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?

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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 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?

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- Poll: 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

- Poll: What is the reproductive number?

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

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- If $\mathcal{R} = 1.2$, then λ

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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 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

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- 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

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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 $N_x(T+1)$

- Poll: 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)]

The structured model
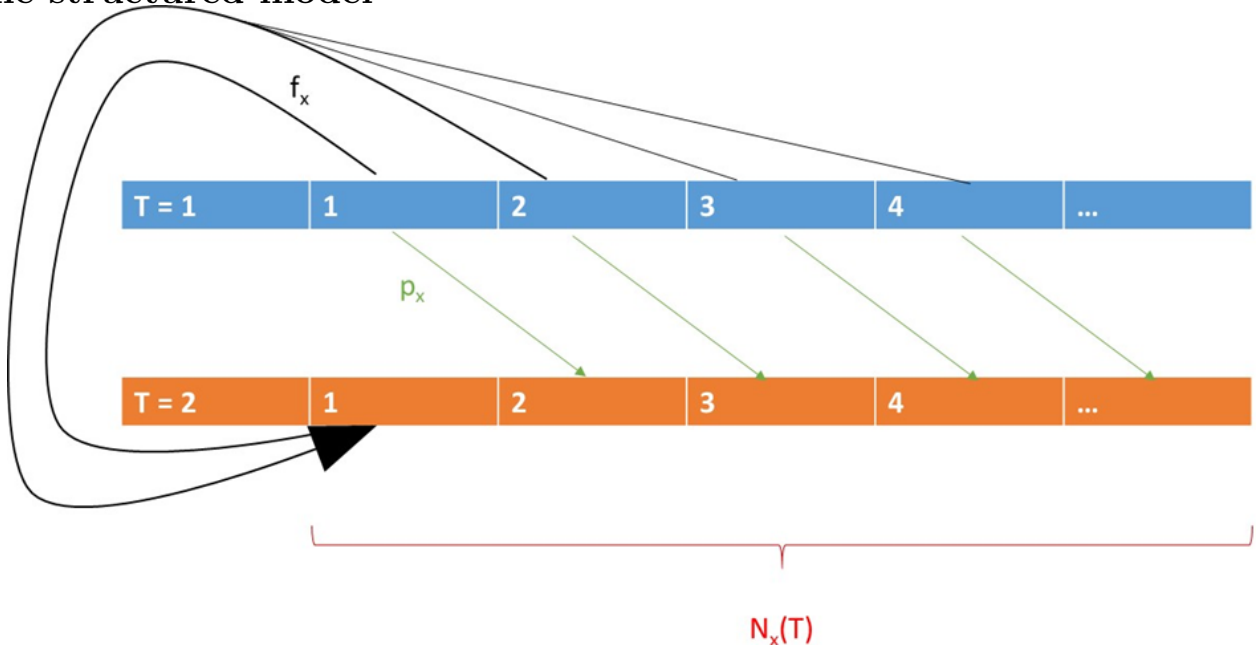
2.1 Model dynamics

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?

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- Skipping calculations, but you can poke if curious

- Spreadsheet link: http://tinyurl.com/DandelionModel2020

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.

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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*

