret graphical results to determine optimal biological strategies.

### 13.2 Key Concepts

The exercise covers several important theoretical concepts, including:

- **Life-history trade-offs:** Organisms allocate limited resources to reproduction, growth, and survival. Increasing one aspect (like clutch size) often decreases another (like offspring survival), creating an evolutionary trade-off.
- **Lack's clutch size trade-off:** British ornithologist David Lack proposed that birds optimize clutch size by balancing the benefits of producing more offspring with the decreasing probability of each chick's survival. It is a classic example of a life-history trade-off.

- **Chick survival probability:** As clutch size increases, the likelihood of parental care for each chick decreases, lowering the chances of chick survival.
- **Expected number of surviving chicks:** Students will calculate this value using the equation:  $\text{Expected number of surviving chicks} = \text{Clutch size} \times \text{Survival probability per chick}$   
The goal is to identify the clutch size that maximizes this value.

### 13.3 Learning Outcomes

- Understand the concept of life-history trade-offs in evolutionary ecology.
- Analyze how clutch size affects offspring survival and identify optimal reproductive strategies.
- Use Excel to create graphs and interpret data on biological trade-offs.

### 13.4 Activity Overview

Suggested timings: - 5 minutes: Introduce the exercise and explain the biological context of trade-offs. - 5 minutes: Students read through the background material and examine the survival data. - 20-25 minutes: Students use Excel to calculate the expected number of surviving chicks and generate corresponding graphs. - 5-10 minutes: Wrap up and discuss the concept of optimal clutch size and other factors that might influence this decision.

### 13.5 Instructions for Facilitating

1. Begin by explaining the concept of life-history trade-offs, specifically Lack's clutch size hypothesis.
2. Ensure students understand the relationship between clutch size and chick survival by reviewing the provided data.
3. Guide students as they enter data into Excel and plot graphs for survival probability and the expected number of surviving chicks.
4. Help students think critically about the results by asking questions about the optimal clutch size and how changing parameters might affect it.

### 13.6 Questions & Model Answers

1. **What is Lack's clutch size trade-off, and why is it considered a fundamental concept in evolutionary ecology?**
  - Lack's clutch size trade-off proposes that birds optimize the number of eggs they lay by balancing the benefits of producing more offspring

with the limitations on parental resources. This concept is fundamental because it highlights the evolutionary strategies organisms use to maximize reproductive success. It is a trade-off between quality and quantity of offspring: should there be many poorly-surviving offspring, or few well-surviving offspring?

**2. How does the trade-off between clutch size and offspring quality manifest in different bird species, and what factors influence their clutch size decisions?**

- The trade-off occurs because as clutch size increases, individual offspring may receive less parental care or resources, reducing their chances of survival. Factors influencing clutch size decisions include food availability, environmental stability, and parental ability to care for offspring.

**3. What are the potential advantages and disadvantages of producing larger clutches with smaller-sized eggs compared to smaller clutches with larger-sized eggs?**

- Larger clutches may increase the number of surviving offspring, but each chick may be smaller and weaker, reducing individual survival chances. Smaller clutches with larger eggs might lead to fewer but stronger and better-cared-for chicks, enhancing individual survival chances.

## 13.7 Teaching Tips

To help students successfully complete the exercise, consider these teaching tips:

- **Ensure students understand the relationship between clutch size and survival:** Explain that as clutch size increases, the survival probability decreases due to resource limitations. The number of mouths to feed per parent.
- **Excel graphing skills:** If students are unfamiliar with Excel, demonstrate how to input data/equations, plot graphs, and create a secondary axis for the expected number of surviving chicks.
- **Encourage critical thinking:** Ask students how changing environmental conditions or parental abilities might shift the optimal clutch size, and if this trade-off applies to other species.

## 13.8 Common Pitfalls

Watch out for these common pitfalls:

- **Confusion about survival probability:** Students may struggle to grasp that the survival probability applies to *each* chick, and not to the whole

clutch. Clarify that they should calculate the survival for each chick and multiply it by the total number of eggs.

- **Excel formula errors:** Ensure students correctly input formulas in Excel, particularly when calculating the expected number of surviving chicks. Remind them to use relative references when copying formulas across multiple rows.

## Chapter 14

# Trade-offs and the Declining Force of Selection

### 14.1 Introduction

This exercise enables students to explore the concept of life history trade-offs, particularly between early reproduction and late-life survival, and understand how the declining force of selection with age influences these trade-offs. By engaging with a simplified life table and manipulating reproductive and survival parameters, students will gain insights into the evolutionary mechanisms shaping aging patterns and life history strategies.

### 14.2 Key Concepts

- **Life History Trade-offs:** The allocation of limited resources between competing biological functions, such as reproduction and maintenance, leading to compromises in one area to benefit another.
- **Force of Selection:** The influence of natural selection on the prevalence of specific traits within a population, which typically diminishes with age, making early-life traits more subject to selection pressures than late-life traits.
- **Net Reproductive Rate ( $R_0$ ):** A measure of the average number of offspring produced by an individual over its lifetime, indicating the fitness of a life history strategy.

