

UNIT 8: Infectious disease

Outline

Introduction

Rate of spread

Single-epidemic model

Epidemic size

Recurrent epidemic models

Dynamics

Reproductive numbers and risk

Pathogen aggressiveness

Infectious disease

- ▶ Extremely common

Infectious disease

- ▶ Extremely common
- ▶ Huge impacts on ecological interactions

Infectious disease

- ▶ Extremely common
- ▶ Huge impacts on ecological interactions
- ▶ A form of exploitation, but doesn't fit well into our previous modeling framework

Infectious disease

- ▶ Extremely common
- ▶ Huge impacts on ecological interactions
- ▶ A form of exploitation, but doesn't fit well into our previous modeling framework
 - ▶ How many people are there?

Infectious disease

- ▶ Extremely common
- ▶ Huge impacts on ecological interactions
- ▶ A form of exploitation, but doesn't fit well into our previous modeling framework
 - ▶ How many people are there?
 - ▶ How many influenza viruses are there?

Infectious disease

- ▶ Extremely common
- ▶ Huge impacts on ecological interactions
- ▶ A form of exploitation, but doesn't fit well into our previous modeling framework
 - ▶ How many people are there?
 - ▶ How many influenza viruses are there?
 - ▶ How do they find each other?

Infectious disease

- ▶ Extremely common
- ▶ Huge impacts on ecological interactions
- ▶ A form of exploitation, but doesn't fit well into our previous modeling framework
 - ▶ How many people are there?
 - ▶ How many influenza viruses are there?
 - ▶ How do they find each other?

Disease agents

- ▶ Name an infectious agent that causes disease in humans.

Disease agents

- ▶ Name an infectious agent that causes disease in humans.
- ▶ Disease agents vary tremendously:

Disease agents

- ▶ Name an infectious agent that causes disease in humans.
- ▶ Disease agents vary tremendously:
 - ▶ Most **viruses** have just a handful of genes that allow them to hijack a cell and get it to make virus copies

Disease agents

- ▶ Name an infectious agent that causes disease in humans.
- ▶ Disease agents vary tremendously:
 - ▶ Most **viruses** have just a handful of genes that allow them to hijack a cell and get it to make virus copies

▶ *

Disease agents

- ▶ Name an infectious agent that causes disease in humans.
- ▶ Disease agents vary tremendously:
 - ▶ Most **viruses** have just a handful of genes that allow them to hijack a cell and get it to make virus copies
 - ▶ * SARS-CoV-2, influenza virus, HIV, measles

Disease agents

- ▶ Name an infectious agent that causes disease in humans.
- ▶ Disease agents vary tremendously:
 - ▶ Most **viruses** have just a handful of genes that allow them to hijack a cell and get it to make virus copies
 - ▶ * SARS-CoV-2, influenza virus, HIV, measles
 - ▶ **Bacteria** are independent, free-living cells with hundreds or thousands of chemical pathways

Disease agents

- ▶ Name an infectious agent that causes disease in humans.
- ▶ Disease agents vary tremendously:
 - ▶ Most **viruses** have just a handful of genes that allow them to hijack a cell and get it to make virus copies
 - ▶ * SARS-CoV-2, influenza virus, HIV, measles
 - ▶ **Bacteria** are independent, free-living cells with hundreds or thousands of chemical pathways
 - ▶ *

Disease agents

- ▶ Name an infectious agent that causes disease in humans.
- ▶ Disease agents vary tremendously:
 - ▶ Most **viruses** have just a handful of genes that allow them to hijack a cell and get it to make virus copies
 - ▶ * SARS-CoV-2, influenza virus, HIV, measles
 - ▶ **Bacteria** are independent, free-living cells with hundreds or thousands of chemical pathways
 - ▶ * Tuberculosis, anthrax, pertussis

Disease agents

- ▶ Name an infectious agent that causes disease in humans.
- ▶ Disease agents vary tremendously:
 - ▶ Most **viruses** have just a handful of genes that allow them to hijack a cell and get it to make virus copies
 - ▶ * SARS-CoV-2, influenza virus, HIV, measles
 - ▶ **Bacteria** are independent, free-living cells with hundreds or thousands of chemical pathways
 - ▶ * Tuberculosis, anthrax, pertussis
 - ▶ **Eukaryotic** pathogens are nucleated cells who are more closely related to you than they are to bacteria

Disease agents

- ▶ Name an infectious agent that causes disease in humans.
- ▶ Disease agents vary tremendously:
 - ▶ Most **viruses** have just a handful of genes that allow them to hijack a cell and get it to make virus copies
 - ▶ * SARS-CoV-2, influenza virus, HIV, measles
 - ▶ **Bacteria** are independent, free-living cells with hundreds or thousands of chemical pathways
 - ▶ * Tuberculosis, anthrax, pertussis
 - ▶ **Eukaryotic** pathogens are nucleated cells who are more closely related to you than they are to bacteria
 - ▶ *

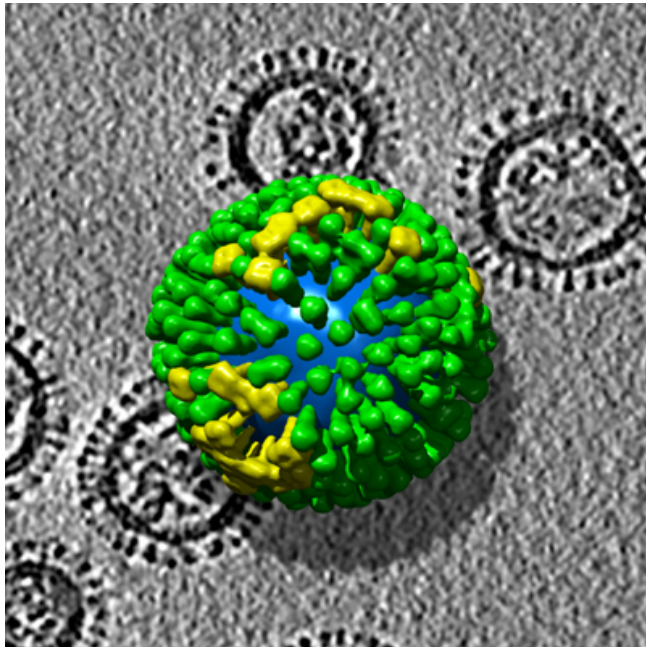
Disease agents

- ▶ Name an infectious agent that causes disease in humans.
- ▶ Disease agents vary tremendously:
 - ▶ Most **viruses** have just a handful of genes that allow them to hijack a cell and get it to make virus copies
 - ▶ * SARS-CoV-2, influenza virus, HIV, measles
 - ▶ **Bacteria** are independent, free-living cells with hundreds or thousands of chemical pathways
 - ▶ * Tuberculosis, anthrax, pertussis
 - ▶ **Eukaryotic** pathogens are nucleated cells who are more closely related to you than they are to bacteria
 - ▶ * Malaria, intestinal worms, trichomoniasis

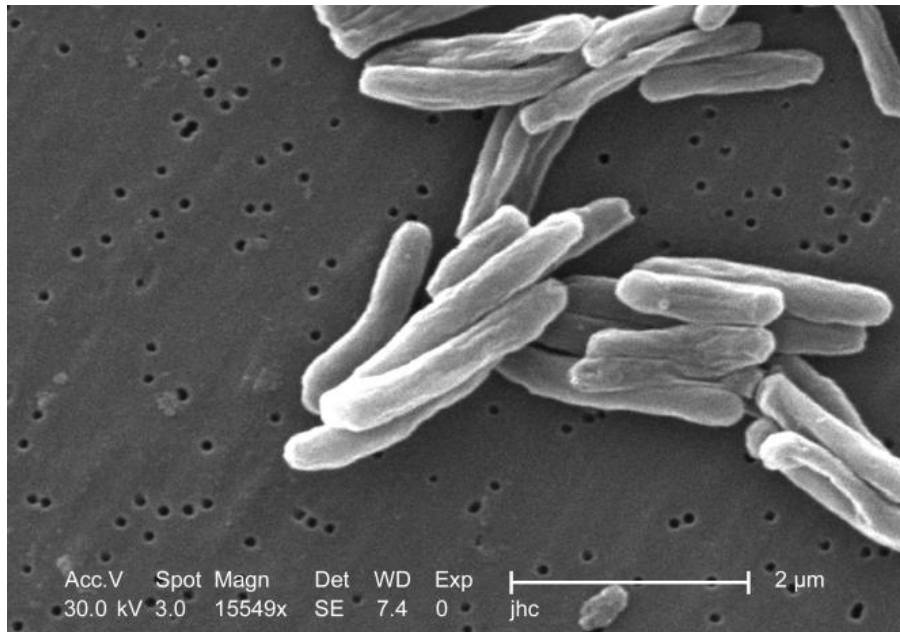
Disease agents

- ▶ Name an infectious agent that causes disease in humans.
- ▶ Disease agents vary tremendously:
 - ▶ Most **viruses** have just a handful of genes that allow them to hijack a cell and get it to make virus copies
 - ▶ * SARS-CoV-2, influenza virus, HIV, measles
 - ▶ **Bacteria** are independent, free-living cells with hundreds or thousands of chemical pathways
 - ▶ * Tuberculosis, anthrax, pertussis
 - ▶ **Eukaryotic** pathogens are nucleated cells who are more closely related to you than they are to bacteria
 - ▶ * Malaria, intestinal worms, trichomoniasis

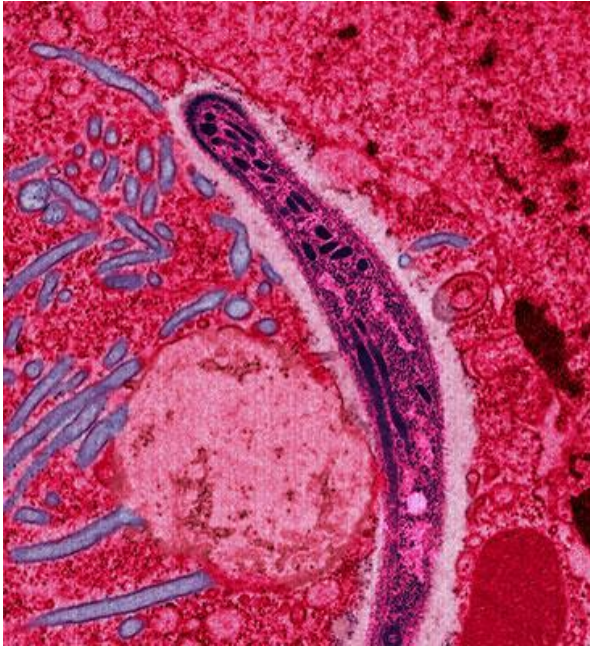
Influenza virus



Tuberculosis bacilli



Malaria sporozoite



Microparasites

- ▶ For infections with small pathogens (viruses and bacteria), we don't attempt to count pathogens, but instead divide disease into stages

Microparasites

- ▶ For infections with small pathogens (viruses and bacteria), we don't attempt to count pathogens, but instead divide disease into stages
 - ▶ Latently infected

Microparasites

- ▶ For infections with small pathogens (viruses and bacteria), we don't attempt to count pathogens, but instead divide disease into stages
 - ▶ Latently infected
 - ▶ Productively infected

Microparasites

- ▶ For infections with small pathogens (viruses and bacteria), we don't attempt to count pathogens, but instead divide disease into stages
 - ▶ Latently infected
 - ▶ Productively infected
 - ▶ Recovered

Microparasites

- ▶ For infections with small pathogens (viruses and bacteria), we don't attempt to count pathogens, but instead divide disease into stages
 - ▶ Latently infected
 - ▶ Productively infected
 - ▶ Recovered

Microparasite models

- ▶ We model microparasites by counting the number of hosts in various **states**:

Microparasite models

- ▶ We model microparasites by counting the number of hosts in various **states**:
 - ▶ **Susceptible** individuals can become infected

Microparasite models

- ▶ We model microparasites by counting the number of hosts in various **states**:
 - ▶ **Susceptible** individuals can become infected
 - ▶ **Infectious** individuals are infected and can infect others

Microparasite models

- ▶ We model microparasites by counting the number of hosts in various **states**:
 - ▶ **Susceptible** individuals can become infected
 - ▶ **Infectious** individuals are infected and can infect others
 - ▶ **Resistant** individuals are not infected and cannot become infected

Microparasite models

- ▶ We model microparasites by counting the number of hosts in various **states**:
 - ▶ **Susceptible** individuals can become infected
 - ▶ **Infectious** individuals are infected and can infect others
 - ▶ **Resistant** individuals are not infected and cannot become infected
- ▶ More complicated models might include other states, such as latently infected hosts who are infected with the pathogen but cannot yet infect others

Microparasite models

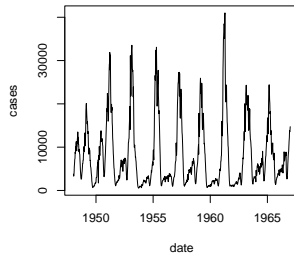
- ▶ We model microparasites by counting the number of hosts in various **states**:
 - ▶ **Susceptible** individuals can become infected
 - ▶ **Infectious** individuals are infected and can infect others
 - ▶ **Resistant** individuals are not infected and cannot become infected
- ▶ More complicated models might include other states, such as latently infected hosts who are infected with the pathogen but cannot yet infect others

Models as tools

- Models are the tools that we use to connect scales:



Measles reports from England and Wales

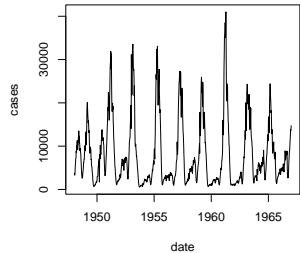


Models as tools

- ▶ Models are the tools that we use to connect scales:
 - ▶ individuals to populations



Measles reports from England and Wales

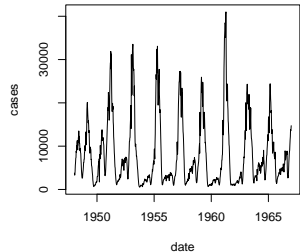


Models as tools

- ▶ Models are the tools that we use to connect scales:
 - ▶ individuals to populations
 - ▶ single actions to trends through time



Measles reports from England and Wales

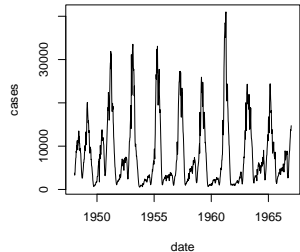


Models as tools

- ▶ Models are the tools that we use to connect scales:
 - ▶ individuals to populations
 - ▶ single actions to trends through time



Measles reports from England and Wales



Outline

Introduction

Rate of spread

Single-epidemic model

Epidemic size

Recurrent epidemic models

Dynamics

Reproductive numbers and risk

Pathogen aggressiveness

Rate of spread

- ▶ For many diseases, especially new diseases, we can *observe* and *estimate* r .

