

BIOL 3295: Population and Evolutionary
Ecology, Winter 2023

Amy Hurford

2023-02-16

Contents

Chapter 1

Syllabus

1.1 Instructor Information

Instructor: Dr. Amy Hurford

Office: CSF 4338

Email: ahurford@mun.ca

I will try to reply to emails within 24 hours (excluding evenings, weekends and holidays). Office hours: Tuesday 1-2pm; Thursday 1-2pm

1.2 Course Information

TR 12.00-12.50pm

F 1-1.50pm

Classroom: SN3060 (unless stated otherwise on the schedule)

All Course Announcements will be made on BrightSpace. Should lectures be remote a WebEx link will be provided on BrightSpace.

Course description:

Population and Evolutionary Ecology is an introduction to the theory and principles of evolutionary ecology and population dynamics. Pre-requisites: BIOL 2600; at least one of BIOL 2010, 2122 or 2210.

Course format:

The course consists of lectures, 4 data analysis assignments, 2 exams and a final exam.

Course expectations:

Please attend lectures and respect the learning environment of other students. If you have COVID-19 please follow university and provincial public health

guidelines.

Learning goals:

The course content emphasizes a deeper understanding of fewer concepts. You have seen much of the course material in pre-requisite courses. In this course, I will revisit the models, clarify the assumptions and when they are appropriate, and we will fit the models to data to estimate parameters. By the end of the course, I hope that if you were given population data, that you would know the key quantities that you might estimate, and could complete the analysis.

Required Text and Resources:

The course materials are online at <https://ahurford.github.io/biol-3295-winter-2023/index.html>.

Most readings are assigned from two textbooks that are available electronically from the library:

- Vandermeer, J.H., Goldberg, D.E., 2013. Population Ecology: First Principles (Second Edition). Princeton University Press, Princeton, United States. [Link](#)
- Otto, Sarah P., and Troy Day. 2007. A Biologist's Guide to Mathematical Modeling in Ecology and Evolution, Princeton University Press. [Link](#)

If you wish to use your own computer for assignments you should install **R** and **RStudio** (see also [here](#)).

1.3 Method of Evaluation

- 4 Assignments - 20%
- 2 Exams - 40%
- Final Exam - 40%

Late assignments and missed exams, and final exams will be accommodated as described by University Regulation 6.7.3 and 6.7.5 (see <https://www.mun.ca/regoff/calendar/sectionNo=REGS-0474> for Regulations). Please discuss missed assignments and exams with me. To accommodate the absence an assignment may be modified or exempted and re-weighted in the grading scheme.

1.4 Additional Policies

1.4.1 Accommodation of students with disabilities

Memorial University of Newfoundland is committed to supporting inclusive education based on the principles of equity, accessibility and collaboration. Accommodations are provided within the scope of the University Policies for the Accommodations for Students with Disabilities see www.mun.ca/policy/site/policy.php?id=239. Students who may need an academic accommodation are asked to initiate the request with the Glenn Roy Blundon Centre at the earliest opportunity (see www.mun.ca/blundon for more information).

1.4.2 Academic misconduct

Students are expected to adhere to those principles, which constitute proper academic conduct. A student has the responsibility to know which actions, as described under Academic Offences in the University Regulations, could be construed as dishonest or improper. Students found guilty of an academic offence may be subject to a number of penalties commensurate with the offence including reprimand, reduction of grade, probation, suspension or expulsion from the University. For more information regarding this policy, students should refer to University Regulation 6.12.

1.4.3 Equity and Diversity

A safe learning environment will be provided for all students regardless of race, colour, nationality, ethnic origin, social origin, religious creed, religion, age, disability, disfigurement, sex (including pregnancy), sexual orientation, gender identity, gender expression, marital status, family status, source of income or political opinion.

You should not photograph or record myself, teaching assistants, or other students in the class without first obtaining permission. Accommodation will be made for students with special needs.

The sound should be turned off on phones and computers during class.

1.5 Additional Supports

Resources for additional support can be found at:

- www.mun.ca/currentstudents/student/
- <https://munsu.ca/resource-centres/>

Chapter 2

Schedule

All lectures are in SN 3060 unless otherwise stated

This is a tentative revision of the schedule following the MUNFA strike.

This revised version of the schedule will be confirmed after discussion with the class.