### 14.3 Learning Outcomes

Students will achieve the following learning outcomes:

- Understand the concept of life history trade-offs.
- Comprehend the force of selection, its age-related decline, and the implications for late-life deleterious genes.

## 14.4 Activity Overview

Suggested timings:

- 5 minutes: Introduce the exercise.
- 5-10 minutes: Students read through instructions and familiarize themselves with the Excel file.
- 25 minutes: Students complete the exercise, exploring different life history strategies.
- 5 minutes: Wrap up and discuss findings.

### Instructions for Facilitating

1. **Introduction:** Begin by explaining the concepts of life history trade-offs and the declining force of selection.
2. **Excel File Familiarization:** Guide students to open the provided Excel file, which contains a simplified life table for a fictional species.
3. **Exercise Execution:** Instruct students to manipulate reproductive and survival parameters in the Excel sheet to observe their effects on  $R_0$  and understand the balance between early reproduction and late-life survival. Focus on how changes early in life are more important than later in life.
4. **Discussion:** Facilitate a discussion on how changes in early and late-life traits impact fitness and the evolutionary implications of these trade-offs. e.g. in human's the declining force of selection is a good explanation for the existence age-related health problems.

### Questions & Model Answers

Students will answer the following questions:

1. **What is the force of selection, and why does it decline with age?**
  - The force of selection refers to the extent to which natural selection influences traits in a population. It declines with age because individuals have already passed on their genes by reproducing early in life, making late-life traits less subject to selection pressures.
2. **How do early-life and late-life trade-offs influence aging patterns in organisms?**

- Trade-offs between early reproduction and late-life survival can lead to increased reproductive success at younger ages but may result in higher mortality or decreased fitness in later life, influencing the aging patterns observed in different species.

### Teaching Tips

- **Excel Proficiency:** Ensure students are comfortable using Excel, particularly in manipulating data and interpreting graphs.
- **Conceptual Emphasis:** Highlight the real-world implications of life history trade-offs, such as how they can explain variations in aging and longevity across species and how they can explain age-related health problems in humans.

### Common Pitfalls

- **Overlooking the Declining Force of Selection:** Students may not fully grasp why late-life traits are less influenced by natural selection. Emphasize the reproductive timeline and its impact on selection pressures.
- **Misinterpreting  $R_0$ :** Clarify that  $R_0$  represents the net reproductive rate and is a key indicator of the fitness of a life history strategy.





## Part III

# Population Genetics and Evolution



## Chapter 15

# Hardy-Weinberg equilibrium

### 15.1 Introduction

This exercise introduces students to the Hardy-Weinberg Equilibrium (HWE), a fundamental principle in population genetics that describes the genetic variation in a population under ideal conditions. Students will engage with problems that involve calculating allele and genotype frequencies, understanding the assumptions of HWE, and exploring factors that can cause deviations from equilibrium. This exercise reinforces concepts such as genetic drift, mutation, migration, and selection, and their roles in evolutionary biology.

### 15.2 Key Concepts

- **Hardy-Weinberg Equilibrium (HWE):** A principle stating that allele and genotype frequencies in a population remain constant from generation to generation in the absence of evolutionary influences.
- **Allele Frequency:** The proportion of a specific allele among all allele copies in a population.
- **Genotype Frequency:** The proportion of a specific genotype among all individuals in a population.
- **Assumptions of HWE:** The conditions under which HWE holds true, including random mating, no mutations, large population size, no migration, and no natural selection.

### 15.3 Learning Outcomes

Students will achieve the following learning outcomes:

- Understand the concept of Hardy-Weinberg Equilibrium and its significance in population genetics.
- Calculate allele and genotype frequencies and apply the Hardy-Weinberg equation.
- Identify and explain factors that can cause deviations from Hardy-Weinberg Equilibrium.

## 15.4 Activity Overview

Suggested timings:

- 5 minutes: Introduce the exercise and review key concepts.
- 10 minutes: Students read through instructions and familiarize themselves with the problems.
- 20-30 minutes: Students work on the problems individually or in groups.
- 5 minutes: Wrap up and answer any questions the students have.

## 15.5 Instructions for Facilitating

1. **Introduction:** Begin by explaining the significance of Hardy-Weinberg Equilibrium in understanding genetic variation and evolution. Emphasise that it is a null model and often used to identify if interesting processes are happening in a population (i.e. if the population is not at HWE, perhaps selection is operating).
2. **Review Key Concepts:** Discuss allele and genotype frequencies, the Hardy-Weinberg equation, and the assumptions underlying the equilibrium.
3. **Problem-Solving:** Let students tackle the problems. Guide them through one of the provided problems to illustrate general methods.
4. **Discussion:** Facilitate a discussion on the results, focusing on how deviations from HWE can indicate evolutionary forces at work.

### Questions & Model Answers

Students will answer the following questions:

1. **What are the key assumptions of Hardy-Weinberg Equilibrium?**
  - The key assumptions are random mating, no mutations, large population size, no migration, and no natural selection.

