

## UNIT 4: Structured populations

### 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?
  - - \*
      - \*
- What are some organisms for which this seems like a good approximation?
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- What are some organisms that don't work so well?
  -

### 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 $\lambda$ ?

- 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?
  -
- Poll: What is  $p$  in this example?
  - 
  -

## 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?
- - 
  -
-

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

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- If  $\mathcal{R} = 1.2$ , then  $\lambda$ 
  - 
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## 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*:
  - 
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## 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
  - I.e., 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
- 
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## ...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
- 
- 
- 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
- \*
- \*

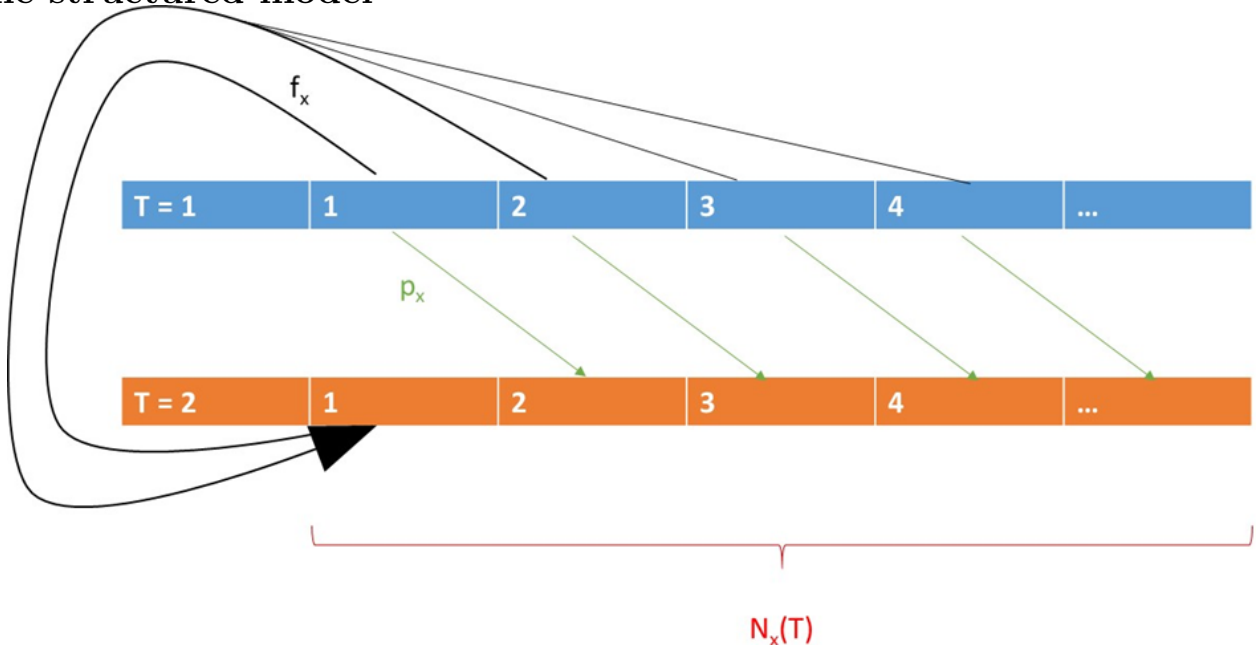
## The conceptual model

- 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  $N_x(T + 1)$
- Poll: What do we need to know?
  - 
  -

## 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  $\lambda$ 
    - \* 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?
  -
- Spreadsheet: <http://tinyurl.com/DandelionModel2020>

## Exception

- Populations with **independent cohorts** do not tend to reach a stable age distribution
  - A **cohort** is a group that enters the population at the same time
  - We say my cohort and your cohort interact if my children might be in the same cohort as your children
  - or my grandchildren might be in the same cohort as your great-grandchildren
  - ...
- As long as all cohorts interact (none are independent), then the unregulated model leads to a stable age distribution (SAD)

## Independent cohorts

- Some populations might have independent cohorts:
  - If salmon reproduce *exactly* every four years, then:
    - \* the 2015 cohort would have offspring in 2019, 2023, 2027, 2031, ...
    - \* the 2016 cohort would have offspring in 2020, 2024, 2028, 2032, ...
    - \* in theory, they could remain independent – distribution would not converge
- Examples could include 17-year locusts, century plants, ...

