

UNIT 3: Structured populations

Outline

Introduction

Example: biennial dandelions

Modeling approach

Constructing a model

Model dynamics

Life tables

Examples

Calculation details

Measuring growth rates

Life-table patterns

Survivorship

Fecundity

Age distributions

Other structured models

Stage structure

Regulated growth

Introduction

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

Introduction

- ▶ Up until now we've tracked populations with a single state variable (population size or population density)
- ▶ **Poll:** What assumption are we making?

Introduction

- ▶ Up until now we've tracked populations with a single state variable (population size or population density)
- ▶ Poll: What assumption are we making?
 - ▶ *

Introduction

- ▶ Up until now we've tracked populations with a single state variable (population size or population density)
- ▶ Poll: **What assumption are we making?**
 - ▶ * All individuals can be counted the same. At least at census time

Introduction

- ▶ Up until now we've tracked populations with a single state variable (population size or population density)
- ▶ Poll: **What assumption are we making?**
 - ▶ * All individuals can be counted the same. At least at census time
 - ▶ *

Introduction

- ▶ Up until now we've tracked populations with a single state variable (population size or population density)
- ▶ Poll: **What assumption are we making?**
 - ▶ * All individuals can be counted the same. At least at census time
 - ▶ * Never exactly true

Introduction

- ▶ Up until now we've tracked populations with a single state variable (population size or population density)
- ▶ Poll: What assumption are we making?
 - ▶ * All individuals can be counted the same. At least at census time
 - ▶ * Never exactly true
- ▶ What are some organisms for which this seems like a good approximation?

Introduction

- ▶ Up until now we've tracked populations with a single state variable (population size or population density)
- ▶ Poll: What assumption are we making?
 - ▶ * All individuals can be counted the same. At least at census time
 - ▶ * Never exactly true
- ▶ What are some organisms for which this seems like a good approximation?
 - ▶ *

Introduction

- ▶ Up until now we've tracked populations with a single state variable (population size or population density)
- ▶ Poll: What assumption are we making?
 - ▶ * All individuals can be counted the same. At least at census time
 - ▶ * Never exactly true
- ▶ What are some organisms for which this seems like a good approximation?
 - ▶ * Dandelions, bacteria, insects

Introduction

- ▶ Up until now we've tracked populations with a single state variable (population size or population density)
- ▶ Poll: **What assumption are we making?**
 - ▶ * All individuals can be counted the same. At least at census time
 - ▶ * Never exactly true
- ▶ What are some organisms for which this seems like a good approximation?
 - ▶ * Dandelions, bacteria, insects
- ▶ **What are some organisms that don't work so well?**

Introduction

- ▶ Up until now we've tracked populations with a single state variable (population size or population density)
- ▶ Poll: **What assumption are we making?**
 - ▶ * All individuals can be counted the same. At least at census time
 - ▶ * Never exactly true
- ▶ What are some organisms for which this seems like a good approximation?
 - ▶ * Dandelions, bacteria, insects
- ▶ What are some organisms that don't work so well?
 - ▶ *

Introduction

- ▶ Up until now we've tracked populations with a single state variable (population size or population density)
- ▶ Poll: **What assumption are we making?**
 - ▶ * All individuals can be counted the same. At least at census time
 - ▶ * Never exactly true
- ▶ What are some organisms for which this seems like a good approximation?
 - ▶ * Dandelions, bacteria, insects
- ▶ What are some organisms that don't work so well?
 - ▶ * Trees, people, codfish

Introduction

- ▶ Up until now we've tracked populations with a single state variable (population size or population density)
- ▶ Poll: **What assumption are we making?**
 - ▶ * All individuals can be counted the same. At least at census time
 - ▶ * Never exactly true
- ▶ What are some organisms for which this seems like a good approximation?
 - ▶ * Dandelions, bacteria, insects
- ▶ What are some organisms that don't work so well?
 - ▶ * 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

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 ...

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

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

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

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

Subsection 1

Example: biennial dandelions

Example: biennial dandelions

- ▶ Imagine a population of dandelions

Example: biennial dandelions

- ▶ Imagine a population of dandelions
 - ▶ Adults produce 80 seeds each year

Example: biennial dandelions

- ▶ Imagine a population of dandelions
 - ▶ Adults produce 80 seeds each year
 - ▶ 1% of seeds survive to become adults

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

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**

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?

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

How to study this population

- ▶ Choose a census time
 - ▶ Before reproduction or after

How to study this population

- ▶ Choose a census time
 - ▶ Before reproduction or after
 - ▶ Since we have complete cycle information, either one should work

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

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



Census choices

- ▶ Before reproduction
 - ▶ All individuals are adults



Census choices

- ▶ Before reproduction
 - ▶ All individuals are adults
 - ▶ We want to know how many adults we will see next year



Census choices

- ▶ Before reproduction
 - ▶ All individuals are adults
 - ▶ We want to know how many adults we will see next year
- ▶ After reproduction



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



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**



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



Example: biennial dandelions

- ▶ Imagine a population of dandelions

Example: biennial dandelions

- ▶ Imagine a population of dandelions
 - ▶ Adults produce 80 seeds each year

Example: biennial dandelions

- ▶ Imagine a population of dandelions
 - ▶ Adults produce 80 seeds each year
 - ▶ 1% of seeds survive to become adults

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

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**

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?

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?

What determines λ ?

- ▶ If we have 20 adults before reproduction, how many do we expect to see next time?

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 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?

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?
 - ▶ *

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?
 - ▶ * 0.8

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?
 - ▶ * 0.8
- ▶ Poll: What is p in this example?

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?
 - ▶ * 0.8
- ▶ Poll: What is p in this example?
 - ▶ *

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?
 - ▶ * 0.8
- ▶ Poll: What is p in this example?
 - ▶ * 0.5 for 1-year-olds and 0 for 2-year-olds.

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?
 - ▶ * 0.8
- ▶ Poll: What is p in this example?
 - ▶ * 0.5 for 1-year-olds and 0 for 2-year-olds.
 - ▶ *

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?
 - ▶ * 0.8
- ▶ Poll: What is p in this example?
 - ▶ * 0.5 for 1-year-olds and 0 for 2-year-olds.
 - ▶ * We can't take an average, because we don't know the population structure

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?
 - ▶ * 0.8
- ▶ Poll: What is p in this example?
 - ▶ * 0.5 for 1-year-olds and 0 for 2-year-olds.
 - ▶ * 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

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 determines \mathcal{R} ?

- ▶ \mathcal{R} is the average total number of offspring produced by an individual over their lifespan
- ▶ Can start at any stage, but need to close the loop
- ▶ **Poll:** What is the reproductive number?

What determines \mathcal{R} ?

- ▶ \mathcal{R} is the average total number of offspring produced by an individual over their lifespan
- ▶ Can start at any stage, but need to close the loop
- ▶ Poll: What is the reproductive number?
- ▶ *

What 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?
- ▶ * If you become an adult you produce (on average)

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?
- ▶ * If you become an adult you produce (on average)
 - ▶ *

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?
- ▶ * If you become an adult you produce (on average)
 - ▶ * 0.8 adults your first year

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?
- ▶ * If you become an adult you produce (on average)
 - ▶ * 0.8 adults your first year
 - ▶ *

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?**
- ▶ * If you become an adult you produce (on average)
 - ▶ * 0.8 adults your first year
 - ▶ * 0.4 adults your second year

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?
- ▶ * If you become an adult you produce (on average)
 - ▶ * 0.8 adults your first year
 - ▶ * 0.4 adults your second year
- ▶ *

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?
- ▶ * If you become an adult you produce (on average)
 - ▶ * 0.8 adults your first year
 - ▶ * 0.4 adults your second year
- ▶ * $\mathcal{R} = 1.2$

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?
- ▶ * If you become an adult you produce (on average)
 - ▶ * 0.8 adults your first year
 - ▶ * 0.4 adults your second year
- ▶ * $\mathcal{R} = 1.2$

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



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

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

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

- ▶ * Population increases when $\mathcal{R} > 1$, so $\lambda > 1$ exactly when $\mathcal{R} > 1$
- ▶ If $\mathcal{R} = 1.2$, then λ

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

- ▶ * Population increases when $\mathcal{R} > 1$, so $\lambda > 1$ exactly when $\mathcal{R} > 1$
- ▶ If $\mathcal{R} = 1.2$, then λ
 - ▶ *

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

- ▶ * Population increases when $\mathcal{R} > 1$, so $\lambda > 1$ exactly when $\mathcal{R} > 1$
- ▶ If $\mathcal{R} = 1.2$, then λ
 - ▶ * > 1 – the population is increasing

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

- ▶ * Population increases when $\mathcal{R} > 1$, so $\lambda > 1$ exactly when $\mathcal{R} > 1$
- ▶ If $\mathcal{R} = 1.2$, then λ
 - ▶ * > 1 – the population is increasing
 - ▶ *

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

- ▶ * Population increases when $\mathcal{R} > 1$, so $\lambda > 1$ exactly when $\mathcal{R} > 1$
- ▶ If $\mathcal{R} = 1.2$, then λ
 - ▶ * > 1 – the population is increasing
 - ▶ * < 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

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

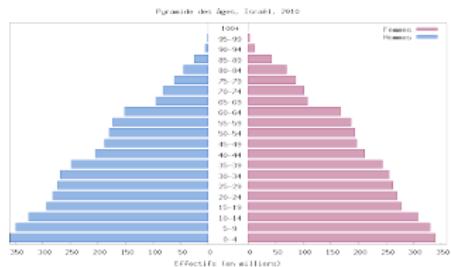
- ▶ * Population increases when $\mathcal{R} > 1$, so $\lambda > 1$ exactly when $\mathcal{R} > 1$
- ▶ If $\mathcal{R} = 1.2$, then λ
 - ▶ * > 1 – the population is increasing
 - ▶ * < 1.2 – the life cycle takes more than 1 year, so it should take more than one year for the population to increase 1.2 times

Subsection 2

Modeling approach

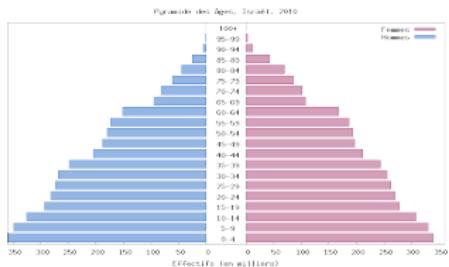
Modeling approach

- In this unit, we will construct *simple* models of structured populations



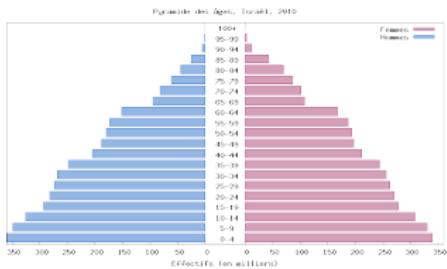
Modeling approach

- ▶ In this unit, we will construct *simple* models of structured populations
 - ▶ To explore how structure might affect population dynamics



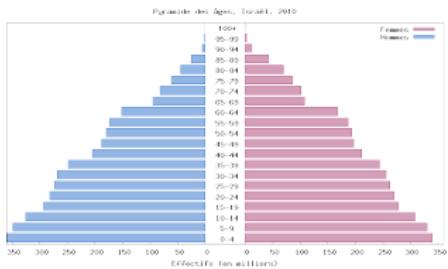
Modeling approach

- ▶ 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



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*

Regulation

- ▶ *Simple* population models with regulation can have extremely complicated dynamics
- ▶ *Structured* population models with regulation can have insanely complicated dynamics

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*:

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*:

▶ *

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*:
 - ▶ * Individuals behave independently, or (equivalently)

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*:
 - ▶ * Individuals behave independently, or (equivalently)
 - ▶ *

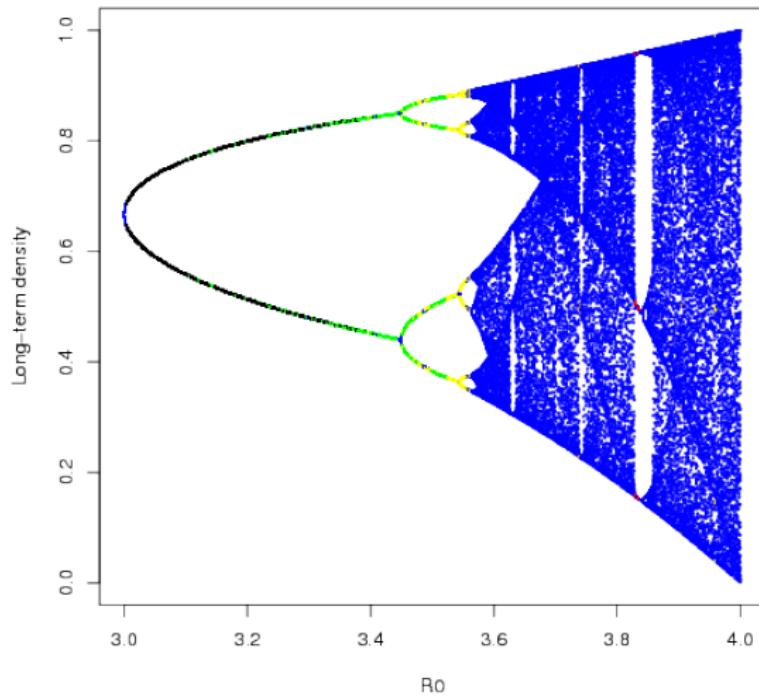
Regulation

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

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

Complexity



Age-structured models

- The most common approach is to structure by age



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”