Rate of spread

- ▶ For many diseases, especially new diseases, we can *observe* and *estimate* r .

▶ *

Rate of spread

- ▶ For many diseases, especially new diseases, we can *observe* and *estimate* r .
 - ▶ * Instantaneous rate of increase (per capita)

Rate of spread

- ▶ For many diseases, especially new diseases, we can *observe* and *estimate* r .
 - ▶ * Instantaneous rate of increase (per capita)

▶ *

Rate of spread

- ▶ For many diseases, especially new diseases, we can *observe* and *estimate* r .
 - ▶ * Instantaneous rate of increase (per capita)
 - ▶ * Units of $1/t$

Rate of spread

- ▶ For many diseases, especially new diseases, we can *observe* and *estimate* r .
 - ▶ * Instantaneous rate of increase (per capita)
 - ▶ * Units of $1/t$
 - ▶ *

Rate of spread

- ▶ For many diseases, especially new diseases, we can *observe* and *estimate* r .
 - ▶ * Instantaneous rate of increase (per capita)
 - ▶ * Units of $1/t$
 - ▶ * Gives the exponential rate of spread

Rate of spread

- ▶ For many diseases, especially new diseases, we can *observe* and *estimate* r .
 - ▶ * Instantaneous rate of increase (per capita)
 - ▶ * Units of $1/t$
 - ▶ * Gives the exponential rate of spread
- ▶ Want to know what factors contribute to that, and how it relates to \mathcal{R} .

Rate of spread

- ▶ For many diseases, especially new diseases, we can *observe* and *estimate* r .
 - ▶ * Instantaneous rate of increase (per capita)
 - ▶ * Units of $1/t$
 - ▶ * Gives the exponential rate of spread
- ▶ Want to know what factors contribute to that, and how it relates to \mathcal{R} .
 - ▶ *

Rate of spread

- ▶ For many diseases, especially new diseases, we can *observe* and *estimate* r .
 - ▶ * Instantaneous rate of increase (per capita)
 - ▶ * Units of $1/t$
 - ▶ * Gives the exponential rate of spread
- ▶ Want to know what factors contribute to that, and how it relates to \mathcal{R} .
 - ▶ * number of new cases per case

Rate of spread

- ▶ For many diseases, especially new diseases, we can *observe* and *estimate* r .
 - ▶ * Instantaneous rate of increase (per capita)
 - ▶ * Units of $1/t$
 - ▶ * Gives the exponential rate of spread
- ▶ Want to know what factors contribute to that, and how it relates to \mathcal{R} .
 - ▶ * number of new cases per case
 - ▶ *

Rate of spread

- ▶ For many diseases, especially new diseases, we can *observe* and *estimate* r .
 - ▶ * Instantaneous rate of increase (per capita)
 - ▶ * Units of $1/t$
 - ▶ * Gives the exponential rate of spread
- ▶ Want to know what factors contribute to that, and how it relates to \mathcal{R} .
 - ▶ * number of new cases per case
 - ▶ * Unitless

Rate of spread

- ▶ For many diseases, especially new diseases, we can *observe* and *estimate* r .
 - ▶ * Instantaneous rate of increase (per capita)
 - ▶ * Units of $1/t$
 - ▶ * Gives the exponential rate of spread
- ▶ Want to know what factors contribute to that, and how it relates to \mathcal{R} .
 - ▶ * number of new cases per case
 - ▶ * Unitless

Basic reproductive number

- ▶ People in the disease field love to talk specifically about \mathcal{R}_0

Basic reproductive number

- ▶ People in the disease field love to talk specifically about \mathcal{R}_0
- ▶ But they don't always mean the same thing when they say \mathcal{R}_0 :

Basic reproductive number

- ▶ People in the disease field love to talk specifically about \mathcal{R}_0
- ▶ But they don't always mean the same thing when they say \mathcal{R}_0 :
 - ▶ Actual value of \mathcal{R} before an epidemic

Basic reproductive number

- ▶ People in the disease field love to talk specifically about \mathcal{R}_0
- ▶ But they don't always mean the same thing when they say \mathcal{R}_0 :
 - ▶ Actual value of \mathcal{R} before an epidemic
 - ▶ Hypothetical value assuming no immunity

Basic reproductive number

- ▶ People in the disease field love to talk specifically about \mathcal{R}_0
- ▶ But they don't always mean the same thing when they say \mathcal{R}_0 :
 - ▶ Actual value of \mathcal{R} before an epidemic
 - ▶ Hypothetical value assuming no immunity
 - ▶ Hypothetical value assuming no immunity and no control efforts whatsoever

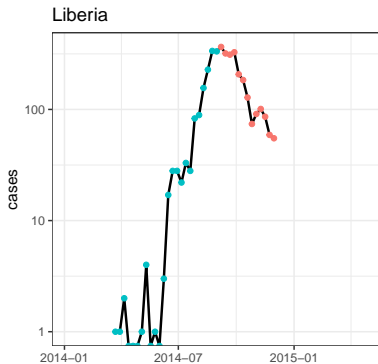
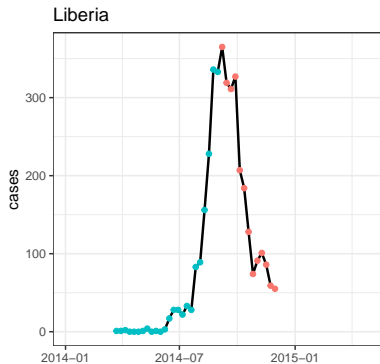
Basic reproductive number

- ▶ People in the disease field love to talk specifically about \mathcal{R}_0
- ▶ But they don't always mean the same thing when they say \mathcal{R}_0 :
 - ▶ Actual value of \mathcal{R} before an epidemic
 - ▶ Hypothetical value assuming no immunity
 - ▶ Hypothetical value assuming no immunity and no control efforts whatsoever
- ▶ Often easier to talk simply about \mathcal{R} .

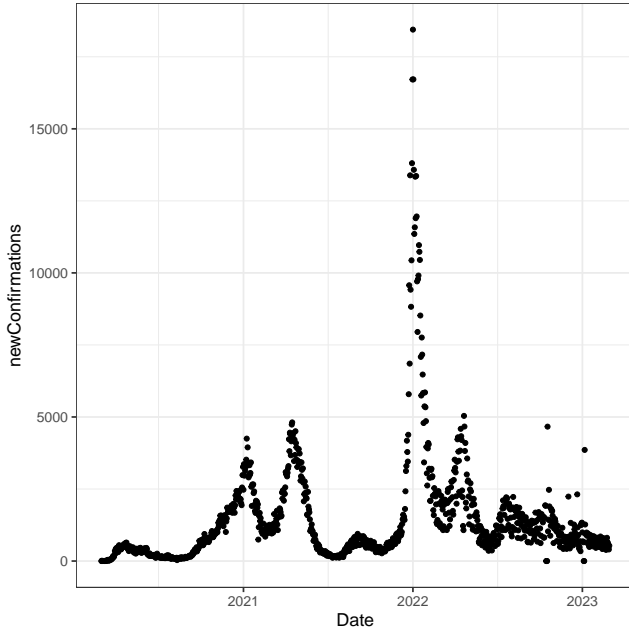
Basic reproductive number

- ▶ People in the disease field love to talk specifically about \mathcal{R}_0
- ▶ But they don't always mean the same thing when they say \mathcal{R}_0 :
 - ▶ Actual value of \mathcal{R} before an epidemic
 - ▶ Hypothetical value assuming no immunity
 - ▶ Hypothetical value assuming no immunity and no control efforts whatsoever
- ▶ Often easier to talk simply about \mathcal{R} .

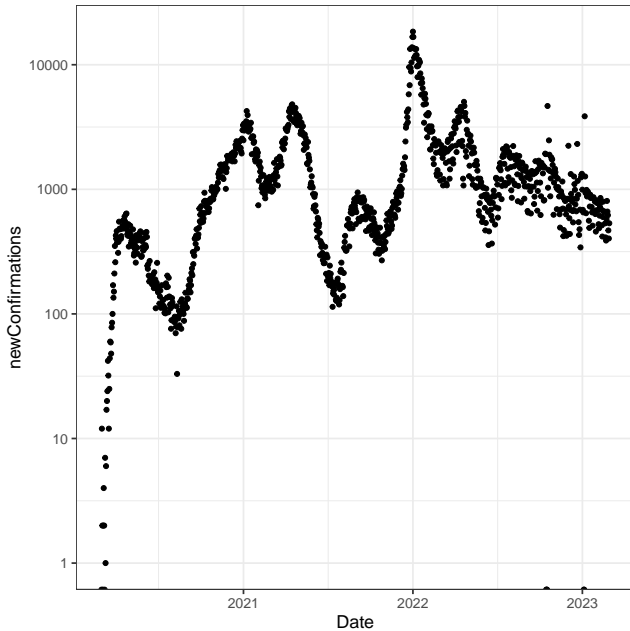
Example: the West African Ebola epidemic



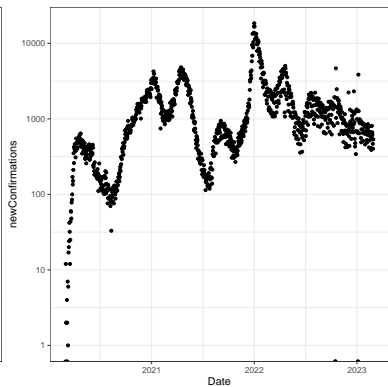
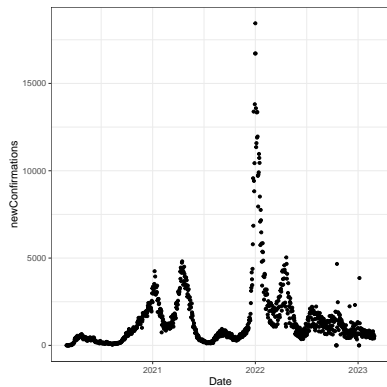
COVID in Ontario (preview)



COVID in Ontario (preview)



COVID in Ontario



Scales

- ▶ Which scale should we look at?

Scales

- ▶ Which scale should we look at?



Scales

- ▶ Which scale should we look at?
 - ▶ * Log scale is better for looking at trends

Scales

- ▶ Which scale should we look at?
 - ▶ * Log scale is better for looking at trends
 - ▶ *

Scales

- ▶ Which scale should we look at?
 - ▶ * Log scale is better for looking at trends
 - ▶ * Linear scale is better for looking at impacts

Scales

- ▶ Which scale should we look at?
 - ▶ * Log scale is better for looking at trends
 - ▶ * Linear scale is better for looking at impacts

Population biology

- ▶ What quantities do we want to look at?

Population biology

- ▶ What quantities do we want to look at?



Population biology

- ▶ What quantities do we want to look at?
 - ▶ * Speed of exponential growth r

Population biology

- ▶ What quantities do we want to look at?
 - ▶ * Speed of exponential growth r
 - ▶ *

Population biology

- ▶ What quantities do we want to look at?
 - ▶ * Speed of exponential growth r
 - ▶ * Finite rate of increase λ

Population biology

- ▶ What quantities do we want to look at?
 - ▶ * Speed of exponential growth r
 - ▶ * Finite rate of increase λ
 - ▶ *

Population biology

- ▶ What quantities do we want to look at?
 - ▶ * Speed of exponential growth r
 - ▶ * Finite rate of increase λ
 - ▶ * Lifetime reproduction, \mathcal{R}

Population biology

- ▶ What quantities do we want to look at?
 - ▶ * Speed of exponential growth r
 - ▶ * Finite rate of increase λ
 - ▶ * Lifetime reproduction, \mathcal{R}

Instantaneous rate of growth r

- ▶ What are the components?

Instantaneous rate of growth r

- ▶ What are the components?



Instantaneous rate of growth r

- ▶ What are the components?
 - ▶ * Birth rate

Instantaneous rate of growth r

▶ What are the components?

▶ * Birth rate

▶ *

Instantaneous rate of growth r

- ▶ What are the components?
 - ▶ * Birth rate
 - ▶ * Instantaneous rate of a case producing new cases

Instantaneous rate of growth r

- ▶ What are the components?
 - ▶ * Birth rate
 - ▶ * Instantaneous rate of a case producing new cases
 - ▶ *

Instantaneous rate of growth r

- ▶ What are the components?
 - ▶ * Birth rate
 - ▶ * Instantaneous rate of a case producing new cases
 - ▶ * $[\text{case}/(\text{case} \cdot \text{time})]$

Instantaneous rate of growth r

- ▶ What are the components?
 - ▶ * Birth rate
 - ▶ * Instantaneous rate of a case producing new cases
 - ▶ * $[\text{case}/(\text{case} \cdot \text{time})]$
 - ▶ *

Instantaneous rate of growth r

- ▶ What are the components?
 - ▶ * Birth rate
 - ▶ * Instantaneous rate of a case producing new cases
 - ▶ * $[\text{case}/(\text{case} \cdot \text{time})]$
 - ▶ * Death rate

Instantaneous rate of growth r

- ▶ What are the components?
 - ▶ * Birth rate
 - ▶ * Instantaneous rate of a case producing new cases
 - ▶ * $[\text{case}/(\text{case} \cdot \text{time})]$
 - ▶ * Death rate
 - ▶ *

Instantaneous rate of growth r

- ▶ What are the components?
 - ▶ * Birth rate
 - ▶ * Instantaneous rate of a case producing new cases
 - ▶ * $[\text{case}/(\text{case} \cdot \text{time})]$
 - ▶ * Death rate
 - ▶ * Virus-centered!

Instantaneous rate of growth r

- ▶ What are the components?
 - ▶ * Birth rate
 - ▶ * Instantaneous rate of a case producing new cases
 - ▶ * $[\text{case}/(\text{case} \cdot \text{time})]$
 - ▶ * Death rate
 - ▶ * Virus-centered!
 - ▶ *

Instantaneous rate of growth r

- ▶ What are the components?
 - ▶ * Birth rate
 - ▶ * Instantaneous rate of a case producing new cases
 - ▶ * $[\text{case}/(\text{case} \cdot \text{time})]$
 - ▶ * Death rate
 - ▶ * Virus-centered!
 - ▶ * Rate of death, recovery, or effective quarantine

Instantaneous rate of growth r

- ▶ What are the components?
 - ▶ * Birth rate
 - ▶ * Instantaneous rate of a case producing new cases
 - ▶ * $[\text{case}/(\text{case} \cdot \text{time})]$
 - ▶ * Death rate
 - ▶ * Virus-centered!
 - ▶ * Rate of death, recovery, or effective quarantine
- ▶ How do you think we estimate?