- Thurs Jan 5: Introduction
- Fri Jan 6: Population biology with discrete and continuous variables
- Tues Jan 10: —
- Thurs Jan 12: **CSF 2218** Introduction to Rmarkdown and tidyverse **Assignment 1 is assigned**
- Fri Jan 13: Geometric growth
- Tues Jan 17: Exponential growth
- Thurs Jan 19: **CSF 2218** Numerical solutions and graphing population data **Assignment 2 is assigned**
- Fri Jan 20: Exponential growth
- Tues Jan 24: Density dependence and logistic growth
- Thurs Jan 26: Density dependence and logistic growth **Assignments 1 & 2 are due**
- Fri Jan 27: Discrete time models with density dependence

MUNFA STRIKE

- Fri Feb 16: Age-structured models
- Tues Feb 17: **CSF 2218** Numerical analysis of stage-structured models **Assignment 3 is assigned**

WINTER BREAK

- Tues Feb 28: Stage-structured models
- Thurs Mar 2: Stage-structured models

- Fri Mar 3: Density dependence in stage-structured models **Assignment 3 is due**
- Tues Mar 7: Metapopulation models
- Thurs Mar 9: Continuous space models
- Fri Mar 10: Disease dynamics
- Tues Mar 14: The net reproduction number
- Thurs Mar 16: **EXAM I** (All material covered to date)
- Fri Mar 17: What is evolutionary ecology?
- Tues Mar 21: Haploid selection model
- Thur Mar 23: Selection coefficients for COVID-19 variants
- Fri Mar 24: **CSF 2218** Estimating selection coefficients **Assignment 4 is assigned**
- Tues Mar 28: The evolutionary ecology of pathogens
- Thurs Mar 30: The evolutionary ecology of COVID-19
- Fri Mar 31: The evolutionary ecology of hosts **Assignment 4 is due**
- Tues Apr 3: The evolution of reproductive effort in plants
- Thurs Apr 5: Evolutionarily stable and convergent stable strategies
- Fri Apr 6: Review

TBD **FINAL EXAM** (all course material)

Chapter 3

Jan 5: Introduction

- Survey of student computer preferences

3.1 Some questions

- What is a population?
- What are some definitions of a population that are given in textbooks?
- In research studies, how are populations discussed in the *Discussion*?
- How are individuals that comprise the sample selected in the *Methods* of a research study?
- List some potential differences between how populations are defined and discussed and the research methods?
- Why does the definition of a population matter?

3.2 References

Vandermeer, J.H., Goldberg, D.E., 2013. Population Ecology: First Principles (Second Edition). Princeton University Press, Princeton, United States. [Link](#)

The Princeton Guide to Ecology, edited by Simon A. Levin, et al., Princeton University Press, 2009. ProQuest Ebook Central, [Link](#)

Sacchi, R., Gentili, A., Razzetti, E., Barbieri, F., 2002. Effects of building features on density and flock distribution of feral pigeons *Columba livia* var. *domestica* in an urban environment. Can. J. Zool. 80, 48-54. [Link](#)

Chapter 4

Jan 6: Discrete and continuous variables

Reading: Otto, Sarah P., and Troy Day. 2007. A Biologist's Guide to Mathematical Modeling in Ecology and Evolution, Princeton University Press. Link **pages 33-38 in Section 2.3**

- Parameters versus variables
- Fitted versus independently estimated parameters

Chapter 5

Jan 12: ASSIGNMENT

Rmarkdown and tidyverse

(Dates changed owing to the university closure for a snow day)

ASSIGNMENT 1 due Jan 26.

PART I is to reproduce a figure and the figure caption of a plot in Vandermeer and Goldberg 2013 or another textbook or a published paper in Rmarkdown and as an output file: .html, .pdf, or .docx. Please choose a figure to reproduce in the area of Population Biology or Evolutionary Ecology.

You can simplify a complex figure if necessary. Your figure should be made in `ggplot()` and have:

- the title (if there is one),
- axes labels,
- points or lines or both,
- approximately the same data as the original figure,
- the correct axes limits.

The objective is for you to learn how to use Rmarkdown to make a synthetic write-up that includes code, a figure and text. Your completed output should have:

1. A brief text description of where I can find the figure you reproduced.
2. Code that makes a figure that is suppressed in the output file.
3. The reproduced figure (or simplified figure).
4. The actual figure

You are to hand-in the .Rmd file and an output file (.html, .pdf, or .docx)

Here, is an example of what a completed PART 1 looks like (as an .html output).

The graph is Figure 3.1 from Population Ecology: First Principles - Second Edition (Vandermeer and Goldberg) on p67.



FIGURE 3.1 Difference in per capita egg production between the O lines and B lines from Rose and Charlesworth's (1981) experiment.



FIGURE 3.1. Difference in per capita egg production between the O lines and B lines from Rose and Charlesworth's (1981) experiment.

Instructions to complete PART I are here.

PART II of this assignment is to clean up messy data. As a biologist, much of my coding work involves getting data into the right format to use in functions, this might be a plot function like `ggplot()`, which you used in PART I, or a statistical function like `lm()`, which will perform a regression, t-test, or analysis of variance. The objective of PART II is to practice cleaning messy data into a useable format.

1. You are to clean the messy data from here enough so you can make a plot using `ggplot()`. Some helpful instructions for how to do this are here. The code that you write **must use the `select()`, `mutate()`, and `ggplot()` functions**. The graph that you make must be different than the example given in the instructions - for example, you might plot the same variables but for Plot 2.