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



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



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



Stage-structured models

- ▶ In stage-structured models, we model how many individuals there are in different stages
 - ▶ I.e., newborns, juveniles, adults



Stage-structured models

- ▶ In stage-structured models, we model how many individuals there are in different stages
 - ▶ I.e., newborns, juveniles, adults
 - ▶ More flexible than an age-structured model



Stage-structured models

- ▶ In stage-structured models, we model how many individuals there are in different stages
 - ▶ I.e., newborns, juveniles, adults
 - ▶ More flexible than an age-structured model
 - ▶ Example: forest trees may survive on very little light for a long time before they have the opportunity to recruit to the sapling stage



Stage-structured models

- ▶ In stage-structured models, we model how many individuals there are in different stages
 - ▶ I.e., newborns, juveniles, adults
 - ▶ More flexible than an age-structured model
 - ▶ Example: forest trees may survive on very little light for a long time before they have the opportunity to recruit to the sapling stage



Discrete vs. continuous time

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

Discrete vs. continuous time

- ▶ Structured models can be done in either discrete or continuous time
- ▶ **Continuous-time models are structurally simpler (and smoother)**

Discrete vs. continuous time

- ▶ Structured models can be done in either discrete or continuous time
- ▶ Continuous-time models are structurally simpler (and smoother)
- ▶ **Poll: How do population characteristics affect the choice?**

Discrete vs. continuous time

- ▶ Structured models can be done in either discrete or continuous time
- ▶ Continuous-time models are structurally simpler (and smoother)
- ▶ Poll: How do population characteristics affect the choice?
 - ▶ *

Discrete vs. continuous time

- ▶ Structured models can be done in either discrete or continuous time
- ▶ Continuous-time models are structurally simpler (and smoother)
- ▶ Poll: How do population characteristics affect the choice?
 - ▶ * Populations with continuous reproduction (e.g. bacteria), may be better suited to continuous-time models

Discrete vs. continuous time

- ▶ Structured models can be done in either discrete or continuous time
- ▶ Continuous-time models are structurally simpler (and smoother)
- ▶ Poll: How do population characteristics affect the choice?
 - ▶ * Populations with continuous reproduction (e.g. bacteria), may be better suited to continuous-time models
 - ▶ *

Discrete vs. continuous time

- ▶ Structured models can be done in either discrete or continuous time
- ▶ Continuous-time models are structurally simpler (and smoother)
- ▶ Poll: How do population characteristics affect the choice?
 - ▶ * Populations with continuous reproduction (e.g. bacteria), may be better suited to continuous-time models
 - ▶ * Populations with **synchronous** reproduction (e.g., moths) may be better suited to discrete-time models

Discrete vs. continuous time

- ▶ Structured models can be done in either discrete or continuous time
- ▶ Continuous-time models are structurally simpler (and smoother)
- ▶ Poll: How do population characteristics affect the choice?
 - ▶ * Populations with continuous reproduction (e.g. bacteria), may be better suited to continuous-time models
 - ▶ * Populations with **synchronous** reproduction (e.g., moths) may be better suited to discrete-time models
- ▶ Adding age structure is conceptually simpler with discrete time

Discrete vs. continuous time

- ▶ Structured models can be done in either discrete or continuous time
- ▶ Continuous-time models are structurally simpler (and smoother)
- ▶ Poll: How do population characteristics affect the choice?
 - ▶ * Populations with continuous reproduction (e.g. bacteria), may be better suited to continuous-time models
 - ▶ * Populations with **synchronous** reproduction (e.g., moths) may be better suited to discrete-time models
- ▶ Adding age structure is conceptually simpler with discrete time
 - ▶ *

Discrete vs. continuous time

- ▶ Structured models can be done in either discrete or continuous time
- ▶ Continuous-time models are structurally simpler (and smoother)
- ▶ Poll: How do population characteristics affect the choice?
 - ▶ * Populations with continuous reproduction (e.g. bacteria), may be better suited to continuous-time models
 - ▶ * Populations with **synchronous** reproduction (e.g., moths) may be better suited to discrete-time models
- ▶ Adding age structure is conceptually simpler with discrete time
 - ▶ * So we'll do that.

Discrete vs. continuous time

- ▶ Structured models can be done in either discrete or continuous time
- ▶ Continuous-time models are structurally simpler (and smoother)
- ▶ Poll: How do population characteristics affect the choice?
 - ▶ * Populations with continuous reproduction (e.g. bacteria), may be better suited to continuous-time models
 - ▶ * Populations with **synchronous** reproduction (e.g., moths) may be better suited to discrete-time models
- ▶ Adding age structure is conceptually simpler with discrete time
 - ▶ * So we'll do that.

Outline

Introduction

Example: biennial dandelions

Modeling approach

Constructing a model

Model dynamics

Life tables

Examples

Calculation details

Measuring growth rates

Life-table patterns

Survivorship

Fecundity

Age distributions

Other structured models

Stage structure

Regulated growth

Constructing a model

- ▶ This section will focus on **linear, discrete-time, age-structured** models

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

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*

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

When to count

- ▶ We will choose a census time that is appropriate for our study
 - ▶ Before reproduction, to have the fewest number of individuals

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

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

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
 - ▶ *

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
 - ▶ * A time when individuals gather together

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
 - ▶ * A time when individuals gather together
 - ▶ *

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
 - ▶ * A time when individuals gather together
 - ▶ * A time when they are easy to find (insect pupae)

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
 - ▶ * A time when individuals gather together
 - ▶ * 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 .

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 $N_x(T)$

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

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 $N_x(T + 1)$

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?

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?
 - ▶ *

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?**
 - ▶ * The survival probability of each age group: p_x

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?**
 - ▶ * The survival probability of each age group: p_x
 - ▶ *

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?**
 - ▶ * The survival probability of each age group: p_x
 - ▶ * The average fecundity of each age group: f_x

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?**
 - ▶ * The survival probability of each age group: p_x
 - ▶ * 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:

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)]

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)]

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)]

Subsection 1

Model dynamics

Short-term dynamics

- ▶ This model's short-term dynamics will depend on parameters ...

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

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

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

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

Long-term dynamics

- ▶ If a population follows a model like this, it will tend to reach
 - ▶ a **stable age distribution**:

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

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**

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

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?

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?**
 - ▶ *

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?
 - ▶ * Exponential growth or exponential decline

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?
 - ▶ * Exponential growth or exponential decline

Exception

- ▶ Populations with **independent cohorts** do not tend to reach a stable age distribution

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

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

Exception

- ▶ Populations with **independent cohorts** do not tend to reach a stable age distribution
 - ▶ A **cohort** is a group that enters the population at the same time
 - ▶ We say my cohort and your cohort interact if my children might be in the same cohort as your children
 - ▶ **or my grandchildren might be in the same cohort as your great-grandchildren**

Exception

- ▶ Populations with **independent cohorts** do not tend to reach a stable age distribution
 - ▶ A **cohort** is a group that enters the population at the same time
 - ▶ We say my cohort and your cohort interact if my children might be in the same cohort as your children
 - ▶ or my grandchildren might be in the same cohort as your great-grandchildren
 - ▶ ...

Exception

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

Exception

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

Independent cohorts

- ▶ Some populations might have independent cohorts:

Independent cohorts

- ▶ Some populations might have independent cohorts:
 - ▶ If salmon reproduce *exactly* every four years, then:

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, ...

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, ...

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**

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, . . .

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, . . .

Outline

Introduction

Example: biennial dandelions

Modeling approach

Constructing a model

Model dynamics

Life tables

Examples

Calculation details

Measuring growth rates

Life-table patterns

Survivorship

Fecundity

Age distributions

Other structured models

Stage structure

Regulated growth

Life tables

- ▶ People often study structured models using **life tables**

Life tables

- ▶ People often study structured models using **life tables**
- ▶ A life table is made *from the perspective of a particular census time*

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:

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)

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)**

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**

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

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 .

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 .

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 .

▶ *

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 .
 - ▶ * $\ell_x = p_1 \times \dots \times p_{x-1}$

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 .
 - ▶ $\ell_x = p_1 \times \dots \times p_{x-1}$
 - ▶ *

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 .
 - ▶ $\ell_x = p_1 \times \dots \times p_{x-1}$
 - ▶ 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)

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 .
 - ▶ $\ell_x = p_1 \times \dots \times p_{x-1}$
 - ▶ 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*

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:

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:
 - ▶ *

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:
 - ▶ $f_x \times \ell_x$

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:
 - ▶ $f_x \times \ell_x$

Subsection 1

Examples

Dandelion example



Example: biennial dandelions

- ▶ Adults produce 80 seeds each

Example: biennial dandelions

- ▶ Adults produce 80 seeds each
- ▶ 1% of seeds survive to become adults

Example: biennial dandelions

- ▶ Adults produce 80 seeds each
- ▶ 1% of seeds survive to become adults
- ▶ 50% of first-year adults survive to reproduce again

Example: biennial dandelions

- ▶ Adults produce 80 seeds each
- ▶ 1% of seeds survive to become adults
- ▶ 50% of first-year adults survive to reproduce again
- ▶ **Second-year adults never survive**

Example: biennial dandelions

- ▶ Adults produce 80 seeds each
- ▶ 1% of seeds survive to become adults
- ▶ 50% of first-year adults survive to reproduce again
- ▶ Second-year adults never survive
- ▶ What does the life table look like?

Example: biennial dandelions

- ▶ Adults produce 80 seeds each
- ▶ 1% of seeds survive to become adults
- ▶ 50% of first-year adults survive to reproduce again
- ▶ Second-year adults never survive
- ▶ What does the life table look like?

Dandelion life table

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

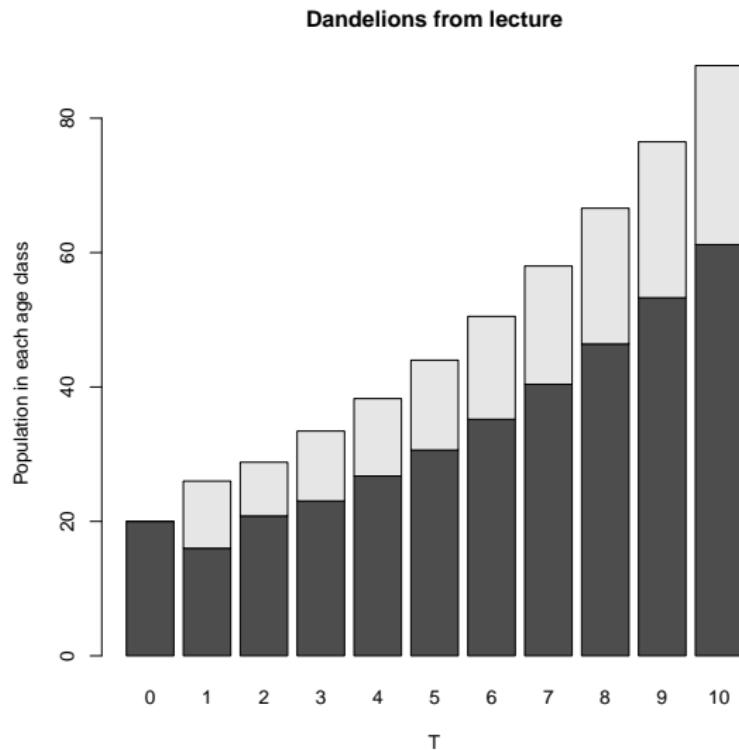
Dandelion life table

x	f_x	p_x	ℓ_x	$\ell_x f_x$
1	0.8	0.5		
2	0.8	0		
R				

Dandelion life table

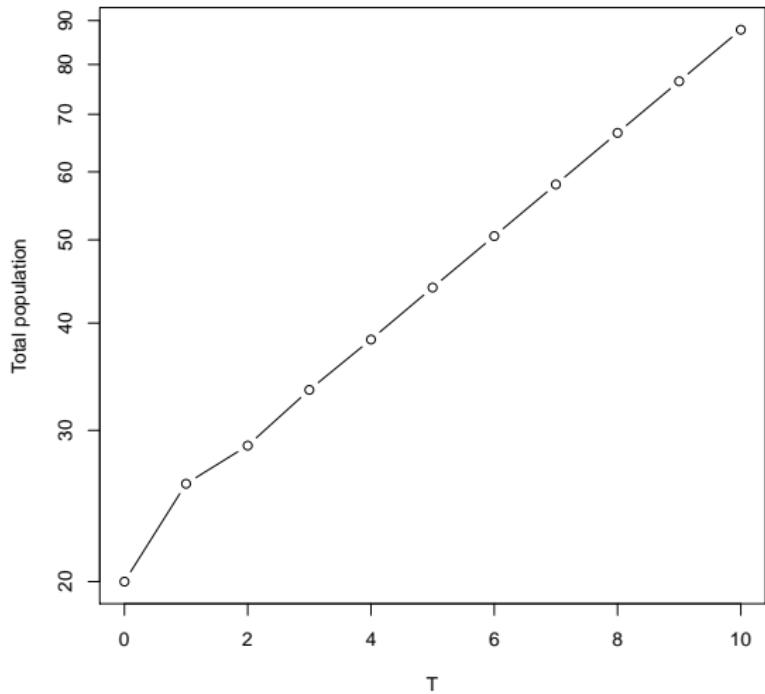
x	f_x	p_x	ℓ_x	$\ell_x f_x$
1	0.8	0.5	1.000	0.800
2	0.8	0	0.500	0.400
R				1.200