### 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  $x$ :  $\ell_x$ .

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#### 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:

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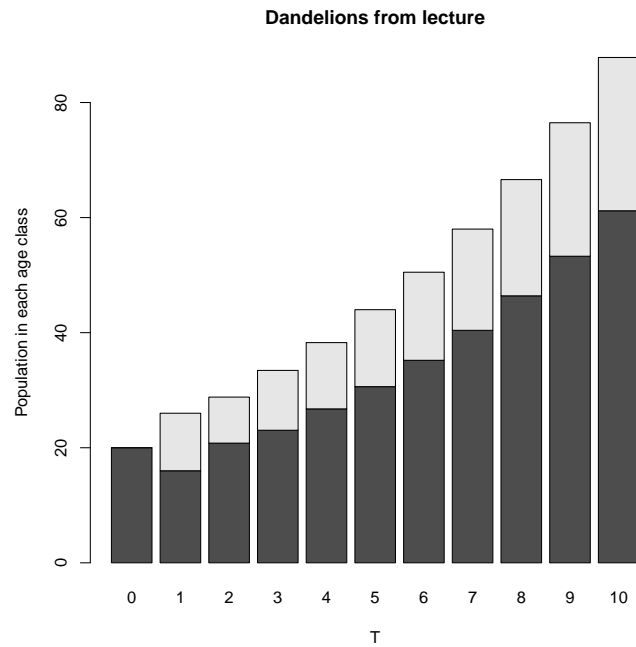
#### 3.1 Examples

##### Dandelion example

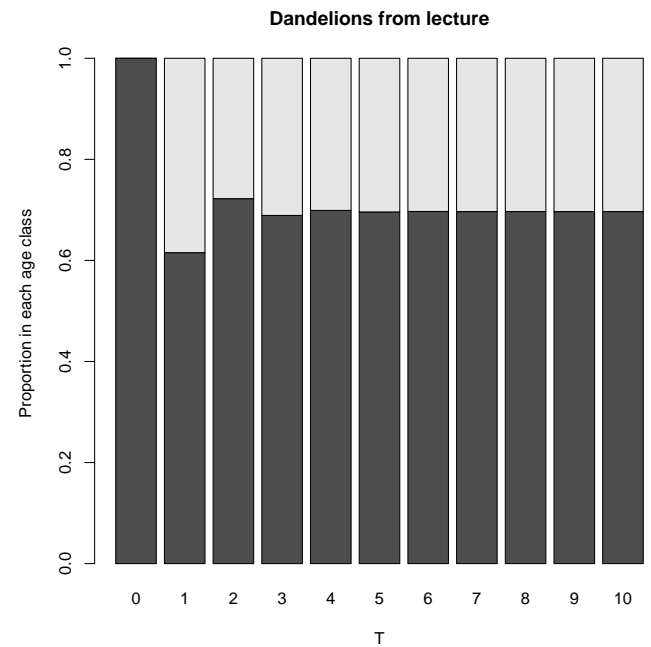
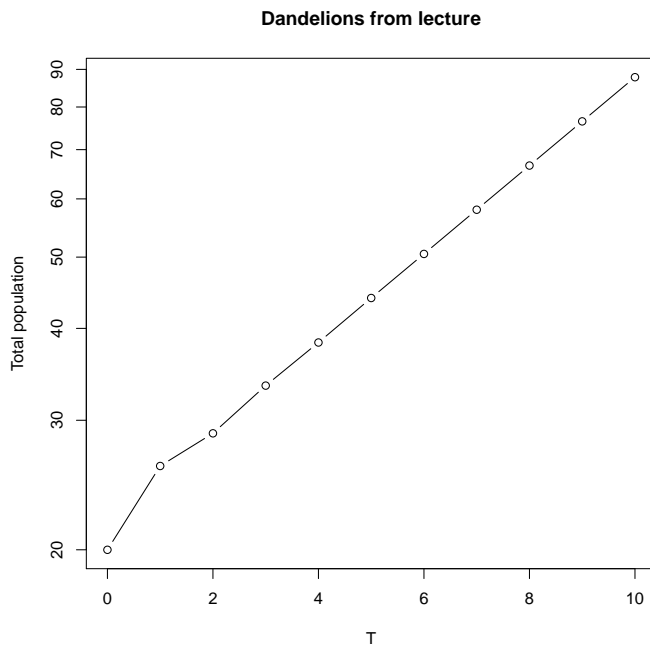
##### Dandelion life table