2. **How can you calculate allele frequencies from genotype frequencies?**

- Allele frequencies can be calculated by adding the frequency of the homozygous genotype for that allele to half the frequency of the heterozygous genotype.

3. **What factors can cause a population to deviate from Hardy-Weinberg Equilibrium?**

- Factors include non-random mating, mutations, genetic drift (especially in small populations), gene flow (migration), and natural selection.

**Teaching Tips**

- **Clarify Assumptions:** Ensure students understand each assumption of HWE and why deviations from these assumptions can lead to evolutionary change.
- **Use Real-World Examples:** Provide examples of populations where HWE is applied, such as in predicting carrier frequencies for genetic diseases.
- **Encourage Critical Thinking:** Prompt students to think about how real populations might differ from the idealized conditions of HWE and what that means for genetic diversity.

**Common Pitfalls**

- **Confusing Allele and Genotype Frequencies:** Students may mix up these concepts. Reinforce the difference: allele frequencies refer to the proportion of a specific allele, while genotype frequencies refer to the proportion of a specific genotype.
- **Basic maths issues:** Students may not know how to get  $p$  from  $p^2$  etc. Guide them through the logic of solving variations of the HWE equation.
- **Overlooking Assumptions:** Students might forget that HWE relies on specific assumptions. Emphasize that real populations often violate these assumptions, leading to evolution.



# Chapter 16

## The Gene Pool Model

### 16.1 Introduction

This exercise introduces students to the concept of genetic drift and its impact on allele frequencies within a population. By utilizing the R programming language, students will simulate how allele frequencies change over generations, providing a practical understanding of evolutionary processes. This hands-on approach reinforces concepts such as genetic drift, population size effects, and the stochastic nature of allele frequency changes.

### 16.2 Key Concepts

- **Genetic Drift:** The random fluctuation of allele frequencies in a population due to chance events, which can lead to significant genetic changes over time, especially in small populations. Evolution can occur via this mechanism, even without natural selection operating.
- **Allele Frequency:** The proportion of a specific allele among all allele copies in a population.
- **Population Size:** The number of individuals in a population, which influences the magnitude of genetic drift; smaller populations experience more pronounced effects.
- **Stochastic Processes:** Random processes that introduce variability into genetic outcomes, highlighting the role of chance in evolution.

### 16.3 Learning Outcomes

Students will achieve the following learning outcomes:

- Understand the concept of genetic drift and its impact on allele frequencies.
- Comprehend how population size influences the magnitude of genetic drift.
- Develop proficiency in using R as a simulation tool.

## 16.4 Activity Overview

Suggested timings:

- 5 minutes: Introduce the exercise and review key concepts.
- 5 minutes: Students read through instructions and set up the initial gene pool in R.
- 20-30 minutes: Students run simulations to observe allele frequency changes over generations.
- 5 minutes: Wrap up and discuss findings.

## 16.5 Instructions for Facilitating

1. **Introduction:** Begin by explaining genetic drift and its significance in evolutionary biology.
2. **R Setup:** Ensure students have R and RStudio installed. Guide them through setting up the initial gene pool using the provided code snippets.
3. **Simulation Execution:** Instruct students to run simulations, varying population sizes to observe the effects on allele frequency changes.
4. **Discussion:** Facilitate a discussion on the results, focusing on how population size affects genetic drift and the implications for genetic diversity.

## 16.6 Questions & Model Answers

Students will answer the following questions:

1. **How does population size affect the magnitude of genetic drift?**
  - Smaller populations experience more significant fluctuations in allele frequencies due to genetic drift, while larger populations exhibit more stable allele frequencies over time.
2. **What is the impact of genetic drift on genetic diversity within a population?**



- Genetic drift can lead to a reduction in genetic diversity, especially in small populations, as certain alleles may become fixed or lost purely by chance.
3. **How does the initial allele frequency influence the outcome of genetic drift?**
- Alleles with higher initial frequencies are more likely to become fixed, while those with lower frequencies are more susceptible to loss due to genetic drift.

## 16.7 Teaching Tips

- **R Proficiency:** Ensure students are comfortable, or at least understand, the basic R operations used by the code. This includes setting up vectors, loops, and using functions like `sample()`.
- **Conceptual Emphasis:** Highlight the real-world implications of genetic drift, such as its role in the evolution of small isolated populations. Make the link to endangered species that typically have small populations and where drift is an important factor.
- **Visualization:** Encourage students to plot allele frequency changes over time to visualize the stochastic nature of genetic drift and how parameters like allele frequency and population size play a role in the outcome.

## 16.8 Common Pitfalls

- **Misunderstanding Stochasticity:** Students may expect deterministic outcomes. Emphasize that genetic drift is a random process, leading to different results in each simulation run.
- **Overlooking Population Size Effects:** Students might not fully grasp how population size influences genetic drift. Encourage them to compare results from simulations with varying population sizes to observe the differences.



## Chapter 17

# Neutral or Adaptive Evolution in Humans: What Drives Evolution of Our Traits?

### 17.1 Introduction

This exercise engages students in exploring the evolutionary mechanisms—natural selection and genetic drift—that shape human traits. By categorizing various human characteristics based on the strength of natural selection acting upon them in different environments, students will develop a nuanced understanding of how adaptive and neutral evolution influence our biology.