Instantaneous rate of growth r

- ▶ What are the components?
 - ▶ * Birth rate
 - ▶ * Instantaneous rate of a case producing new cases
 - ▶ * $[\text{case}/(\text{case} \cdot \text{time})]$
 - ▶ * Death rate
 - ▶ * Virus-centered!
 - ▶ * Rate of death, recovery, or effective quarantine
- ▶ How do you think we estimate?
 - ▶ *

Instantaneous rate of growth r

- ▶ What are the components?
 - ▶ * Birth rate
 - ▶ * Instantaneous rate of a case producing new cases
 - ▶ * $[\text{case}/(\text{case} \cdot \text{time})]$
 - ▶ * Death rate
 - ▶ * Virus-centered!
 - ▶ * Rate of death, recovery, or effective quarantine
- ▶ How do you think we estimate?
 - ▶ * We estimate r from the population-level increase in disease

Instantaneous rate of growth r

- ▶ What are the components?
 - ▶ * Birth rate
 - ▶ * Instantaneous rate of a case producing new cases
 - ▶ * $[\text{case}/(\text{case} \cdot \text{time})]$
 - ▶ * Death rate
 - ▶ * Virus-centered!
 - ▶ * Rate of death, recovery, or effective quarantine
- ▶ How do you think we estimate?
 - ▶ * We estimate r from the population-level increase in disease
 - ▶ *

Instantaneous rate of growth r

- ▶ What are the components?
 - ▶ * Birth rate
 - ▶ * Instantaneous rate of a case producing new cases
 - ▶ * $[\text{case}/(\text{case} \cdot \text{time})]$
 - ▶ * Death rate
 - ▶ * Virus-centered!
 - ▶ * Rate of death, recovery, or effective quarantine
- ▶ How do you think we estimate?
 - ▶ * We estimate r from the population-level increase in disease
 - ▶ * Then we use that to estimate $b = d + r$

Instantaneous rate of growth r

- ▶ What are the components?
 - ▶ * Birth rate
 - ▶ * Instantaneous rate of a case producing new cases
 - ▶ * $[\text{case}/(\text{case} \cdot \text{time})]$
 - ▶ * Death rate
 - ▶ * Virus-centered!
 - ▶ * Rate of death, recovery, or effective quarantine
- ▶ How do you think we estimate?
 - ▶ * We estimate r from the population-level increase in disease
 - ▶ * Then we use that to estimate $b = d + r$
- ▶ *

Instantaneous rate of growth r

- ▶ What are the components?
 - ▶ * Birth rate
 - ▶ * Instantaneous rate of a case producing new cases
 - ▶ * $[\text{case}/(\text{case} \cdot \text{time})]$
 - ▶ * Death rate
 - ▶ * Virus-centered!
 - ▶ * Rate of death, recovery, or effective quarantine
- ▶ How do you think we estimate?
 - ▶ * We estimate r from the population-level increase in disease
 - ▶ * Then we use that to estimate $b = d + r$
 - ▶ * Models go both directions!

Instantaneous rate of growth r

- ▶ What are the components?
 - ▶ * Birth rate
 - ▶ * Instantaneous rate of a case producing new cases
 - ▶ * $[\text{case}/(\text{case} \cdot \text{time})]$
 - ▶ * Death rate
 - ▶ * Virus-centered!
 - ▶ * Rate of death, recovery, or effective quarantine
- ▶ How do you think we estimate?
 - ▶ * We estimate r from the population-level increase in disease
 - ▶ * Then we use that to estimate $b = d + r$
 - ▶ * Models go both directions!
 - ▶ Individuals \leftrightarrow Populations

Instantaneous rate of growth r

- ▶ What are the components?
 - ▶ * Birth rate
 - ▶ * Instantaneous rate of a case producing new cases
 - ▶ * $[\text{case}/(\text{case} \cdot \text{time})]$
 - ▶ * Death rate
 - ▶ * Virus-centered!
 - ▶ * Rate of death, recovery, or effective quarantine
- ▶ How do you think we estimate?
 - ▶ * We estimate r from the population-level increase in disease
 - ▶ * Then we use that to estimate $b = d + r$
 - ▶ * Models go both directions!
 - ▶ Individuals \leftrightarrow Populations

Finite rate of growth λ

- Why do we want this?

Finite rate of growth λ

► Why do we want this?

► *

Finite rate of growth λ

- ▶ Why do we want this?
 - ▶ * to communicate with policy-makers or the public

Finite rate of growth λ

- ▶ Why do we want this?
 - ▶ * to communicate with policy-makers or the public
 - ▶ *

Finite rate of growth λ

- ▶ Why do we want this?
 - ▶ * to communicate with policy-makers or the public
 - ▶ * maybe to make concrete predictions, though we could use r

Finite rate of growth λ

- ▶ Why do we want this?
 - ▶ * to communicate with policy-makers or the public
 - ▶ * maybe to make concrete predictions, though we could use r
- ▶ How do we calculate it?

Finite rate of growth λ

- ▶ Why do we want this?
 - ▶ * to communicate with policy-makers or the public
 - ▶ * maybe to make concrete predictions, though we could use r
- ▶ How do we calculate it?
 - ▶ *

Finite rate of growth λ

- ▶ Why do we want this?
 - ▶ * to communicate with policy-makers or the public
 - ▶ * maybe to make concrete predictions, though we could use r
- ▶ How do we calculate it?
 - ▶ * Pick a time step (week? year?)

Finite rate of growth λ

- ▶ Why do we want this?
 - ▶ * to communicate with policy-makers or the public
 - ▶ * maybe to make concrete predictions, though we could use r
- ▶ How do we calculate it?
 - ▶ * Pick a time step (week? year?)
 - ▶ *

Finite rate of growth λ

- ▶ Why do we want this?
 - ▶ * to communicate with policy-makers or the public
 - ▶ * maybe to make concrete predictions, though we could use r
- ▶ How do we calculate it?
 - ▶ * Pick a time step (week? year?)
 - ▶ * Use a formula $\lambda = \exp(r\Delta t)$

Finite rate of growth λ

- ▶ Why do we want this?
 - ▶ * to communicate with policy-makers or the public
 - ▶ * maybe to make concrete predictions, though we could use r
- ▶ How do we calculate it?
 - ▶ * Pick a time step (week? year?)
 - ▶ * Use a formula $\lambda = \exp(r\Delta t)$

Example

- ▶ $r \approx 0.14$ / day for early COVID spread

Example

- ▶ $r \approx 0.14$ / day for early COVID spread
- ▶ What is λ ?

Example

- ▶ $r \approx 0.14$ /day for early COVID spread
- ▶ What is λ ?
 - ▶ At a time scale of a day?

Example

- ▶ $r \approx 0.14$ /day for early COVID spread
- ▶ What is λ ?
 - ▶ At a time scale of a day?
 - ▶ At a time scale of a week?

Example

- ▶ $r \approx 0.14/\text{day}$ for early COVID spread
- ▶ What is λ ?
 - ▶ At a time scale of a day?
 - ▶ At a time scale of a week?

Reproductive number \mathcal{R}

- ▶ What is it?

Reproductive number \mathcal{R}

► What is it?

► *

Reproductive number \mathcal{R}

- ▶ What is it?
 - ▶ * Expected number of new cases per case over the lifetime of a case

Reproductive number \mathcal{R}

- ▶ What is it?
 - ▶ * Expected number of new cases per case over the lifetime of a case
- ▶ Why do we want this?

Reproductive number \mathcal{R}

- ▶ What is it?
 - ▶ * Expected number of new cases per case over the lifetime of a case
- ▶ Why do we want this?
 - ▶ *

Reproductive number \mathcal{R}

- ▶ What is it?
 - ▶ * Expected number of new cases per case over the lifetime of a case
- ▶ Why do we want this?
 - ▶ * An important measure of how hard the epidemic will be to stop

Reproductive number \mathcal{R}

- ▶ What is it?
 - ▶ * Expected number of new cases per case over the lifetime of a case
- ▶ Why do we want this?
 - ▶ * An important measure of how hard the epidemic will be to stop
- ▶ How do we calculate it?

Reproductive number \mathcal{R}

- ▶ What is it?
 - ▶ * Expected number of new cases per case over the lifetime of a case
- ▶ Why do we want this?
 - ▶ * An important measure of how hard the epidemic will be to stop
- ▶ How do we calculate it?
 - ▶ *

Reproductive number \mathcal{R}

- ▶ What is it?
 - ▶ * Expected number of new cases per case over the lifetime of a case
- ▶ Why do we want this?
 - ▶ * An important measure of how hard the epidemic will be to stop
- ▶ How do we calculate it?
 - ▶ * $\mathcal{R} = b/d$; if we can estimate those

Reproductive number \mathcal{R}

- ▶ What is it?
 - ▶ * Expected number of new cases per case over the lifetime of a case
- ▶ Why do we want this?
 - ▶ * An important measure of how hard the epidemic will be to stop
- ▶ How do we calculate it?
 - ▶ * $\mathcal{R} = b/d$; if we can estimate those

Example

► $r \approx 0.14/\text{day}$

Example

- ▶ $r \approx 0.14/\text{day}$
- ▶ What is our estimate of \mathcal{R} ?

Example

- ▶ $r \approx 0.14/\text{day}$
- ▶ What is our estimate of \mathcal{R} ?
 - ▶ When average length of infection $L = 5$ day?

Example

- ▶ $r \approx 0.14/\text{day}$
- ▶ What is our estimate of \mathcal{R} ?
 - ▶ When average length of infection $L = 5$ day?
 - ▶ *

Example

- ▶ $r \approx 0.14/\text{day}$
- ▶ What is our estimate of \mathcal{R} ?
 - ▶ When average length of infection $L = 5 \text{ day}$?
 - ▶ * $d = 1/(5 \text{ day}) = 0.2/\text{day}$

Example

- ▶ $r \approx 0.14/\text{day}$
- ▶ What is our estimate of \mathcal{R} ?
 - ▶ When average length of infection $L = 5 \text{ day}$?
 - ▶ * $d = 1/(5 \text{ day}) = 0.2/\text{day}$
 - ▶ *

Example

- ▶ $r \approx 0.14/\text{day}$
- ▶ What is our estimate of \mathcal{R} ?
 - ▶ When average length of infection $L = 5 \text{ day}$?
 - ▶ * $d = 1/(5 \text{ day}) = 0.2/\text{day}$
 - ▶ * $b = 0.14 \text{ day} + 0.2 \text{ day} = 0.34/\text{day}$

Example

- ▶ $r \approx 0.14/\text{day}$
- ▶ What is our estimate of \mathcal{R} ?
 - ▶ When average length of infection $L = 5 \text{ day}$?
 - ▶ * $d = 1/(5 \text{ day}) = 0.2/\text{day}$
 - ▶ * $b = 0.14 \text{ day} + 0.2 \text{ day} = 0.34/\text{day}$
 - ▶ *

Example

- ▶ $r \approx 0.14/\text{day}$
- ▶ What is our estimate of \mathcal{R} ?
 - ▶ When average length of infection $L = 5 \text{ day}$?
 - ▶ * $d = 1/(5 \text{ day}) = 0.2/\text{day}$
 - ▶ * $b = 0.14 \text{ day} + 0.2 \text{ day} = 0.34/\text{day}$
 - ▶ * $\mathcal{R} = 0.34/0.2 = 1.7$

Example

- ▶ $r \approx 0.14/\text{day}$
- ▶ What is our estimate of \mathcal{R} ?
 - ▶ When average length of infection $L = 5$ day?
 - ▶ * $d = 1/(5 \text{ day}) = 0.2/\text{day}$
 - ▶ * $b = 0.14 \text{ day} + 0.2 \text{ day} = 0.34/\text{day}$
 - ▶ * $\mathcal{R} = 0.34/0.2 = 1.7$
 - ▶ When average length of infection $L = 10$ day?

Example

- ▶ $r \approx 0.14/\text{day}$
- ▶ What is our estimate of \mathcal{R} ?
 - ▶ When average length of infection $L = 5$ day?
 - ▶ * $d = 1/(5 \text{ day}) = 0.2/\text{day}$
 - ▶ * $b = 0.14 \text{ day} + 0.2 \text{ day} = 0.34/\text{day}$
 - ▶ * $\mathcal{R} = 0.34/0.2 = 1.7$
 - ▶ When average length of infection $L = 10$ day?
 - ▶ *

Example

- ▶ $r \approx 0.14/\text{day}$
- ▶ What is our estimate of \mathcal{R} ?
 - ▶ When average length of infection $L = 5$ day?
 - ▶ * $d = 1/(5 \text{ day}) = 0.2/\text{day}$
 - ▶ * $b = 0.14 \text{ day} + 0.2 \text{ day} = 0.34/\text{day}$
 - ▶ * $\mathcal{R} = 0.34/0.2 = 1.7$
 - ▶ When average length of infection $L = 10$ day?
 - ▶ * $d = 1/(10 \text{ day}) = 0.1/\text{day}$

Example

- ▶ $r \approx 0.14/\text{day}$
- ▶ What is our estimate of \mathcal{R} ?
 - ▶ When average length of infection $L = 5$ day?
 - ▶ * $d = 1/(5 \text{ day}) = 0.2/\text{day}$
 - ▶ * $b = 0.14 \text{ day} + 0.2 \text{ day} = 0.34/\text{day}$
 - ▶ * $\mathcal{R} = 0.34/0.2 = 1.7$
 - ▶ When average length of infection $L = 10$ day?
 - ▶ * $d = 1/(10 \text{ day}) = 0.1/\text{day}$
 - ▶ *

Example

- ▶ $r \approx 0.14/\text{day}$
- ▶ What is our estimate of \mathcal{R} ?
 - ▶ When average length of infection $L = 5$ day?
 - ▶ * $d = 1/(5 \text{ day}) = 0.2/\text{day}$
 - ▶ * $b = 0.14 \text{ day} + 0.2 \text{ day} = 0.34/\text{day}$
 - ▶ * $\mathcal{R} = 0.34/0.2 = 1.7$
 - ▶ When average length of infection $L = 10$ day?
 - ▶ * $d = 1/(10 \text{ day}) = 0.1/\text{day}$
 - ▶ * $b = 0.14 \text{ day} + 0.1 \text{ day} = 0.24/\text{day}$

Example

- ▶ $r \approx 0.14/\text{day}$
- ▶ What is our estimate of \mathcal{R} ?
 - ▶ When average length of infection $L = 5 \text{ day}$?
 - ▶ * $d = 1/(5 \text{ day}) = 0.2/\text{day}$
 - ▶ * $b = 0.14 \text{ day} + 0.2 \text{ day} = 0.34/\text{day}$
 - ▶ * $\mathcal{R} = 0.34/0.2 = 1.7$
 - ▶ When average length of infection $L = 10 \text{ day}$?
 - ▶ * $d = 1/(10 \text{ day}) = 0.1/\text{day}$
 - ▶ * $b = 0.14 \text{ day} + 0.1 \text{ day} = 0.24/\text{day}$
 - ▶ *