$x$	$f_x$	$p_x$	$\ell_x$	$\ell_x f_x$
1				
2				
R				

## Dandelion dynamics



## Dandelion dynamics



## Squirrel example

### Gray squirrel population example



$x$	$f_x$	$p_x$	$\ell_x$	$\ell_x f_x$
1	0	0.25		
2	1.28	0.46		
3	2.28	0.77		
4	2.28	0.65		
5	2.28	0.67		
6	2.28	0.64		
7	2.28	0.88		
8	2.28	0.0		
R				

## Squirrel observations

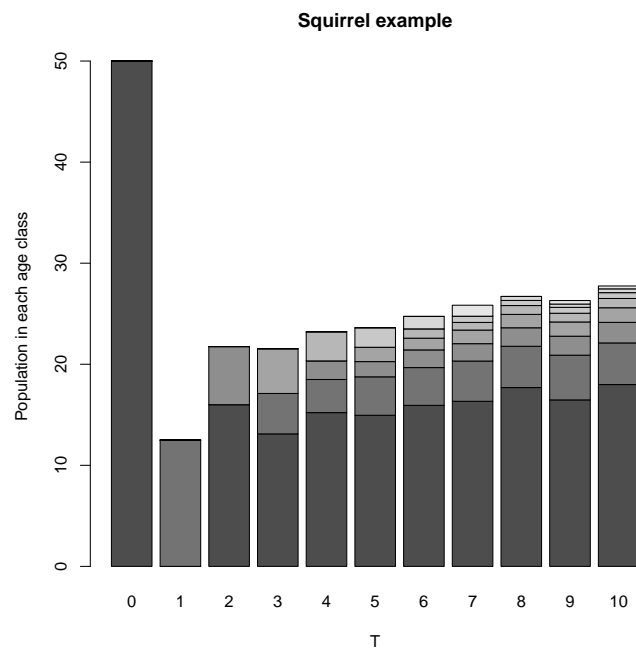
- Poll: Do you notice anything strange about the squirrel life table?

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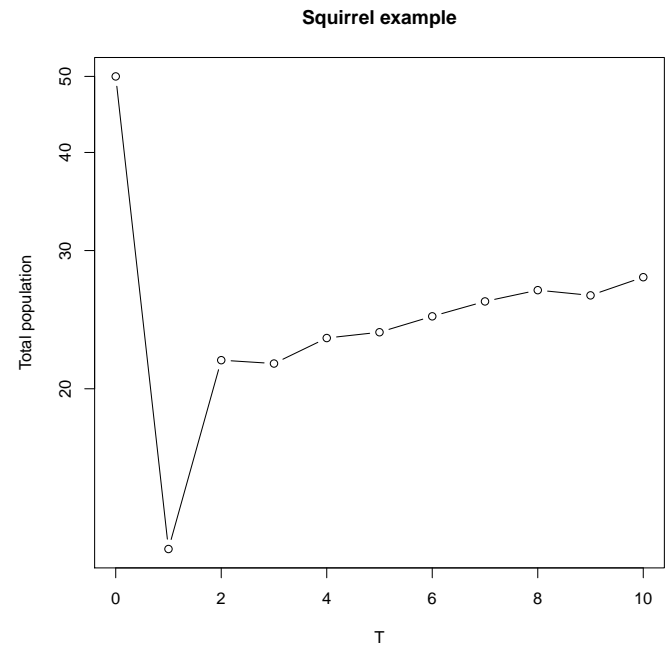
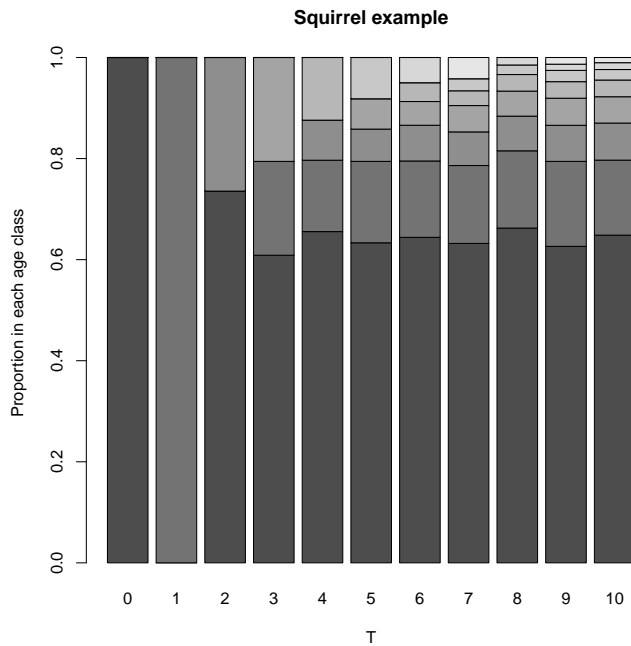
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## Gray squirrel dynamics