(perhaps this sounds easy - this data is pretty messy - I found it quite hard!)

TO HAND IN

1. Hand in an `.Rmd` file and an output file (`.html`, `.docx`, or `.pdf`) with the solutions to both PART I and PART II of this assignment. Each part is 10 marks for a total of 20 marks.

Chapter 6

Jan 13: Geometric growth

6.1 Reading

Vandermeer, J.H., Goldberg, D.E., 2013. Population Ecology: First Principles (Second Edition). Princeton University Press, Princeton, United States. **p1-3**. [Link](#)

- Von Foerster human population become effectively infinite on Nov 13 2026
- Lilly pads replicate once per week. If it take a year for 1/2 a pond to be covered, when will it be completely covered? See also the wheat and chessboard
- $N_{t+1} = \lambda N_t$ equation 3 in Vandermeer and Goldberg. For what values of λ will the population size, N_t , grow?
- $N_t = N_0 \lambda^t$ is equation 4 in Vandermeer and Goldberg (but written more generally). With $N_0 > 0$ sketch a graph of N_t for different values of λ . If $N_0 = 0$, sketch a graph of N_t .
- If $N_0 = 1.1$ individuals per km^2 , $\lambda = 2$, what is the population size at time $t = 10$?
- Consider population growth of pheasants on Protection Island. If we were to apply the geometric growth model to the pheasant population, what are some assumptions? How might this affect our parameterization (i.e., our estimate of λ) for the pheasant population?
- How can we understand what λ is in a population that has births and deaths?

Chapter 7

Jan 17: Geometric growth

7.1 Reading

Download the .pdf of the MSc thesis below and read the Abstract (the first two pages prior to the title page). Pay specific attention to the number of pheasants at different points in time, these might be N_{t+1} and N_t in the geometric growth model formula; and the number of births and deaths that occur, these may help you estimate λ in the geometric growth formula. Pay attention to the length of time that births and deaths are reported over, and what time of the year the population size is reported.

Newcomb, HR. 1940. Ring-necked pheasant studies on Protection Island in the Strait of Juan de Fuca, Washington. MS thesis. Oregon State University. [two pages prior to the title page]

Noteably,

- a. Pheasant chicks are born during the summer.
- b. In May 1937, 10 pheasants were introduced to the island. Before the next breeding season there were 35.
- c. November 10, 1938 a census estimated 110 pheasants.
- d. October 13, 1939 a census estimated 400 pheasants.
- e. Between the 1938 and 1939 censuses, Newcomb observed that 17 adult birds died.
- f. During the 1938 nesting season there were 5.86 eggs/nest. 83.57% of eggs hatched.
- g. During the 1939 nesting season there were 8.73 eggs/nest. 64.58% hatched.
- h. During the 1939 nesting season: Average number of chicks per clutch was 6.93.¹
- i. You can assume the sex ratio is 50:50 male to female. Pheasants are a sexually reproducing species.

¹ Note that g. and h. appear to be contradictory.

7.2 Questions

This approach is called independent parameter estimation because we will estimate the birth and mortality rates independently of the population size data for different years.

1. $b > 0$ is the per capita number of births each year. The estimation of b for a geometric growth model is more subtle. First, b is estimated as the number of births (occurring between t and $t + 1$), divided by the number of individuals that could have given birth, N_t . You might average this value across multiple years if sufficient data are available. Furthermore, to correctly project the future population size, we should consider what we have assumed about survival of the pheasant chicks, given the time step of our model. **Given a.-i. estimate b . Write down any assumptions you have made.**
2. Is the probability that pheasants survive from one time step to the next. Estimate d .
3. What is the value of λ given your estimate of b and d from previous questions? Is this population is expected to grow over time?
4. Lets assume that the pheasant population on Protection Island grows geometrically (i.e. exponentially but for a discrete time model) where the geometric growth rate, λ , is the value that you estimated in question 3. Let $N_0 = 10$ and let t be the number of years since May 1937. Recall that when a population grows geometrically,

$$N_t = N_0 \lambda^t$$

Use the formula and your answer to 3. to predict the number of pheasants in May 1938, May 1939, May 1940, and May 1950.

Chapter 8

Jan 19: ASSIGNMENT

Estimating the geometric growth rate

ASSIGNMENT 2 due Jan 26.

You are to write an Rmarkdown report that estimates the geometric growth rate, λ , for the Protection Island pheasant population. Your report needs to consider two methods for estimating the geometric growth rate: fitting; and estimation from independent data.

The code you will need to complete this assignment is below. You may copy and paste this code into your Rmarkdown report. Sometimes you will need to change the values.

The requirements of the report follow the code.

