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?
  - **Answer:** All individuals can be counted the same. At least at census time
  - **Answer:** Never exactly true
- 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
- What is f in this example?
  - **Answer:** 0.8
- 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
- What is the reproductive number?
- **Answer:** If you become an adult you produce (on average)
  - **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?

- **Answer:** Population increases when $\mathcal{R} > 1$, so $\lambda > 1$ exactly when $\mathcal{R} > 1$
- If $\mathcal{R} = 1.2$, then λ
  - **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*:
  - **<u>Answer</u>:** Individuals behave independently, or (equivalently)
  - **<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

- Structured models can be done in either discrete or continuous time
- Continuous-time models are structurally simpler (and smoother)
- How do population characteristics affect the choice?
  - **<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
- Adding age structure is conceptually simpler with discrete time
  - **<u>Answer</u>:** So we'll do that.

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)

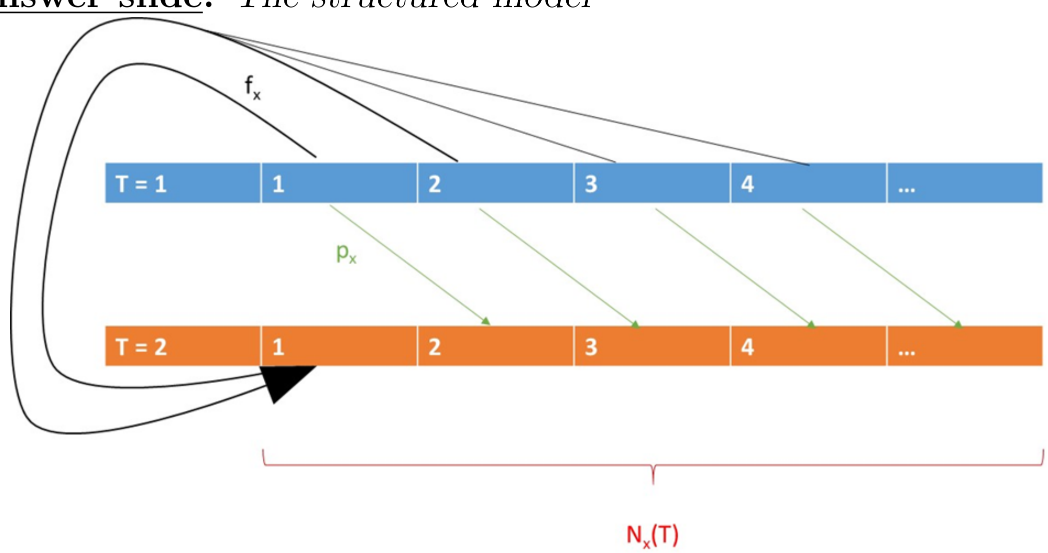
The conceptual model

- 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 do we need to know?
  - **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)]

Answer slide: *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
- What are the long-term dynamics of such a system?
  - **Answer:** Exponential growth or exponential decline

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: 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:** $f_x \times \ell_x$

