**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?

  - **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 $\lambda$?

- 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?

  - **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 $\lambda$?

- **Answer:** Population increases when $\mathcal{R} > 1$, so $\lambda > 1$ exactly when $\mathcal{R} > 1$

- If $\mathcal{R} = 1.2$, then $\lambda$

  - **Answer:** $> 1$ – the population is increasing
  - **Answer:** $< 1.2$ – 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*:

  - **Answer:** Individuals behave independently, or (equivalently)
  - **Answer:** Average per capita rates do not depend on population size

# Comment slide: *Complexity*
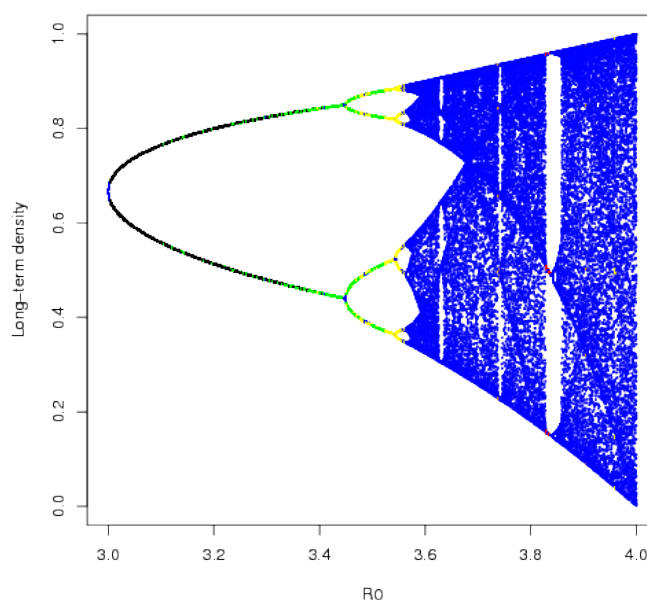
### Age-structured models

- 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

  - **Answer:** At the census time
  - **Answer:** 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

  - **Answer:** Populations with continuous reproduction (e.g. bacteria), may be better suited to continuous-time models
  - **Answer:** 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
    * **Answer:** A time when individuals gather together
    * **Answer:** 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 do we need to know? — 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
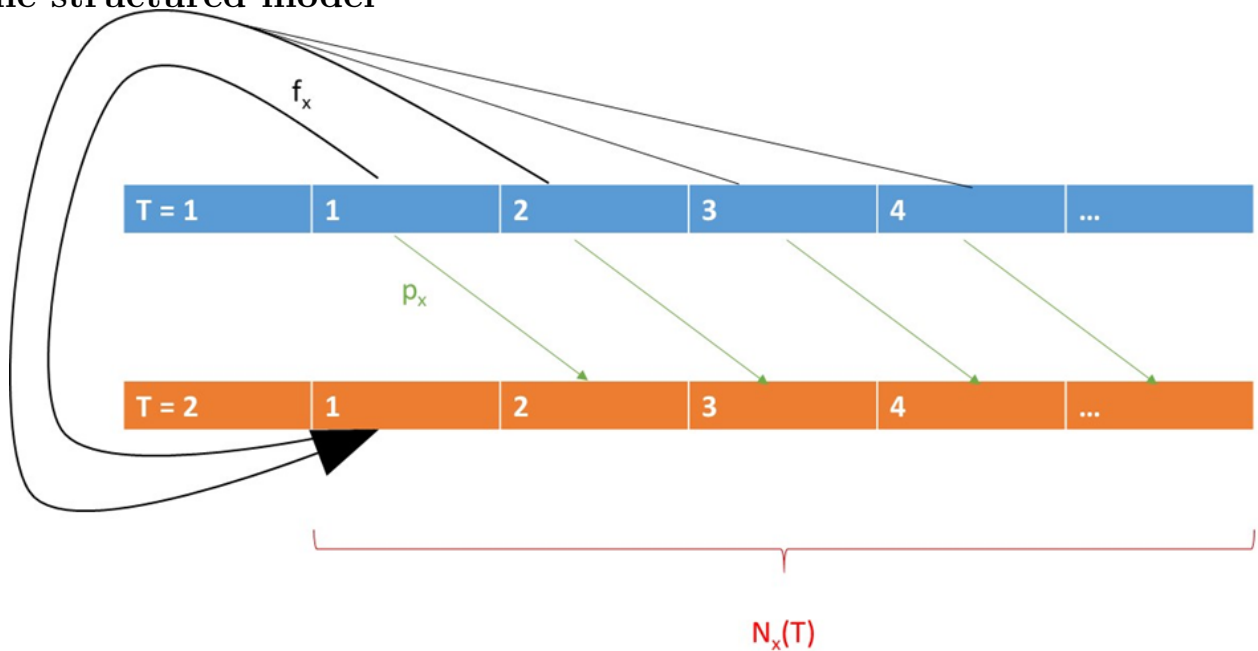


## 2.1  Model dynamics

### 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 $\lambda$
        * 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?
    - **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 $x$: $\ell_x$.

