**UNIT 3: Structured populations**

# 1 Introduction

- Up until now we've tracked populations with a single state variable (population size or population density)

- What assumption are we making?

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- 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?

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## 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

- What is $f$ in this example?

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- What is $p$ in this example?

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## 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

- What is the reproductive number?

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## 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

  – 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

- Structured models can be done in either discrete or continuous time

- Continuous-time models are structurally simpler (and smoother)

- do population characteristics affect the choice?

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- Adding age structure is conceptually simpler with discrete time

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# 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

    *

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## 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 do we need to know?

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## 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)]

## 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

- What are the long-term dynamics of such a system?

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## 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-grandchlidren
    - ...

- 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*

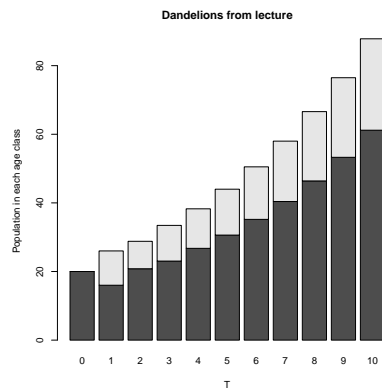    – We figure out expected contribution given you were ever counted by multiplying:
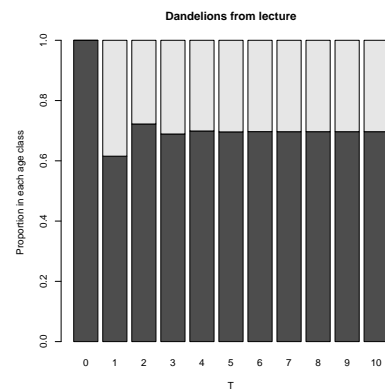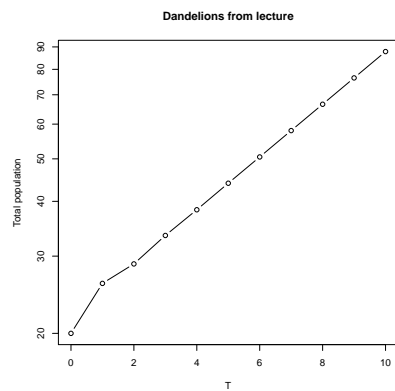
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## 3.1 Examples

**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

- Do you notice anything strange about the life table?
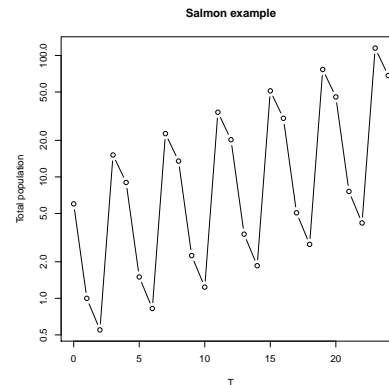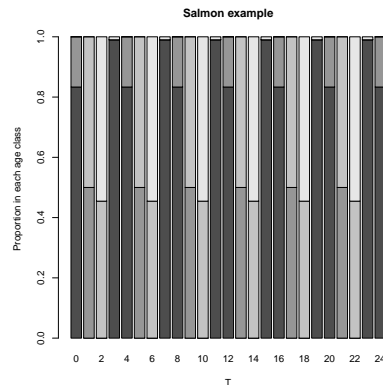
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## Gray squirrel dynamics
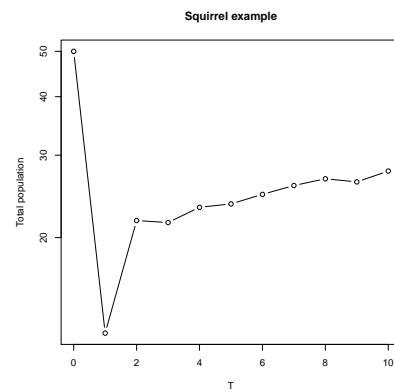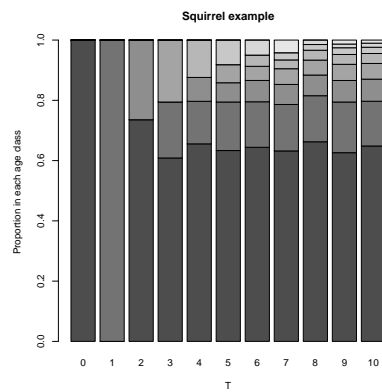


## Salmon example

- What happens when a population has independent cohorts?