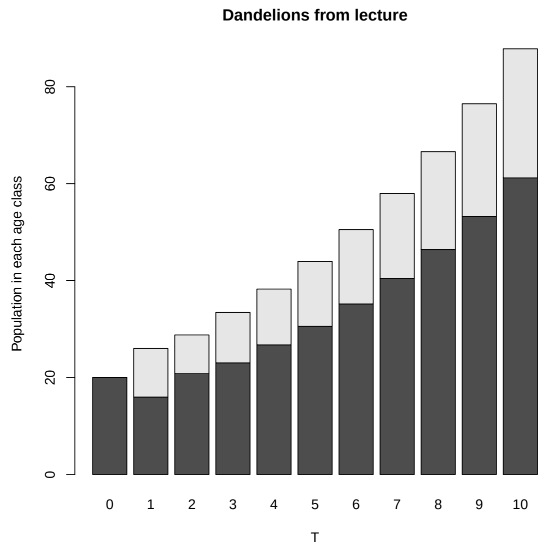
3.1 Examples

Dandelion example

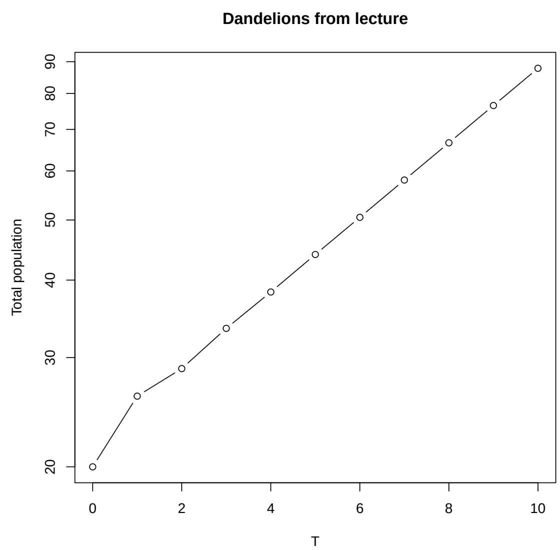
Answer slide: *Dandelion life table*

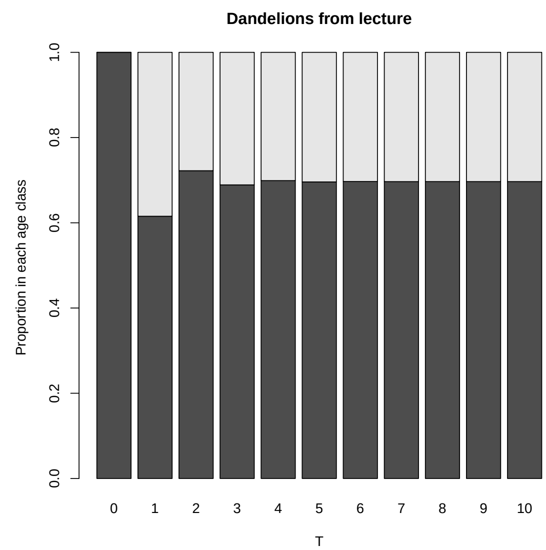
x	f_x	p_x	ℓ_x	$\ell_x f_x$
1	0.8	0.5	1.000	0.800
2	0.8	0	0.500	0.400
R				1.200

Dandelion dynamics



Dandelion dynamics





Squirrel example

Squirrel observations

- Do you notice anything strange about the squirrel life table?
  - **Answer:** Older age groups seem to be grouped for fecundity.

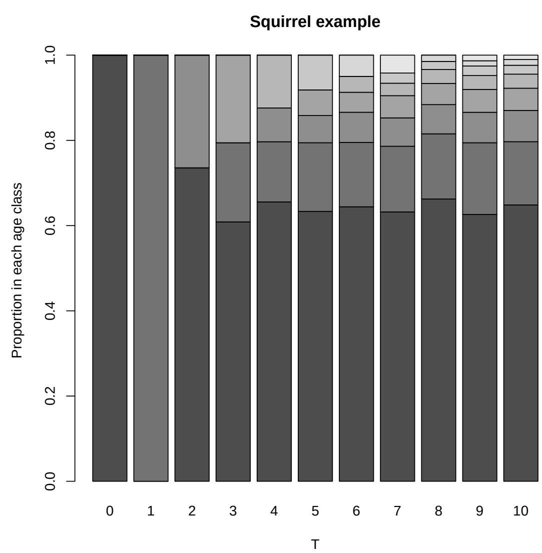
– **Answer:** Strange pattern in survivorship; do we really believe nobody survives past the last year?

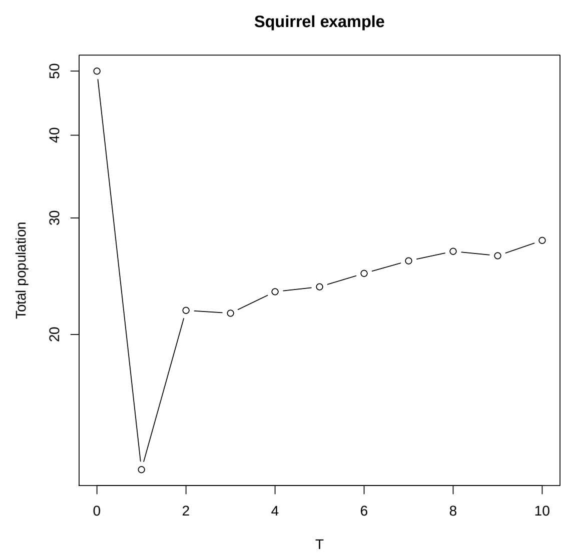
– **Answer:** Might be better to use a model where they keep track of 1 year, 2 year, and "adult" – not much harder.