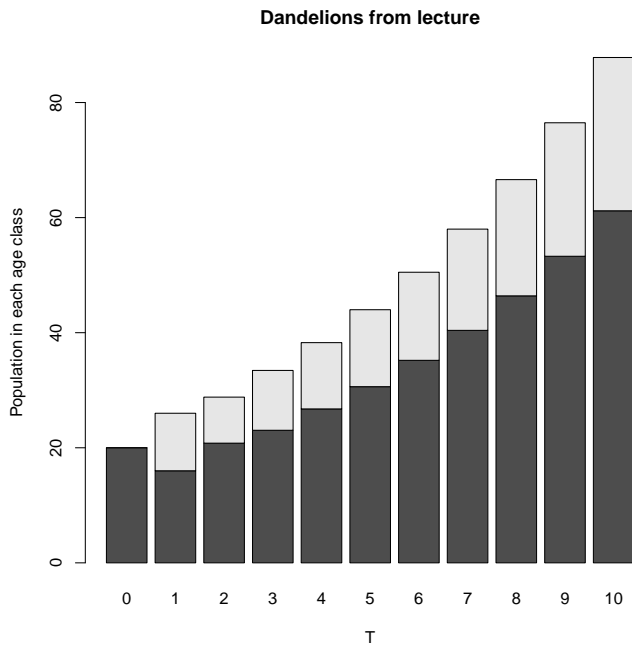 - We figure out expected contribution given you were ever counted by multiplying:
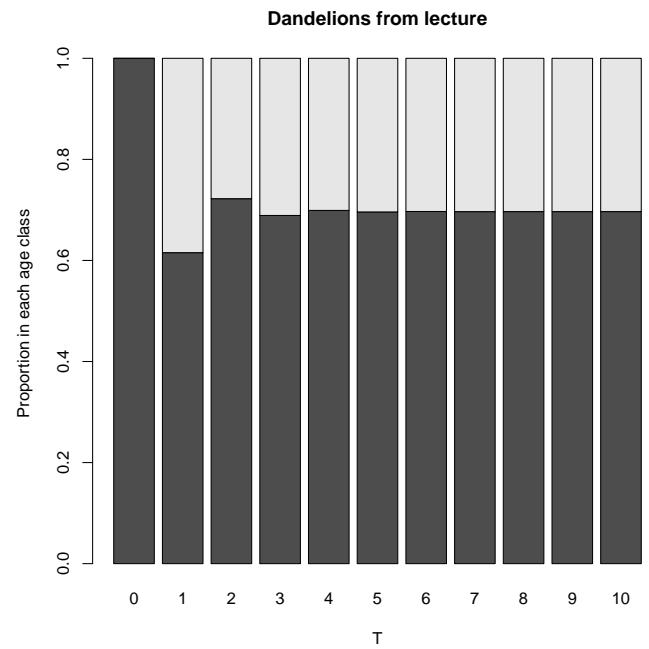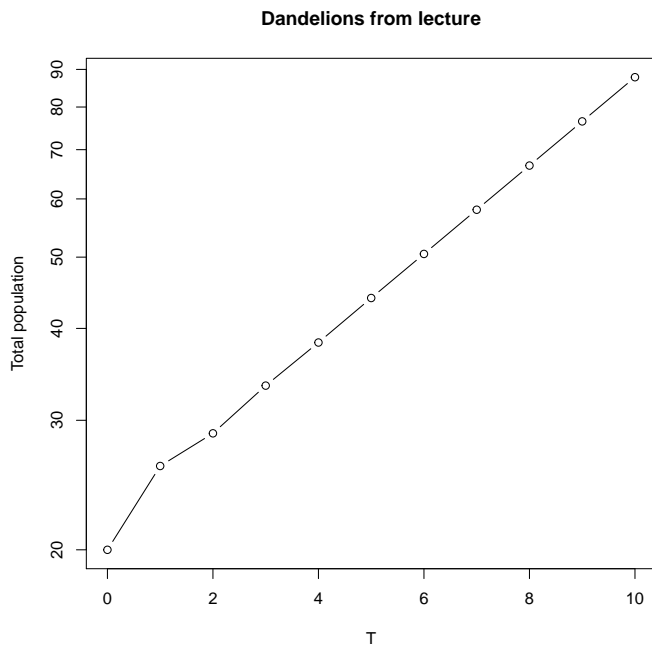
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3.1 Examples

Dandelion example
Dandelion life table

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

Dandelion dynamics

Dandelions from lecture

Dandelion dynamics

Dandelions from lecture

Dandelions from lecture

Squirrel example
Gray squirrel population example

x	f_x	p_x	ℓ_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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Gray squirrel dynamics