    – Does not necessarily converge to a SAD

## 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 $x$

- What is the relationship?

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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 $\mathcal{R}$?
    - 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 $\ell_x f_x$
    - Extreme how?
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- Reproductive potential of old individuals *may* or *may not* be important

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## 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?

## $\lambda$ 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*

- What relationship do we expect for an annual population (individuals die every year):

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- For a long-lived population

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## 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 $\mathcal{R}$.

- A common error is to assume that periods of exponential *growth* are more important to ecology and evolution the periods of exponential *decline*. In the long term, these should balance.

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# 4 Life-table patterns

## 4.1 Survivorship

### Patterns of survivorship

- What sort of patterns do you expect to see in $p_x$?

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- What about $\ell_x$?

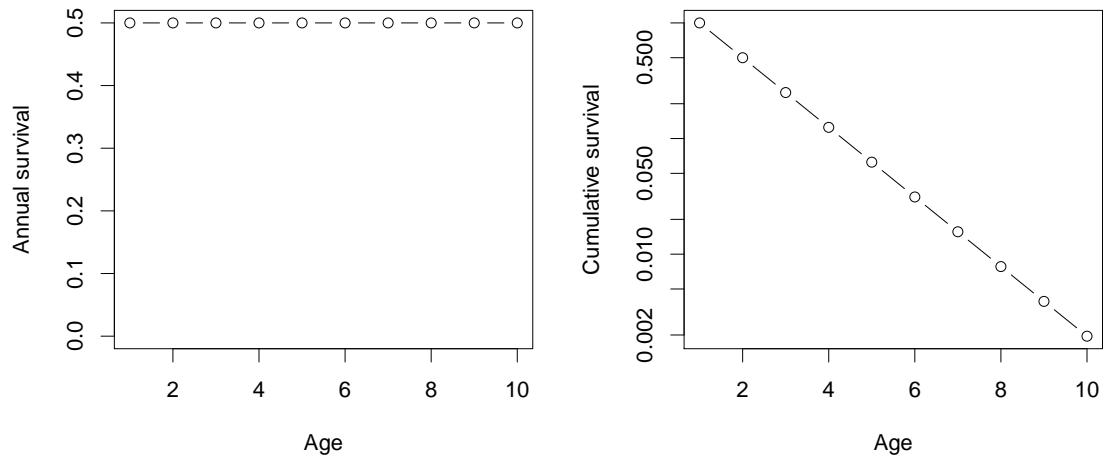    –

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### Starting off

- Recall: we always start from age *class* 1

    – If we count newborns, we still call them class 1.

- 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
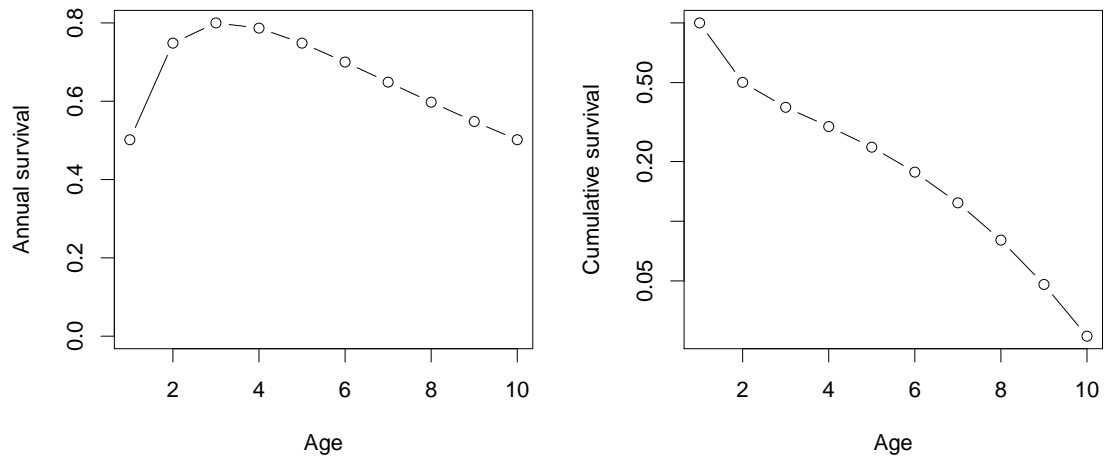
## 4.2  Fecundity