Answer 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





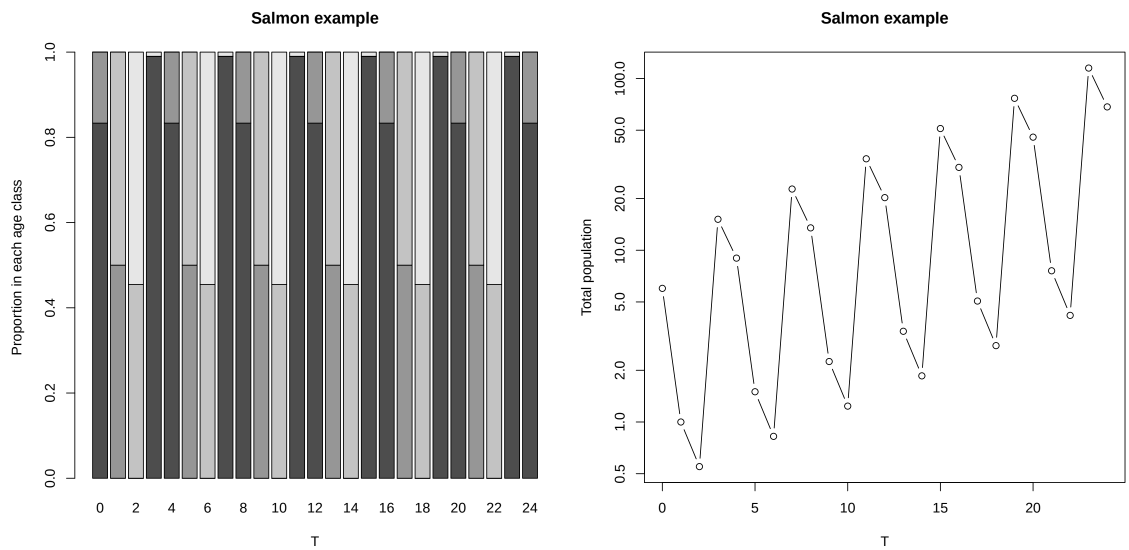
Salmon example

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

<u>Answer slide</u>: *Salmon example*

x	f_x	p_x	ℓ_x	$\ell_x f_x$
1	0	0.1	1.000	0.000
2	0	0.5	0.100	0.000
3	0	0.6	0.050	0.000
4	50	0	0.030	1.500
R				1.500

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?
  - **<u>Answer</u>:** To get f_x we multiply m_x by one or more survival terms, depending on when the census is
  - **<u>Answer</u>:** Need 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.

<u>Answer slide</u>: *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

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 $\mathcal{R}$?
  - Which values of p_x and f_x is $\mathcal{R}$ sensitive to?
    - **<u>Answer</u>:** The ps for young individuals affect all the ℓs.

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 $\ell_x f_x$
  - Extreme how?
  - **Answer:** In most populations ℓ 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 tree populations, most trees don't survive to get huge, but the huge trees may have most of the total reproduction
  - **Answer:** In bird populations, old birds produce fairly well, but not nearly enough to outweigh the low probability of being old.

Comment slide: *Old individuals*

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 λ bigger (or smaller) than the previous one
  - λ is the finite rate of increase, like before
- Looking back in time, the cohort x years ago is λ^{-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 λ 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 λ, would it continue to grow at rate λ.
- On the left-side each cohort started as λ times smaller than the one after it
  - Then got multiplied by ℓ_x.
- Under this assumption, is the next generation λ times bigger again?