Squirrel example

Gray squirrel dynamics

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Squirrel example   **Squirrel example**
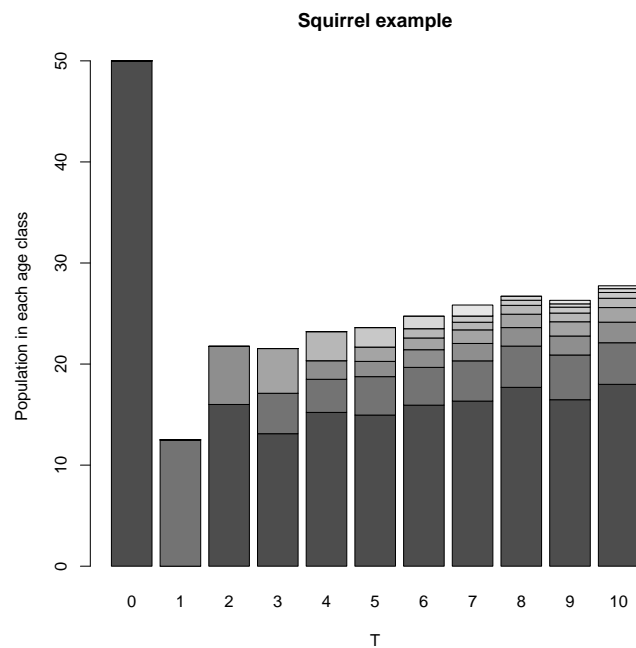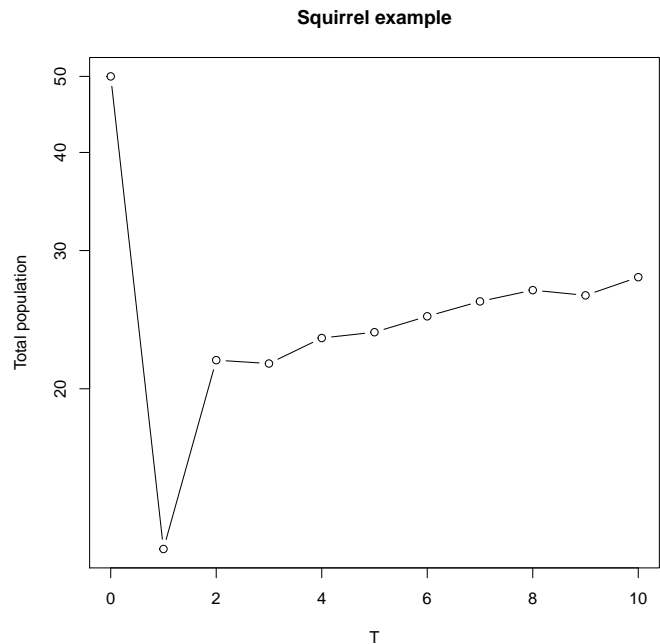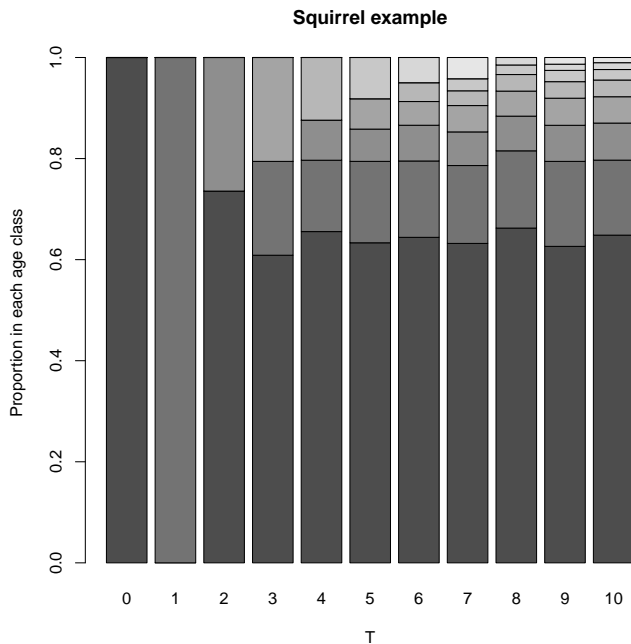
3.2 Calculation details

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?

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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

  – $\mathcal{R} = \sum_x \ell_x f_x$

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– 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 ℓ can be extreme

  – The contribution of an age class to $\mathcal{R}$ is $\ell_x f_x$

  – Poll: 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

λ and $\mathcal{R}$

- If the life table doesn't change, then λ is given by $\sum_x \ell_x f_x \lambda^{-x} = 1$

  – What's the relationship between λ 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 λ tell the same story about whether the population is increasing

Time scales

- λ 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)?

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- Poll: For a long-lived population?

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Studying population growth

- λ and $\mathcal{R}$ give related information about your population

- $\mathcal{R}$ is easier to calculate, and more generally useful

- But λ 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 λ

    – Complicated, but well-developed, theory

    – In a growing population, what happens early in life is more important to λ than to $\mathcal{R}$.