  - **Answer:** $\ell_x = p_1 \times \ldots p_{x-1}$

  - **Answer:** $\ell_x$ 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:

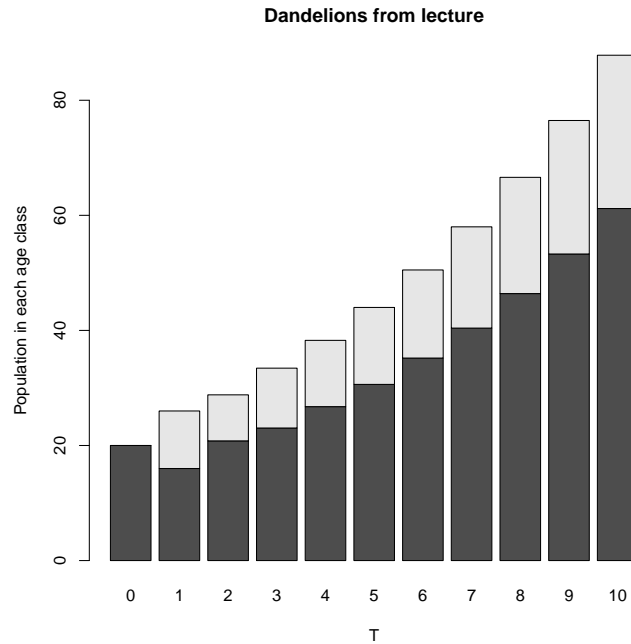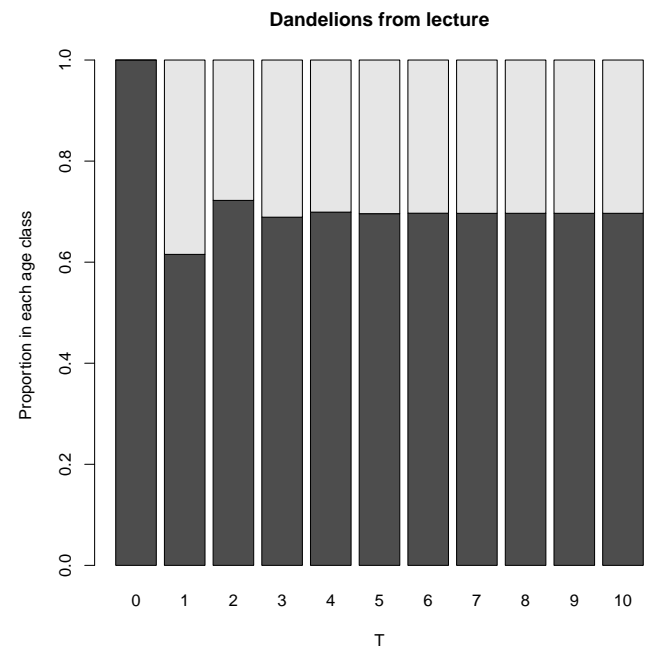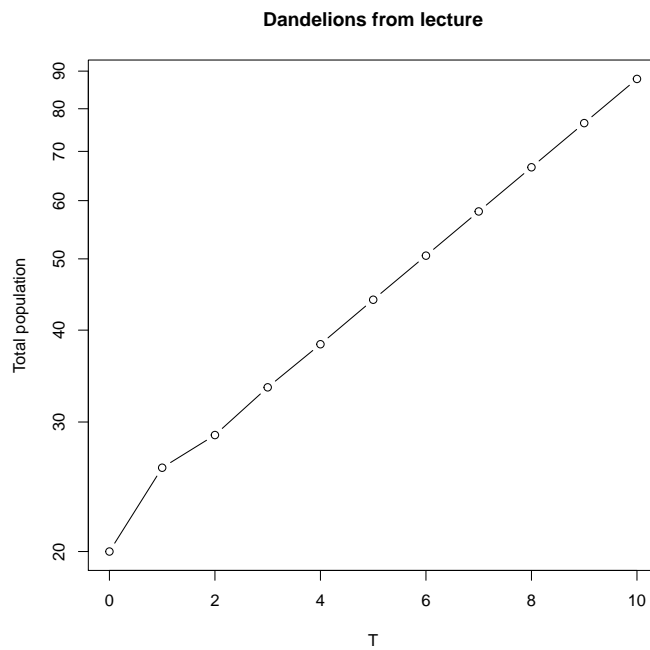  - **Answer:** $f_x \times \ell_x$