## Gray squirrel dynamics



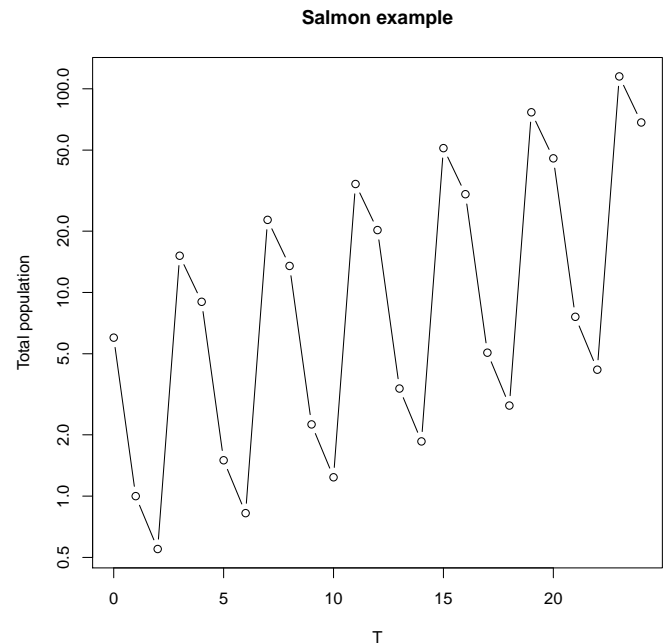
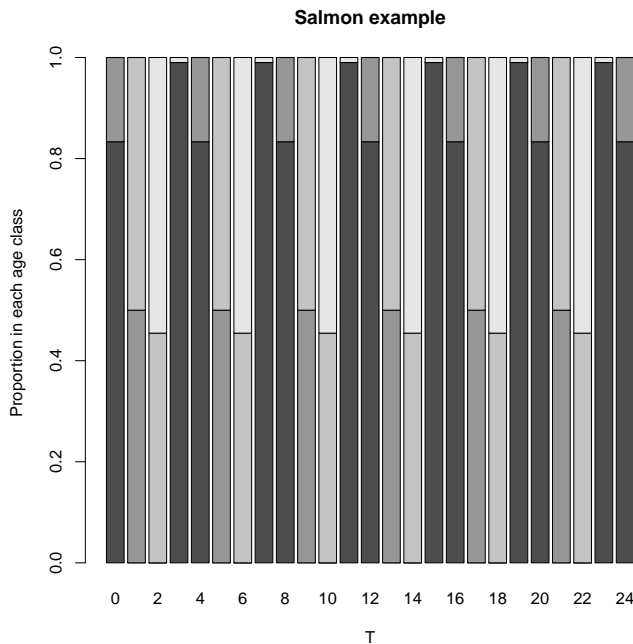
## Salmon example

- What happens when a population has independent cohorts?
  - Does not necessarily converge to a SAD

## Salmon example

$x$	$f_x$	$p_x$	$\ell_x$	$\ell_x f_x$
1	0	0.1		
2	0	0.5		
3	0	0.6		
4	50	0		
R				

## Salmon 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?

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## 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.