Dandelion dynamics

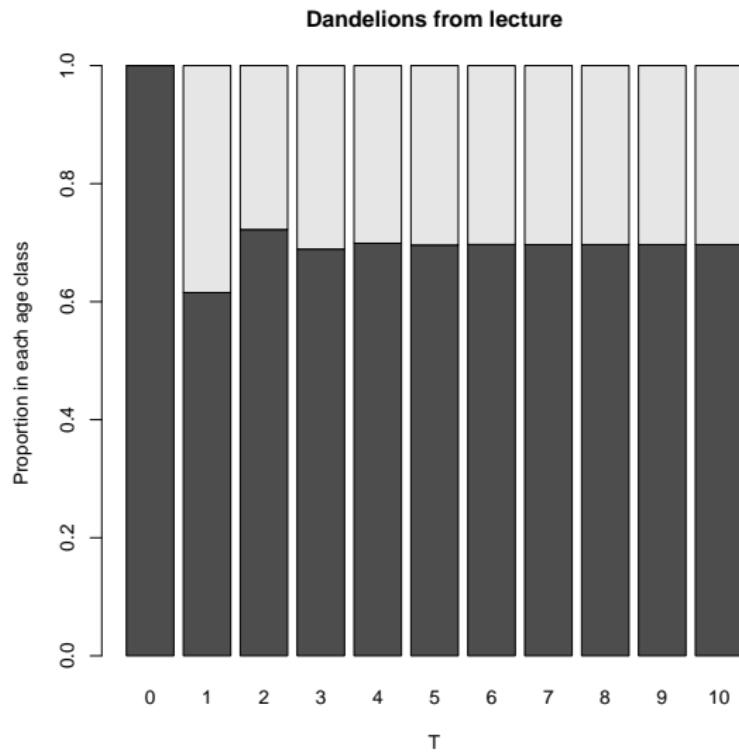


Dandelion dynamics

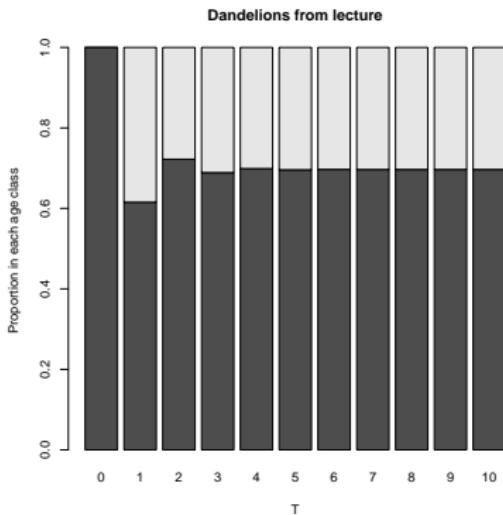
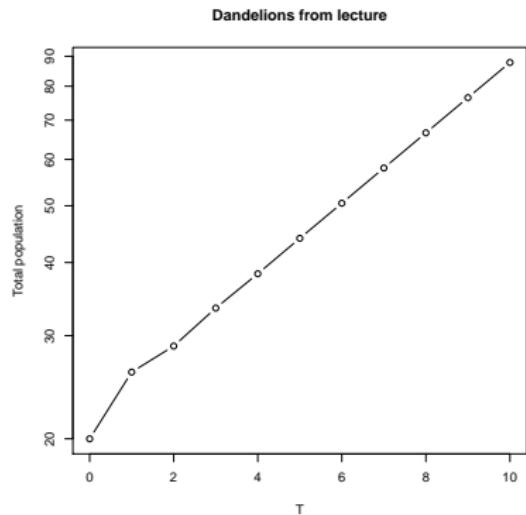
Dandelions from lecture



Dandelion dynamics



Dandelion dynamics



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?

Squirrel observations

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

Squirrel observations

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

Squirrel observations

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

Squirrel observations

- ▶ Poll: Do you notice anything strange about the squirrel life table?
 - ▶ * Older age groups seem to be grouped for fecundity.
 - ▶ * Strange pattern in survivorship; do we really believe nobody survives past the last year?

Squirrel observations

- ▶ Poll: Do you notice anything strange about the squirrel life table?
 - ▶ * Older age groups seem to be grouped for fecundity.
 - ▶ * Strange pattern in survivorship; do we really believe nobody survives past the last year?
 - ▶ *

Squirrel observations

- ▶ Poll: Do you notice anything strange about the squirrel life table?
 - ▶ * Older age groups seem to be grouped for fecundity.
 - ▶ * Strange pattern in survivorship; do we really believe nobody survives past the last year?
 - ▶ * Might be better to use a model where they keep track of 1 year, 2 year, and "adult" – not much harder.

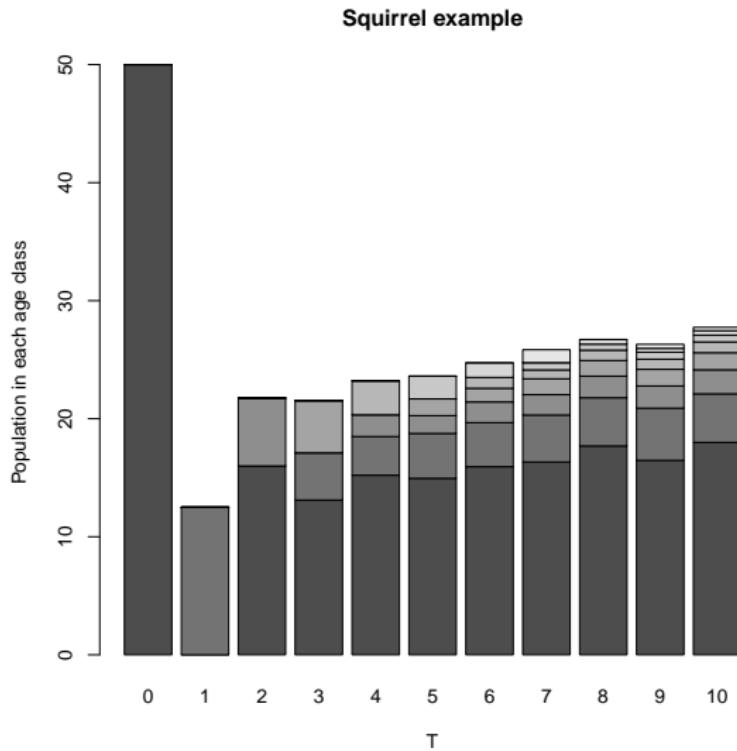
Squirrel observations

- ▶ Poll: Do you notice anything strange about the squirrel life table?
 - ▶ * Older age groups seem to be grouped for fecundity.
 - ▶ * Strange pattern in survivorship; do we really believe nobody survives past the last year?
 - ▶ * Might be better to use a model where they keep track of 1 year, 2 year, and "adult" – not much harder.

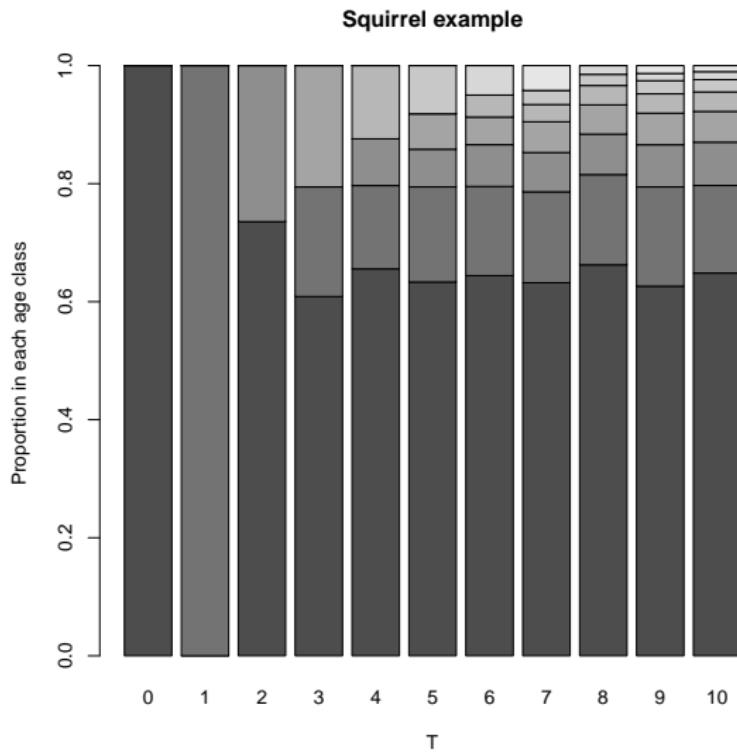
Gray squirrel population example

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

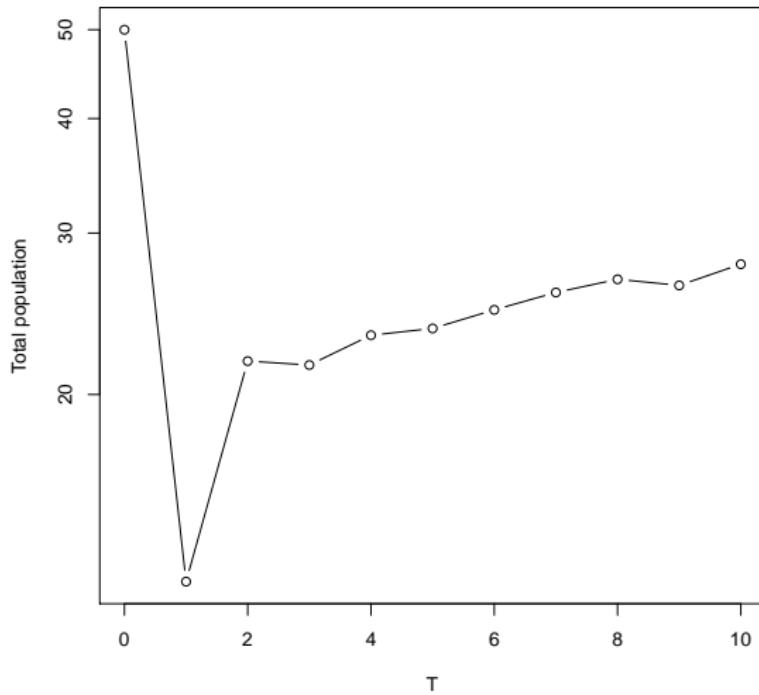


Gray squirrel dynamics

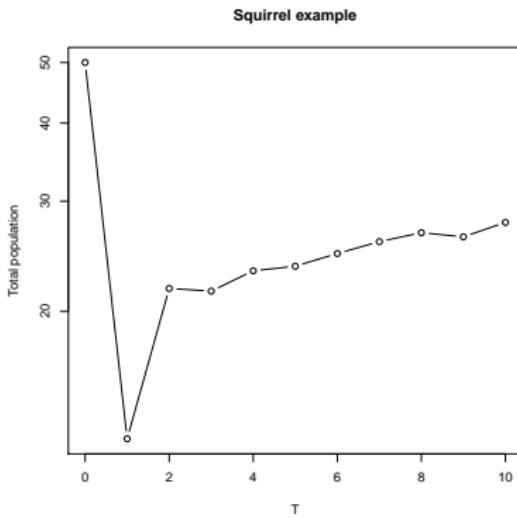
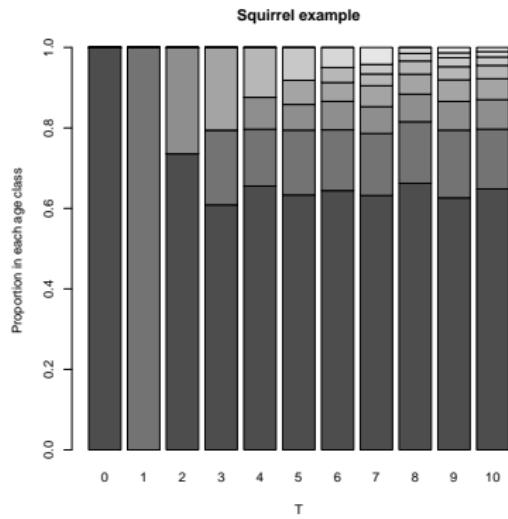