### 17.2 Key Concepts

- **Adaptive Evolution:** The process by which traits that enhance survival and reproduction become more common in a population due to natural selection.
- **Neutral Evolution:** The change in allele frequencies within a population due to random genetic drift, rather than selective pressures.
- **Natural Selection:** The differential survival and reproduction of individuals due to differences in phenotype, leading to adaptive evolution.
- **Genetic Drift:** Random fluctuations in allele frequencies within a population, which can lead to neutral evolution, especially in small populations.

### 17.3 Learning Outcomes

Students will achieve the following learning outcomes:

- Interpret the influence of selection pressure: Categorize traits based on the level of natural selection acting upon them and articulate reasons for their categorization.
- Distinguish between adaptive and neutral evolution: Differentiate traits evolving due to adaptive evolution from those likely evolving through genetic drift.
- Apply terminology accurately: Utilize correct scientific terminology to articulate viewpoints about trait evolution in different populations.
- Evaluate environmental factors: Assess how different environments (e.g., hunter-gatherer societies vs. modern industrialized countries) impact the strength of natural selection on various traits.
- Engage in collaborative argumentation: Collaboratively argue and defend their categorization of traits, providing evidence or logical reasoning for their views.
- Engage in critical thinking: Develop analytical skills in evaluating the role of selection and drift in trait evolution.

### 17.4 Activity Overview

Suggested timings:

- 5 minutes: Introduce the exercise and explain key concepts.
- 5 minutes: Students write the traits on Post-it notes.
- 10 minutes: In small groups, students discuss and categorize traits based on the strength of natural selection in hunter-gatherer societies.
- 15 minutes: Repeat the categorization for modern industrialized societies like Denmark.
- 10 minutes: Class discussion to compare categorizations and reflect on differences.

### 17.5 Instructions for Facilitating

1. **Introduction:** Begin by explaining the concepts of adaptive and neutral evolution, natural selection, and genetic drift.
2. **Trait Preparation:** Provide students with the list of traits and instruct them to write each trait on a separate Post-it note.

3. **Group Discussion:** Divide students into small groups and have them categorize the traits based on the strength of natural selection in hunter-gatherer societies.
4. **Modern Context:** Instruct groups to repeat the categorization for modern industrialized societies, noting any differences.
5. **Class Discussion:** Facilitate a discussion where groups share their categorizations and reasoning, highlighting how environmental contexts influence evolutionary pressures.

## 17.6 Questions & Model Answers

Students will answer the following questions:

1. **Were there any traits that were categorized differently between the two types of societies? Why?**

Here's how each trait might be categorized in hunter-gatherer societies compared to modern post-industrial societies:

**Metabolic Efficiency:** - *Hunter-Gatherer*: High metabolic efficiency would be advantageous for survival during food shortages, leading to strong positive selection. - *Modern Post-Industrial*: With abundant food supply and sedentary lifestyles, high metabolic efficiency can contribute to obesity and related health issues, so the selection pressure would be weaker or possibly negative.

**Face Symmetry:** - *Hunter-Gatherer*: Facial symmetry may have been associated with health and genetic quality, leading to some degree of selection related to mate choice. - *Modern Post-Industrial*: While facial symmetry still influences attractiveness, it has a lesser impact on survival and reproduction, so selection pressures are primarily social rather than environmental.

**Amount of Body Hair:** - *Hunter-Gatherer*: Body hair might have provided insulation in cold environments or protection from insects, leading to context-dependent selection pressures. - *Modern Post-Industrial*: Body hair has little impact on survival due to clothing and technology, and preferences are more influenced by cultural norms, resulting in weak or neutral selection.

**Running Speed:** - *Hunter-Gatherer*: High running speed would have been crucial for hunting and escaping predators, likely under strong positive selection. - *Modern Post-Industrial*: Running speed is far less important for daily survival, so selection pressure is minimal, except in specific contexts like sports.

**Singing Ability:** - *Hunter-Gatherer*: Singing ability may have played a role in social cohesion, communication, or mate attraction, contributing to weak but present selection pressure. - *Modern Post-Industrial*: While still valued in cultural and social settings, singing ability has little impact on overall fitness, so selection pressure is neutral or purely social.

**Height:** - *Hunter-Gatherer*: Height could have been selected for based on environmental factors, such as taller individuals being better suited for open environments or shorter individuals for dense forests. - *Modern Post-Industrial*: Height influences social and sexual attractiveness but is less tied to survival, so selection is primarily driven by mate preferences rather than environmental pressures.

**Intelligence:** - *Hunter-Gatherer*: Cognitive abilities like problem-solving and planning would have been highly advantageous for survival, leading to strong selection. - *Modern Post-Industrial*: Intelligence remains important for navigating complex social and technological environments, so selection pressure persists but is expressed differently, with an emphasis on academic and professional success.