8.1 Code

8.1.1 Loading and plotting the data

Load the data. I copied the data on to a website, so it can be loaded with the command below. Click here to view the code on the website.

```
data = read.csv("https://raw.githubusercontent.com/ahurford/biol-4605-data/main/data/protection-i
```

Let's plot the data. We select only columns 1 and 2 of the data because column 3 contains comments. We plot **year** on the horizontal (x-) axis and **size** on the (y-) vertical axis.

```
require(ggplot2)
protection.island <- data[,1:2]

g1 = ggplot(data = protection.island, aes(x = year, y = size)) +
  geom_point() +
  xlab("year")+
  ylab("population size")+
  ggtitle("Protection Island")
g1
```



8.1.2 Function for geometric growth

Below is the definition of a geometric growth function with time, t , specifically defined for the number of years of Protection Island pheasant data, and the initial population size, N_0 , defined specifically for the Protection Island data. You need to give this function in your code *before* you call the function.

```
geo.pred <- function(lambda){
  t = protection.island$year - protection.island$year[1]
  N0 = protection.island$size[1]
  size = N0*lambda^t
  pred = data.frame(year = protection.island$year, size = size)
}
```

The function is called by running `geo.pred(lambda)` in the console, where you enter a specific value for `lambda`.

After you have run the code (i.e. in the Console) that defines the `geo.pred(lambda)` function (above), try `lambda = 3` as:

```
result = geo.pred(3)
result
```

```
##   year size
## 1 1936   10
## 2 1937   30
## 3 1938   90
## 4 1939  270
```

Question 1 The `geo.pred()` function works by running the lines of code inside the `geo.pred()` function definition for the value of `lambda` that you supply (inside the parentheses in the function call). In the function definition, what are the lines of code that are pasted below doing? (Hint: What is the data frame `protection.island`? Note that `data[1]` selects the first value of a list of values and the `$` selects a particular column of a data frame).

```
t = protection.island$year - protection.island$year[1]
N0 = protection.island$size[1]
```

8.1.3 Fitting lambda

We have defined a function that will predict the population size of pheasants on Protection Island for different user supplied values of `lambda`. But what value of `lambda` is most likely given the data?

To answer this question we will use a statistical method known as maximum likelihood.

Our first step is to define a function that quantifies the fit of a given `lambda` value. This function assumes that deviations of the recorded data from the model-predicted values follow a Poisson distribution:

```
geofit <- function(lambda){
  pred=geo.pred(lambda=lambda)
  Ypred = pred$size
  -sum(dpois(protection.island$size, Ypred, log=T))
}
```

After running the `geo.fit(lambda)` function (in the Console), let's try to use the function and get some values of the negative log likelihood (i.e. the fit):

```
geofit(3)
```

```
## [1] 41.64846
```

```
geofit(1)
```

```
## [1] 1280.129
```

This result tells us that given the data `lambda = 3` is much more likely than `lambda = 1` because the negative log likelihood value (41.65) is much smaller.

But what value of `lambda` is most likelihood given the data? i.e., for what value of `lambda` is the negative log likelihood minimized? To answer this question we need to call a function that will perform an optimization. This requires the `mle2` function from the `bbmle` package, and you will need to install this package prior to using this function.

```
library(bbmle)

## Loading required package: stats4
fit.geo <- mle2(geofit, start=list(lambda=3))
summary(fit.geo)

## Maximum likelihood estimation
##
## Call:
## mle2(minuslogl = geofit, start = list(lambda = 3))
##
## Coefficients:
##           Estimate Std. Error z value    Pr(z)
## lambda 3.408974    0.053472  63.752 < 2.2e-16 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## -2 log L: 24.32396
confint(fit.geo)

##      2.5 %   97.5 %
## 3.304256 3.513845
```

The output above tells us that the maximum likelihood estimate of `lambda` is 3.41 and that the 95% confidence interval is [3.30, 3.51].

8.1.4 Plotting the fit

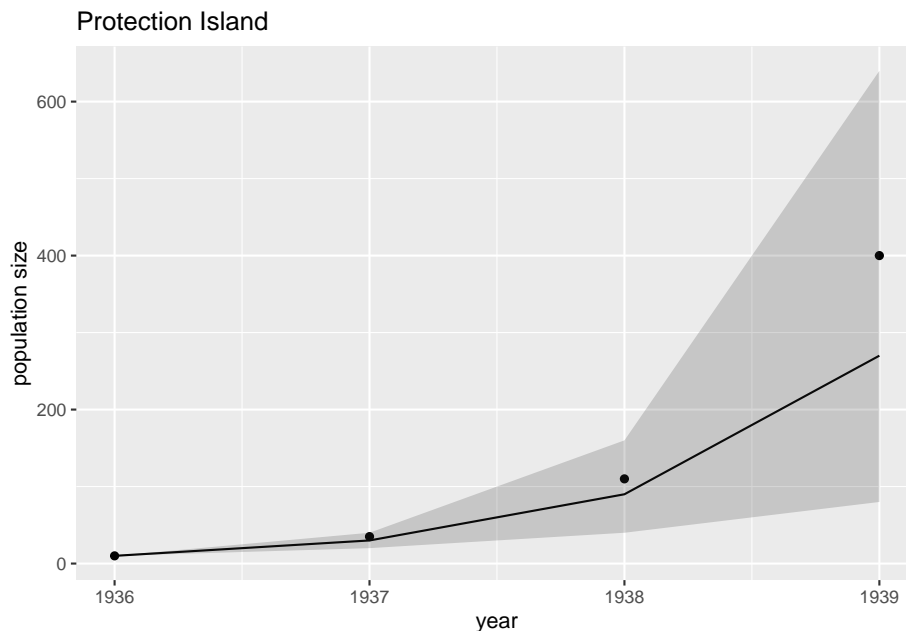
Finally, we would like to use our estimate values of `lambda` in the geometric growth function and compare the fitted values with the observed data.