## Calculating $\mathcal{R}$

- The reproductive number  $\mathcal{R}$  gives the average lifetime reproduction of an individual, and is a valuable summary of the information in the life table

$$- \mathcal{R} = \sum_x \ell_x f_x$$

- If  $\mathcal{R} > 1$  in the long (or medium) term, the population will increase
  - If  $\mathcal{R}$  is persistently  $< 1$ , the population is in trouble
  - We can ask (for example):
    - Which ages have a large *contribution* to  $\mathcal{R}$ ?
    - Poll: Which values of  $p_x$  and  $f_x$  is  $\mathcal{R}$  sensitive to?
- \*

## The effect of old individuals

- Estimating the effects of old individuals on a population can be difficult, because both  $f$  and  $\ell$  can be extreme
    - The contribution of an age class to  $\mathcal{R}$  is  $\ell_x f_x$
    - Poll: Extreme how?
- \*
- \*
- Reproductive potential of old individuals *may* or *may not* be important
    - 
    -

## 3.3 Measuring growth rates

- In a constant population, each age class replaces itself:
  - $\mathcal{R} = \sum_x \ell_x f_x = 1$
- In an exponentially changing population, each year's **cohort** is a factor of  $\lambda$  bigger (or smaller) than the previous one
  - $\lambda$  is the finite rate of increase, like before
- Looking back in time, the cohort  $x$  years ago is  $\lambda^{-x}$  as large as the current one
- The existing cohorts need to make the next one:
  - $\sum_x \ell_x f_x \lambda^{-x} = 1$

## The Euler equation

- If the life table doesn't change, then  $\lambda$  is given by  $\sum_x \ell_x f_x \lambda^{-x} = 1$
- We basically ask, if the population has the structure we would expect from growing at rate  $\lambda$ , would it continue to grow at rate  $\lambda$ .
- On the left-side each cohort started as  $\lambda$  times smaller than the one after it
  - Then got multiplied by  $\ell_x$ .
- Under this assumption, is the next generation  $\lambda$  times bigger again?
- Example from spreadsheet

## $\lambda$ and $\mathcal{R}$

- If the life table doesn't change, then  $\lambda$  is given by  $\sum_x \ell_x f_x \lambda^{-x} = 1$ 
  - What's the relationship between  $\lambda$  and  $\mathcal{R}$ ?
- When  $\lambda = 1$ , the left hand side is just  $\mathcal{R}$ .
  - If  $\mathcal{R} > 1$ , the population more than replaces itself when  $\lambda = 1$ . We must make  $\lambda > 1$  to decrease LHS and balance.
  - If  $\mathcal{R} < 1$ , the population fails to replace itself when  $\lambda = 1$ . We must make  $\lambda < 1$  to increase LHS and balance.
- So  $\mathcal{R}$  and  $\lambda$  tell the same story about whether the population is increasing

## Time scales

- $\lambda$  gives the number of individuals per individual *every year*
- $\mathcal{R}$  gives the number of individuals per individual *over a lifetime*
- Poll: What relationship do we expect for an annual population (individuals die every year)?
  -
- Poll: For a long-lived population?
  - - \*
    - \*

## Studying population growth

- $\lambda$  and  $\mathcal{R}$  give similar information about your population
- $\mathcal{R}$  is easier to calculate, and more generally useful
- But  $\lambda$  gives the actual rate of growth
  - More useful in cases where we expect the life table to be constant with exponential growth or decline for a long time

## Growth and decline

- If we think a particular period of growth or decline is important, we might want to study how factors affect  $\lambda$ 
  - Complicated, but well-developed, theory
  - In a growing population, what happens early in life is more important to  $\lambda$  than to  $\mathcal{R}$ .
  - In a declining population, what happens late in life is more important to  $\lambda$  than to  $\mathcal{R}$ .
- Poll: Which is likely to be more important to ecology and evolution?
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## 4 Life-table patterns