**Resistance to Bubonic Plague:** - *Hunter-Gatherer*: This trait would not have been relevant, as the bubonic plague is a more recent selective pressure in human history. - *Modern Post-Industrial*: The selection pressure for resistance has diminished due to advancements in medicine and public health, also making it less significant than e.g. in the middle ages.

**Iris Structure:** - *Hunter-Gatherer*: The structure of the iris likely had little impact on fitness, resulting in neutral selection pressure. - *Modern Post-Industrial*: Iris structure remains under neutral selection, primarily serving as a trait for individual identification rather than affecting survival or reproduction.

**Sense of Smell:** - *Hunter-Gatherer*: A keen sense of smell would have been important for detecting food (and food quality), predators, or environmental hazards, leading to some positive selection. - *Modern Post-Industrial*: The sense of smell is less critical for daily survival, so selection pressure has likely weakened, except in contexts related to food and social interaction.

**Sperm Motility:** - *Hunter-Gatherer*: High sperm motility would have been under strong selection pressure to increase reproductive success. - *Modern Post-Industrial*: While reproductive fitness remains important, medical interventions and assisted reproductive technologies reduce the impact of natural selection on this trait.

**Resistance to Common Cold:** - *Hunter-Gatherer*: Resistance to common infections would have been advantageous, though the cold viruses we know today may not have been widespread. Lots of uncertainty here! - *Modern Post-Industrial*: While still beneficial, selection pressure is moderate due to medical treatments and the relatively low mortality associated with common colds.

**Muscle Strength:** - *Hunter-Gatherer*: Muscle strength would have been critical for hunting, gathering, and defense, making it subject to strong selection. - *Modern Post-Industrial*: Physical strength is less crucial for survival, so selection pressure is significantly weaker, except in specific contexts like athletic performance.

**Eyesight Acuity:** - *Hunter-Gatherer*: Sharp eyesight would have been essential for hunting and avoiding predators, leading to strong selection pressure. - *Modern Post-Industrial*: With the advent of corrective lenses and modern technology, selection pressure on eyesight acuity has lessened considerably, though good vision is still advantageous.

These comparisons illustrate how the selective pressures on traits can change dramatically with shifts in lifestyle, technology, and societal norms.

**2. Did the exercise challenge any preconceived notions you had about trait evolution?**

- Students may realize that not all traits are solely the result of adaptive evolution; some may be influenced by genetic drift, especially in different environmental contexts. It is important that they grasp the difference between genetic drift and natural selection. It may also be useful to talk about how population size (typically small in hunter gatherers) could increase the importance of drift.

**3. Can you think of any other traits that would be interesting to add to this exercise?**

- This is rather open and gives the students a chance to think about a range of human traits. Traits like lactose tolerance, alcohol metabolism, skin pigmentation, sweat gland density, and dietary adaptations could provide additional insights into how environmental pressures shape human evolution.

## 17.7 Teaching Tips

- **Clarify Concepts:** Ensure students understand the difference between adaptive and neutral evolution, and how natural selection and genetic drift operate.
- **Encourage Critical Thinking:** Prompt students to consider how environmental changes over time influence the evolutionary pressures on different traits.
- **Facilitate Discussion:** Encourage groups to share their reasoning and engage in constructive debate to deepen understanding. Ask them if they think modern humans are still evolving (they are, but natural selection is likely less important than genetic drift).

## 17.8 Common Pitfalls

- **Overemphasis on Natural Selection:** Students may assume all traits are a result of adaptive evolution. Emphasize the role of genetic drift and neutral evolution.
- **Assuming a simple driver for traits:** Students may mistakenly think that traits evolved for a single reason. Emphasize that many traits are shaped by multiple, interacting factors (e.g., both genetic and cultural influences on traits like height or intelligence).

- **Modern bias:** Students may project modern views and values onto hunter-gatherer societies, leading to misconceptions about what traits would have been advantageous. Encourage them to think critically about the survival challenges faced by ancient humans and how these differ from modern environments.
- **Environmental Context Overlooked:** Students might not consider how different environments affect selection pressures. Highlight the importance of context in evolutionary biology.



## Chapter 18

# Heritability from a linear regression

### 18.1 Introduction\*\*

This exercise enables students to estimate heritability by analyzing the relationship between parent and offspring trait values through linear regression. By plotting these values and fitting a linear model, students will learn to interpret the slope as an estimate of heritability. This process reinforces concepts in quantitative genetics and statistical analysis, providing practical skills in data manipulation and interpretation.

### 18.2 Key Concepts

- **Heritability:** A measure of how much of the variation in a trait is due to genetic factors. In this exercise, heritability is estimated by the slope of the regression line between parent and offspring trait values.
- **Linear Regression:** A statistical method used to model the relationship between two continuous variables. Here, it helps determine the strength and direction of the relationship between parent and offspring traits.

### 18.3 Learning Outcomes

Students will achieve the following learning outcomes:

- Learn to import and manipulate data in R or Excel for the purpose of heritability estimation.
- Develop a conceptual understanding of heritability and its importance in trait evolution.

- Gain practical skills in performing linear regression analysis to estimate heritability.