Example

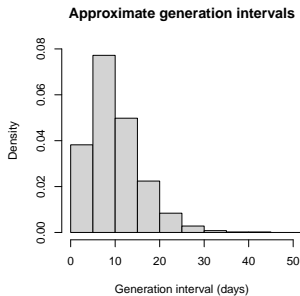
- ▶ $r \approx 0.14/\text{day}$
- ▶ What is our estimate of \mathcal{R} ?
 - ▶ When average length of infection $L = 5 \text{ day}$?
 - ▶ * $d = 1/(5 \text{ day}) = 0.2/\text{day}$
 - ▶ * $b = 0.14 \text{ day} + 0.2 \text{ day} = 0.34/\text{day}$
 - ▶ * $\mathcal{R} = 0.34/0.2 = 1.7$
 - ▶ When average length of infection $L = 10 \text{ day}$?
 - ▶ * $d = 1/(10 \text{ day}) = 0.1/\text{day}$
 - ▶ * $b = 0.14 \text{ day} + 0.1 \text{ day} = 0.24/\text{day}$
 - ▶ * $\mathcal{R} = 0.24/0.1 = 2.4$

Example

- ▶ $r \approx 0.14/\text{day}$
- ▶ What is our estimate of \mathcal{R} ?
 - ▶ When average length of infection $L = 5$ day?
 - ▶ * $d = 1/(5 \text{ day}) = 0.2/\text{day}$
 - ▶ * $b = 0.14 \text{ day} + 0.2 \text{ day} = 0.34/\text{day}$
 - ▶ * $\mathcal{R} = 0.34/0.2 = 1.7$
 - ▶ When average length of infection $L = 10$ day?
 - ▶ * $d = 1/(10 \text{ day}) = 0.1/\text{day}$
 - ▶ * $b = 0.14 \text{ day} + 0.1 \text{ day} = 0.24/\text{day}$
 - ▶ * $\mathcal{R} = 0.24/0.1 = 2.4$

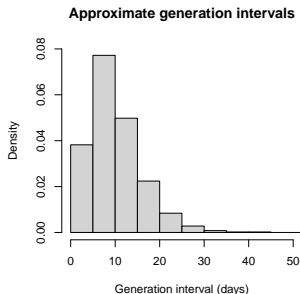
Generation intervals

- Researchers try to estimate the *proportion* of transmission that happens for different **ages of infection**



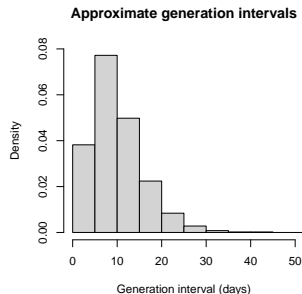
Generation intervals

- ▶ Researchers try to estimate the *proportion* of transmission that happens for different **ages of infection**
- ▶ How long from the time you are *infected* to the time you *infect someone else*?



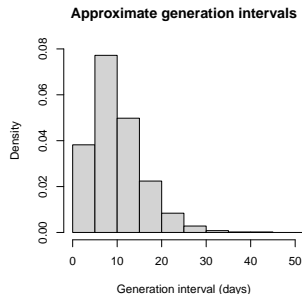
Generation intervals

- ▶ Researchers try to estimate the *proportion* of transmission that happens for different **ages of infection**
- ▶ How long from the time you are *infected* to the time you *infect someone else*?
- ▶ Analogous to a life table



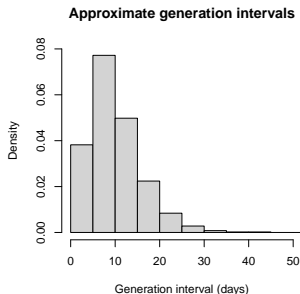
Generation intervals

- ▶ Researchers try to estimate the *proportion* of transmission that happens for different **ages of infection**
- ▶ How long from the time you are *infected* to the time you *infect someone else*?
- ▶ Analogous to a life table
- ▶ The effective generation time \hat{G} has units of time



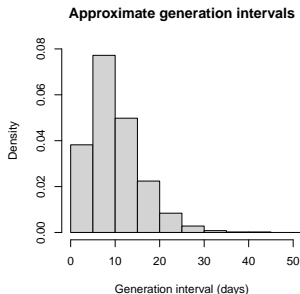
Generation intervals

- ▶ Researchers try to estimate the *proportion* of transmission that happens for different **ages of infection**
- ▶ How long from the time you are *infected* to the time you *infect someone else*?
- ▶ Analogous to a life table
- ▶ The effective generation time \hat{G} has units of time
 - ▶ \hat{G} is fairly deep; we'll skip the details



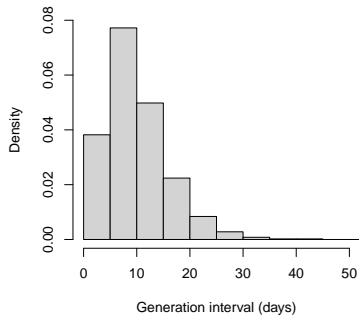
Generation intervals

- ▶ Researchers try to estimate the *proportion* of transmission that happens for different **ages of infection**
- ▶ How long from the time you are *infected* to the time you *infect someone else*?
- ▶ Analogous to a life table
- ▶ The effective generation time \hat{G} has units of time
 - ▶ \hat{G} is fairly deep; we'll skip the details

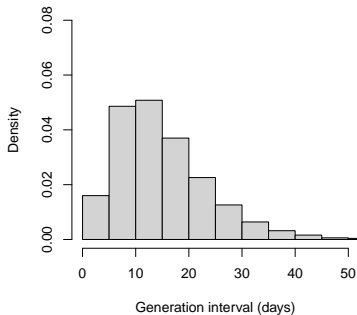


Generation intervals

Approximate generation intervals

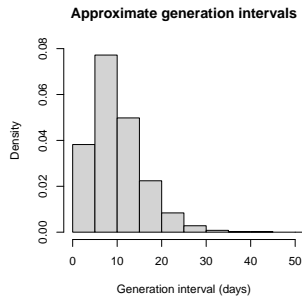


Approximate generation intervals



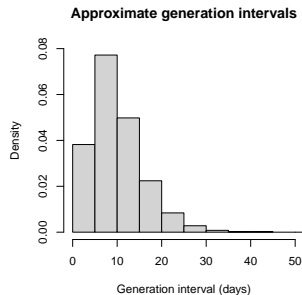
Speed and risk

- Which is more dangerous, a fast disease, or a slow disease?



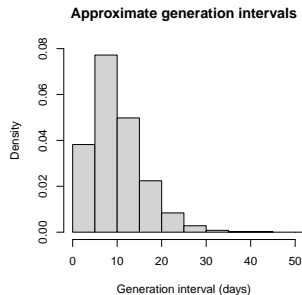
Speed and risk

- ▶ Which is more dangerous, a fast disease, or a slow disease?
 - ▶ How are we measuring speed?



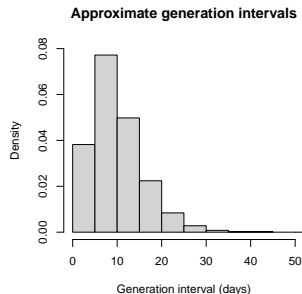
Speed and risk

- ▶ Which is more dangerous, a fast disease, or a slow disease?
 - ▶ How are we measuring speed?
 - ▶ How are we measuring danger?



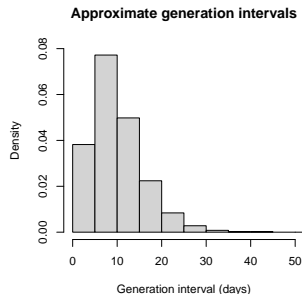
Speed and risk

- ▶ Which is more dangerous, a fast disease, or a slow disease?
 - ▶ How are we measuring speed?
 - ▶ How are we measuring danger?
 - ▶ *What do we already know?*



Speed and risk

- ▶ Which is more dangerous, a fast disease, or a slow disease?
 - ▶ How are we measuring speed?
 - ▶ How are we measuring danger?
 - ▶ *What do we already know?*



Fighting Ebola



Generation time and risk

- ▶ If we know \mathcal{R} , what does the generation time tell us about r ?

Generation time and risk

- ▶ If we know \mathcal{R} , what does the generation time tell us about r ?
 - ▶ *

Generation time and risk

- ▶ If we know \mathcal{R} , what does the generation time tell us about r ?
 - ▶ * The faster the generations (small \hat{G}), the faster the exponential growth (large r)

Generation time and risk

- ▶ If we know \mathcal{R} , what does the generation time tell us about r ?
 - ▶ * The faster the generations (small \hat{G}), the faster the exponential growth (large r)
- ▶ If we know r , what does the generation time tell us about \mathcal{R} ?

Generation time and risk

- ▶ If we know \mathcal{R} , what does the generation time tell us about r ?
 - ▶ * The faster the generations (small \hat{G}), the faster the exponential growth (large r)
- ▶ If we know r , what does the generation time tell us about \mathcal{R} ?
 - ▶ *

Generation time and risk

- ▶ If we know \mathcal{R} , what does the generation time tell us about r ?
 - ▶ * The faster the generations (small \hat{G}), the faster the exponential growth (large r)
- ▶ If we know r , what does the generation time tell us about \mathcal{R} ?
 - ▶ * The faster the generations (small \hat{G}), the *smaller* the strength of the epidemic (small reproductive number \mathcal{R})

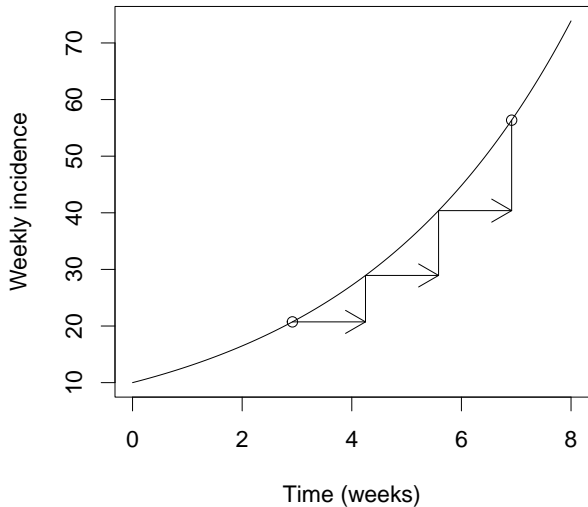
Generation time and risk

- ▶ If we know \mathcal{R} , what does the generation time tell us about r ?
 - ▶ * The faster the generations (small \hat{G}), the faster the exponential growth (large r)
 - ▶ If we know r , what does the generation time tell us about \mathcal{R} ?
 - ▶ * The faster the generations (small \hat{G}), the *smaller* the strength of the epidemic (small reproductive number \mathcal{R})
- ▶ $\mathcal{R} = \exp(r\hat{G})$

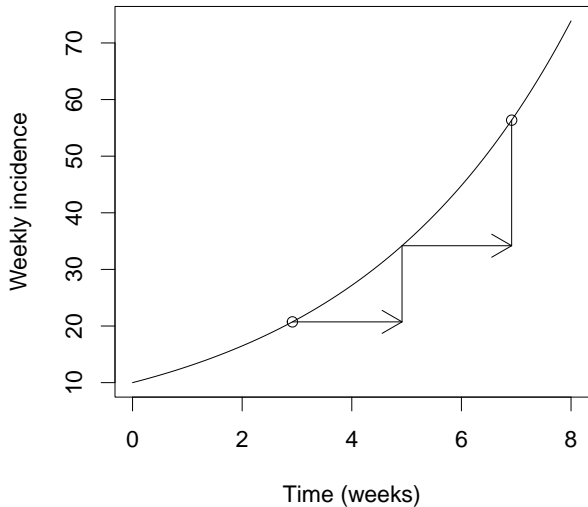
Generation time and risk

- ▶ If we know \mathcal{R} , what does the generation time tell us about r ?
 - ▶ * The faster the generations (small \hat{G}), the faster the exponential growth (large r)
- ▶ If we know r , what does the generation time tell us about \mathcal{R} ?
 - ▶ * The faster the generations (small \hat{G}), the *smaller* the strength of the epidemic (small reproductive number \mathcal{R})
- ▶ $\mathcal{R} = \exp(r\hat{G})$

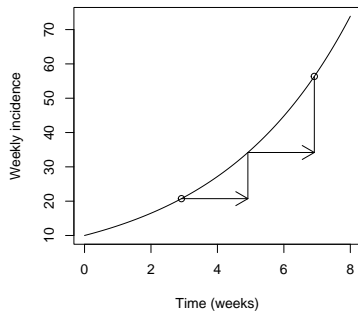
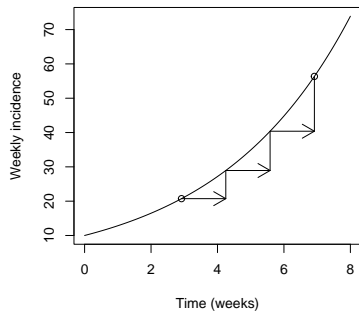
Generation time and risk (repeat)



Generation time and risk (repeat)



Generation time and risk



Generation time and risk

► $\mathcal{R} = \exp(r\hat{G})$

Generation time and risk

▶ $\mathcal{R} = \exp(r\hat{G})$

▶ An intuitive view:

Generation time and risk

- ▶ $\mathcal{R} = \exp(r\hat{G})$
- ▶ An intuitive view:
 - ▶ Epidemic speed = Generation strength \times Generation speed

Generation time and risk

- ▶ $\mathcal{R} = \exp(r\hat{G})$
- ▶ An intuitive view:
 - ▶ Epidemic speed = Generation strength \times Generation speed
 - ▶ *Mathematically:* $r = \log(\mathcal{R}) * (1/\hat{G})$

Generation time and risk

- ▶ $\mathcal{R} = \exp(r\hat{G})$
- ▶ An intuitive view:
 - ▶ Epidemic speed = Generation strength \times Generation speed
 - ▶ *Mathematically:* $r = \log(\mathcal{R}) * (1/\hat{G})$
- ▶ If we know generation speed, then a faster epidemic speed means:

Generation time and risk

- ▶ $\mathcal{R} = \exp(r\hat{G})$
- ▶ An intuitive view:
 - ▶ Epidemic speed = Generation strength \times Generation speed
 - ▶ *Mathematically:* $r = \log(\mathcal{R}) * (1/\hat{G})$
- ▶ If we know generation speed, then a faster epidemic speed means:
 - ▶ *

Generation time and risk

- ▶ $\mathcal{R} = \exp(r\hat{G})$
- ▶ An intuitive view:
 - ▶ Epidemic speed = Generation strength \times Generation speed
 - ▶ *Mathematically:* $r = \log(\mathcal{R}) * (1/\hat{G})$
- ▶ If we know generation speed, then a faster epidemic speed means:
 - ▶ * More strength required (greater \mathcal{R})

Generation time and risk

- ▶ $\mathcal{R} = \exp(r\hat{G})$
- ▶ An intuitive view:
 - ▶ Epidemic speed = Generation strength \times Generation speed
 - ▶ *Mathematically:* $r = \log(\mathcal{R}) * (1/\hat{G})$
- ▶ If we know generation speed, then a faster epidemic speed means:
 - ▶ * More strength required (greater \mathcal{R})
- ▶ If we know epidemic speed, a faster generation speed means