Gray squirrel dynamics

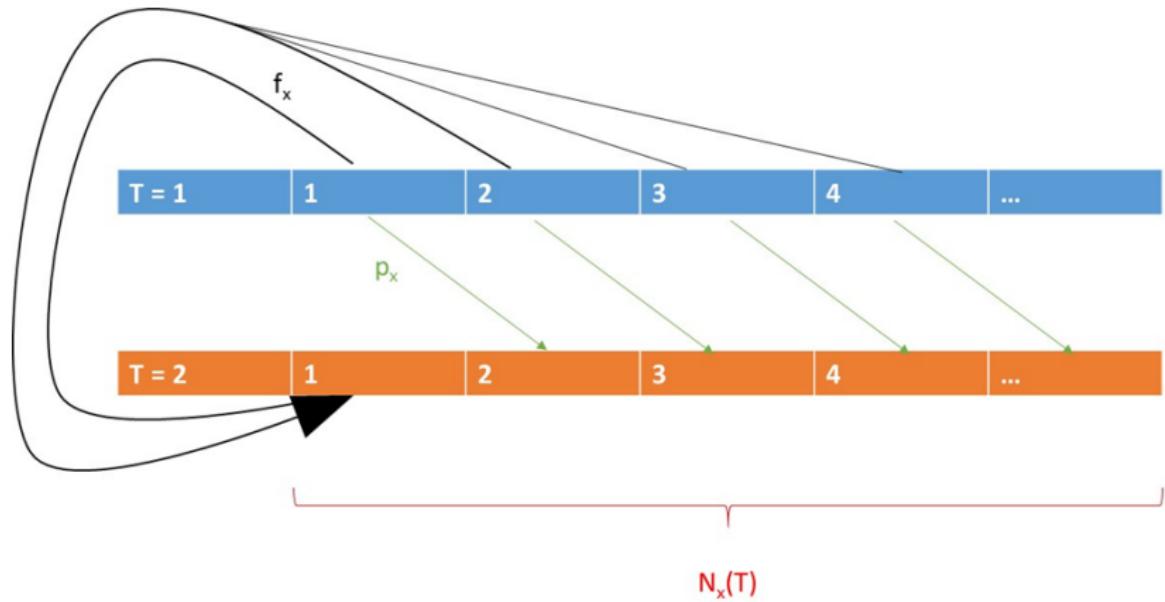
Squirrel example



Gray squirrel dynamics



The structured model



Salmon example

- ▶ What happens when a population has independent cohorts?

Salmon example

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

Salmon example

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

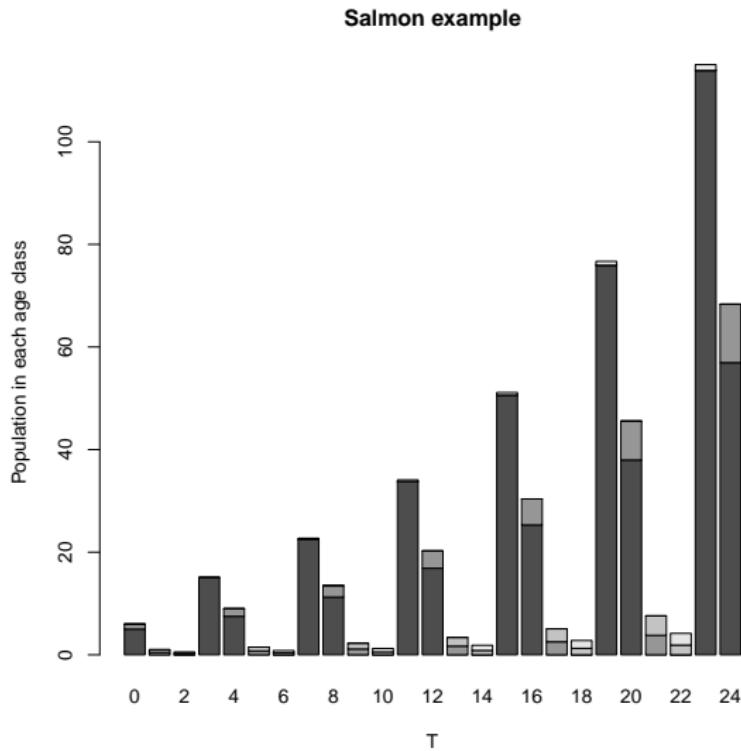
Salmon example

x	f_x	p_x	ℓ_x	$\ell_x f_x$
1	0	0.2		
2	0	0.6		
3	0	0.8		
4	10	0		
R				

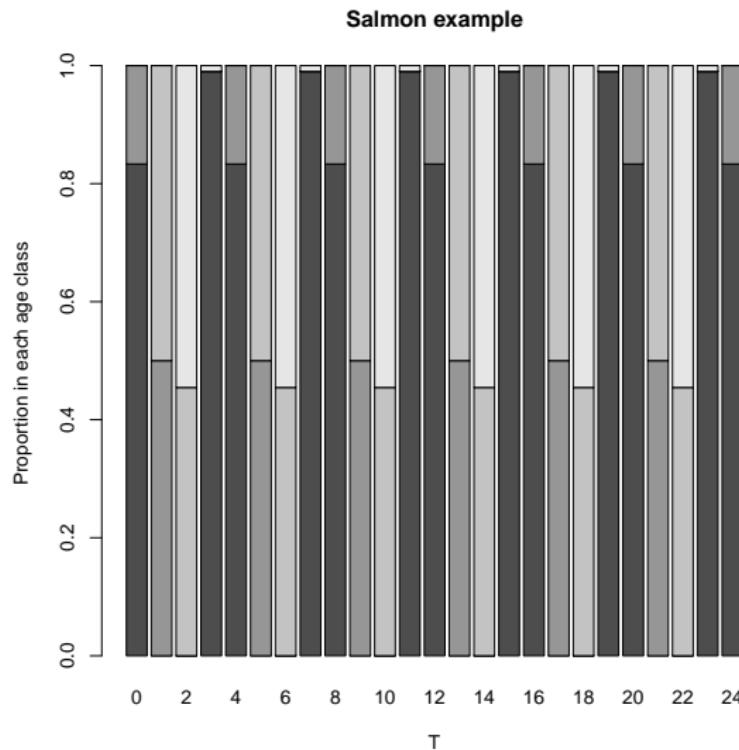
Salmon example



Salmon dynamics

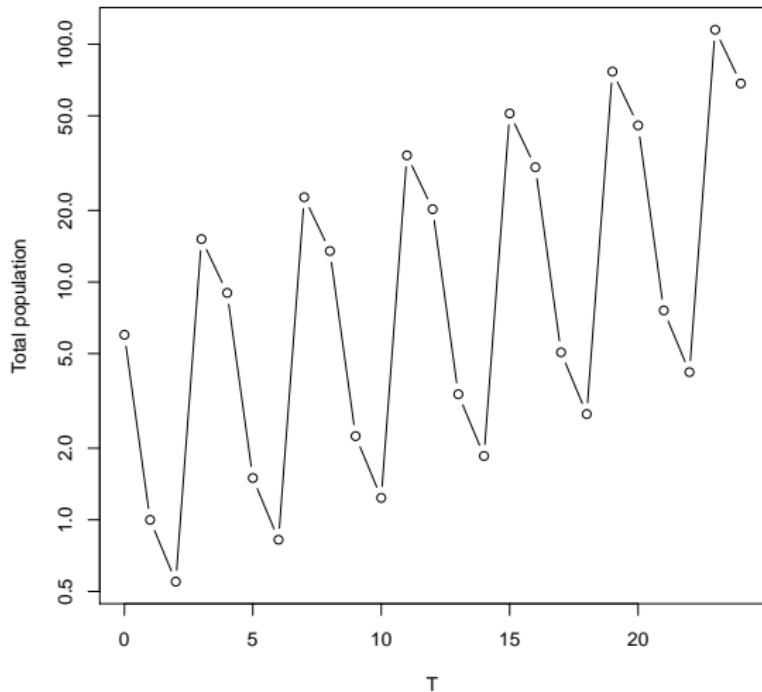


Salmon dynamics

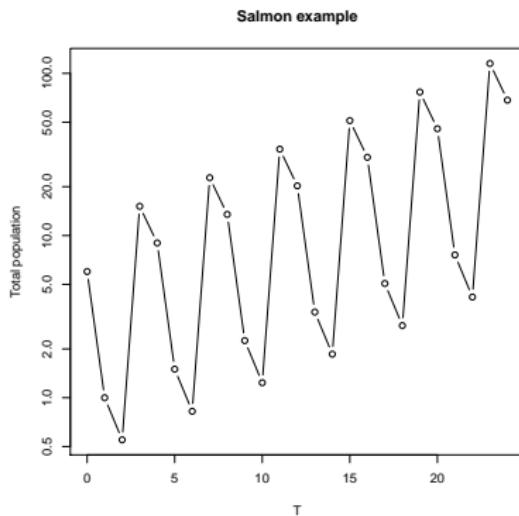
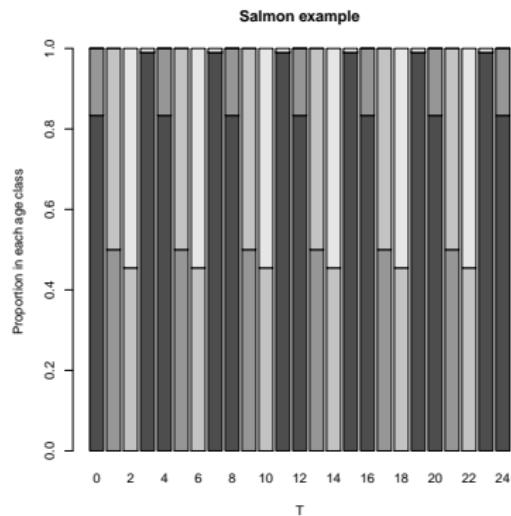


Salmon dynamics

Salmon example



Salmon dynamics



Subsection 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

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

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: What is the relationship?**

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: **What is the relationship?**

▶ *

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: **What is the relationship?**
 - ▶ * To get f_x we multiply m_x by one or more survival terms, depending on when the census is

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: **What is the relationship?**
 - ▶ * To get f_x we multiply m_x by one or more survival terms, depending on when the census is
 - ▶ *

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: **What is the relationship?**
 - ▶ * To get f_x we multiply m_x by one or more survival terms, depending on when the census is
 - ▶ * Need to close the loop from one census to the next

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: **What is the relationship?**
 - ▶ * To get f_x we multiply m_x by one or more survival terms, depending on when the census is
 - ▶ * 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?

When do we start counting?

- ▶ Is the first age class called 0, or 1?
 - ▶ In this course, we will start from age class 1

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.

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.

Example: biennial dandelions

- ▶ Adults produce 80 seeds each (m_x)

Example: biennial dandelions

- ▶ Adults produce 80 seeds each (m_x)
- ▶ 1% of seeds survive to become adults

Example: biennial dandelions

- ▶ Adults produce 80 seeds each (m_x)
- ▶ 1% of seeds survive to become adults
- ▶ 50% of first-year adults survive to reproduce again

Example: biennial dandelions

- ▶ Adults produce 80 seeds each (m_x)
- ▶ 1% of seeds survive to become adults
- ▶ 50% of first-year adults survive to reproduce again
- ▶ **Second-year adults never survive**

Example: biennial dandelions

- ▶ Adults produce 80 seeds each (m_x)
- ▶ 1% of seeds survive to become adults
- ▶ 50% of first-year adults survive to reproduce again
- ▶ Second-year adults never survive
- ▶ What does the life table look like?

Example: biennial dandelions

- ▶ Adults produce 80 seeds each (m_x)
- ▶ 1% of seeds survive to become adults
- ▶ 50% of first-year adults survive to reproduce again
- ▶ Second-year adults never survive
- ▶ What does the life table look like?

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

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

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

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

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

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

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):

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} ?

Calculating \mathcal{R}

- ▶ The reproductive number \mathcal{R} gives the average lifetime reproduction of an individual, and is a valuable summary of the information in the life table
 - ▶ $\mathcal{R} = \sum_x \ell_x f_x$
 - ▶ If $\mathcal{R} > 1$ in the long (or medium) term, the population will increase
 - ▶ If \mathcal{R} is persistently < 1 , the population is in trouble
- ▶ We can ask (for example):
 - ▶ Which ages have a large *contribution* to \mathcal{R} ?
 - ▶ **Poll:** Which values of p_x and f_x is \mathcal{R} sensitive to?