### 4.1 Survivorship

#### Patterns of survivorship

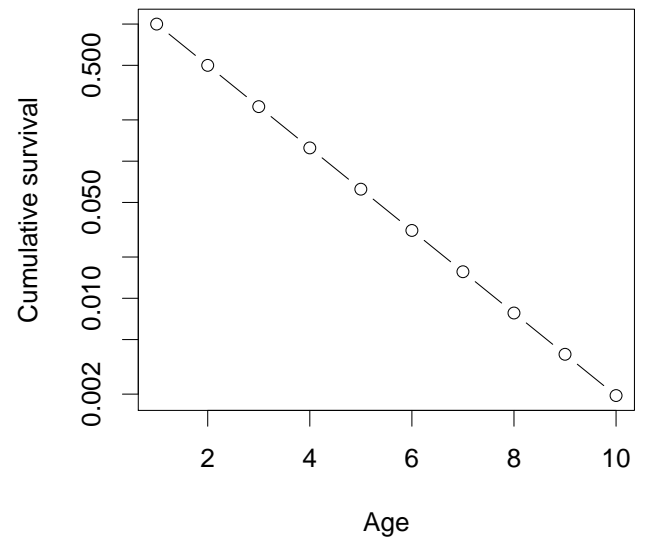
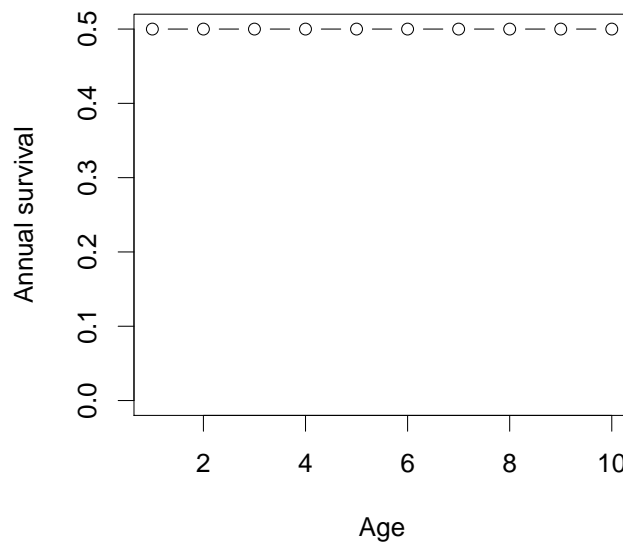
- Poll: What sort of patterns do you expect to see in  $p_x$ ?
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- What about  $\ell_x$ ?
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## Starting off

- Recall: we always start from age *class* 1
  - If we count newborns, we still call them class 1.
- Poll: What is  $\ell_1$  when we count before reproduction?

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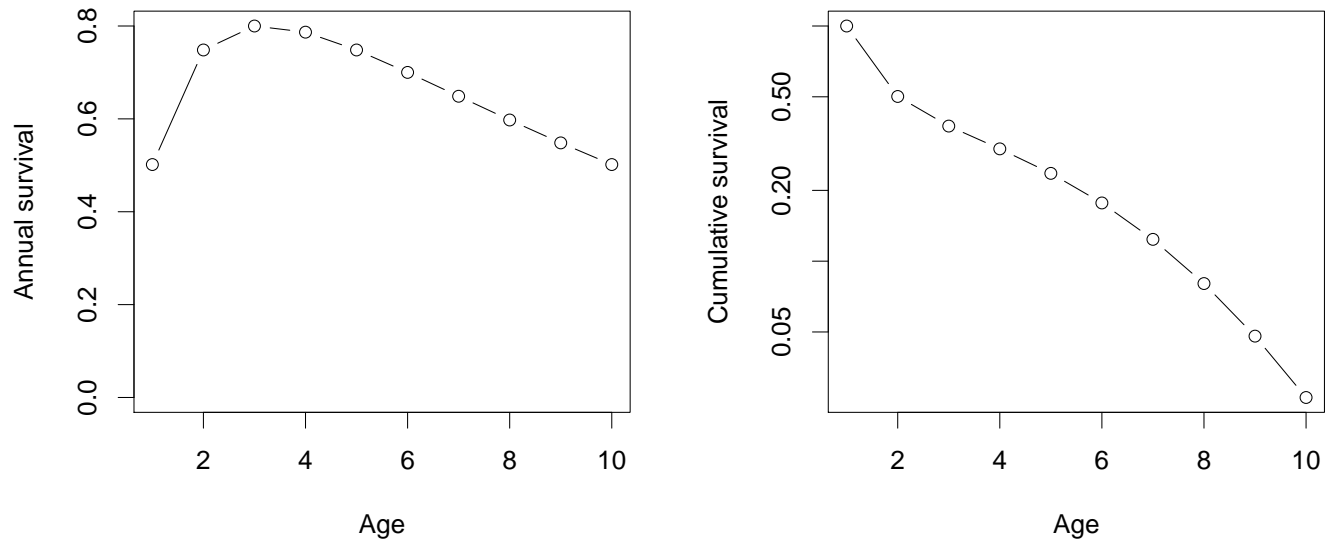
## Constant survivorship



## “Types” of survivorship

- There is a history of defining survivorship as:
  - Type I, II or III depending on whether it increases, stays constant or decreases with age (*don't memorize this, just be aware in case you encounter it later in life*).
  - Real populations tend to be more complicated
- Most common pattern is: high mortality at high and low ages, with less mortality between

## Changing survivorship



### 4.2 Fecundity

- Just as in our simple population growth models, we define fecundity as the expected number of offspring at the next census produced by an individual observed at this census
  - Parent must survive from counting to reproduction
  - Parent must give birth
  - Offspring must survive from birth to counting
- Remember to think clearly about gender when necessary
  - Are we tracking females, or everyone?