Generation time and risk

- ▶ $\mathcal{R} = \exp(r\hat{G})$
- ▶ An intuitive view:
 - ▶ Epidemic speed = Generation strength \times Generation speed
 - ▶ *Mathematically:* $r = \log(\mathcal{R}) * (1/\hat{G})$
- ▶ If we know generation speed, then a faster epidemic speed means:
 - ▶ * More strength required (greater \mathcal{R})
- ▶ If we know epidemic speed, a faster generation speed means
 - ▶ *

Generation time and risk

- ▶ $\mathcal{R} = \exp(r\hat{G})$
- ▶ An intuitive view:
 - ▶ Epidemic speed = Generation strength \times Generation speed
 - ▶ *Mathematically:* $r = \log(\mathcal{R}) * (1/\hat{G})$
- ▶ If we know generation speed, then a faster epidemic speed means:
 - ▶ * More strength required (greater \mathcal{R})
- ▶ If we know epidemic speed, a faster generation speed means
 - ▶ * Less strength required (smaller \mathcal{R})

Generation time and risk

- ▶ $\mathcal{R} = \exp(r\hat{G})$
- ▶ An intuitive view:
 - ▶ Epidemic speed = Generation strength \times Generation speed
 - ▶ *Mathematically:* $r = \log(\mathcal{R}) * (1/\hat{G})$
- ▶ If we know generation speed, then a faster epidemic speed means:
 - ▶ * More strength required (greater \mathcal{R})
- ▶ If we know epidemic speed, a faster generation speed means
 - ▶ * Less strength required (smaller \mathcal{R})

Outline

Introduction

Rate of spread

Single-epidemic model

Epidemic size

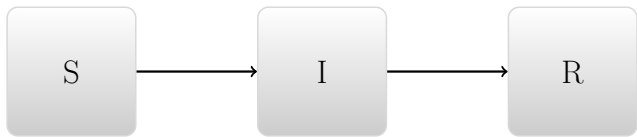
Recurrent epidemic models

Dynamics

Reproductive numbers and risk

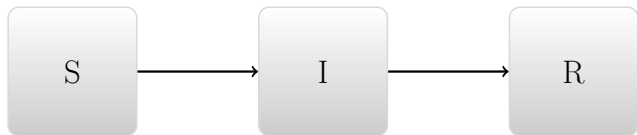
Pathogen aggressiveness

Single-epidemic model



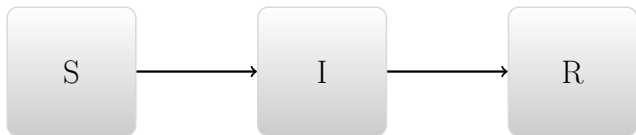
► Susceptible → Infectious → Recovered

Single-epidemic model



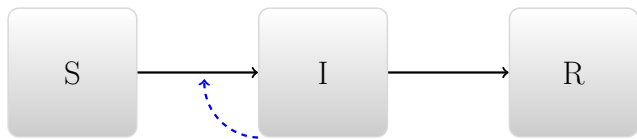
- ▶ Susceptible \rightarrow Infectious \rightarrow Recovered
- ▶ We also use N to mean the total population

Single-epidemic model



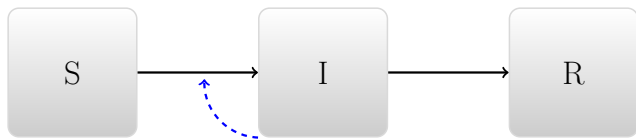
- ▶ Susceptible \rightarrow Infectious \rightarrow Recovered
- ▶ We also use N to mean the total population

Transition rates



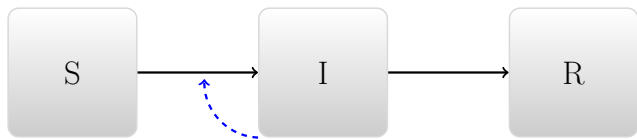
- What factors govern movement through the boxes?

Transition rates



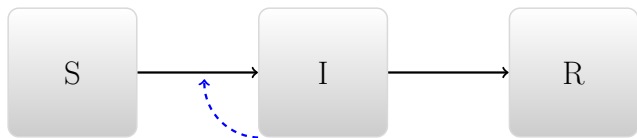
- ▶ What factors govern movement through the boxes?
 - ▶ People get better independently

Transition rates



- ▶ What factors govern movement through the boxes?
 - ▶ People get better independently
 - ▶ People get infected by infectious people

Transition rates



- ▶ What factors govern movement through the boxes?
 - ▶ People get better independently
 - ▶ People get infected by infectious people

Conceptual modeling

- What happens in the long term if we introduce an infectious individual?



Conceptual modeling

- ▶ What happens in the long term if we introduce an infectious individual?



Conceptual modeling

- ▶ What happens in the long term if we introduce an infectious individual?
 - ▶ * *There may be an epidemic*
 - an outbreak of disease



Conceptual modeling

- ▶ What happens in the long term if we introduce an infectious individual
 - ▶ * There *may be* an **epidemic**
 - an outbreak of disease
 - ▶ *



Conceptual modeling

- ▶ What happens in the long term if we introduce an infectious individual?
 - ▶ * There *may be* an **epidemic**
 - an outbreak of disease
 - ▶ * Disease burns out



Conceptual modeling

- ▶ What happens in the long term if we introduce an infectious individual?
 - ▶ * There *may be* an **epidemic**
 - an outbreak of disease
 - ▶ * Disease burns out
 - ▶ *



Conceptual modeling

- ▶ What happens in the long term if we introduce an infectious individual?
 - ▶ * There *may be* an **epidemic**
 - an outbreak of disease
 - ▶ * Disease burns out
 - ▶ * Everyone winds up recovered



Conceptual modeling

- ▶ What happens in the long term if we introduce an infectious individual?
 - ▶ * There *may be* an **epidemic**
 - an outbreak of disease
 - ▶ * Disease burns out
 - ▶ * Everyone winds up recovered



Conceptual modeling

- ▶ What happens in the long term if we introduce an infectious individual?
 - ▶ * There *may be* an **epidemic**
 - an outbreak of disease
 - ▶ * Disease burns out
 - ▶ * Everyone winds up recovered
 - ▶ * ... or susceptible



Conceptual modeling

- ▶ What happens in the long term if we introduce an infectious individual?
 - ▶ * There *may be* an **epidemic**
 - an outbreak of disease
 - ▶ * Disease burns out
 - ▶ * Everyone winds up recovered
 - ▶ * ... or susceptible
 - ▶ *



Conceptual modeling

- ▶ What happens in the long term if we introduce an infectious individual?
 - ▶ * There *may be* an **epidemic** – an outbreak of disease
 - ▶ * Disease burns out
 - ▶ * Everyone winds up recovered
 - ▶ * ... or susceptible
 - ▶ * Or, there may not be an outbreak



Conceptual modeling

- ▶ What happens in the long term if we introduce an infectious individual?
 - ▶ * There *may be* an **epidemic** – an outbreak of disease
 - ▶ * Disease burns out
 - ▶ * Everyone winds up recovered
 - ▶ * ... or susceptible
 - ▶ * Or, there may not be an outbreak



Interpreting

- ▶ Why might there not be an epidemic?

Interpreting

- ▶ Why might there not be an epidemic?



Interpreting

- ▶ Why might there not be an epidemic?
 - ▶ * If the disease can't spread well enough in the population

Interpreting

- ▶ Why might there not be an epidemic?
 - ▶ * If the disease can't spread well enough in the population
 - ▶ *

Interpreting

- ▶ Why might there not be an epidemic?
 - ▶ * If the disease can't spread well enough in the population
 - ▶ * Could depend on season, or immunity ...

Interpreting

- ▶ Why might there not be an epidemic?
 - ▶ * If the disease can't spread well enough in the population
 - ▶ * Could depend on season, or immunity ...
- ▶ *

Interpreting

- ▶ Why might there not be an epidemic?
 - ▶ * If the disease can't spread well enough in the population
 - ▶ * Could depend on season, or immunity ...
 - ▶ * Demographic stochasticity: if we only start with one individual, we expect an element of chance

Interpreting

- ▶ Why might there not be an epidemic?
 - ▶ * If the disease can't spread well enough in the population
 - ▶ * Could depend on season, or immunity ...
 - ▶ * Demographic stochasticity: if we only start with one individual, we expect an element of chance
- ▶ Why doesn't everyone get infected?

Interpreting

- ▶ Why might there not be an epidemic?
 - ▶ * If the disease can't spread well enough in the population
 - ▶ * Could depend on season, or immunity ...
 - ▶ * Demographic stochasticity: if we only start with one individual, we expect an element of chance
- ▶ Why doesn't everyone get infected?
 - ▶ *

Interpreting

- ▶ Why might there not be an epidemic?
 - ▶ * If the disease can't spread well enough in the population
 - ▶ * Could depend on season, or immunity ...
 - ▶ * Demographic stochasticity: if we only start with one individual, we expect an element of chance
- ▶ Why doesn't everyone get infected?
 - ▶ *

Interpreting

- ▶ Why might there not be an epidemic?
 - ▶ * If the disease can't spread well enough in the population
 - ▶ * Could depend on season, or immunity ...
 - ▶ * Demographic stochasticity: if we only start with one individual, we expect an element of chance
- ▶ Why doesn't everyone get infected?
 - ▶ *

Implementing the model

- ▶ The simplest way to implement this conceptual model is with differential equations:



Implementing the model

- ▶ The simplest way to implement this conceptual model is with differential equations:



$$\frac{dS}{dt} = -\beta \frac{SI}{N}$$



Implementing the model

- ▶ The simplest way to implement this conceptual model is with differential equations:

- ▶
$$\frac{dS}{dt} = -\beta \frac{SI}{N}$$

- ▶
$$\frac{dI}{dt} = \beta \frac{SI}{N} - \gamma I$$



Implementing the model

- ▶ The simplest way to implement this conceptual model is with differential equations:



$$\frac{dS}{dt} = -\beta \frac{SI}{N}$$



$$\frac{dI}{dt} = \beta \frac{SI}{N} - \gamma I$$



$$\frac{dR}{dt} = \gamma I$$



Implementing the model

- ▶ The simplest way to implement this conceptual model is with differential equations:

- ▶
$$\frac{dS}{dt} = -\beta \frac{SI}{N}$$

- ▶
$$\frac{dI}{dt} = \beta \frac{SI}{N} - \gamma I$$

- ▶
$$\frac{dR}{dt} = \gamma I$$

- ▶
$$N = S + I + R$$



Implementing the model

- ▶ The simplest way to implement this conceptual model is with differential equations:

- ▶
$$\frac{dS}{dt} = -\beta \frac{SI}{N}$$

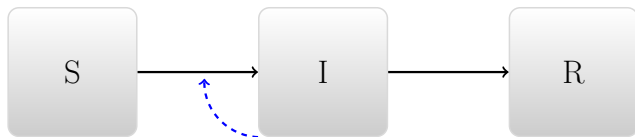
- ▶
$$\frac{dI}{dt} = \beta \frac{SI}{N} - \gamma I$$

- ▶
$$\frac{dR}{dt} = \gamma I$$

- ▶
$$N = S + I + R$$



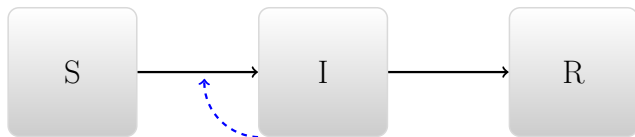
Quantities



State variables

- S, I, R, N : [people] or [people/ha]

Quantities



State variables

- ▶ S, I, R, N : [people] or [people/ha]

Quantities

Parameters

- ▶ Susceptible people have **potentially effective** contacts at rate β (units [1/time])

Parameters

- ▶ Susceptible people have **potentially effective** contacts at rate β (units [1/time])
 - ▶ These are contacts that would lead to infection if the person contacted is infectious

Parameters

- ▶ Susceptible people have **potentially effective** contacts at rate β (units [1/time])
 - ▶ These are contacts that would lead to infection if the person contacted is infectious
 - ▶ Total infection rate is $\beta I/N$, because I/N is the proportion of the population infectious

Quantities

Parameters

- ▶ Susceptible people have **potentially effective** contacts at rate β (units [1/time])
 - ▶ These are contacts that would lead to infection if the person contacted is infectious
 - ▶ Total infection rate is $\beta I/N$, because I/N is the proportion of the population infectious
- ▶ Infectious people recover at *per capita* rate γ (units [1/time])

Quantities

Parameters

- ▶ Susceptible people have **potentially effective** contacts at rate β (units [1/time])
 - ▶ These are contacts that would lead to infection if the person contacted is infectious
 - ▶ Total infection rate is $\beta I/N$, because I/N is the proportion of the population infectious
- ▶ Infectious people recover at *per capita* rate γ (units [1/time])
 - ▶ Total recovery rate is γI

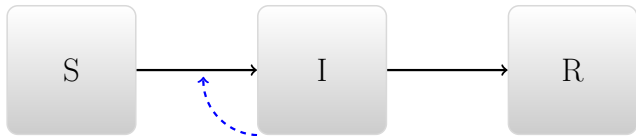
Parameters

- ▶ Susceptible people have **potentially effective** contacts at rate β (units [1/time])
 - ▶ These are contacts that would lead to infection if the person contacted is infectious
 - ▶ Total infection rate is $\beta I/N$, because I/N is the proportion of the population infectious
- ▶ Infectious people recover at *per capita* rate γ (units [1/time])
 - ▶ Total recovery rate is γI
 - ▶ Mean time infectious is $D = 1/\gamma$ (units [time])

Parameters

- ▶ Susceptible people have **potentially effective** contacts at rate β (units [1/time])
 - ▶ These are contacts that would lead to infection if the person contacted is infectious
 - ▶ Total infection rate is $\beta I/N$, because I/N is the proportion of the population infectious
- ▶ Infectious people recover at *per capita* rate γ (units [1/time])
 - ▶ Total recovery rate is γI
 - ▶ Mean time infectious is $D = 1/\gamma$ (units [time])

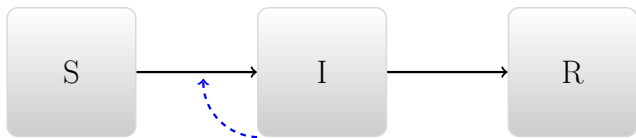
Quantities (repeat)



State variables

- S, I, R, N : [people] or [people/ha]

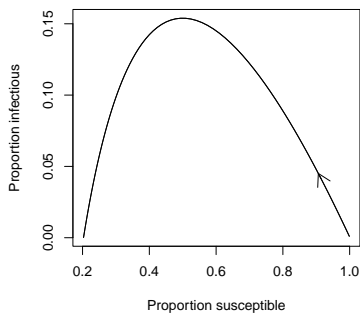
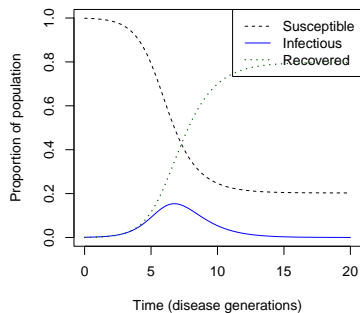
Quantities (repeat)



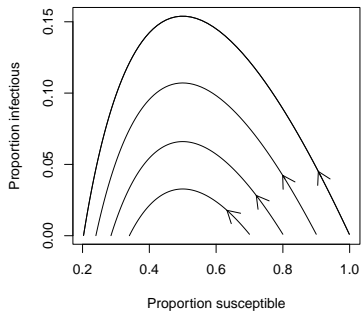
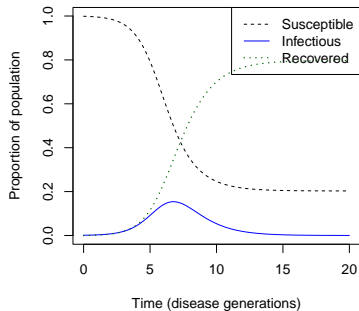
State variables

- ▶ S, I, R, N : [people] or [people/ha]

Simulating the model (repeat)



Simulating the model



Basic reproductive number

- ▶ What *unitless* parameter can you make from the model above?