Calculating \mathcal{R}

- ▶ The reproductive number \mathcal{R} gives the average lifetime reproduction of an individual, and is a valuable summary of the information in the life table
 - ▶ $\mathcal{R} = \sum_x \ell_x f_x$
 - ▶ If $\mathcal{R} > 1$ in the long (or medium) term, the population will increase
 - ▶ If \mathcal{R} is persistently < 1 , the population is in trouble
- ▶ We can ask (for example):
 - ▶ Which ages have a large *contribution* to \mathcal{R} ?
 - ▶ Poll: Which values of p_x and f_x is \mathcal{R} sensitive to?
 - ▶ *

Calculating \mathcal{R}

- ▶ The reproductive number \mathcal{R} gives the average lifetime reproduction of an individual, and is a valuable summary of the information in the life table
 - ▶ $\mathcal{R} = \sum_x \ell_x f_x$
 - ▶ If $\mathcal{R} > 1$ in the long (or medium) term, the population will increase
 - ▶ If \mathcal{R} is persistently < 1 , the population is in trouble
- ▶ We can ask (for example):
 - ▶ Which ages have a large *contribution* to \mathcal{R} ?
 - ▶ Poll: Which values of p_x and f_x is \mathcal{R} sensitive to?
 - ▶ * The p_s for young individuals affect all the ℓ_s .

Calculating \mathcal{R}

- ▶ The reproductive number \mathcal{R} gives the average lifetime reproduction of an individual, and is a valuable summary of the information in the life table
 - ▶ $\mathcal{R} = \sum_x \ell_x f_x$
 - ▶ If $\mathcal{R} > 1$ in the long (or medium) term, the population will increase
 - ▶ If \mathcal{R} is persistently < 1 , the population is in trouble
- ▶ We can ask (for example):
 - ▶ Which ages have a large *contribution* to \mathcal{R} ?
 - ▶ Poll: Which values of p_x and f_x is \mathcal{R} sensitive to?
 - ▶ * The p_s for young individuals affect all the ℓ_s .

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 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 $\ell_x f_x$

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?

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?**
 - ▶ *

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?**
 - ▶ * In most populations ℓ can be very small for large 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?**
 - ▶ * In most populations ℓ can be very small for large 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?**
 - ▶ * In most populations ℓ can be very small for large x
 - ▶ * In many populations, f can be very large for large 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?**
 - ▶ * In most populations ℓ can be very small for large x
 - ▶ * In many populations, f can be very large for large x
- ▶ Reproductive potential of old individuals *may or may not* be important

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?**
 - ▶ * In most populations ℓ can be very small for large x
 - ▶ * In many populations, f can be very large for large x
- ▶ Reproductive potential of old individuals *may* or *may not* be important
 - ▶ *

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?**
 - ▶ * In most populations ℓ can be very small for large x
 - ▶ * In many populations, f can be very large for large x
- ▶ Reproductive potential of old individuals *may* or *may not* be important
 - ▶ * In tree populations, most trees don't survive to get huge, but the huge trees may have most of the total reproduction

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?**
 - ▶ * In most populations ℓ can be very small for large x
 - ▶ * In many populations, f can be very large for large x
- ▶ Reproductive potential of old individuals *may* or *may not* be important
 - ▶ * In tree populations, most trees don't survive to get huge, but the huge trees may have most of the total reproduction
 - ▶ *

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?**
 - ▶ * In most populations ℓ can be very small for large x
 - ▶ * In many populations, f can be very large for large x
- ▶ Reproductive potential of old individuals *may* or *may not* be important
 - ▶ * In tree populations, most trees don't survive to get huge, but the huge trees may have most of the total reproduction
 - ▶ * In bird populations, old birds produce fairly well, but not nearly enough to outweigh the low probability of being old.

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?**
 - ▶ * In most populations ℓ can be very small for large x
 - ▶ * In many populations, f can be very large for large x
- ▶ Reproductive potential of old individuals *may* or *may not* be important
 - ▶ * In tree populations, most trees don't survive to get huge, but the huge trees may have most of the total reproduction
 - ▶ * In bird populations, old birds produce fairly well, but not nearly enough to outweigh the low probability of being old.

Old individuals



Subsection 3

Measuring growth rates

Measuring growth rates

- In a constant population, each age class replaces itself:

Measuring growth rates

- ▶ In a constant population, each age class replaces itself:
 - ▶ $\mathcal{R} = \sum_x \ell_x f_x = 1$

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

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

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

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:

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

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

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

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 .

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

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 .

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?

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

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} ?

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} .

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.

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.

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

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*

Time scales

- ▶ λ gives the number of individuals per individual *every year*
- ▶ \mathcal{R} gives the number of individuals per individual *over a lifetime*

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)?

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)?
 - ▶ *

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

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)?
 - ▶ * $\mathcal{R} = \lambda$; each organism observed reproduces \mathcal{R} offspring on average, all in one time step
- ▶ Poll: For a long-lived population?

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)?
 - ▶ * $\mathcal{R} = \lambda$; each organism observed reproduces \mathcal{R} offspring on average, all in one time step
- ▶ Poll: For a long-lived population?
 - ▶ *

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)?
 - ▶ * $\mathcal{R} = \lambda$; each organism observed reproduces \mathcal{R} offspring on average, all in one time step
- ▶ Poll: For a long-lived population?
 - ▶ * The \mathcal{R} offspring are produced slowly, so population changes slowly

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)?
 - ▶ * $\mathcal{R} = \lambda$; each organism observed reproduces \mathcal{R} offspring on average, all in one time step
- ▶ Poll: For a long-lived population?
 - ▶ * The \mathcal{R} offspring are produced slowly, so population changes slowly
 - ▶ *

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)?
 - ▶ * $\mathcal{R} = \lambda$; each organism observed reproduces \mathcal{R} offspring on average, all in one time step
- ▶ Poll: For a long-lived population?
 - ▶ * The \mathcal{R} offspring are produced slowly, so population changes slowly
 - ▶ * λ should be closer to 1 than \mathcal{R} is.

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)?
 - ▶ * $\mathcal{R} = \lambda$; each organism observed reproduces \mathcal{R} offspring on average, all in one time step
- ▶ Poll: For a long-lived population?
 - ▶ * The \mathcal{R} offspring are produced slowly, so population changes slowly
 - ▶ * λ should be closer to 1 than \mathcal{R} is.
 - ▶ *

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)?
 - ▶ * $\mathcal{R} = \lambda$; each organism observed reproduces \mathcal{R} offspring on average, all in one time step
- ▶ Poll: For a long-lived population?
 - ▶ * The \mathcal{R} offspring are produced slowly, so population changes slowly
 - ▶ * λ should be closer to 1 than \mathcal{R} is.
 - ▶ * But on the same side (same answer about whether population is growing)

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)?
 - ▶ * $\mathcal{R} = \lambda$; each organism observed reproduces \mathcal{R} offspring on average, all in one time step
- ▶ Poll: For a long-lived population?
 - ▶ * The \mathcal{R} offspring are produced slowly, so population changes slowly
 - ▶ * λ should be closer to 1 than \mathcal{R} is.
 - ▶ * 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

Studying population growth

- ▶ λ and \mathcal{R} give similar information about your population
- ▶ \mathcal{R} is easier to calculate, and more generally useful

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

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

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

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

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} .

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} .

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 than the periods of exponential *decline*. In the long term, these should balance.

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 than the periods of exponential *decline*. In the long term, these should balance.
 - ▶ *

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 than the periods of exponential *decline*. In the long term, these should balance.
 - ▶ * Because otherwise the population would go to zero or infinity

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 than the periods of exponential *decline*. In the long term, these should balance.
 - ▶ * Because otherwise the population would go to zero or infinity

Outline

Introduction

Example: biennial dandelions

Modeling approach

Constructing a model

Model dynamics

Life tables

Examples

Calculation details

Measuring growth rates

Life-table patterns

Survivorship

Fecundity

Age distributions

Other structured models

Stage structure

Regulated growth

Subsection 1

Survivorship

Survivorship

Patterns of survivorship

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

Patterns of survivorship

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

Patterns of survivorship

- ▶ Poll: What sort of patterns do you expect to see in p_x ?
 - ▶ * Younger individuals usually have lower survivorship

Patterns of survivorship

- ▶ Poll: What sort of patterns do you expect to see in p_x ?
 - ▶ * Younger individuals usually have lower survivorship
 - ▶ *

Patterns of survivorship

- ▶ Poll: What sort of patterns do you expect to see in p_x ?
 - ▶ * Younger individuals usually have lower survivorship
 - ▶ * Older individuals often have lower survivorship

Patterns of survivorship

- ▶ Poll: What sort of patterns do you expect to see in p_x ?
 - ▶ * Younger individuals usually have lower survivorship
 - ▶ * Older individuals often have lower survivorship
- ▶ What about ℓ_x ?

Patterns of survivorship

- ▶ Poll: What sort of patterns do you expect to see in p_x ?
 - ▶ * Younger individuals usually have lower survivorship
 - ▶ * Older individuals often have lower survivorship
- ▶ What about ℓ_x ?
 - ▶ *

Patterns of survivorship

- ▶ Poll: What sort of patterns do you expect to see in p_x ?
 - ▶ * Younger individuals usually have lower survivorship
 - ▶ * Older individuals often have lower survivorship
- ▶ What about ℓ_x ?
 - ▶ * It goes down

Patterns of survivorship

- ▶ Poll: What sort of patterns do you expect to see in p_x ?
 - ▶ * Younger individuals usually have lower survivorship
 - ▶ * Older individuals often have lower survivorship
- ▶ What about ℓ_x ?
 - ▶ * It goes down
 - ▶ *

Patterns of survivorship

- ▶ Poll: What sort of patterns do you expect to see in p_x ?
 - ▶ * Younger individuals usually have lower survivorship
 - ▶ * Older individuals often have lower survivorship
- ▶ What about ℓ_x ?
 - ▶ * It goes down
 - ▶ * But sometimes faster and sometimes slower

Patterns of survivorship

- ▶ Poll: What sort of patterns do you expect to see in p_x ?
 - ▶ * Younger individuals usually have lower survivorship
 - ▶ * Older individuals often have lower survivorship
- ▶ What about ℓ_x ?
 - ▶ * It goes down
 - ▶ * But sometimes faster and sometimes slower
 - ▶ *

Patterns of survivorship

- ▶ Poll: What sort of patterns do you expect to see in p_x ?
 - ▶ * Younger individuals usually have lower survivorship
 - ▶ * Older individuals often have lower survivorship
- ▶ What about ℓ_x ?
 - ▶ * It goes down
 - ▶ * But sometimes faster and sometimes slower
 - ▶ * Best understood on a log scale

Patterns of survivorship

- ▶ Poll: What sort of patterns do you expect to see in p_x ?
 - ▶ * Younger individuals usually have lower survivorship
 - ▶ * Older individuals often have lower survivorship
- ▶ What about ℓ_x ?
 - ▶ * It goes down
 - ▶ * But sometimes faster and sometimes slower
 - ▶ * Best understood on a log scale

Starting off

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

Starting off

- ▶ Recall: we always start from age *class 1*
 - ▶ If we count newborns, we still call them class 1.

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?

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?
 - ▶ *

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?
 - ▶ * 1

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?
 - ▶ * 1
 - ▶ *

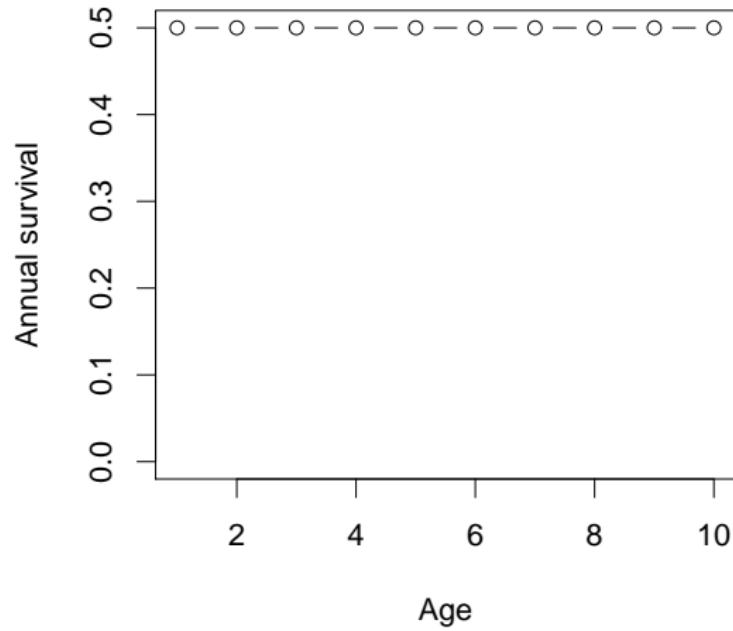
Starting off

- ▶ 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?
 - ▶ * 1
 - ▶ * We don't count individuals that we don't count