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*
- 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
- For a long-lived population?

- **Answer:** The $\mathcal{R}$ offspring are produced slowly, so population changes slowly
  * **Answer:** λ 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

- λ and $\mathcal{R}$ give similar 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 $\mathcal{R}$.
- 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.
  - **Answer:** Because otherwise the population would go to zero or infinity

4 Life-table patterns

4.1 Survivorship

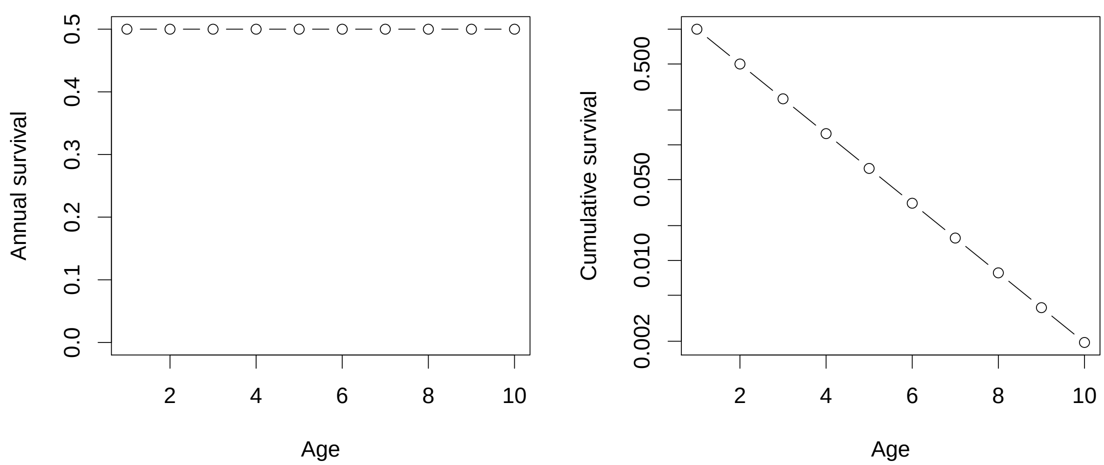
Patterns of survivorship

- 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 ℓ_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.
- What is ℓ_1 when we count before reproduction?
  - **Answer:** 1
  - **Answer:** ℓ_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

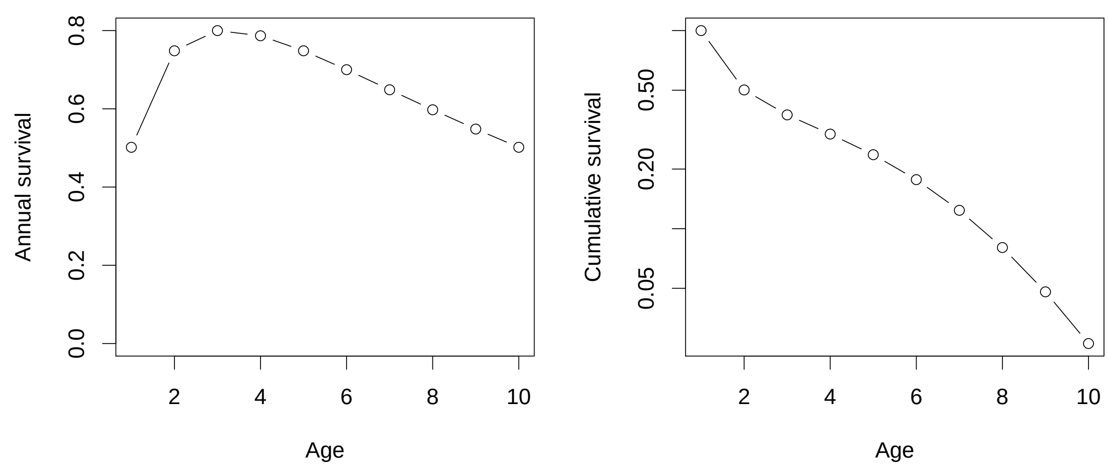
Constant survivorship



"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 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
  - **Answer:** Birds, large mammals
- It may also go up and then come down
  - **Answer:** people
- It may also go up and up as organisms get older
  - **Answer:** Fish, trees