In the code below, `lambda = 3` is the estimated `lambda` value, and the 95% confidence interval is [2,4]. To use this code for your assignment you will need to substitute different values.

```
fit.predictions = geo.pred(3)$size
lower.fit = geo.pred(2)$size
upper.fit = geo.pred(4)$size
```

We had already made a plot of the data and we named our graph `g1`. We can now add some more layers to the graph as shown below. Note that the line is the value of `fit.predictions` as defined above (i.e., set =3 as an example), and the shaded ribbon spans from `lower.fit` to `upper.fit` (i.e., set to 1 and 2 as an example).

```
g2 = g1 +
  geom_line(aes(y=fit.predictions)) +
  geom_ribbon(aes(ymin = lower.fit, ymax = upper.fit), alpha = .2)
g2
```



8.2 To hand in

1. Answer Question 1 which appears in bold in the *Function for geometric growth* section.
2. Write an Rmarkdown report that estimates λ (i.e. `lambda`) in the geometric growth rate function using maximum likelihood fitting. You must include a graph that shows:
 - The data (shown as dots);
 - The predicted values for the maximum likelihood estimate of `lambda` (shown as a line);
 - The predicted values for the 95% confidence interval for the estimate of `lambda` (shown as a shaded region);

You must include a figure caption that explains the main point of your graph,

and what the symbols are.

Your Rmarkdown file must contain a sequence of R commands that produces the graph.

3. Estimate λ from data independent of the time series describing the population size of pheasants on Protection Island. This means that you cannot use more than one value of the population size to estimate one value of a quantity (you should be using the population size in a given year to calculate per capita rates by dividing only). Your goal is to keep your parameter estimation method independent from the time series of pheasant population size so that you can *validate* the assumptions of your geometric growth model. In your Rmarkdown report you should:
 - Derive a formula for λ in terms of b the per capita birth rate, and the probability of mortality d each year. Do this based on the class discussion on January 17 or by reading Otto and Day, 2007 *Section 2.5.1 Discrete-Time Models* p47-50 and omit migration, $m = 0$ for the application to the Protection Island pheasant population.
 - State some important assumptions of your λ formula.
 - Estimate b and d using some of the information given here. Calculate λ given the formula you derived.
 - Use the `geo.pred(lambda)` function to predict the population size of pheasants on Protection Island for your independently estimated λ value. The code to do this must be included in your Rmarkdown file.
 - Make a plot of your predictions relative to the reported data. Include a figure caption that describes the main point of your figure and defines all the symbols.

Chapter 9

Jan 20: Exponential growth

9.1 Required reading

Vandermeer, J.H., Goldberg, D.E., 2013. Population Ecology: First Principles (Second Edition). Princeton University Press, Princeton, United States. p4-8. [Link](#)

We now have two ways of describing how population size changes with time whereby each individual has the same average number of offspring per unit time and the same probability of dying.

- 1) Discrete time geometric growth:

$$N_t = N_0 \lambda^t \quad (9.1)$$

and,

- 2) Continuous time exponential growth:

$$N(t) = N(0)e^{rt} \quad (9.2)$$

Notably, for both these models the per capita birth and death rates do not change over time, and do not change with density or age.

The notation N_t and $N(t)$ is conventional for discrete time versus continuous time formulations respectively, however, these notations both mean the same: the population size at a particular time, t . When $t = 0$ we have the population size at time 0: N_0 or $N(0)$.

As noted in the reading, when $\lambda = e^r$ the equations are the same.

Note that e is the exponential function, `exp()` or e^x .

9.2 Discrete or continuous time formulations

It is appropriate to use the discrete time formulation when births are synchronous.

It is appropriate to use the continuous time formulation when births occur throughout the year.

For example, for many animals there is a distinct breeding season: a short proportion of the year when offspring are born (synchronous reproduction). As such, there is very little temporal overlap between the times of year when births and deaths occur. Humans are an example of a species that might reasonably be modelled as continuous time because babies are born year round.