Basic reproductive number

- ▶ What *unitless* parameter can you make from the model above?

▶ *

Basic reproductive number

- ▶ What *unitless* parameter can you make from the model above?
 - ▶ * $\mathcal{R}_0 = \beta D = \beta/\gamma$ is the **basic reproductive number**

Basic reproductive number

- ▶ What *unitless* parameter can you make from the model above?
 - ▶ * $\mathcal{R}_0 = \beta D = \beta/\gamma$ is the **basic reproductive number**
 - ▶ *

Basic reproductive number

- ▶ What *unitless* parameter can you make from the model above?
 - ▶ * $\mathcal{R}_0 = \beta D = \beta/\gamma$ is the **basic reproductive number**
 - ▶ * The *potential* number of infections caused by an average infectious individual

Basic reproductive number

- ▶ What *unitless* parameter can you make from the model above?
 - ▶ * $\mathcal{R}_0 = \beta D = \beta/\gamma$ is the **basic reproductive number**
 - ▶ * The *potential* number of infections caused by an average infectious individual
 - ▶ *

Basic reproductive number

- ▶ What *unitless* parameter can you make from the model above?
 - ▶ * $\mathcal{R}_0 = \beta D = \beta/\gamma$ is the **basic reproductive number**
 - ▶ * The *potential* number of infections caused by an average infectious individual
 - ▶ * That is: the number they would cause on average if everyone else were susceptible

Basic reproductive number

- ▶ What *unitless* parameter can you make from the model above?
 - ▶ * $\mathcal{R}_0 = \beta D = \beta/\gamma$ is the **basic reproductive number**
 - ▶ * The *potential* number of infections caused by an average infectious individual
 - ▶ * That is: the number they would cause on average if everyone else were susceptible

▶ *

Basic reproductive number

- ▶ What *unitless* parameter can you make from the model above?
 - ▶ * $\mathcal{R}_0 = \beta D = \beta/\gamma$ is the **basic reproductive number**
 - ▶ * The *potential* number of infections caused by an average infectious individual
 - ▶ * That is: the number they would cause on average if everyone else were susceptible
 - ▶ * The product of the rate β (units [1/t]) and the duration D ([t])

Basic reproductive number

- ▶ What *unitless* parameter can you make from the model above?
 - ▶ * $\mathcal{R}_0 = \beta D = \beta/\gamma$ is the **basic reproductive number**
 - ▶ * The *potential* number of infections caused by an average infectious individual
 - ▶ * That is: the number they would cause on average if everyone else were susceptible
 - ▶ * The product of the rate β (units [1/t]) and the duration D ([t])

Basic reproductive number implications

- ▶ What happens early in the epidemic if $\mathcal{R}_0 > 1$?

Basic reproductive number implications

- ▶ What happens early in the epidemic if $\mathcal{R}_0 > 1$?



Basic reproductive number implications

- ▶ What happens early in the epidemic if $\mathcal{R}_0 > 1$?
 - ▶ * Number of infected individuals grows exponentially

Basic reproductive number implications

- ▶ What happens early in the epidemic if $\mathcal{R}_0 > 1$?
 - ▶ * Number of infected individuals grows exponentially
- ▶ What happens early in the epidemic if $\mathcal{R}_0 < 1$?

Basic reproductive number implications

- ▶ What happens early in the epidemic if $\mathcal{R}_0 > 1$?
 - ▶ * Number of infected individuals grows exponentially
- ▶ What happens early in the epidemic if $\mathcal{R}_0 < 1$?
 - ▶ *

Basic reproductive number implications

- ▶ What happens early in the epidemic if $\mathcal{R}_0 > 1$?
 - ▶ * Number of infected individuals grows exponentially
- ▶ What happens early in the epidemic if $\mathcal{R}_0 < 1$?
 - ▶ * Number of infected individuals does not grow (disease cannot invade)

Basic reproductive number implications

- ▶ What happens early in the epidemic if $\mathcal{R}_0 > 1$?
 - ▶ * Number of infected individuals grows exponentially
- ▶ What happens early in the epidemic if $\mathcal{R}_0 < 1$?
 - ▶ * Number of infected individuals does not grow (disease cannot invade)

Effective reproductive number

- ▶ The effective reproductive number gives the number of new infections per infectious individual in a partially susceptible population:

Effective reproductive number

- ▶ The effective reproductive number gives the number of new infections per infectious individual in a partially susceptible population:

▶ *

Effective reproductive number

- ▶ The effective reproductive number gives the number of new infections per infectious individual in a partially susceptible population:
 - ▶ * $\mathcal{R}_{\text{eff}} = \mathcal{R}_0 S/N$

Effective reproductive number

- ▶ The effective reproductive number gives the number of new infections per infectious individual in a partially susceptible population:
 - ▶ * $\mathcal{R}_{\text{eff}} = \mathcal{R}_0 S/N$
- ▶ Is the disease increasing or decreasing?

Effective reproductive number

- ▶ The effective reproductive number gives the number of new infections per infectious individual in a partially susceptible population:
 - ▶ * $\mathcal{R}_{\text{eff}} = \mathcal{R}_0 S/N$
- ▶ Is the disease increasing or decreasing?
 - ▶ *

Effective reproductive number

- ▶ The effective reproductive number gives the number of new infections per infectious individual in a partially susceptible population:
 - ▶ * $\mathcal{R}_{\text{eff}} = \mathcal{R}_0 S/N$
- ▶ Is the disease increasing or decreasing?
 - ▶ * It will increase when $\mathcal{R}_{\text{eff}} > 1$ (more than one case per case)

Effective reproductive number

- ▶ The effective reproductive number gives the number of new infections per infectious individual in a partially susceptible population:
 - ▶ * $\mathcal{R}_{\text{eff}} = \mathcal{R}_0 S/N$
- ▶ Is the disease increasing or decreasing?
 - ▶ * It will increase when $\mathcal{R}_{\text{eff}} > 1$ (more than one case per case)
 - ▶ *

Effective reproductive number

- ▶ The effective reproductive number gives the number of new infections per infectious individual in a partially susceptible population:
 - ▶ * $\mathcal{R}_{\text{eff}} = \mathcal{R}_0 S/N$
- ▶ Is the disease increasing or decreasing?
 - ▶ * It will increase when $\mathcal{R}_{\text{eff}} > 1$ (more than one case per case)
 - ▶ * This happens when $S/N > 1/\mathcal{R}_0$

Effective reproductive number

- ▶ The effective reproductive number gives the number of new infections per infectious individual in a partially susceptible population:
 - ▶ * $\mathcal{R}_{\text{eff}} = \mathcal{R}_0 S/N$
- ▶ Is the disease increasing or decreasing?
 - ▶ * It will increase when $\mathcal{R}_{\text{eff}} > 1$ (more than one case per case)
 - ▶ * This happens when $S/N > 1/\mathcal{R}_0$
- ▶ Why doesn't everyone get infected?

Effective reproductive number

- ▶ The effective reproductive number gives the number of new infections per infectious individual in a partially susceptible population:
 - ▶ * $\mathcal{R}_{\text{eff}} = \mathcal{R}_0 S/N$
- ▶ Is the disease increasing or decreasing?
 - ▶ * It will increase when $\mathcal{R}_{\text{eff}} > 1$ (more than one case per case)
 - ▶ * This happens when $S/N > 1/\mathcal{R}_0$
- ▶ Why doesn't everyone get infected?
 - ▶ *

Effective reproductive number

- ▶ The effective reproductive number gives the number of new infections per infectious individual in a partially susceptible population:
 - ▶ * $\mathcal{R}_{\text{eff}} = \mathcal{R}_0 S/N$
- ▶ Is the disease increasing or decreasing?
 - ▶ * It will increase when $\mathcal{R}_{\text{eff}} > 1$ (more than one case per case)
 - ▶ * This happens when $S/N > 1/\mathcal{R}_0$
- ▶ Why doesn't everyone get infected?
 - ▶ * When susceptibles are low enough $\mathcal{R}_{\text{eff}} < 1$

Effective reproductive number

- ▶ The effective reproductive number gives the number of new infections per infectious individual in a partially susceptible population:
 - ▶ * $\mathcal{R}_{\text{eff}} = \mathcal{R}_0 S/N$
- ▶ Is the disease increasing or decreasing?
 - ▶ * It will increase when $\mathcal{R}_{\text{eff}} > 1$ (more than one case per case)
 - ▶ * This happens when $S/N > 1/\mathcal{R}_0$
- ▶ Why doesn't everyone get infected?
 - ▶ * When susceptibles are low enough $\mathcal{R}_{\text{eff}} < 1$
 - ▶ *

Effective reproductive number

- ▶ The effective reproductive number gives the number of new infections per infectious individual in a partially susceptible population:
 - ▶ * $\mathcal{R}_{\text{eff}} = \mathcal{R}_0 S/N$
- ▶ Is the disease increasing or decreasing?
 - ▶ * It will increase when $\mathcal{R}_{\text{eff}} > 1$ (more than one case per case)
 - ▶ * This happens when $S/N > 1/\mathcal{R}_0$
- ▶ Why doesn't everyone get infected?
 - ▶ * When susceptibles are low enough $\mathcal{R}_{\text{eff}} < 1$
 - ▶ * When $\mathcal{R}_{\text{eff}} < 1$, the disease dies out on its own (less than one case per case)

Effective reproductive number

- ▶ The effective reproductive number gives the number of new infections per infectious individual in a partially susceptible population:
 - ▶ * $\mathcal{R}_{\text{eff}} = \mathcal{R}_0 S/N$
- ▶ Is the disease increasing or decreasing?
 - ▶ * It will increase when $\mathcal{R}_{\text{eff}} > 1$ (more than one case per case)
 - ▶ * This happens when $S/N > 1/\mathcal{R}_0$
- ▶ Why doesn't everyone get infected?
 - ▶ * When susceptibles are low enough $\mathcal{R}_{\text{eff}} < 1$
 - ▶ * When $\mathcal{R}_{\text{eff}} < 1$, the disease dies out on its own (less than one case per case)

Outline

Introduction

Rate of spread

Single-epidemic model

Epidemic size

Recurrent epidemic models

Dynamics

Reproductive numbers and risk

Pathogen aggressiveness

Epidemic size

- ▶ In this model, the epidemic always burns out

Epidemic size

- ▶ In this model, the epidemic always burns out
 - ▶ No source of new susceptibles

Epidemic size

- ▶ In this model, the epidemic always burns out
 - ▶ No source of new susceptibles
- ▶ Epidemic size is determined by:

Epidemic size

- ▶ In this model, the epidemic always burns out
 - ▶ No source of new susceptibles
- ▶ Epidemic size is determined by:
 - ▶ *

Epidemic size

- ▶ In this model, the epidemic always burns out
 - ▶ No source of new susceptibles
- ▶ Epidemic size is determined by:
 - ▶ * \mathcal{R}_0 : larger \mathcal{R}_0 leads to a bigger epidemic

Epidemic size

- ▶ In this model, the epidemic always burns out
 - ▶ No source of new susceptibles
- ▶ Epidemic size is determined by:
 - ▶ * \mathcal{R}_0 : larger \mathcal{R}_0 leads to a bigger epidemic
 - ▶ *

Epidemic size

- ▶ In this model, the epidemic always burns out
 - ▶ No source of new susceptibles
- ▶ Epidemic size is determined by:
 - ▶ * \mathcal{R}_0 : larger \mathcal{R}_0 leads to a bigger epidemic
 - ▶ * The number of susceptibles at the beginning of the epidemic

Epidemic size

- ▶ In this model, the epidemic always burns out
 - ▶ No source of new susceptibles
- ▶ Epidemic size is determined by:
 - ▶ * \mathcal{R}_0 : larger \mathcal{R}_0 leads to a bigger epidemic
 - ▶ * The number of susceptibles at the beginning of the epidemic
 - ▶ *

Epidemic size

- ▶ In this model, the epidemic always burns out
 - ▶ No source of new susceptibles
- ▶ Epidemic size is determined by:
 - ▶ * \mathcal{R}_0 : larger \mathcal{R}_0 leads to a bigger epidemic
 - ▶ * The number of susceptibles at the beginning of the epidemic
 - ▶ * More susceptibles leads to a bigger epidemic

Epidemic size

- ▶ In this model, the epidemic always burns out
 - ▶ No source of new susceptibles
- ▶ Epidemic size is determined by:
 - ▶ * \mathcal{R}_0 : larger \mathcal{R}_0 leads to a bigger epidemic
 - ▶ * The number of susceptibles at the beginning of the epidemic
 - ▶ * More susceptibles leads to a bigger epidemic
 - ▶ *

Epidemic size

- ▶ In this model, the epidemic always burns out
 - ▶ No source of new susceptibles
- ▶ Epidemic size is determined by:
 - ▶ * \mathcal{R}_0 : larger \mathcal{R}_0 leads to a bigger epidemic
 - ▶ * The number of susceptibles at the beginning of the epidemic
 - ▶ * More susceptibles leads to a bigger epidemic
 - ▶ * ...and *fewer* susceptibles at the end

Epidemic size

- ▶ In this model, the epidemic always burns out
 - ▶ No source of new susceptibles
- ▶ Epidemic size is determined by:
 - ▶ * \mathcal{R}_0 : larger \mathcal{R}_0 leads to a bigger epidemic
 - ▶ * The number of susceptibles at the beginning of the epidemic
 - ▶ * More susceptibles leads to a bigger epidemic
 - ▶ * ...and *fewer* susceptibles at the end
 - ▶ *