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?
  - **Answer:** Distribution should be proportional to ℓ_x
- What if population is growing?
  - **Answer:** We expect proportionally more individuals in younger age classes
    - **Answer:** Number of births in more recent cohorts is larger

Stable age distribution

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

Patterns

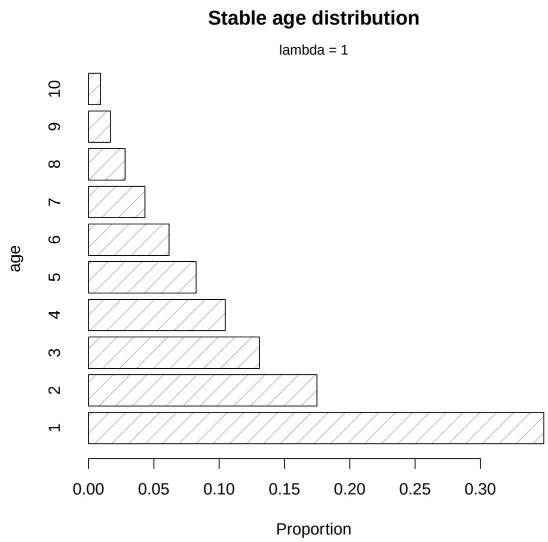
- Populations tend to be bottom-heavy (more individuals at lower age classes)
  - Many individuals born, few survive to older age classes
- If population is growing, this increases the lower classes further
  - More individuals born more recently
- If population is *declining*, this shifts the age distribution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

University cohorts

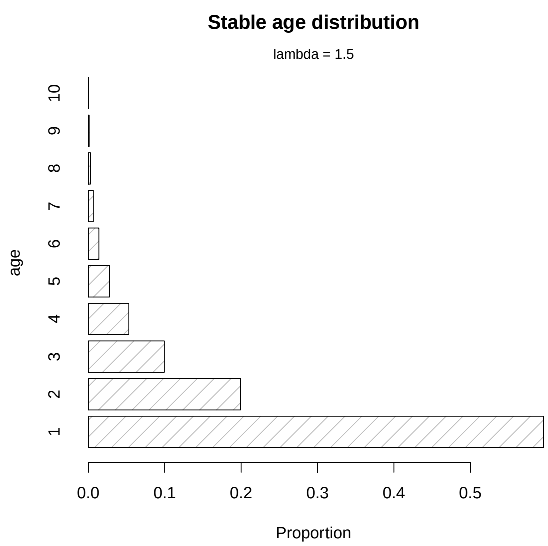
- McMaster accepts only first-year students. For any given stage (e.g., end of third year) the same proportion drop out each year
- What can you say about the relative size of the classes if:
  - The same number of students is admitted each year?
    * **Answer:** The lower classes are larger
  - More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

- Fewer students are admitted each year?
    * **Answer:** Anything could happen (drop outs and size change are operating in different directions)

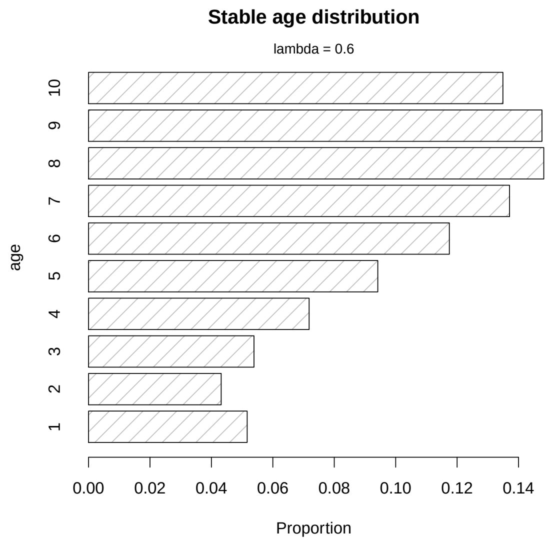
Age distributions



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?
- 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)

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
  - **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 λ (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 λ
  - 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 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
  - **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 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