9.3 Questions

1. For what values of r does the population size increase over time? Note that r might be negative, and I am asking not if the population size, $N(t)$ is positive, but if the population is increasing, i.e., if $N(t)$ is getting larger in value over time.
2. As described in the reading, b is a per capita birth rate, and d is a per capita death rate, and $r = b - d$. For continuous time exponential growth, both b and d must be non-negative and can take any values bigger than 0. Note that this differs from the discrete time model formulation where $0 \leq d \leq 1$. When $d > 1$ in the continuous time formulation, this means that the average lifespan is less than one time step (i.e., the average life span is $1/d$). For example, when $d = 2$ this means that the average life expectancy for an individual is $1/2$ a time step (i.e., days or year, however, the time unit is defined in the model). When the population size increases over time, what is true of b relative to d ?
3. For what value of r does $N(t)$ not change over time? Hint: if $N(t)$ is not changing then $N(t) = N(0)$ for all t .
4. Consider the equation:

$$\frac{dN(t)}{dt} = rN(t).$$

As described in the reading, this is an alternative way to write the continuous time exponential growth equation. The quantity $\frac{dN(t)}{dt}$ can be understood as the slope of a graph where population size is on the vertical axis and time is on the horizontal axis. As such, if the slope is zero, $\frac{dN(t)}{dt} = 0$, then the population size is not changing. If $\frac{dN(t)}{dt} < 0$, then the population size is decreasing. For what value of r does the population size decrease? What is true about b relative to d in this instance?

5. Which population would be more appropriate to be modelled as a continuous time formulation: *E. coli* bacteria or moose?

6. Calculate the formula for the doubling time for continuous time exponential growth (equation (??)). This is the time for the population to double in size. The value of $N(0)$, the population size at $t = 0$ doesn't matter as long as it is a positive number. When the population has doubled, $N(t) = 2N(0)$. To answer this question you need to find t such that $N(t) = 2N(0)$. You may need to revisit some rules about working with logarithms to complete this question (i.e. see here, specifically the *Product*, *Quotient*, *Power*, and *Root* table).

Chapter 10

Jan 24: Density dependent growth

10.1 Required reading

Vandermeer, J.H., Goldberg, D.E., 2013. Population Ecology: First Principles (Second Edition). Princeton University Press, Princeton, United States. p9-17.
[Link](#)

10.2 Questions

1. What is the equation for continuous time logistic growth in its *classic form*? Define all the symbols in the equation by writing their meanings in words. Can K be negative?
2. What does dN/dt mean?
3. Assume that $N < K$. For what values of r will N increase over time?
4. Assume that $r > 0$ and $K > N$. Will N increase or decrease in size over time?
5. Assume that $r, K \neq 0$. For what values of N is the population size constant (i.e., not changing over time)?
6. What is the main difference between exponential and logistic growth?
7. Sketch a graph of the logistic growth equation, $\frac{dN(t)}{dt} = rN(t) \left(1 - \frac{N(t)}{K}\right)$, with time, t , on the horizontal axis (x-axis), and population size $N(t)$, on the vertical (y-axis).

- a. Add to your graph a dashed line corresponding to the carrying capacity, $N(t) = K$.
 - b. Label on your graph, $N(0)$: the population size at $t = 0$.
 - c. As drawn in your graph, is $N(0) < K$? i.e. is the population size at $t = 0$ less than the carrying capacity, K ?
 - d. As drawn, is $r > 0$? i.e. is the net reproductive rate when the population size is small, positive?
 - e. What does it mean if $r < 0$ in terms of the per capita birth rate when the population size is small, b , relative to the per capita death rate when the population size is small, d ?
 - f. If you answered 'yes' to c. add another line for $N(t)$, but when $N(0) > K$ (assume $r > 0$). Note that $N(0) > K$ means that at time $t = 0$ the population size, $N(0)$, is greater than the carrying capacity, K .
1. Draw a graph of a. exponential growth, $N(t) = N(0)e^{rt}$ or $\frac{dN(t)}{dt} = rN(t)$ (both are the same equation), and b. logistic growth $\frac{dN(t)}{dt} = rN(t) \left(1 - \frac{N(t)}{K}\right)$, where the value of r is the same for both a. and b.
 2. Draw a graph of logistic growth, where the population size is decreasing $\frac{dN(t)}{dt} < 0$, but positive $N(t) > 0$. Give a condition on the initial value of $N(0)$ or the per capita net reproductive rate when the population size is small, r , such that the population size is decreasing, $\frac{dN(t)}{dt} < 0$, but positive, $N(t) > 0$.

Chapter 11

Jan 26: Density dependence

I give the derivation of the logistic growth equation as from Vandermeer and Goldberg here.

However, the logistic growth equation, in its classic form does not have a strong mechanistic basis making it difficult to parameterize.