- 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

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- It may also go up and then come down

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- 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/

## 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 $\lambda$.
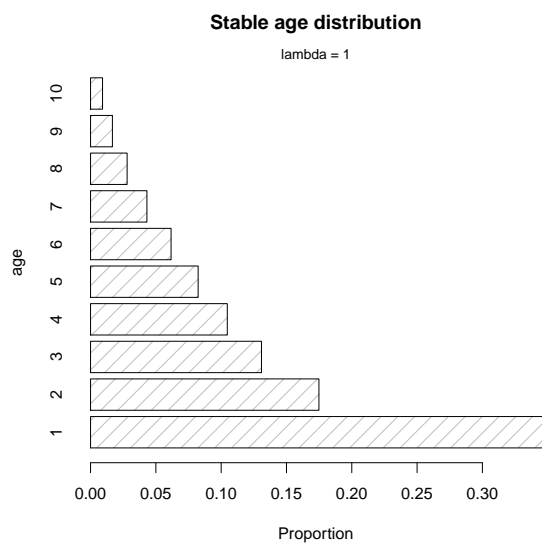
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## Patterns

- 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
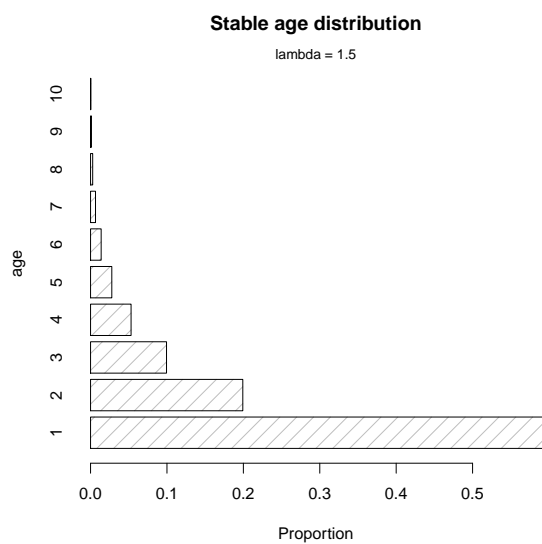  - Declining populations may be bottom-heavy, top-heavy or just jumbled

## 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

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  - More students are admitted each year
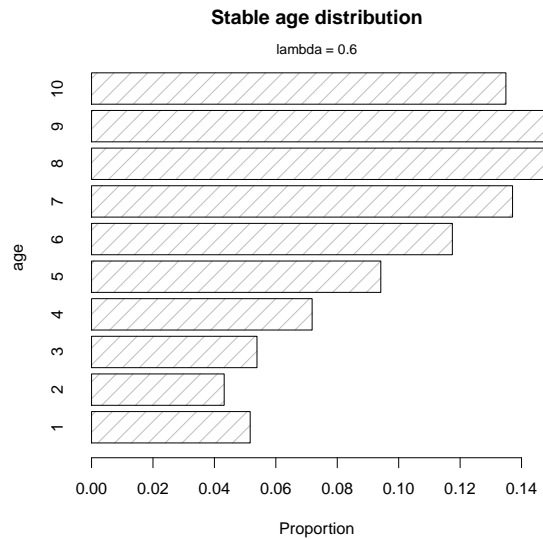
    *

  - Fewer students are admitted each year

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# Age distributions

**Stable age distribution**

lambda = 1



# Age distributions

**Stable age distribution**

lambda = 1.5



# Age distributions

**Stable age distribution**

lambda = 0.6

# 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?

- 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
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        *
    - 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