## 18.4 Activity Overview

Suggested timings:

- 5 minutes: Introduce the exercise
- 10 minutes: Students read through instructions
- 20-30 minutes: Students complete the exercise
- 5 minutes: Wrap up and discuss answers

## 18.5 Instructions for Facilitating

1. **Introduction:** Briefly explain the purpose of the exercise and its relevance to understanding genetic inheritance.
2. **Data Import:** Guide students in importing the provided datasets into R or Excel.
3. **Data Visualization:** Assist students in plotting parent trait values on the x-axis and offspring trait values on the y-axis.
4. **Linear Regression:** Help students fit a linear regression model to the data and interpret the slope as the heritability estimate.
5. **Comparative Analysis:** Encourage students to repeat the analysis with the second dataset and compare results.
6. **Discussion:** Facilitate a discussion on the implications of the findings and the assumptions underlying the methods used.

## 18.6 Questions & Model Answers

Students will answer the following questions:

1. **What does the heritability tell us about the amount of variation explained by genetic factors?**
  - Heritability indicates the proportion of total variation in a trait that is attributable to genetic differences among individuals.
2. **What other factors might explain the remaining variation?**

- Environmental influences, measurement errors, and gene-environment interactions can contribute to the remaining variation.
3. **How would the heritability estimate change if you used a different trait (e.g., beak length instead of wing length)?**
    - The heritability estimate may differ because different traits can have varying degrees of genetic and environmental influences.
  4. **What does the heritability tell us about how fast a trait might change due to selection?**
    - Higher heritability suggests that a trait can respond more rapidly to selection pressures, leading to faster evolutionary change. This is related to the Breeders Equation ( $R = h^2 \times S$ )
  5. **You can calculate  $V_P$  from the phenotype values. Use this information to calculate  $V_A$  based on the equation  $V_A = h^2 \times V_P$ .**
    - By calculating the total phenotypic variance ( $V_P$ ) and knowing the heritability ( $h^2$ ), students can estimate the additive genetic variance ( $V_A$ ).
  6. **What does the heritability tell us this time?**
    - Comparing heritability estimates between datasets can reveal differences in genetic and environmental contributions to trait variation across populations.
  7. **Can you identify any environmental factors that might explain the difference?**
    - Differences in habitat, diet, climate, or other environmental conditions between populations could account for variations in heritability estimates.
  8. **Can you think of any real-world applications where understanding heritability would be important?**
    - Applications include selective breeding programs, conservation genetics, and understanding the genetic basis of diseases in humans.

## 18.7 Teaching Tips

- **Data Handling:** Ensure students are comfortable with importing and manipulating datasets in R or Excel. Provide guidance as needed.
- **Statistical Concepts:** Clarify the interpretation of the regression slope as an estimate of heritability and discuss the assumptions of linear regression.
- **Assumptions Discussion:** Emphasize the importance of understanding the assumptions underlying heritability estimation, such as additive genetic effects and the absence of shared environmental influences.

## 18.8 Common Pitfalls

- **Misinterpreting Heritability:** Students may confuse heritability with the proportion of a trait caused by genes in an individual. Clarify that heritability refers to variation within a population.
- **Overlooking Assumptions:** Failing to consider the assumptions of linear regression and heritability estimation can lead to incorrect conclusions. Encourage critical evaluation of these assumptions.
- **Data Entry Errors:** Mistakes in data import or manipulation can affect results. Advise students to double-check their data handling processes. In particular, importing data into R is a common headache.

## Part IV

# Interactions Between Species and Community Structure



## Chapter 19

# Lotka-Volterra competition

### 19.1 Introduction

This exercise, which should be run over TWO sessions, involves programming the Lotka-Volterra competition model in a spreadsheet (e.g., Excel) to simulate interspecific competition between two species. Students will manually create a spreadsheet model from scratch, entering formulae and parameters to investigate the conditions under which species coexist or exclude each other. This hands-on activity enhances understanding of mathematical modeling in ecology, emphasising the relationship between competition coefficients, carrying capacities, and species interactions.

### 19.2 Key Concepts

- **Lotka-Volterra Competition Model:** This model uses differential equations to describe the population dynamics of two competing species. The equations incorporate competition coefficients that quantify the impact of each species on the other's population growth.
- **Interspecific Competition:** Describes the interaction between species that compete for the same resources, affecting population sizes and influencing species coexistence.
- **Competitive Exclusion Principle:** A key ecological principle derived from the model, which states that two species cannot coexist indefinitely if they compete for the same limited resources unless they differ significantly in their use of these resources.
- **Zero Net Growth Isoclines (ZNGIs):** Graphical representations where the population growth rate of a species is zero. These lines are used to determine conditions for species coexistence or exclusion.

### 19.3 Learning Outcomes

Students will achieve the following learning outcomes:

- Experience programming a population biology model (Lotka-Volterra Competition model) in a spreadsheet and using it to explore population dynamics.
- Understand and explain the competitive exclusion principle and its ecological significance.
- Analyse the effects of different competition coefficients, carrying capacities, and initial population sizes on species interactions.
- Visualise and interpret phase diagrams and population trajectories to identify conditions for species coexistence or competitive exclusion.