These issues are discussed here

Chapter 12

Jan 27: Density dependence (discrete time)

Density-yield and discrete time density dependence

12.1 Required reading

Vandermeer, J.H., Goldberg, D.E., 2013. Population Ecology: First Principles (Second Edition). Princeton University Press, Princeton, United States. p17-19 and 28-29. [Link](#)

There are also slides on BrightSpace: Additional resources > Density Dependence DT.pdf

12.2 Questions

1. Logistic growth assumes density dependence in the population growth rate. This, however, may be insufficient in many applications. In the section, *The Yield-Density Relationship* what solution is proposed?
2. As written in Vandermeer and Goldberg the Shinozaki-Kira equation is presented without an =. Write the complete equation, by adding in an equals and quantity on the other side of the equals. Define all the parameters and variables in the equation.
3. The Beverton-Holt equation is equation (28) on p29. There are two values of N_t such that $N_t = N_{t+1}$. One value can be found by re-arranging,

$$1 = \frac{\lambda}{1 + \alpha N_t},$$

until N_t is isolated on one side. To find the other value inspect the equation,

$$N_{t+1} = \frac{\lambda N_t}{1 + \alpha N_t}.$$

What is another value of N_t such that $N_{t+1} = N_t$.

Chapter 13

Feb 16: Stage structure

We will start by discussing the syllabus for the remainder of the semester.

13.1 Required Reading

Vandermeer, J.H., Goldberg, D.E., 2013. Population Ecology: First Principles (Second Edition). Princeton University Press, Princeton, United States. p30-34. [Link](#)

The reading mentions ‘*readers who have forgotten their linear algebra*’, however, linear algebra is not a pre-requisite for BIOL 3295. To learn enough linear algebra to complete today’s questions you might watch this 4 minute video explaining how to multiply a matrix by a column vector on the right.

We are learning a little bit of linear algebra now because the notation is compact and because later this formulation will be helpful to calculate the year-to-year multiplicative change in the population size.

Let’s consider an age-structured population where:

- Individuals aged less than 1 year old do not reproduce, and will survive to 1 year old with a probability of 0.5.
- Individuals aged less than 2 years old have 2 offspring and then die.

We can write the equations for the number of individuals in each stage one year from now as:

$$\begin{aligned} N_{1,t+1} &= 2N_{2,t}, \\ N_{2,t+1} &= 0.5N_{1,t}, \end{aligned} \tag{13.1}$$

where $N_{1,t+1}$ is the number of individuals aged less than 1 year at time $t + 1$, and $N_{2,t+1}$ is the number of individuals aged between 1 and 2 years at time $t + 1$. Try out the system of equations: suppose, $N_{1,0} = 10$ and $N_{2,0} = 5$, what is $N_{1,1}$ and $N_{2,1}$?

Note that in the system of equations (??), some of the values that were zeros were omitted, i.e.,

$$\begin{aligned} N_{1,t+1} &= 0N_{1,t} + 2N_{2,t}, \\ N_{2,t+1} &= 0.5N_{1,t} + 0N_{2,t}, \end{aligned} \quad (13.2)$$

Note that as written above, consistency with the ordering is necessary: $N_{1,t+1}$ appears above $N_{2,t+1}$, and on the other side of the $=$ $N_{1,t}$ always appears to the left of $N_{2,t}$. When written as the system of equations (??), we can now more easily write the system of equations (??) in matrix notation:

$$\begin{bmatrix} N_{1,t+1} \\ N_{2,t+1} \end{bmatrix} = \begin{bmatrix} 0 & 2 \\ 0.5 & 0 \end{bmatrix} \begin{bmatrix} N_{1,t} \\ N_{2,t} \end{bmatrix} \quad (13.3)$$

Again, let $N_{1,0} = 10$ and $N_{2,0} = 5$. Using the system of equations (??), and remembering how to multiply a matrix by a column vector, what is $N_{1,1}$ and $N_{2,1}$? Did you get the same answer (but now formatted as a vector) as you did to this same question, but when the problem wasn't in matrix notation (i.e., equation (??))? Yes? Super!

Now, we have two equivalent ways to write our population models with age structure. This may seem unhelpful now, but remember that later matrix notation will be helpful to calculate the rate of population increase and the ratio of individuals in the age or stage classes.

13.2 Questions

1. Consider an age-structured population where:
 - Individuals aged less than 1 year old do not reproduce, and will survive to 1 year old with a probability of 0.2.
 - Individuals aged less than 2 years old have 4 offspring and then die.

Write the equations for the number of individuals in each age class in one year from now, in the format of the system of equations (??)

2. Using your system of equations from question 1, assume that at $t = 0$ there are 4 individuals aged less than 1 year, and 4 individuals aged 1 to 2 years. Calculate the number of individuals in each of the two age classes at $t = 1$.

Chapter 14

Feb 17: ASSIGNMENT

Stage-structured population dynamics

Class will be in CSF 2218

ASSIGNMENT 3 is due on March 3.