### Fecundity patterns

- $f_x$  is the average number of new individuals *counted* next census per individual in age class  $x$  *counted* this census
- Fecundity often goes up early in life and then remains constant
  -
- It may also go up and then come down
  -
- It may also go up and up as organisms get older



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## 5 Age distributions

- <http://www.gapminder.org/population/tool/>
- [https://en.wikipedia.org/wiki/Population\\_pyramid](https://en.wikipedia.org/wiki/Population_pyramid)

### Learning from the model

- If a population has constant size (ie., the same number of individuals are born every year), what determines the proportion of individuals in each age class?

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- What if population is growing?

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\*

### Stable age distribution

- If a population has reached a SAD, and is increasing at rate  $\lambda$  (given by the Euler equation):
  - the  $x$  year old cohort, born  $x$  years ago originally had a size  $\lambda^{-x}$  relative to the current one
  - a proportion  $\ell_x$  of this cohort has survived
  - thus, the relative size of cohort  $x$  is  $\lambda^{-x}\ell_x$
  - SAD depends only on survival distribution  $\ell_x$  and  $\lambda$ .

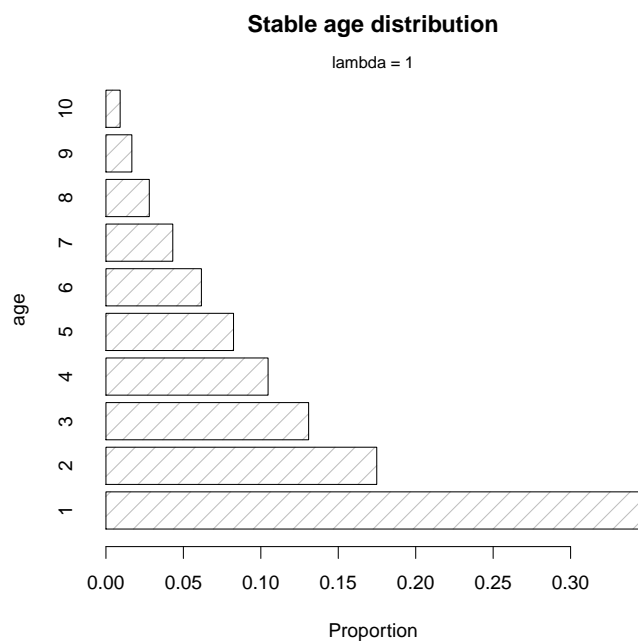
### Patterns

- Populations tend to be bottom-heavy (more individuals at lower age classes)
  - Many individuals born, few survive to older age classes
- If population is growing, this increases the lower classes further
  - More individuals born more recently
- If population is *declining*, this shifts the age distribution in the opposite direction
  - Results can be complicated
  - Declining populations may be bottom-heavy, top-heavy or just jumbled