    – In a declining population, what happens late in life is more important to λ 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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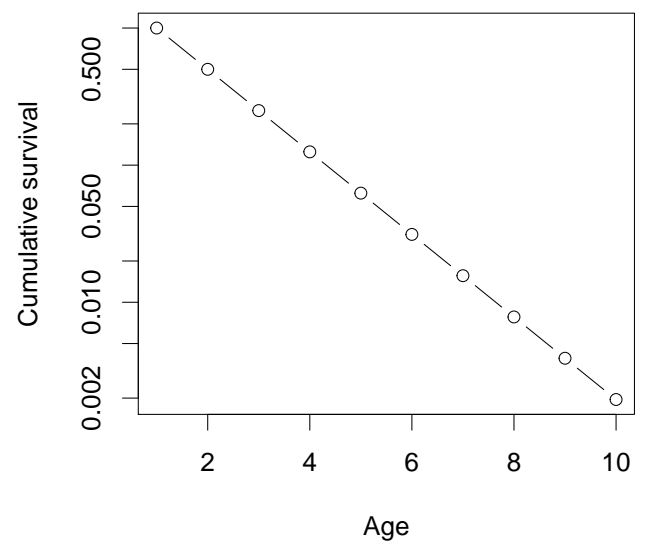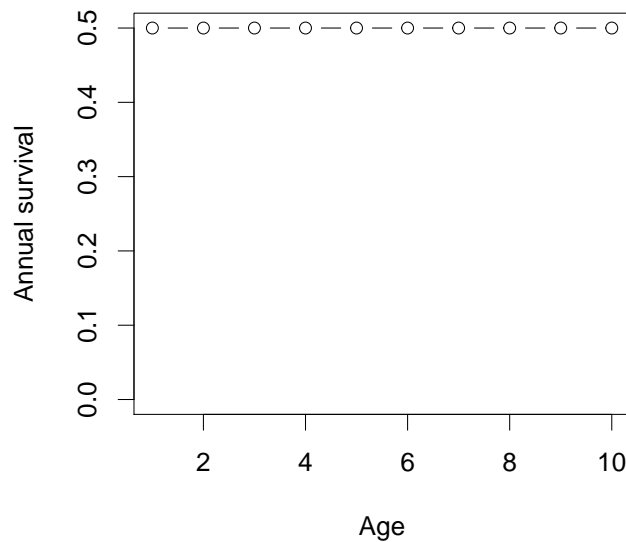 –

- What about ℓ_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 ℓ_1 when we count before reproduction?

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Constant survivorship

Age

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"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
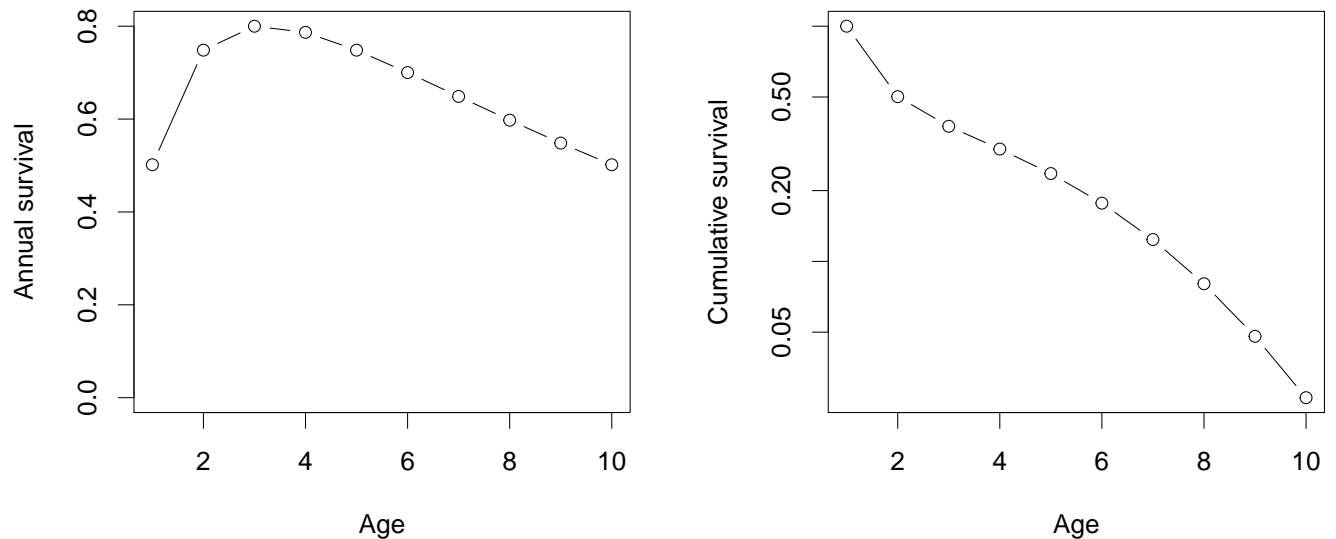
4.2 Fecundity

- 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?

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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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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?

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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
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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 λ (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 λ
  - 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 λ 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 λ 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:

  - ℓ_x, and
  - whether the population has been growing or declining recently