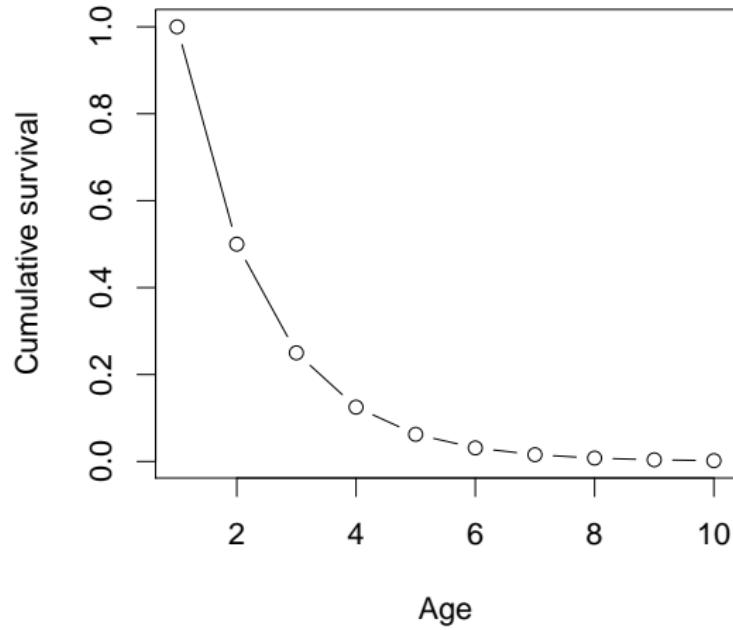
Starting off

- ▶ 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?
 - ▶ * 1
 - ▶ * We don't count individuals that we don't count

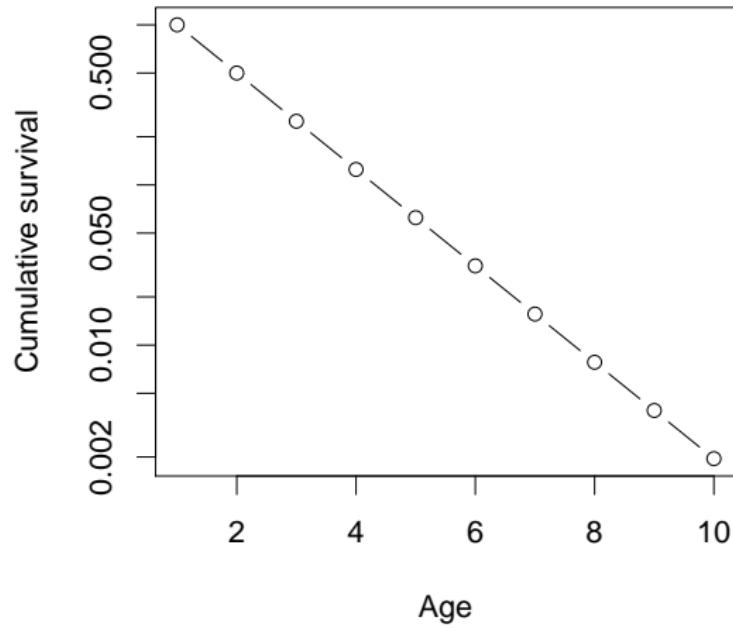
Constant survivorship



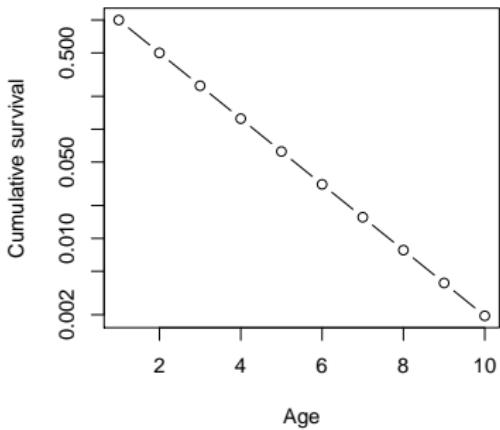
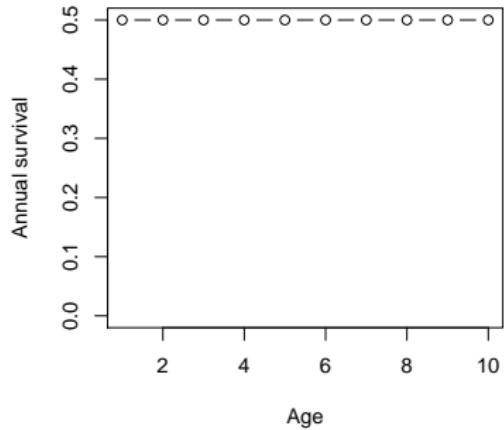
Constant survivorship



Constant survivorship



Constant survivorship



“Types” of survivorship

- ▶ There is a history of defining survivorship as:

“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*).

“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

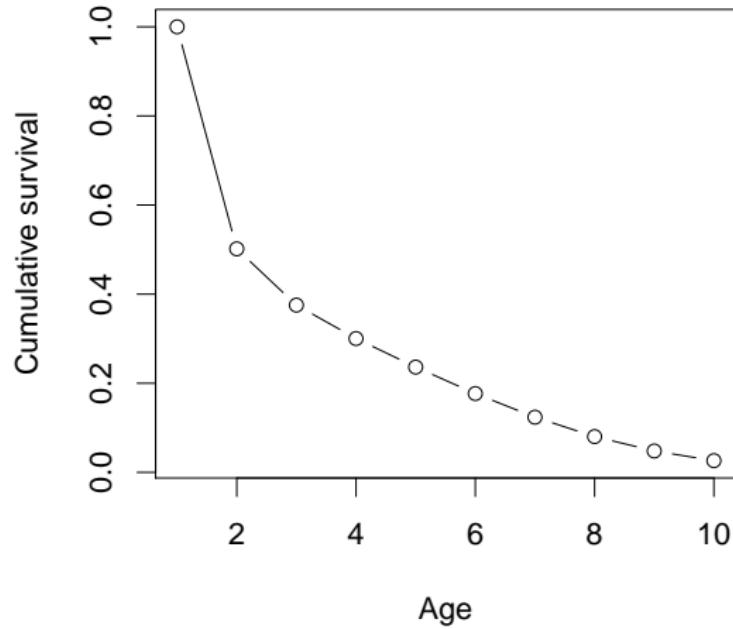
“Types” of survivorship

- ▶ 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

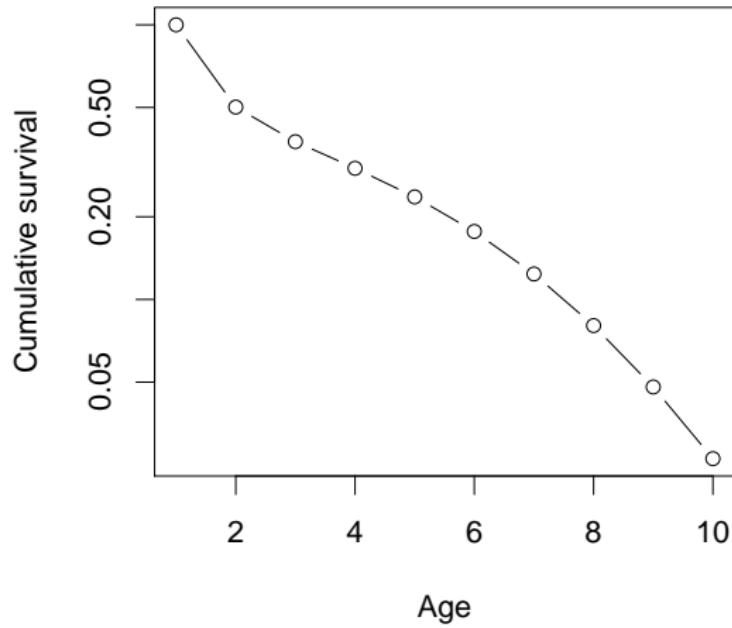
“Types” of survivorship

- ▶ 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

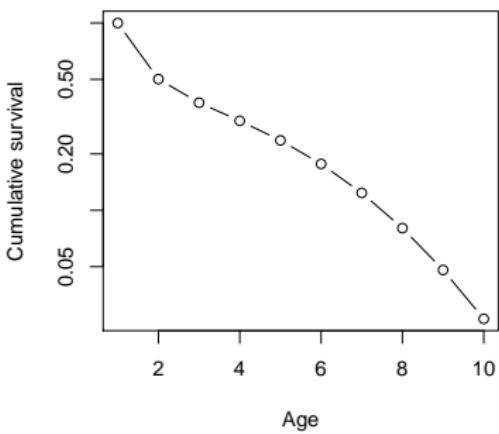
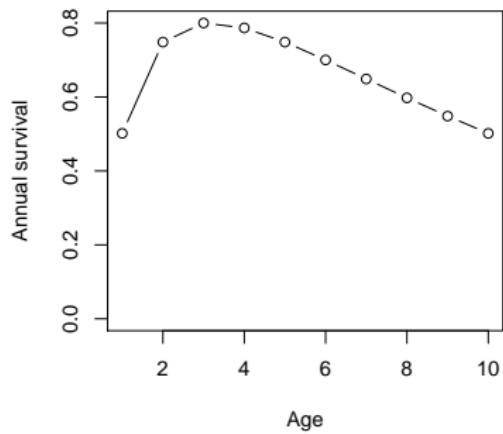
Changing survivorship



Changing survivorship



Changing survivorship



Subsection 2

Fecundity

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

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

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**

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**

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

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

- ▶ 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 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

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

▶ *

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
 - ▶ * Birds, large mammals

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
 - ▶ * Birds, large mammals
- ▶ It may also go up and then come down

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
 - ▶ * Birds, large mammals
- ▶ It may also go up and then come down
 - ▶ *

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
 - ▶ * Birds, large mammals
- ▶ It may also go up and then come down
 - ▶ * people

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
 - ▶ * Birds, large mammals
- ▶ It may also go up and then come down
 - ▶ * people
- ▶ It may also go up and up as organisms get older

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
 - ▶ * Birds, large mammals
- ▶ It may also go up and then come down
 - ▶ * people
- ▶ It may also go up and up as organisms get older
 - ▶ *

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

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

Outline

Introduction

Example: biennial dandelions

Modeling approach

Constructing a model

Model dynamics

Life tables

Examples

Calculation details

Measuring growth rates

Life-table patterns

Survivorship

Fecundity

Age distributions

Other structured models

Stage structure

Regulated growth

Age distributions

► <http://www.gapminder.org/population/tool/>

Age distributions

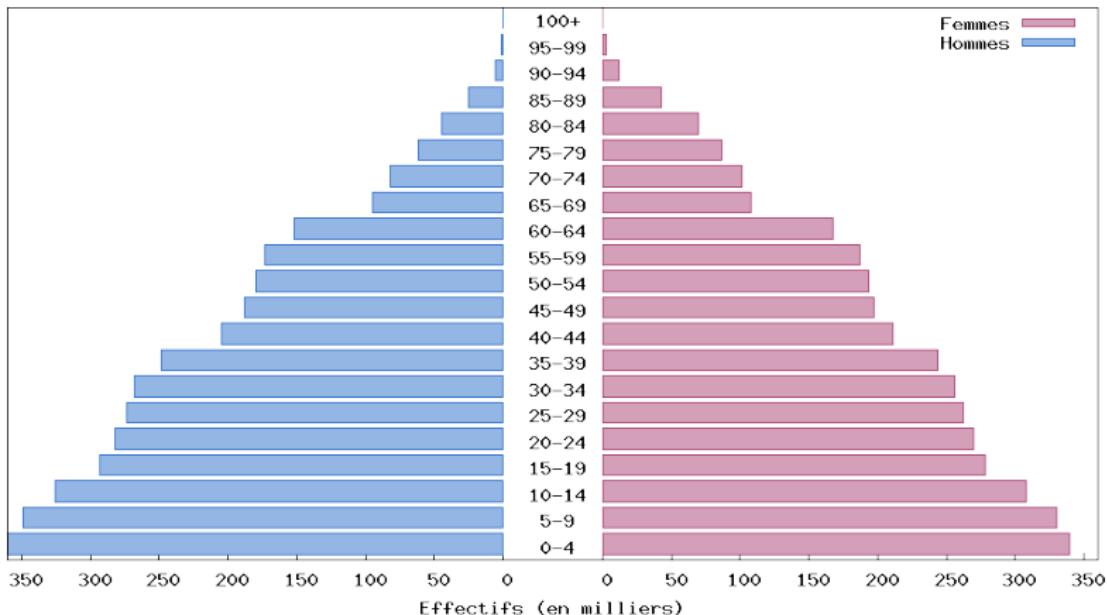
- ▶ <http://www.gapminder.org/population/tool/>
- ▶ <https://en.wikipedia.org/>