Epidemic size

- ▶ In this model, the epidemic always burns out
 - ▶ No source of new susceptibles
- ▶ Epidemic size is determined by:
 - ▶ * \mathcal{R}_0 : larger \mathcal{R}_0 leads to a bigger epidemic
 - ▶ * The number of susceptibles at the beginning of the epidemic
 - ▶ * More susceptibles leads to a bigger epidemic
 - ▶ * ...and *fewer* susceptibles at the end
 - ▶ * The number of infected individuals at the beginning of the epidemic

Epidemic size

- ▶ In this model, the epidemic always burns out
 - ▶ No source of new susceptibles
- ▶ Epidemic size is determined by:
 - ▶ * \mathcal{R}_0 : larger \mathcal{R}_0 leads to a bigger epidemic
 - ▶ * The number of susceptibles at the beginning of the epidemic
 - ▶ * More susceptibles leads to a bigger epidemic
 - ▶ * ...and *fewer* susceptibles at the end
 - ▶ * The number of infected individuals at the beginning of the epidemic
 - ▶ *

Epidemic size

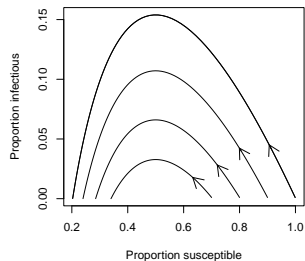
- ▶ In this model, the epidemic always burns out
 - ▶ No source of new susceptibles
- ▶ Epidemic size is determined by:
 - ▶ * \mathcal{R}_0 : larger \mathcal{R}_0 leads to a bigger epidemic
 - ▶ * The number of susceptibles at the beginning of the epidemic
 - ▶ * More susceptibles leads to a bigger epidemic
 - ▶ * ...and *fewer* susceptibles at the end
 - ▶ * The number of infected individuals at the beginning of the epidemic
 - ▶ * Usually relatively small (and a relatively small effect)

Epidemic size

- ▶ In this model, the epidemic always burns out
 - ▶ No source of new susceptibles
- ▶ Epidemic size is determined by:
 - ▶ * \mathcal{R}_0 : larger \mathcal{R}_0 leads to a bigger epidemic
 - ▶ * The number of susceptibles at the beginning of the epidemic
 - ▶ * More susceptibles leads to a bigger epidemic
 - ▶ * ...and *fewer* susceptibles at the end
 - ▶ * The number of infected individuals at the beginning of the epidemic
 - ▶ * Usually relatively small (and a relatively small effect)

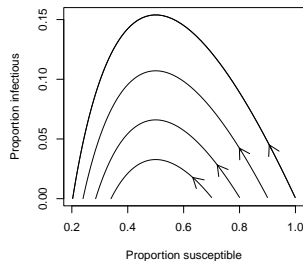
Overshoot

- Why does more susceptibles at the beginning mean fewer susceptibles at the end?



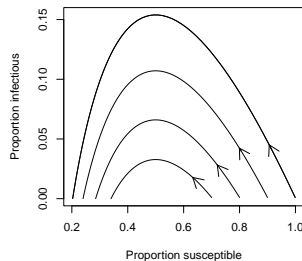
Overshoot

- Why does more susceptibles at the beginning mean fewer susceptibles at the end?



Overshoot

- ▶ Why does more susceptibles at the beginning mean fewer susceptibles at the end?
 - ▶ * More susceptibles \Rightarrow

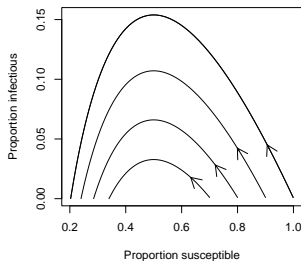


Overshoot

- ▶ Why does more susceptibles at the beginning mean fewer susceptibles at the end?

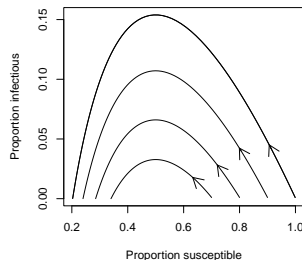
▶ * More susceptibles \Rightarrow

▶ *



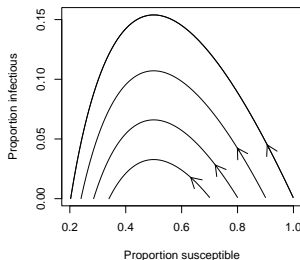
Overshoot

- ▶ Why does more susceptibles at the beginning mean fewer susceptibles at the end?
 - ▶ * More susceptibles \Rightarrow
 - ▶ * Faster initial growth \Rightarrow



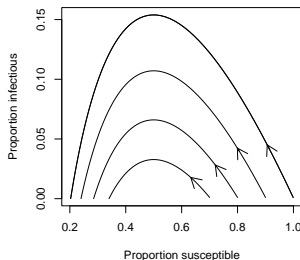
Overshoot

- ▶ Why does more susceptibles at the beginning mean fewer susceptibles at the end?
 - ▶ * More susceptibles \Rightarrow
 - ▶ * Faster initial growth \Rightarrow
 - ▶ *



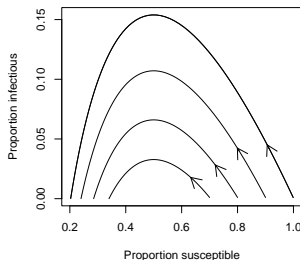
Overshoot

- ▶ Why does more susceptibles at the beginning mean fewer susceptibles at the end?
 - ▶ * More susceptibles \Rightarrow
 - ▶ * Faster initial growth \Rightarrow
 - ▶ * Bigger epidemic \Rightarrow



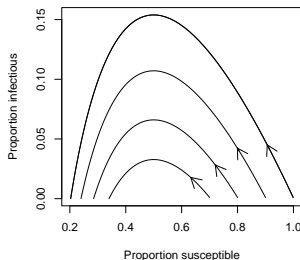
Overshoot

- ▶ Why does more susceptibles at the beginning mean fewer susceptibles at the end?
 - ▶ * More susceptibles \Rightarrow
 - ▶ * Faster initial growth \Rightarrow
 - ▶ * Bigger epidemic \Rightarrow
 - ▶ *



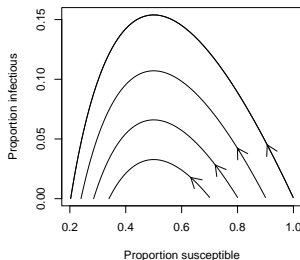
Overshoot

- ▶ Why does more susceptibles at the beginning mean fewer susceptibles at the end?
 - ▶ * More susceptibles \Rightarrow
 - ▶ * Faster initial growth \Rightarrow
 - ▶ * Bigger epidemic \Rightarrow
 - ▶ * More infections at peak (same number of susceptibles) \Rightarrow



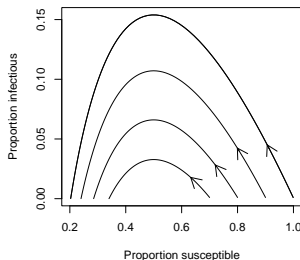
Overshoot

- ▶ Why does more susceptibles at the beginning mean fewer susceptibles at the end?
 - ▶ * More susceptibles \Rightarrow
 - ▶ * Faster initial growth \Rightarrow
 - ▶ * Bigger epidemic \Rightarrow
 - ▶ * More infections at peak (same number of susceptibles) \Rightarrow
- ▶ *



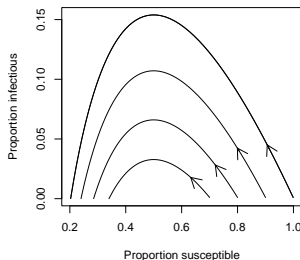
Overshoot

- ▶ Why does more susceptibles at the beginning mean fewer susceptibles at the end?
 - ▶ * More susceptibles \Rightarrow
 - ▶ * Faster initial growth \Rightarrow
 - ▶ * Bigger epidemic \Rightarrow
 - ▶ * More infections at peak (same number of susceptibles) \Rightarrow
 - ▶ * More generations needed for disease to fade out \Rightarrow



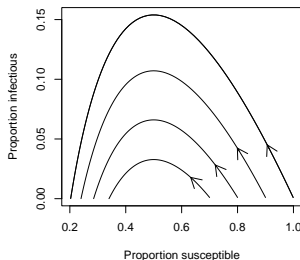
Overshoot

- ▶ Why does more susceptibles at the beginning mean fewer susceptibles at the end?
 - ▶ * More susceptibles \Rightarrow
 - ▶ * Faster initial growth \Rightarrow
 - ▶ * Bigger epidemic \Rightarrow
 - ▶ * More infections at peak (same number of susceptibles) \Rightarrow
 - ▶ * More generations needed for disease to fade out \Rightarrow
- ▶ *



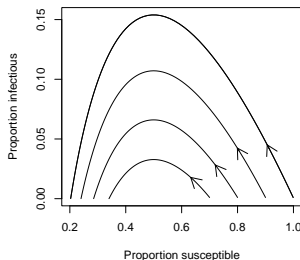
Overshoot

- ▶ Why does more susceptibles at the beginning mean fewer susceptibles at the end?
 - ▶ * More susceptibles \Rightarrow
 - ▶ * Faster initial growth \Rightarrow
 - ▶ * Bigger epidemic \Rightarrow
 - ▶ * More infections at peak (same number of susceptibles) \Rightarrow
 - ▶ * More generations needed for disease to fade out \Rightarrow
 - ▶ * More infections after peak
 - ...



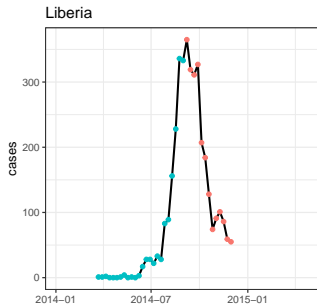
Overshoot

- ▶ Why does more susceptibles at the beginning mean fewer susceptibles at the end?
 - ▶ * More susceptibles \Rightarrow
 - ▶ * Faster initial growth \Rightarrow
 - ▶ * Bigger epidemic \Rightarrow
 - ▶ * More infections at peak (same number of susceptibles) \Rightarrow
 - ▶ * More generations needed for disease to fade out \Rightarrow
 - ▶ * More infections after peak
 - ...



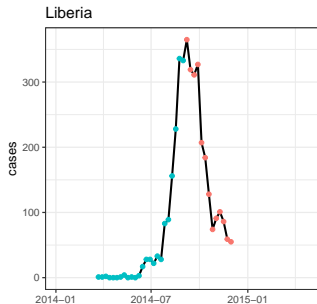
Ebola example

- ▶ In September, the US CDC predicted “as many as” 1.5 million Ebola cases in Liberia by January



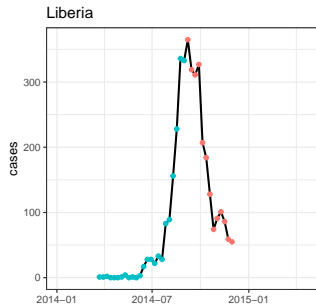
Ebola example

- ▶ In September, the US CDC predicted “as many as” 1.5 million Ebola cases in Liberia by January
- ▶ In fact, their model predicted many *more* cases than that by April



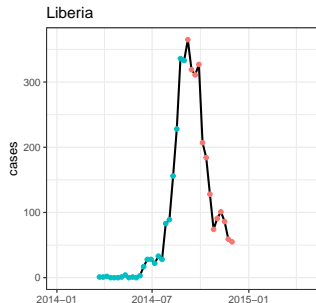
Ebola example

- ▶ In September, the US CDC predicted “as many as” 1.5 million Ebola cases in Liberia by January
- ▶ In fact, their model predicted many *more* cases than that by April
- ▶ What happened?



Ebola example

- ▶ In September, the US CDC predicted “as many as” 1.5 million Ebola cases in Liberia by January
- ▶ In fact, their model predicted many *more* cases than that by April
- ▶ What happened?



What limits epidemics?

- ▶ What limits epidemics in our simple models?

What limits epidemics?

- ▶ What limits epidemics in our simple models?



What limits epidemics?

- ▶ What limits epidemics in our simple models?
 - ▶ * Depletion of susceptibles

What limits epidemics?

- ▶ What limits epidemics in our simple models?
 - ▶ * Depletion of susceptibles
- ▶ What else limits epidemics in real life?

What limits epidemics?

- ▶ What limits epidemics in our simple models?
 - ▶ * Depletion of susceptibles
- ▶ What else limits epidemics in real life?
 - ▶ *

What limits epidemics?

- ▶ What limits epidemics in our simple models?
 - ▶ * Depletion of susceptibles
- ▶ What else limits epidemics in real life?
 - ▶ * Interventions; changes in government policy, medicine, vaccines

What limits epidemics?

- ▶ What limits epidemics in our simple models?
 - ▶ * Depletion of susceptibles
- ▶ What else limits epidemics in real life?
 - ▶ * Interventions; changes in government policy, medicine, vaccines
 - ▶ *

What limits epidemics?

- ▶ What limits epidemics in our simple models?
 - ▶ * Depletion of susceptibles
- ▶ What else limits epidemics in real life?
 - ▶ * Interventions; changes in government policy, medicine, vaccines
 - ▶ * Behaviour change; people stay home, wear masks, avoid sick people

What limits epidemics?

- ▶ What limits epidemics in our simple models?
 - ▶ * Depletion of susceptibles
- ▶ What else limits epidemics in real life?
 - ▶ * Interventions; changes in government policy, medicine, vaccines
 - ▶ * Behaviour change; people stay home, wear masks, avoid sick people
 - ▶ *

What limits epidemics?

- ▶ What limits epidemics in our simple models?
 - ▶ * Depletion of susceptibles
- ▶ What else limits epidemics in real life?
 - ▶ * Interventions; changes in government policy, medicine, vaccines
 - ▶ * Behaviour change; people stay home, wear masks, avoid sick people
 - ▶ * Heterogeneity (differences between hosts, locations, etc.)

What limits epidemics?

- ▶ What limits epidemics in our simple models?
 - ▶ * Depletion of susceptibles
- ▶ What else limits epidemics in real life?
 - ▶ * Interventions; changes in government policy, medicine, vaccines
 - ▶ * Behaviour change; people stay home, wear masks, avoid sick people
 - ▶ * Heterogeneity (differences between hosts, locations, etc.)

Outline

Introduction

Rate of spread

Single-epidemic model

Epidemic size

Recurrent epidemic models

Dynamics

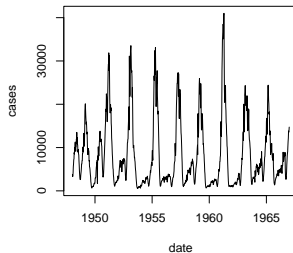
Reproductive numbers and risk

Pathogen aggressiveness

Recurrent epidemic models

- If epidemics tend to burn out, why do we often see repeated epidemics?