[currently unfinished]

We will do this exact example in lecture. Here we are verifying that we can get the same conclusions using R.

Install and load the `popbio` package.

```
require("popbio")
```

```
## Loading required package: popbio
```

Define our projection matrix:

```
A = matrix(c(0,2,0.5,.1), 2,2, byrow=TRUE)
```

Type `A` into the console to check that `A` has the correct number of rows and columns and the numerical entries in the correct place.

The function `eigen()` is a built-in function that will calculate the eigenvalues and eigenvectors for the projection matrix `A`:

```
ev = eigen(A)
```

Type `ev` into the console. There are two eigenvalues. Why are there two? Which is the dominant eigenvalue? Will this population grow (for a positive

initial number of individuals)?

There is an eigenvector (2 rows x 1 column) associated with each eigenvalue (= 2 eigenvectors). The eigenvector associated with the n^{th} eigenvalue is in column n .

The dominant eigenvalue is the first one. Therefore, the associated right eigenvector, that will tell us about the long-term relative stage abundance, is in the first column.

```
vec1 = ev$eigenvectors[,1]
```

Eigenvectors are not unique - they can be multiplied by a constant and are still the same eigenvector:

```
norm.vec1 = -100*vec1
```

What happens if our initial population size is a right eigenvector?

```
vec2 = A%*%norm.vec1
vec3 = A%*%vec2
```

How does this compare to if the right eigenvector is multiplied by the dominant eigenvalue?

```
1.05*norm.vec1
```

```
## [1] 92.94288 48.85306
```

Let's simulate the long term population dynamics:

Chapter 15

Feb 28: Stage-structured population dynamics

15.1 Required Reading

Vandermeer, J.H., Goldberg, D.E., 2013. Population Ecology: First Principles (Second Edition). Princeton University Press, Princeton, United States. p39-40. [Link](#)

Where \mathbb{P} is a projection matrix, the element p_{ij} is the contribution *from* individuals in stage j at time t , *to* stage i at time $t + 1$,

$$\mathbb{P} = \begin{bmatrix} p_{11} & p_{12} & \cdots & \cdots & p_{1n} \\ p_{21} & p_{22} & \cdots & \cdots & p_{2n} \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ p_{n1} & \cdots & \cdots & \cdots & p_{nn} \end{bmatrix}. \quad (15.1)$$

Note that it is convention for both age-structured and stage-structured population models that the most immature stages: i.e, newborns, eggs, or offspring are indexed as $i, j = 1$, and progressively more mature stages are indexed with progressively larger indexes. For example, in Question 3 below the sensible choice of indexes is:

$i, j = 1$: larvae

$i, j = 2$: pupae

$i, j = 3$: adults

15.2 Questions

1. Consider the projection matrix of the age-structured model from the previous class:

$$\begin{bmatrix} 0 & 2 \\ 0.5 & 0 \end{bmatrix} \quad (15.2)$$

What are the special characteristics of the projection matrix for an age-structured population model (Leslie-Lewis matrix), that don't necessarily occur for a stage-structured population model (Leftkovitch matrix)?

2. Which elements of the Leftkovitch matrix may be larger than 1? Note that elements of the matrix occurring in a horizontal line are called rows, and elements occurring in a vertical line are called columns.
3. Complete Exercise 2.15 on p40 of Vandermeer and Goldberg (2013). This question is a bit tricky, so here's a hint. The correct answer for the projection matrix has this form:

$$\mathbb{P} = \begin{bmatrix} p_{11} & p_{12} & 50 \\ p_{21} & p_{22} & p_{23} \\ p_{31} & p_{32} & p_{33} \end{bmatrix}. \quad (15.3)$$

Note that it isn't necessary to include eggs as a stage because after a month either all eggs have become larvae or died.

Chapter 16

Mar 2: Eigenvalues and eigenvectors

16.1 Required Reading

Vandermeer, J.H., Goldberg, D.E., 2013. Population Ecology: First Principles (Second Edition). Princeton University Press, Princeton, United States. p37-39. [Link](#)

Today we will learn how to determine if a population with age- or stage-structure is expected to increase or decrease over time. Recall, that for discrete time, without age- or stage-structure, and for exponential (also called geometric) growth we had:

$$N_{t+1} = \lambda N_t,$$

where the population size, N_t , increases over time if $\lambda > 1$. For age- and stage-structured populations, rather than a scalar, λ , (i.e. just one number) we have a matrix, \mathbb{P} , containing many numbers:

$$\mathbb{P} = \begin{bmatrix} p_{11} & p_{12} & \cdots & \cdots & p_{1n} \\ p_{21} & p_{22} & \cdots & \cdots & p_{2n} \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ p_{n1} & \cdots & \cdots & \cdots & p_{nn} \end{bmatrix}, \quad (16.1)$$

where each number represents the contribution that one of the age- or stage-classes makes to another.

Recall that to calculate the population size at the next time step, we use matrix multiplication: