UNIT Extra notes

1 Introduction

- Up until now we've tracked populations with a single state variable (population size or population density)
- Poll: What assumption are we making?
  - **Answer:** All individuals are similar enough to be counted as if they are the same
    - **Answer:** Always (continuous time)
    - **Answer:** At census time (discrete time)
- What are some organisms for which this seems like a good approximation?
  - **Answer:** Dandelions, bacteria, insects
- What are some organisms that don't work so well?
  - **Answer:** Trees, people, codfish

Structured populations

- If we think age or size is important to understanding a population, we might model it as an **structured** population
- Instead of just keeping track of the total number of individuals in our population ...
  - Keeping track of how many individuals of each age
    - or size
    - or developmental stage

1.1 Example: biennial dandelions

- Imagine a population of dandelions
  - Adults produce 80 seeds each year
  - 1% of seeds survive to become adults
  - 50% of first-year adults survive to reproduce again
  - Second-year adults never survive
- Will this population increase or decrease through time?

How to study this population

- Choose a census time
  - Before reproduction or after
  - Since we have complete cycle information, either one should work
- Figure out how to predict the population at the next census

Census choices

- Before reproduction
  - All individuals are adults
  - We want to know how many adults we will see next year
- After reproduction
  - Seeds, one-year-olds and two-year-olds
  - Two-year-olds have already produced their seeds; once these seeds are counted, the two-year-olds can be ignored, since they will not reproduce or survive again

What determines λ?

- If we have 20 adults *before* reproduction, how many do we expect to see next time?
- $\lambda = p + f$ is the total number of individuals per individual after one time step
- Poll: What is f in this example?
  - **Answer:** 0.8
- Poll: What is p in this example?
  - **Answer:** 0.5 for 1-year-olds and 0 for 2-year-olds.
  - **Answer:** We can't take an average, because we don't know the population structure

What determines $\mathcal{R}$?

- $\mathcal{R}$ is the average total number of offspring produced by an individual over their lifespan
- Can start at any stage, but need to close the loop
- Poll: What is the reproductive number?
- **Answer:** If you become an adult you produce (on average)
  - *Comment:* Blackboard!
  - **Answer:** 0.8 adults your first year
  - **Answer:** 0.4 adults your second year
- **Answer:** $\mathcal{R} = 1.2$

What does $\mathcal{R}$ tell us about λ?

- **<u>Answer</u>:** Population increases when $\mathcal{R} > 1$, so $\lambda > 1$ exactly when $\mathcal{R} > 1$
- If $\mathcal{R} = 1.2$, then λ
  - **<u>Answer</u>:** > 1 – the population is increasing
  - **<u>Answer</u>:** < 1.2 – the life cycle takes more than 1 year, so it should take more than one year for the population to increase 1.2 times

1.2 Modeling approach

- In this unit, we will construct *simple* models of structured populations
  - To explore how structure might affect population dynamics
  - To investigate how to interpret structured data

Regulation

- *Simple* population models with regulation can have extremely complicated dynamics
- *Structured* population models with regulation can have insanely complicated dynamics
- Here we will focus on understanding structured population models *without regulation*:
  - **<u>Answer</u>:** Individuals behave independently, meaning. . .
  - **<u>Answer</u>:** Average per capita rates do not depend on population size

Age-structured models

- The most common approach is to structure by age
- In age-structured models we model how many individuals there are in each "age class"
  - Typically, we use age classes of one year
  - Example: salmon live in the ocean for roughly a fixed number of years; if we know how old a salmon is, that strongly affects how likely it is to reproduce

Stage-structured models

- In stage-structured models, we model how many individuals there are in different stages
  - Ie., newborns, juveniles, adults
  - More flexible than an age-structured model
  - Example: forest trees may survive on very little light for a long time before they have the opportunity to recruit to the sapling stage

Discrete vs. continuous time in unstructured models

- continuous-time models are structurally simpler (and smoother)
- discrete-time models only need to assume everyone's the same sometimes
  - **<u>Answer</u>:** At the census time
  - **<u>Answer</u>:** More realistic

...in structured models

- We no longer assume everyone is the same (we keep track of age or size)
- Poll: So it should be mostly about reproduction
  - **<u>Answer</u>:** Populations with continuous reproduction (e.g. bacteria), may be better suited to continuous-time models
  - **<u>Answer</u>:** Populations with **synchronous** reproduction (e.g., moths) may be better suited to discrete-time models
- Continuous time with structure gives people headaches
  - So we won't do it here, even though it may be better for many applications

2 Constructing a model

- This section will focus on **linear, discrete-time, age-structured** models
- State variables: how many individuals of each age at any given time
- Parameters: p and f *for each age that we are modeling*

When to count

- We will choose a census time that is appropriate for our study
  - Before reproduction, to have the fewest number of individuals
  - After reproduction, to have the most information about the population processes
  - Some other time, for convenience in counting
    - **<u>Answer</u>:** A time when individuals gather together
    - **<u>Answer</u>:** A time when they are easy to find (insect pupae)

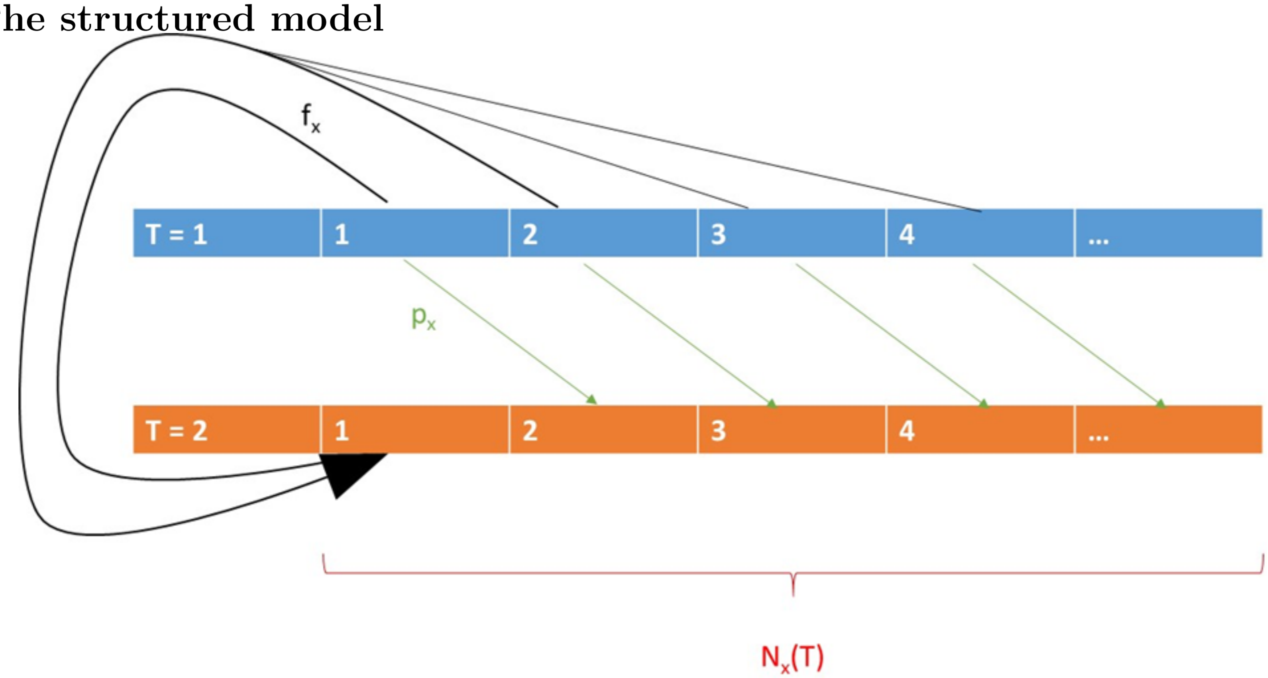
The conceptual model

- Once we choose a census time, we imagine we know the population for each age x after time step T.
  - We call these values $N_x(T)$
- Now we want to calculate the expected number of individuals in each age class at the next time step
  - We call these values $N_x(T+1)$
- What are the parameters? — What do we need to know to calculate population for next time?
  - **Answer:** The survival probability of each age group: p_x
  - **Answer:** The average fecundity of each age group: f_x

Closing the loop

- f_x and p_x must close the loop back to the census time, so we can use them to simulate our model:
  - f_x has units [new indiv (at census time)]/[age x indiv (at census time)]
  - p_x has units [age $x+1$ indiv (at census time)]/[age x indiv (at census time)]

The structured model



2.1 Model dynamics

Short-term dynamics

- This model's short-term dynamics will depend on parameters ...
  - It is more likely to go up if fecundities and survival probabilities are high
- ... and starting conditions
  - If we start with mostly very old or very young individuals, it might go down; with lots of reproductive adults it might go up

Long-term dynamics

- If a population follows a model like this, it will tend to reach
  - a **stable age distribution**:
    - the *proportion* of individuals in each age class is constant
  - a stable value of λ
    - if the proportions are constant, then we can average over f_x and p_x, and the system will behave like our simple model
- Poll: What are the long-term dynamics of such a system?
  - **Answer:** Exponential growth or exponential decline
- Skipping calculations, but you can poke if curious
- Spreadsheet link

3 Life tables

- People often study structured models using **life tables**
- A life table is made *from the perspective of a particular census time*
- It contains the information necessary to project to the next census:
  - How many survivors do we expect at the next census for each individual we see at this census? (p_x in our model)
  - How many offspring do we expect at the next census for each individual we see at this census? (f_x in our model)

Cumulative survivorship

- The first key to understanding how much each organism will contribute to the population is **survivorship**
- In the field, we estimate the probability of survival from age x to age $x+1$: p_x
  - This is the probability you will be *counted* at age $x+1$, given that you were *counted* at age x.
- To understand how individuals contribute to the population, we are also interested in the overall probability that individuals survive to age x: ℓ_x.
  - **Answer:** $\ell_x = p_1 \times \ldots p_{x-1}$
  - **Answer:** ℓ_x measures the probability that an individual survives to be counted at age x, given that it is ever counted at all (ie., it survives to its first census)

Calculating $\mathcal{R}$

- We calculate $\mathcal{R}$ by figuring out the estimated contribution at each age group, *per individual who was ever counted*
  - We figure out expected contribution given you were ever counted by multiplying:
  - **Answer:** $f_x \times \ell_x$

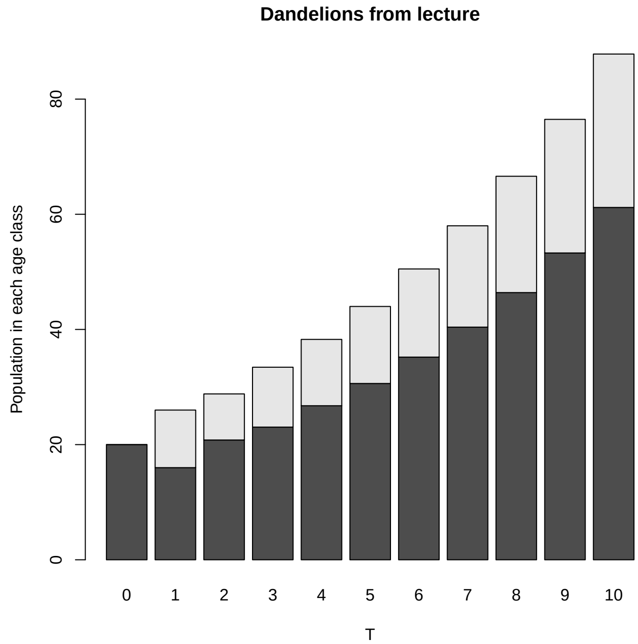
3.1 Examples

Dandelion example

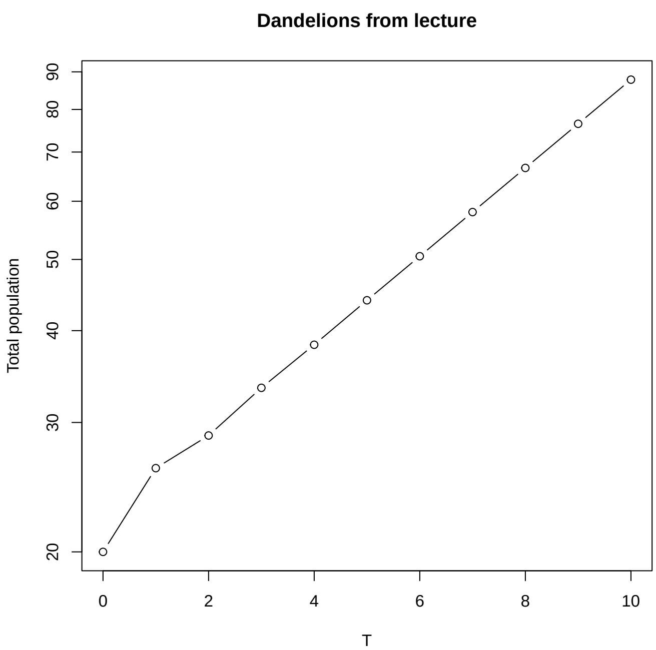
Answer slide: *Dandelion life table*

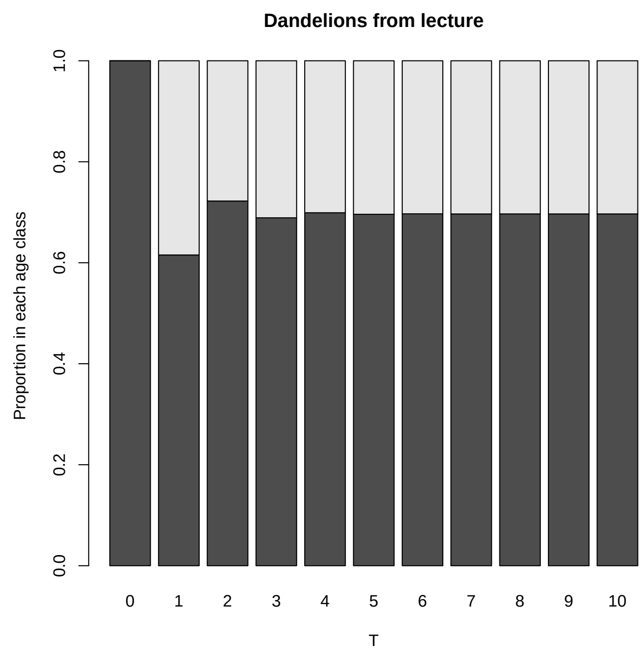
x	f_x	p_x	ℓ_x	$\ell_x f_x$
1	0.8	0.5	1.000	0.800
2	0.8	0	0.500	0.400
R				1.200

Dandelion dynamics



Dandelion dynamics





Squirrel example

Squirrel observations

- Poll: Do you notice anything strange?
  - **<u>Answer</u>:** Older age groups seem to be grouped for fecundity.
  - **<u>Answer</u>:** Strange pattern in survivorship; do we really believe nobody survives past the last year?

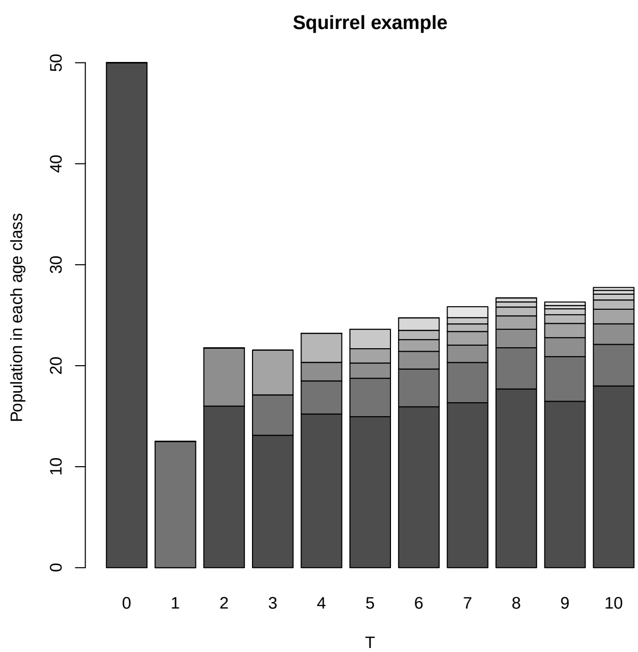
– **Answer:** Might be better to use a model where they keep track of 1 year, 2 year, and "adult" – not much harder.

  * **Answer:** This is what we call stage structure

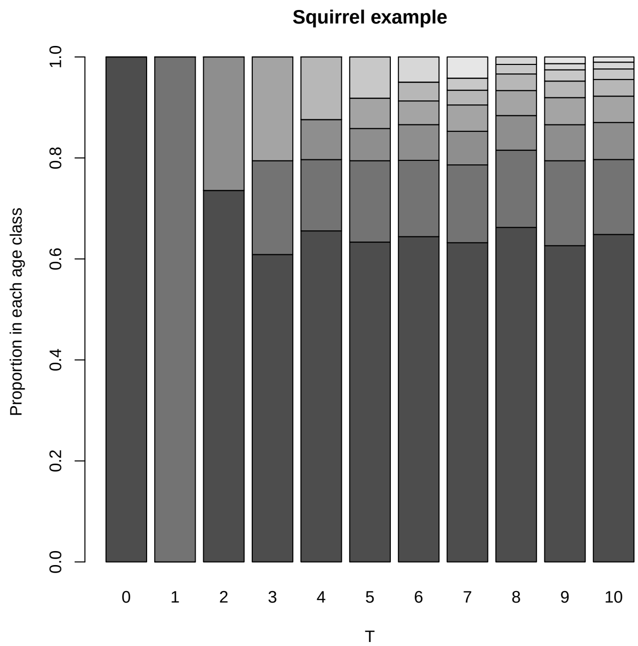
Answer slide: *Gray squirrel population example*

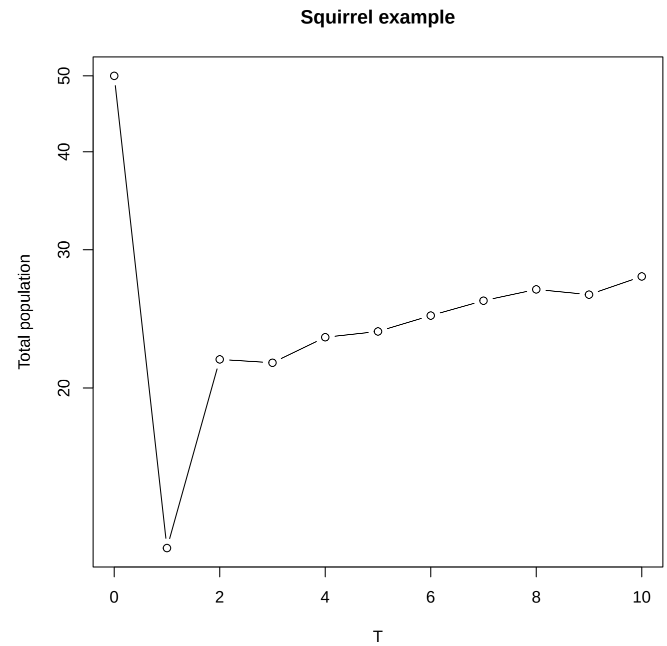
x	f_x	p_x	ℓ_x	$\ell_x f_x$
1	0	0.25	1.000	0.000
2	1.28	0.46	0.250	0.320
3	2.28	0.77	0.115	0.262
4	2.28	0.65	0.089	0.202
5	2.28	0.67	0.058	0.131
6	2.28	0.64	0.039	0.088
7	2.28	0.88	0.025	0.056
8	2.28	0.0	0.022	0.050
R				1.109

Gray squirrel dynamics



Gray squirrel dynamics





3.2 Calculation details

f_x vs. m_x

- Here we focus on f_x – the number of offspring seen at the next census (next year) per organism of age x seen at this census
- An alternative perspective is m_x: the total number of offspring per reproducing individual of age x
- Poll: How would I calculate one from the other?
  - **Answer:** To get f_x we multiply m_x by one or more survival terms, depending on when the census is
  - **Answer:** f_x needs to close the loop from one census to the next

When do we start counting?

- Is the first age class called 0, or 1?
  - In this course, we will start from age class 1
  - If we count right *after* reproduction, this means we are calling newborns age class 1. Don't get confused.

Answer slide: *Dandelion life table*

x	f_x	p_x	ℓ_x	$\ell_x f_x$
1	0.8	0.5	1.000	0.800
2	0.8	0	0.500	0.400
R				1.200

<u>Answer slide</u>: *Counting* after *reproduction*

x	f_x	p_x	ℓ_x	$\ell_x f_x$
1	0.8	0.01	1.000	0.800
2	40	0	0.010	0.400
R				1.200

<u>Comment</u>: There are two different approaches to the third age class: if we assume that we count the two-year old adults ($x = 3$), we can write $p_2 = 0.5$; $f_3 = 0$, and get the same answer (with one extra row that has zero contribution).