Age distributions

- ▶ <http://www.gapminder.org/population/tool/>
 - ▶ <https://en.wikipedia.org/>

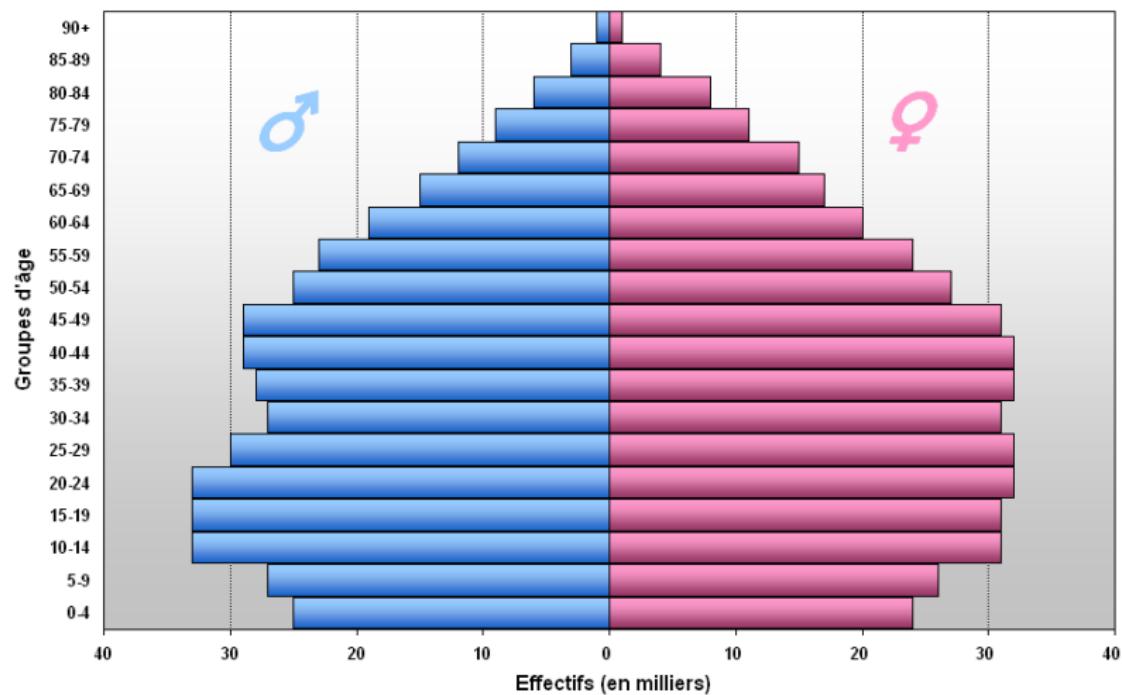
Age distributions

Pyramide des âges, Israël, 2010



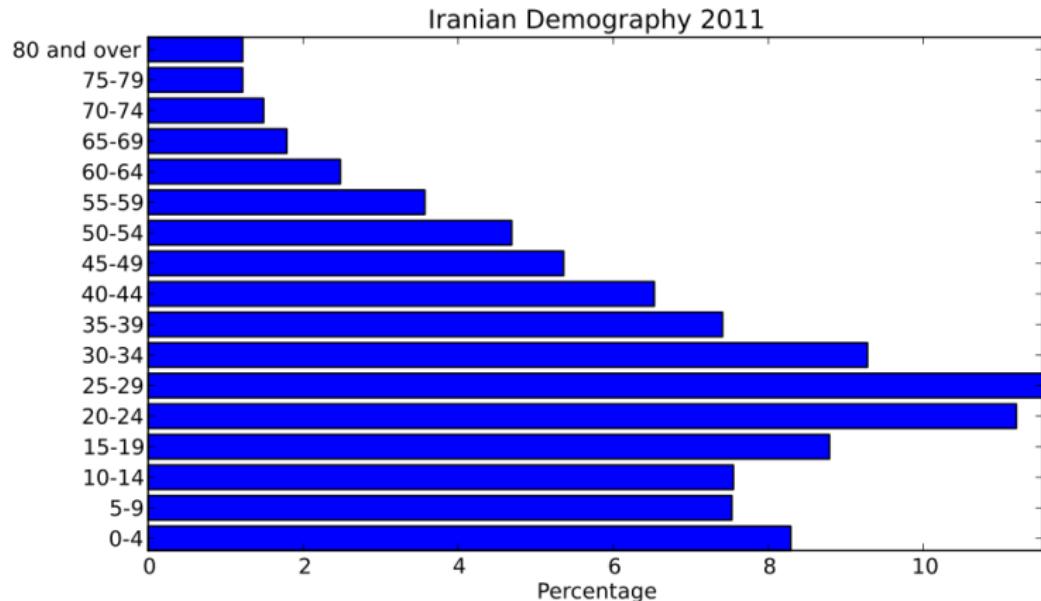
Age distributions

Pyramide des âges, Chypre, 2005

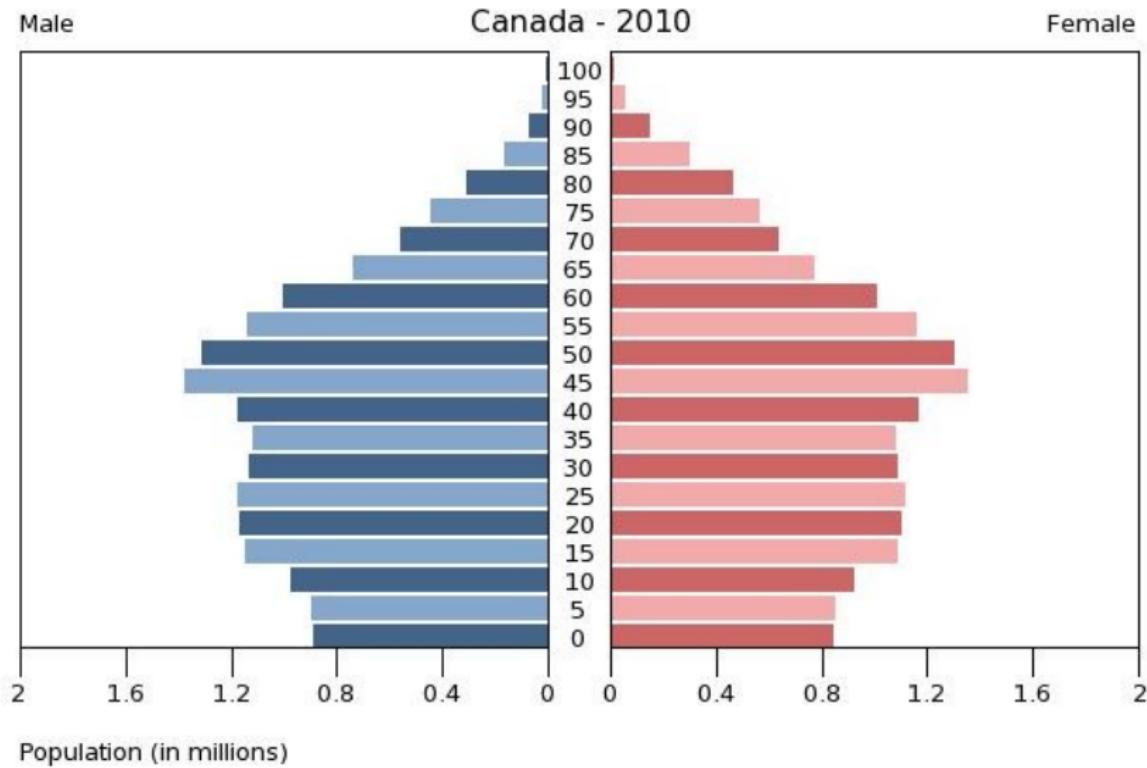


Source: Organisation des Nations Unies (World Population Prospects: The 2004 Revision)

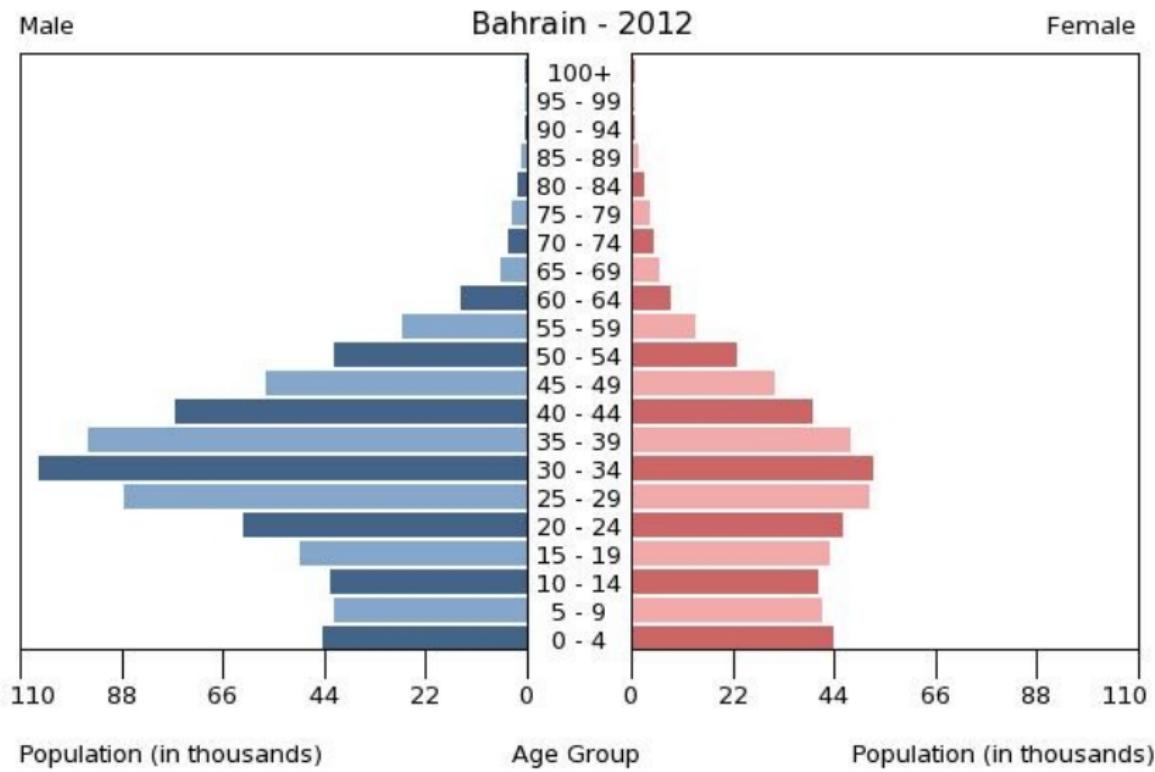
Age distributions



Age distributions

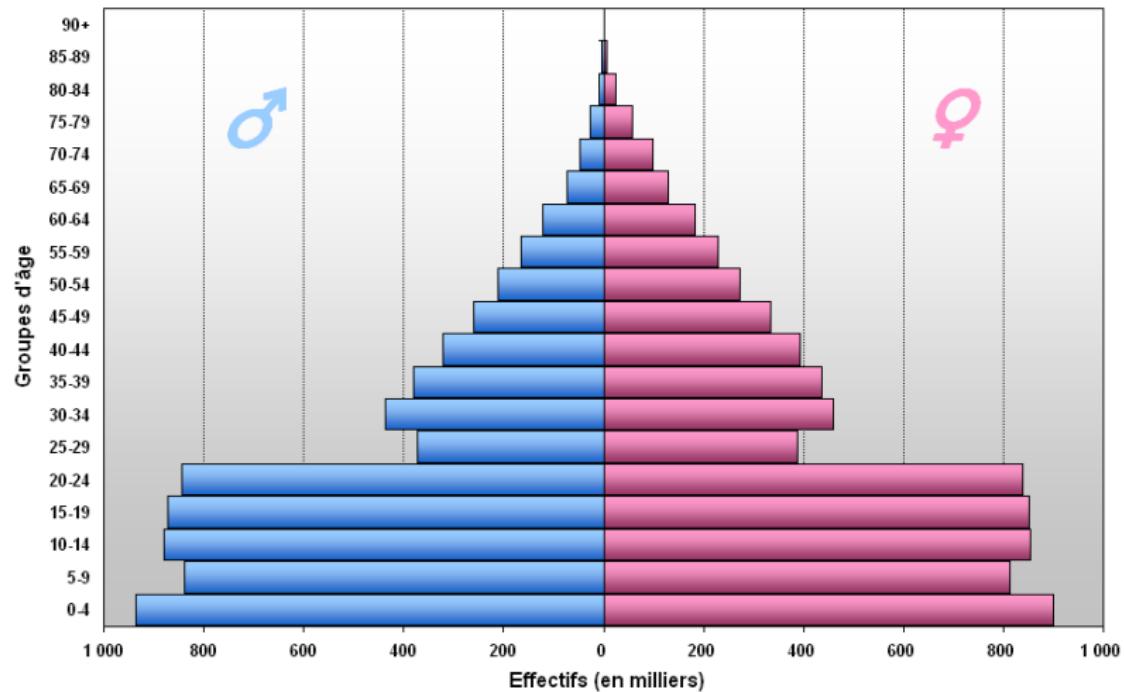


Age distributions



Age distributions

Pyramide des âges, Cambodge, 2005



Source: Organisation des Nations Unies (World Population Prospects: The 2004 Revision)

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?