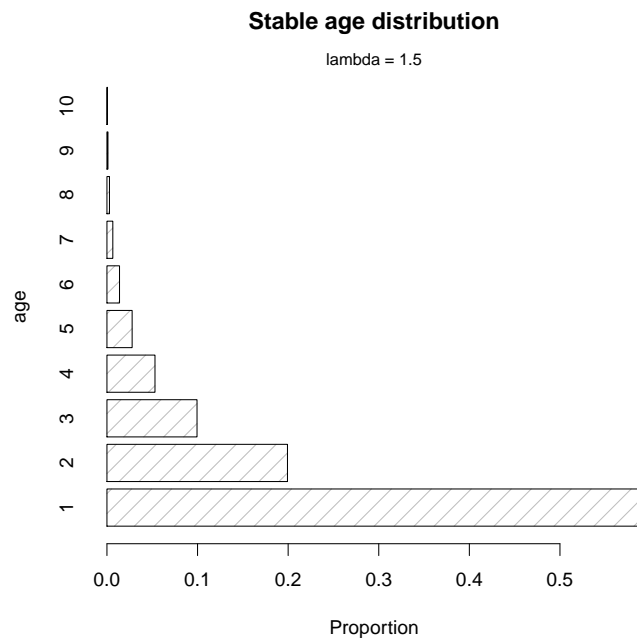
## University cohorts

- McMaster accepts only first-year students. For any given stage (e.g., end of third year) the same proportion drop out each year
- What can you say about the relative size of the classes if:
  - The same number of students is admitted each year?
    - \*
  - Poll: More students are admitted each year?
    - \*
  - Poll: Fewer students are admitted each year?
    - \*

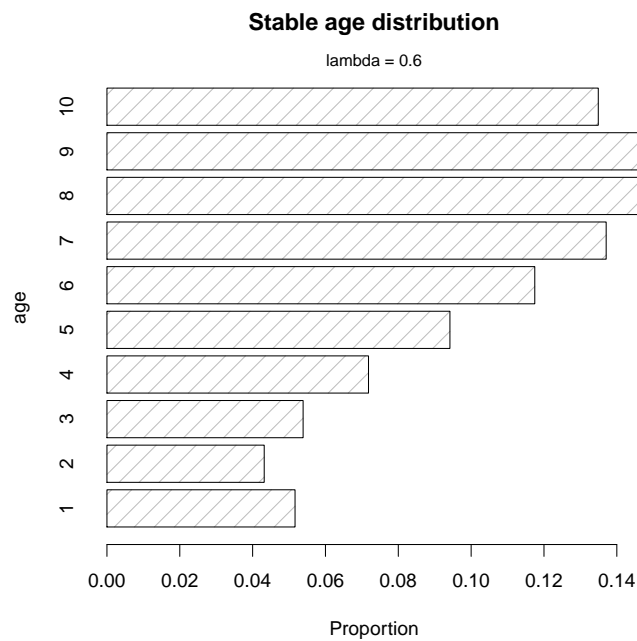
## Age distributions



## Age distributions



## Age distributions



## 6 Other structured models

### Forest example

- Forests have obvious population structure
- They also seem to remain stable for long periods of time

- Populations are presumably *regulated* at some time scale

## Forest size classes

- When we go to an apparently stable forest ecosystem, it seems to be dominated by large trees, not small ones. What up?
- Poll: How is it possible that these systems are dominated by large trees?
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## 6.1 Stage structure

- Stage structure works just like age structure, except that what stage you are in is not strictly predicted by how old you are
  - Age-structured models need fecundity, and survival probability
  - 
  - \*
  - \*
  - More complicated models are also possible

## Advantages

- Stage structured models don't need a maximum age
- Nor one box for every single age class

## Unregulated growth

- What happens if you have a constant stage table (no regulation)?
  - Fecundity, and survival and recruitment probabilities are constant
- Similar to constant life table
  - Can calculate  $\mathcal{R}$  and  $\lambda$  (will be consistent with each other)
  - Can calculate a stable stage distribution
- Unregulated growth cannot persist

## Summary

- If the life table remains constant (no regulation or stochasticity):
  - Reach a stable age (or stage) distribution
  - Grow or decline with a constant  $\lambda$
  - Factors behind age distribution can be understood

## 6.2 Regulated growth

- Our models up until now have assumed that individuals are independent
- In this case, we expect populations to grow (or decline) exponentially
- We do not expect that the long-term average value of  $\mathcal{R}$  or  $\lambda$  will be exactly 1.

## The value of simple models

- There is a lot of mathematical study of unregulated, age-structured populations, but it should be taken with a grain of salt
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- Understanding this behaviour is helpful:
  - interpreting age structures in real populations
  - beginning to understand more complicated systems

## Regulation and structure

- We expect real populations to be regulated
- The long-term average value of  $\lambda$  under regulation *could* be exactly 1
- There is also likely to be substantial variation from year to year, due to changing conditions and other random-seeming forces

## Dynamics

- We expect to see smooth behaviour in many cases
- Cycles and complex behaviour should arise for reasons similar to our unstructured models:
  - Delays in the system
  - Strong population response to density

- Age distribution will be determined by:
  - $\ell_x$ , and
  - whether the population has been growing or declining recently