## 3.1 Examples

## Dandelion example

**Answer slide:** *Dandelion life table*

| $x$ | $f_x$ | $p_x$ | $\ell_x$ | $\ell_x f_x$ |
|---|---|---|---|---|
| 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?

  - **Answer:** Older age groups seem to be grouped for fecundity.
  - **Answer:** 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.
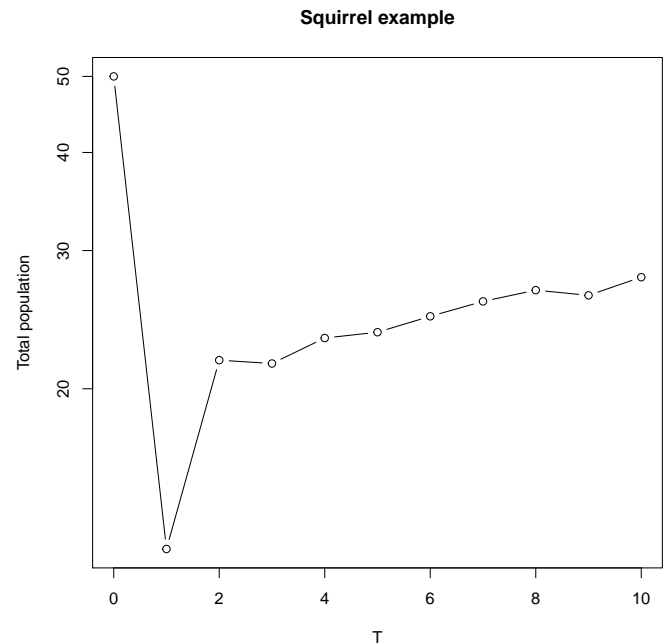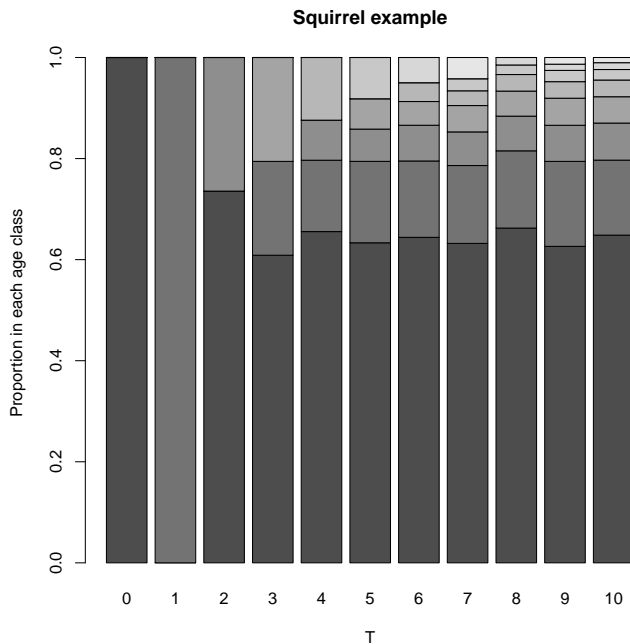    - ∗ **Answer:** This is what we call stage structure

## Answer slide: *Gray squirrel population example*

| $x$ | $f_x$ | $p_x$ | $\ell_x$ | $\ell_x f_x$ |
|---|---|---|---|---|
| 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