### 19.4 Activity Overview

Suggested timings:

- 5 minutes: Introduce the exercise and explain the objectives.
- 10 minutes: Students review the provided detailed instructions on creating the spreadsheet.
- 20-30 minutes: Students set up and complete the spreadsheet, entering data, formulae, and creating graphs.
- 5 minutes: Wrap up with a discussion about their findings and the ecological implications of the model.

#### Instructions for Facilitating

1. **Introduction:** Start by discussing the importance of understanding species interactions in ecology and the role of mathematical models like Lotka-Volterra in predicting outcomes of competition.
2. **Spreadsheet Setup:**
  - Guide students to download the instructions PDF for setting up their spreadsheet.
  - Explain that they will build the model step-by-step, entering population parameters, setting up a time series, and programming the Lotka-Volterra equations.
  - Clarify that they will be able to modify model parameters to explore their impact on the population processes.
3. **Entering Formulae:**
  - Assist students in using absolute and relative cell references as specified in the instructions to avoid errors.



- Explain the equations and ensure students understand how parameters like carrying capacity ( $K$ ) and competition coefficients ( $\alpha_{12}$  and  $\alpha_{21}$ ) are used.

#### 4. Graphing:

- Guide students in creating two types of graphs: (1) Population sizes over time, and (2) a phase diagram showing ZNGIs and population trajectories.
- Emphasise proper labeling of axes and data points to aid in interpretation.

5. **Analysis and Interpretation:** Facilitate discussions on how changing model parameters (e.g., competition coefficients) affects the outcomes, leading to coexistence or competitive exclusion. Use the PowerPoint or mirror your screen to the projector to show examples using the completed spreadsheet.

6. **Wrap-Up:** Discuss real-world examples of interspecific competition and how such models are used in ecological research and conservation.

### Questions & Model Answers

Students will answer the following questions:

1. **What parameter values will cause species 1 to exclude species 2 from the habitat? What do these values mean ecologically?**
  - High competition coefficient ( $\alpha_{12}$ ) values indicate strong negative impacts from species 2 on species 1, leading to exclusion. These values represent a scenario where species 1 is outcompeted for resources.
2. **What parameter values will reverse this outcome?**
  - Lowering  $\alpha_{12}$  or increasing  $\alpha_{21}$  may favor species 2 over species 1, reversing the exclusion outcome. Ecologically, this represents a shift where species 2 becomes the stronger competitor.
3. **Under what conditions can the two species coexist stably?**
  - Coexistence is possible when the competition coefficients are such that each species limits its own population growth more than it limits the other's. This requires  $\alpha_{12} < 1$  and  $\alpha_{21} < 1$ , meaning intraspecific competition is stronger than interspecific competition.
4. **Are there parameter values that make the outcome depend on initial population sizes?**
  - Yes, in cases where the system has multiple stable equilibria, initial conditions can determine which equilibrium the system approaches. Ecologically, this suggests that historical population sizes can influence competitive outcomes.

### Teaching Tips

- **Formula Entry:** Remind students to double-check formulae for errors and use proper cell references. Provide assistance as needed to ensure accuracy.
- **Graph Interpretation:** Spend time discussing how to interpret ZNGIs and the significance of phase diagrams in understanding population dynamics.
- **Parameter Sensitivity:** Encourage students to experiment with different values to observe how sensitive the model is to changes in competition coefficients and carrying capacities.

### Common Pitfalls

- **Formula Errors:** Students may struggle with using correct formulae and cell references. Encourage careful entry and checking of formulae.
- **Confusing Parameters:** Clarify the distinction between intraspecific and interspecific competition to avoid misunderstandings.
- **Misinterpreting Graphs:** Ensure students understand how to read and interpret the graphs, especially the phase diagrams, and what they reveal about species interactions.

## Chapter 20

# Lotka-Volterra predator-prey dynamics

### 20.1 Introduction

This exercise guides students through building a spreadsheet model from scratch to simulate the Lotka-Volterra predator-prey dynamics. Students will explore how predator and prey populations interact, modify the model to include prey refuges and carrying capacities, and analyse the effects of various parameters on population stability. The activity introduces foundational concepts in population ecology and demonstrates how mathematical models can capture complex biological interactions.

### 20.2 Key Concepts

- **Lotka-Volterra Predator-Prey Model:** A mathematical model using differential equations to describe the oscillatory dynamics between predator and prey populations. The model predicts population cycles resulting from the interactions between prey availability and predator abundance.
- **Equilibrium Points:** States at which predator and prey populations remain constant. Understanding these points provides insights into the conditions under which both populations can coexist or one species may face extinction.
- **Model Modifications:** The exercise includes modifications to account for factors like prey refuges and carrying capacities, adding ecological realism to the model.

### 20.3 Learning Outcomes

Students will achieve the following learning outcomes:

- Practice constructing spreadsheets model to simulate biological processes and using them to boost their understanding.
- Understanding of predator-prey dynamics described by the Lotka-Volterra equations.
- Understand and explain how model parameters (e.g., prey growth rate, predator attack rate) influence population stability and oscillations.
- Understanding how models can be modified to include additional ecological features such as prey refuges and carrying capacities.
- Interpret the results and evaluate the model's applicability to real-world predator-prey interactions.