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?
 - ▶ *

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?
 - ▶ * Distribution should be proportional to ℓ_x

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?
 - ▶ * Distribution should be proportional to ℓ_x
- ▶ What if population is growing?

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?
 - ▶ * Distribution should be proportional to ℓ_x
- ▶ What if population is growing?
 - ▶ *

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?
 - ▶ * Distribution should be proportional to ℓ_x
- ▶ What if population is growing?
 - ▶ * We expect proportionally more individuals in younger age classes

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?
 - ▶ * Distribution should be proportional to ℓ_x
- ▶ What if population is growing?
 - ▶ * We expect proportionally more individuals in younger age classes
 - ▶ *

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

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?
 - ▶ * Distribution should be proportional to ℓ_x
- ▶ What if population is growing?
 - ▶ * We expect proportionally more individuals in younger age classes
 - ▶ * 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):

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

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

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 $\lambda^{-x}\ell_x$

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 .**

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)

Patterns

- ▶ Populations tend to be bottom-heavy (more individuals at lower age classes)
 - ▶ Many individuals born, few survive to older age classes

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

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

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

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

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

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

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:

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?

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?
 - ▶ *

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?
 - ▶ * The lower classes are larger

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?
 - ▶ * The lower classes are larger
 - ▶ Poll: More students are admitted each year?

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?
 - ▶ * The lower classes are larger
 - ▶ Poll: More students are admitted each year?
 - ▶ *

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?
 - ▶ * The lower classes are larger
 - ▶ Poll: More students are admitted each year?
 - ▶ * The lower classes are larger (even more so)

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?
 - ▶ * The lower classes are larger
 - ▶ Poll: More students are admitted each year?
 - ▶ * The lower classes are larger (even more so)
 - ▶ Poll: Fewer students are admitted each year?

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?
 - ▶ * The lower classes are larger
 - ▶ Poll: More students are admitted each year?
 - ▶ * The lower classes are larger (even more so)
 - ▶ Poll: Fewer students are admitted each year?
 - ▶ *

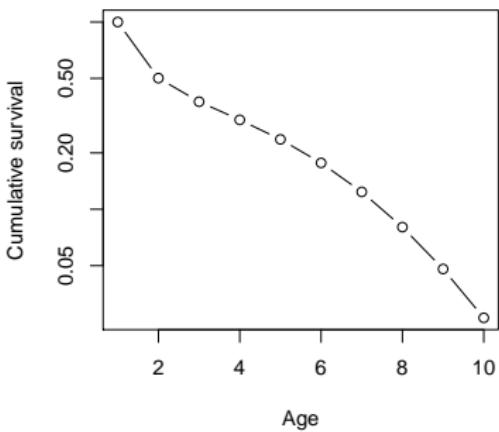
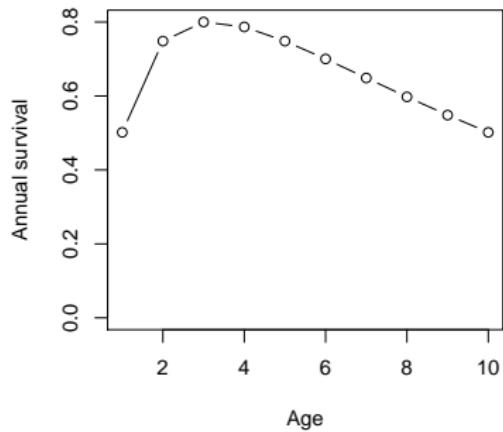
University cohorts

- ▶ 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?
 - ▶ * The lower classes are larger
 - ▶ Poll: More students are admitted each year?
 - ▶ * The lower classes are larger (even more so)
 - ▶ Poll: Fewer students are admitted each year?
 - ▶ * Anything could happen (drop outs and size change are operating in different directions)

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?
 - ▶ * The lower classes are larger
 - ▶ Poll: More students are admitted each year?
 - ▶ * The lower classes are larger (even more so)
 - ▶ Poll: Fewer students are admitted each year?
 - ▶ * Anything could happen (drop outs and size change are operating in different directions)

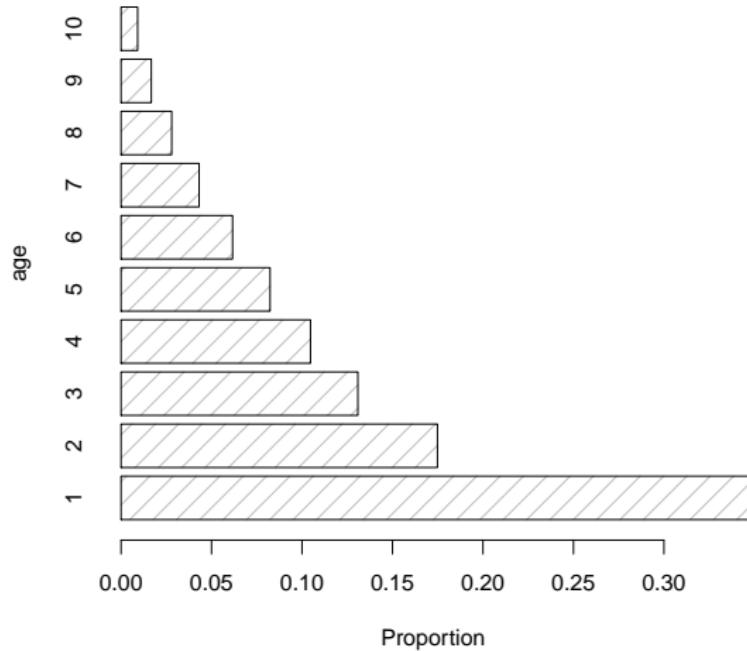
Changing survivorship



Age distributions

Stable age distribution

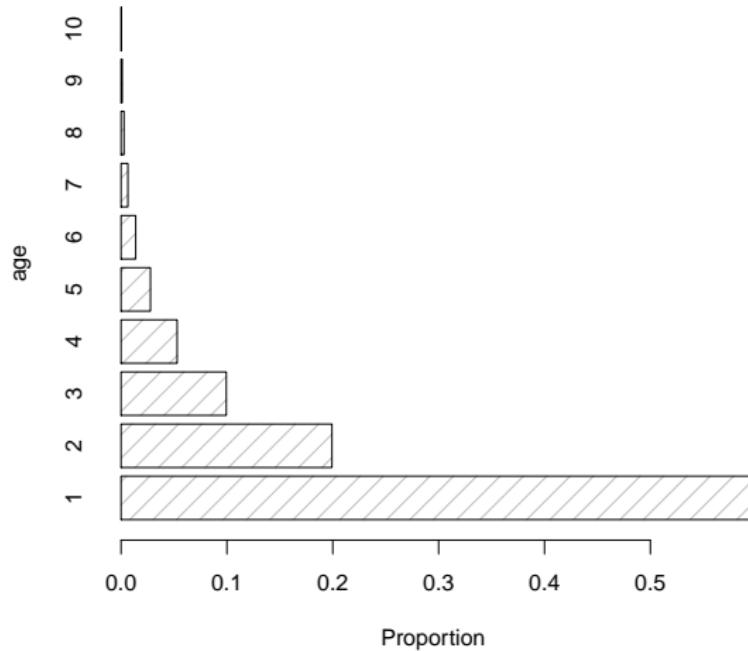
$\lambda = 1$



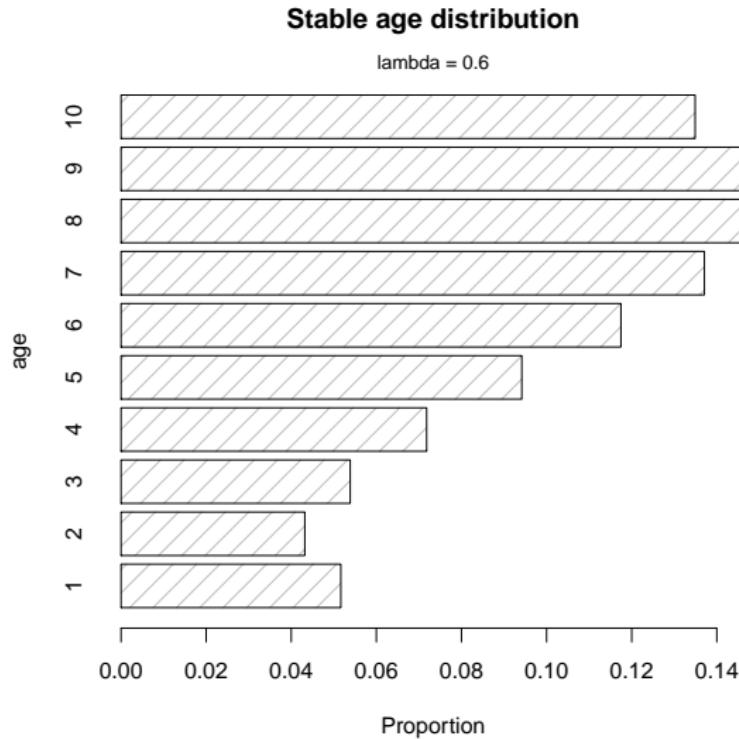
Age distributions

Stable age distribution

$\lambda = 1.5$



Age distributions



Outline

Introduction

Example: biennial dandelions

Modeling approach

Constructing a model

Model dynamics

Life tables

Examples

Calculation details

Measuring growth rates

Life-table patterns

Survivorship

Fecundity

Age distributions

Other structured models

Stage structure

Regulated growth

Forest example

- ▶ Forests have obvious population structure



Forest example

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



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 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?

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?

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?
 - ▶ *

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?
 - ▶ * Large trees are larger

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?
 - ▶ * Large trees are larger
 - ▶ *

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?
 - ▶ * Large trees are larger
 - ▶ * Population may be declining

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?
 - ▶ * Large trees are larger
 - ▶ * Population may be declining
 - ▶ *

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?
 - ▶ * Large trees are larger
 - ▶ * Population may be declining
 - ▶ * Trees may spend longer in some size classes than in others

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?
 - ▶ * Large trees are larger
 - ▶ * Population may be declining
 - ▶ * Trees may spend longer in some size classes than in others
 - ▶ *

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

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

Subsection 1

Stage structure

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

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

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
 - ▶ *

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
 - ▶ * In stage-structured models survival is typically broken into:

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
 - ▶ * In stage-structured models survival is typically broken into:
 - ▶ *

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
 - ▶ * In stage-structured models survival is typically broken into:
 - ▶ * Survival into same stage

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
 - ▶ * In stage-structured models survival is typically broken into:
 - ▶ * Survival into same stage
 - ▶ *

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
 - ▶ * In stage-structured models survival is typically broken into:
 - ▶ * Survival into same stage
 - ▶ * Survival with recruitment (ie., to the next larger class of individuals)

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
 - ▶ * In stage-structured models survival is typically broken into:
 - ▶ * Survival into same stage
 - ▶ * Survival with recruitment (ie., to the next larger class of individuals)
 - ▶ More complicated models are also possible

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
 - ▶ * In stage-structured models survival is typically broken into:
 - ▶ * Survival into same stage
 - ▶ * 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

Advantages

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

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)?

Unregulated growth

- ▶ What happens if you have a constant stage table (no regulation)?
 - ▶ Fecundity, and survival and recruitment probabilities are constant

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

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)

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

- ▶ 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
 - ▶ \mathcal{R} is *about the same as in age structured model*

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
 - ▶ \mathcal{R} is *about the same as in age structured model*
- ▶ Unregulated growth cannot persist

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
 - ▶ \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):

Summary

- ▶ If the life table remains constant (no regulation or stochasticity):
 - ▶ Reach a stable age (or stage) distribution

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**

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

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

Subsection 2

Regulated growth

Regulated growth

- ▶ Our models up until now have assumed that individuals are independent

Regulated growth

- ▶ Our models up until now have assumed that individuals are independent
- ▶ In this case, we expect populations to grow (or decline) exponentially

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.

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

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

▶ *

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
 - ▶ * We know that real populations are regulated

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
 - ▶ * We know that real populations are regulated
 - ▶ *

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

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
 - ▶ * We know that real populations are regulated
 - ▶ * Populations can't increase or decrease exponentially for very long
- ▶ Understanding this behaviour is helpful:

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
 - ▶ * We know that real populations are regulated
 - ▶ * Populations can't increase or decrease exponentially for very long
- ▶ Understanding this behaviour is helpful:
 - ▶ interpreting age structures in real populations

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
 - ▶ * We know that real populations are regulated
 - ▶ * 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

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
 - ▶ * We know that real populations are regulated
 - ▶ * 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

Regulation and structure

- ▶ We expect real populations to be regulated
- ▶ The long-term average value of λ under regulation *could* be exactly 1

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

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

Dynamics

- ▶ We expect to see smooth behaviour in many cases
- ▶ Cycles and complex behaviour should arise for reasons similar to our unstructured models:

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

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

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:

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

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

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