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**Squirrel example**      **Squirrel example**
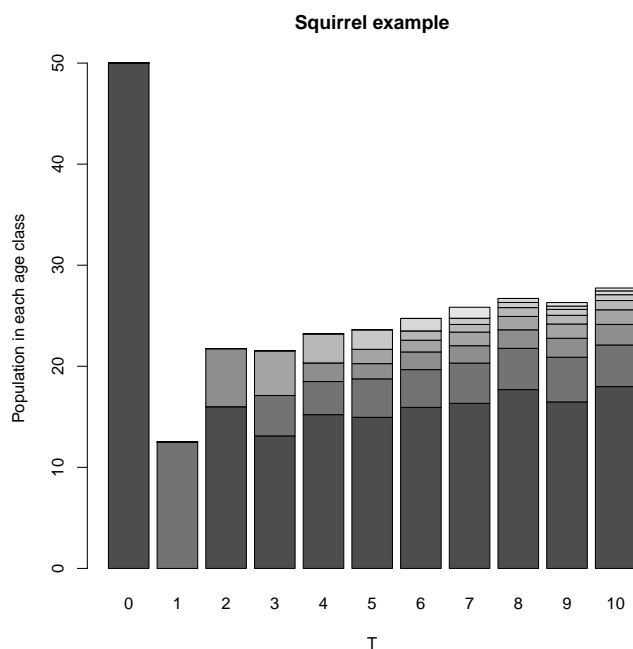
## 3.2 Calculation details

$f_x$ **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*

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

**Answer slide:** *Counting* after *reproduction*

    *Comment:* There are two different approaches

## 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 $\mathcal{R}$?
    - How does $\mathcal{R}$ respond to changes in various $p_x$ and $f_x$?

## 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?
        * **Answer:** In most populations $\ell$ can be very small for large $x$
        * **Answer:** In many populations, $f$ can be very large for large $x$

- Reproductive potential of old individuals *may* or *may not* be important

    - **Answer:** In many tree populations, most individuals don't survive to get huge, but the huge trees may have most of the total reproduction
    - **Answer:** In many bird populations, old birds produce well, but not enough to outweigh the low probability of surviving to get old.

## Comment slide: *Old individuals*

## 3.3  Measuring growth rates

## Comment slide: *Calculating $\lambda$*

- 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:

    - $\sum_x \ell_x f_x \lambda^{-x} = 1$

## $\lambda$ 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)?

    - **Answer:** $\mathcal{R} = \lambda$; each organism observed reproduces $\mathcal{R}$ offspring on average, all in one time step

- Poll: For a long-lived population?

    - **Answer:** The $\mathcal{R}$ offspring are produced slowly, so population changes slowly
        * **Answer:** $\lambda$ should be closer to 1 than $\mathcal{R}$ is.
        * **Answer:** But on the same side (same answer about whether population is growing)

## Studying population growth

- $\lambda$ and $\mathcal{R}$ give related 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?

  - **Answer:** The two phases (growth and decline) will be roughly balanced
  - **Answer:** Because otherwise the population would go to zero or infinity


# 4 Life-table patterns

## 4.1 Survivorship

## Patterns of survivorship

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

  - **Answer:** Younger individuals usually have lower survivorship
  - **Answer:** Older individuals often have lower survivorship

- What about $\ell_x$?

  - **Answer:** It goes down
  - **Answer:** But sometimes faster and sometimes slower
  - **Answer:** Best understood on a log scale

## 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?

  - **Answer:** 1
  - **Answer:** $\ell_1$ is the probability you're counted at age class 1, *given that* you're counted at age class 1.
  - **Answer:** We don't count individuals that we don't count