## 20.4 Activity Overview

Suggested timings:

- 5 minutes: Introduce the exercise and discuss the ecological significance of predator-prey dynamics.
- 10 minutes: Students review the provided PDF instructions for creating the spreadsheet.
- 20-30 minutes: Students set up the spreadsheet, input formulas, and generate graphs.
- 5 minutes: Wrap up with a discussion on model results and implications.

## 20.5 Instructions for Facilitating

1. **Introduction:** Explain the purpose of modelling predator-prey interactions and the significance of understanding these dynamics in ecology. Highlight how the Lotka-Volterra model forms the basis of more complex ecological models.
2. **Spreadsheet Setup:**
  - Direct students to the detailed PDF instructions for setting up their spreadsheet.
  - Explain the process of creating a linear time series, entering initial values for prey and predator populations, and defining parameters such as prey growth rate ( $R$ ), predator attack rate ( $a$ ), and predator starvation rate ( $q$ ).
  - Ensure students understand how the model uses these parameters to simulate population changes over discrete time intervals.
3. **Entering Formulas:**
  - Guide students in inputting the equations for prey and predator population changes, using the Lotka-Volterra equations (though this should be clear from the PDF instructions):
    - Prey population:  $V_{t+1} = V_t + R \times V_t - a \times C_t \times V_t$

– Predator population:  $C_{t+1} = C_t + f \times a \times V_t \times C_t - q \times C_t$

- Use absolute and relative cell references where necessary and explain the importance of using the IF function to prevent negative population sizes.

#### 4. Graphing:

- Help students create graphs to visualise predator and prey populations over time, using separate y-axes for clarity.
- Guide them in plotting phase diagrams (prey population on the x-axis and predator population on the y-axis) to observe the cyclical nature of the interactions.

#### 5. Model Modifications:

- Instruct students on how to modify the model to include prey refuges, adjusting the prey equation to ensure a minimum number of prey individuals always survive.
- Later, guide them through adding a carrying capacity for the prey population and discuss how this changes the model dynamics.

#### 6. Analysis and Discussion:

- Facilitate discussions on the ecological implications of the model. Ask students to experiment with different parameter values and observe how these changes affect population stability and cycles.
- Encourage critical thinking about the model's assumptions and limitations, such as the exclusion of environmental variability or alternative prey-predator behaviours.

## 20.6 Questions & Model Answers

### 1. Does a larger prey population growth rate (R) increase or decrease the stability of the predator-prey interaction?

- A higher prey growth rate generally leads to more pronounced population cycles, which may destabilise the interaction.

### 2. What happens if the predators starve more quickly? Less quickly?

- Faster predator starvation reduces predator numbers, potentially allowing the prey population to grow unchecked. Slower starvation increases predator pressure on the prey population.

### 3. What happens if the predator is more efficient at converting prey into offspring? Less efficient?

- Higher efficiency leads to faster predator population growth, intensifying predation pressure. Lower efficiency reduces predator growth, potentially stabilising the system.

4. **What happens if the predator is better at finding prey? Worse?**

- A higher attack rate increases predation pressure, which may drive the prey population lower and lead to predator-prey instability. A lower attack rate reduces predation, allowing the prey population to increase.

5. **Is the behaviour of the model sensitive to starting populations?**

- Yes, initial conditions can influence the trajectory of population cycles, especially when populations start near equilibrium points.

6. **What factors not included in the model may explain differences between predictions and real-world observations?**

- Real ecosystems include additional factors such as environmental variability, multiple prey and predator species, and resource limitations that the simple model does not account for.

## 20.7 Teaching Tips

- **Formula Accuracy:** Emphasise the importance of correctly entering formulas and using absolute references. Double-check formulas to ensure the model runs as expected.
- **Graph Interpretation:** Spend time explaining how to interpret the graphs, especially the significance of phase diagrams in understanding population cycles.
- **Model Assumptions:** Discuss the simplifying assumptions of the model and how they may limit its application to real-world scenarios.

## 20.8 Common Pitfalls

- **Incorrect Formulae:** Students may input formulas incorrectly, leading to unrealistic results. Encourage careful formula entry and cross-verification.
- **Language issues:** Excel commands vary between English and Danish localisations (e.g. HVIS or IF). Check the students are using the right ones.
- **Misunderstanding Parameters:** Clarify the roles of parameters like attack rate and conversion efficiency to avoid confusion.
- **Understanding Graphs:** Ensure students can understand what the graphs are showing.

## Part V

# Animal behaviour, altruism and sexual selection





## Chapter 21

# Game theory: Hawks and doves

Coming soon. . .



## Part VI

# Appendix - extras



## Chapter 22

# Exponential growth in detail

Coming soon. . .



## Chapter 23

# The legend of Ambalapuzha

Coming soon. . .





## Chapter 24

# From population biology to fitness

Coming soon. . .