# Constant survivorship
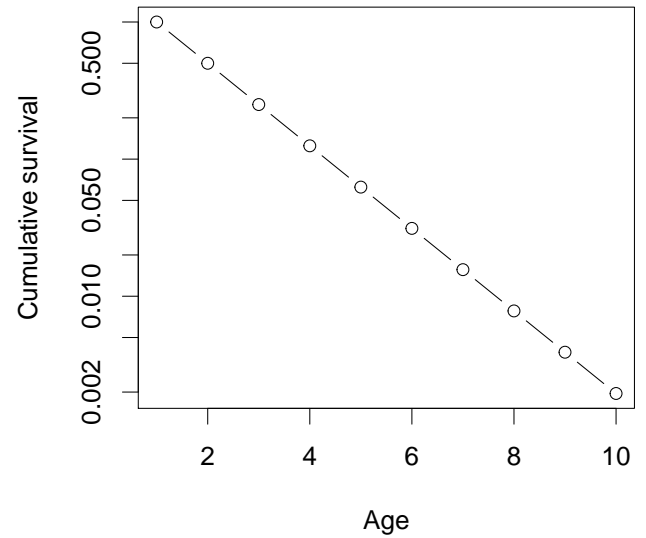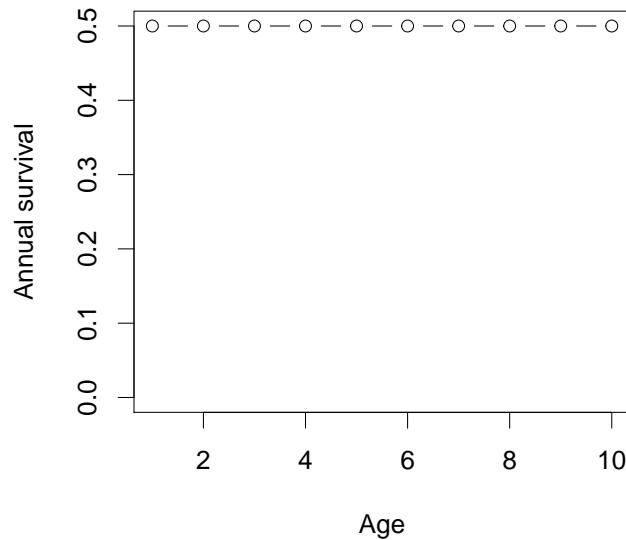


## "Types" of survivorship

- 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
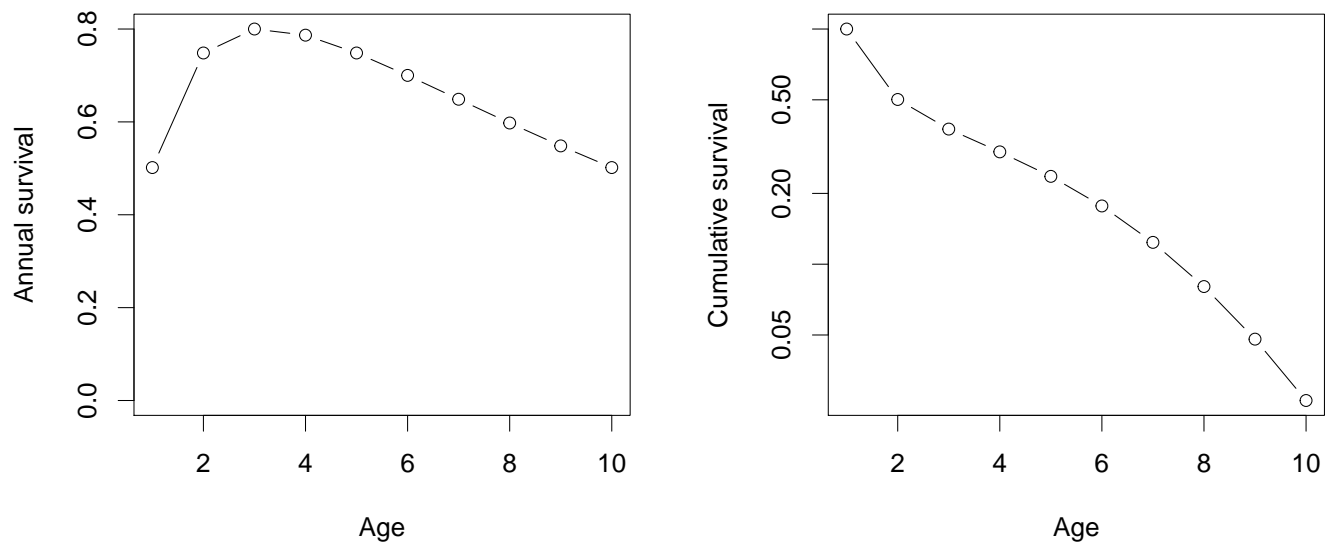
## 4.2 Fecundity

- 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 sex 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

  - **<u>Answer:</u>** Most birds, many large mammals

- It may also go up and then come down

  - **<u>Answer:</u>** people

- It may also go up and up as organisms get older

  - **<u>Answer:</u>** Many fish, many trees

### Age distributions

- Not covered this year

- `http://www.gapminder.org/population/tool/`

- `https://en.wikipedia.org/wiki/Population_pyramid`

# 5  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?

  - **Answer:** Large trees are larger
  - **Answer:** Population may be declining
  - **Answer:** Trees may spend longer in some size classes than in others
  - **Answer:** Life table may not be constant (smaller trees may recruit at certain times and places)

## 5.1  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
  - **Answer:** In stage-structured models survival is typically broken into:
    * **Answer:** Survival into same stage
    * **Answer:** Survival with recruitment (ie., to the next larger class of individuals)
  - 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
  - *Comment:* $\mathcal{R}$ is about the same as in age structured model

- 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


## 5.2 Regulated growth

- Our models in this unit assume 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

  - **Answer:** We know that real populations are regulated
  - **Answer:** Populations can't increase or decrease exponentially for very long

- 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