Measles reports from England and Wales

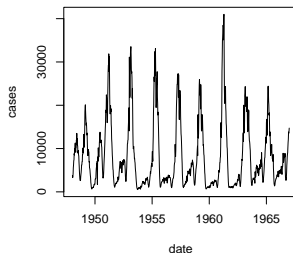


Recurrent epidemic models

- ▶ If epidemics tend to burn out, why do we often see repeated epidemics?



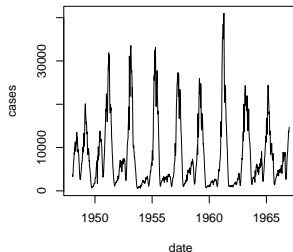
Measles reports from England and Wales



Recurrent epidemic models

- ▶ If epidemics tend to burn out, why do we often see repeated epidemics?
 - ▶ * People might lose immunity

Measles reports from England and Wales



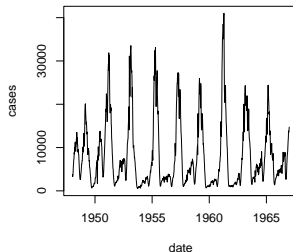
Recurrent epidemic models

- ▶ If epidemics tend to burn out, why do we often see repeated epidemics?

- ▶ * People might lose immunity

- ▶ *

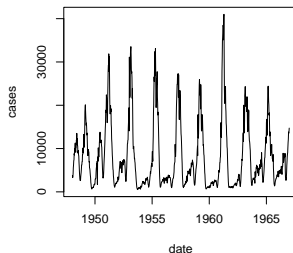
Measles reports from England and Wales



Recurrent epidemic models

- ▶ If epidemics tend to burn out, why do we often see repeated epidemics?
 - ▶ * People might lose immunity
 - ▶ * Births and deaths; newborns are susceptible

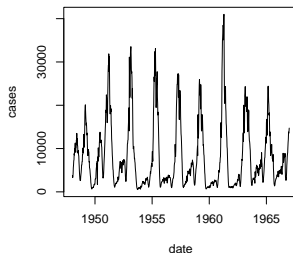
Measles reports from England and Wales



Recurrent epidemic models

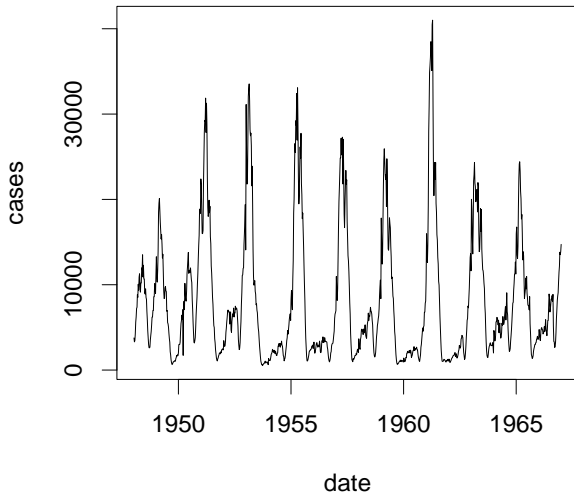
- ▶ If epidemics tend to burn out, why do we often see repeated epidemics?
 - ▶ * People might lose immunity
 - ▶ * Births and deaths; newborns are susceptible

Measles reports from England and Wales

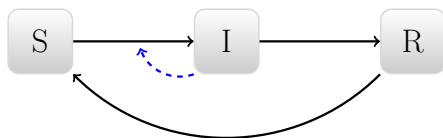


Recurrent epidemics

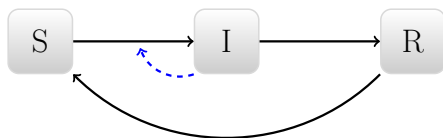
Measles reports from England and Wales



Closing the circle

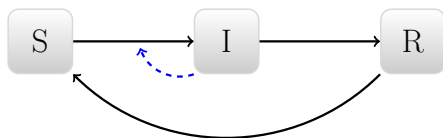


Closing the circle



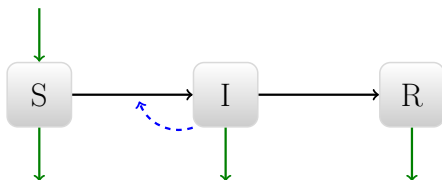
- * Loss of immunity

Closing the circle

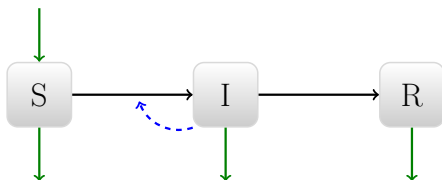


- * Loss of immunity

Closing the circle

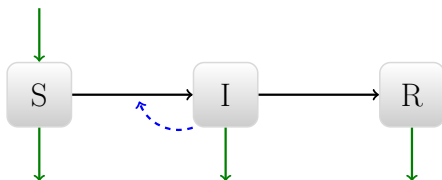


Closing the circle



► * Births and deaths

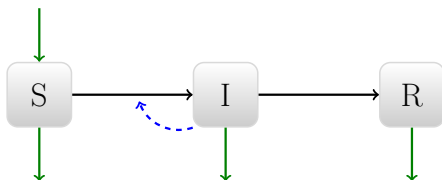
Closing the circle



► * Births and deaths

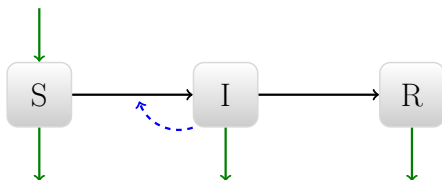
► *

Closing the circle



- ▶ * Births and deaths
 - ▶ * Effect on dynamics is similar to loss of immunity

Closing the circle

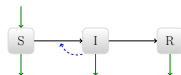


- ▶ * Births and deaths
 - ▶ * Effect on dynamics is similar to loss of immunity

Births and deaths



$$\frac{dS}{dt} = bN - \beta \frac{SI}{N} - dS$$



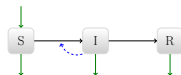
Births and deaths



$$\frac{dS}{dt} = bN - \beta \frac{SI}{N} - dS$$



$$\frac{dI}{dt} = \beta \frac{SI}{N} - \gamma I - dI$$



Births and deaths



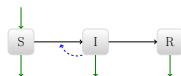
$$\frac{dS}{dt} = bN - \beta \frac{SI}{N} - dS$$



$$\frac{dI}{dt} = \beta \frac{SI}{N} - \gamma I - dI$$



$$\frac{dR}{dt} = \gamma I - dR$$



Births and deaths



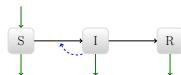
$$\frac{dS}{dt} = bN - \beta \frac{SI}{N} - dS$$



$$\frac{dI}{dt} = \beta \frac{SI}{N} - \gamma I - dI$$



$$\frac{dR}{dt} = \gamma I - dR$$



► We often assume $b = d$

Births and deaths



$$\frac{dS}{dt} = bN - \beta \frac{SI}{N} - dS$$



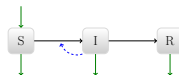
$$\frac{dI}{dt} = \beta \frac{SI}{N} - \gamma I - dI$$



$$\frac{dR}{dt} = \gamma I - dR$$

► We often assume $b = d$

► \implies population is constant



Births and deaths



$$\frac{dS}{dt} = bN - \beta \frac{SI}{N} - dS$$



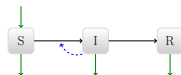
$$\frac{dI}{dt} = \beta \frac{SI}{N} - \gamma I - dI$$



$$\frac{dR}{dt} = \gamma I - dR$$

► We often assume $b = d$

► \implies population is constant



Outline

Introduction

Rate of spread

Single-epidemic model

Epidemic size

Recurrent epidemic models

Dynamics

Reproductive numbers and risk

Pathogen aggressiveness

Equilibrium

- ▶ At equilibrium, we know that $\mathcal{R}_{\text{eff}} = 1$

Equilibrium

- ▶ At equilibrium, we know that $\mathcal{R}_{\text{eff}} = 1$
 - ▶ One case per case

Equilibrium

- ▶ At equilibrium, we know that $\mathcal{R}_{\text{eff}} = 1$
 - ▶ One case per case
 - ▶ Number of susceptibles at equilibrium determined by the number required to keep infection in balance

Equilibrium

- ▶ At equilibrium, we know that $\mathcal{R}_{\text{eff}} = 1$
 - ▶ One case per case
 - ▶ Number of susceptibles at equilibrium determined by the number required to keep infection in balance
 - ▶ $S/N = 1/\mathcal{R}_0$

Equilibrium

- ▶ At equilibrium, we know that $\mathcal{R}_{\text{eff}} = 1$
 - ▶ One case per case
 - ▶ Number of susceptibles at equilibrium determined by the number required to keep infection in balance
 - ▶ $S/N = 1/\mathcal{R}_0$
- ▶ What does this remind you of?

Equilibrium

- ▶ At equilibrium, we know that $\mathcal{R}_{\text{eff}} = 1$
 - ▶ One case per case
 - ▶ Number of susceptibles at equilibrium determined by the number required to keep infection in balance
 - ▶ $S/N = 1/\mathcal{R}_0$
- ▶ What does this remind you of?
 - ▶ *

Equilibrium

- ▶ At equilibrium, we know that $\mathcal{R}_{\text{eff}} = 1$
 - ▶ One case per case
 - ▶ Number of susceptibles at equilibrium determined by the number required to keep infection in balance
 - ▶ $S/N = 1/\mathcal{R}_0$
- ▶ What does this remind you of?
 - ▶ * Reciprocal control!

Equilibrium

- ▶ At equilibrium, we know that $\mathcal{R}_{\text{eff}} = 1$
 - ▶ One case per case
 - ▶ Number of susceptibles at equilibrium determined by the number required to keep infection in balance
 - ▶ $S/N = 1/\mathcal{R}_0$
- ▶ What does this remind you of?
 - ▶ * Reciprocal control!

Equilibrium

- ▶ Number of infectious individuals determined by number required to keep susceptibles in balance.

Equilibrium

- ▶ Number of infectious individuals determined by number required to keep susceptibles in balance.
- ▶ As susceptibles go up, what happens?

Equilibrium

- ▶ Number of infectious individuals determined by number required to keep susceptibles in balance.
- ▶ As susceptibles go up, what happens?
 - ▶ Per capita replenishment goes down

Equilibrium

- ▶ Number of infectious individuals determined by number required to keep susceptibles in balance.
- ▶ As susceptibles go up, what happens?
 - ▶ Per capita replenishment goes down
 - ▶ Infections required goes down

Equilibrium

- ▶ Number of infectious individuals determined by number required to keep susceptibles in balance.
- ▶ As susceptibles go up, what happens?
 - ▶ Per capita replenishment goes down
 - ▶ Infections required goes down

Reciprocal control

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to *R* class)?

Reciprocal control

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to R class)?



Reciprocal control

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to R class)?
 - ▶ * Equation for dl/dt does not change

Reciprocal control

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to *R* class)?
 - ▶ * Equation for dl/dt does not change
 - ▶ *

Reciprocal control

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to R class)?
 - ▶ * Equation for dl/dt does not change
 - ▶ * Number of susceptibles at equilibrium does not change

Reciprocal control

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to *R* class)?
 - ▶ * Equation for dl/dt does not change
 - ▶ * Number of susceptibles at equilibrium does not change
 - ▶ *

Reciprocal control

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to *R* class)?
 - ▶ * Equation for dl/dt does not change
 - ▶ * Number of susceptibles at equilibrium does not change
 - ▶ * Fewer susceptibles removed by infection (some are removed by us)

Reciprocal control

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to R class)?
 - ▶ * Equation for dl/dt does not change
 - ▶ * Number of susceptibles at equilibrium does not change
 - ▶ * Fewer susceptibles removed by infection (some are removed by us)
 - ▶ *

Reciprocal control

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to R class)?
 - ▶ * Equation for dl/dt does not change
 - ▶ * Number of susceptibles at equilibrium does not change
 - ▶ * Fewer susceptibles removed by infection (some are removed by us)
 - ▶ * Less disease

Reciprocal control

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to R class)?
 - ▶ * Equation for dl/dt does not change
 - ▶ * Number of susceptibles at equilibrium does not change
 - ▶ * Fewer susceptibles removed by infection (some are removed by us)
 - ▶ * Less disease
- ▶ What else could happen?

Reciprocal control

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to *R* class)?
 - ▶ * Equation for dl/dt does not change
 - ▶ * Number of susceptibles at equilibrium does not change
 - ▶ * Fewer susceptibles removed by infection (some are removed by us)
 - ▶ * Less disease
- ▶ What else could happen?
 - ▶ *

Reciprocal control

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to *R* class)?
 - ▶ * Equation for dl/dt does not change
 - ▶ * Number of susceptibles at equilibrium does not change
 - ▶ * Fewer susceptibles removed by infection (some are removed by us)
 - ▶ * Less disease
- ▶ What else could happen?
 - ▶ * If we remove susceptibles fast enough, infection could go extinct

Reciprocal control

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to *R* class)?
 - ▶ * Equation for dl/dt does not change
 - ▶ * Number of susceptibles at equilibrium does not change
 - ▶ * Fewer susceptibles removed by infection (some are removed by us)
 - ▶ * Less disease
- ▶ What else could happen?
 - ▶ * If we remove susceptibles fast enough, infection could go extinct
 - ▶ *

Reciprocal control

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to *R* class)?
 - ▶ * Equation for dl/dt does not change
 - ▶ * Number of susceptibles at equilibrium does not change
 - ▶ * Fewer susceptibles removed by infection (some are removed by us)
 - ▶ * Less disease
- ▶ What else could happen?
 - ▶ * If we remove susceptibles fast enough, infection could go extinct
 - ▶ * If we keep increasing the rate ...

Reciprocal control

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to *R* class)?
 - ▶ * Equation for dl/dt does not change
 - ▶ * Number of susceptibles at equilibrium does not change
 - ▶ * Fewer susceptibles removed by infection (some are removed by us)
 - ▶ * Less disease
- ▶ What else could happen?
 - ▶ * If we remove susceptibles fast enough, infection could go extinct
 - ▶ * If we keep increasing the rate ...
 - ▶ *

Reciprocal control

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to *R* class)?
 - ▶ * Equation for dl/dt does not change
 - ▶ * Number of susceptibles at equilibrium does not change
 - ▶ * Fewer susceptibles removed by infection (some are removed by us)
 - ▶ * Less disease
- ▶ What else could happen?
 - ▶ * If we remove susceptibles fast enough, infection could go extinct
 - ▶ * If we keep increasing the rate ...
 - ▶ * Number of susceptibles goes down

Reciprocal control

- ▶ What happens to *equilibrium* if we protect susceptibles (move them to *R* class)?
 - ▶ * Equation for dl/dt does not change
 - ▶ * Number of susceptibles at equilibrium does not change
 - ▶ * Fewer susceptibles removed by infection (some are removed by us)
 - ▶ * Less disease
- ▶ What else could happen?
 - ▶ * If we remove susceptibles fast enough, infection could go extinct
 - ▶ * If we keep increasing the rate ...
 - ▶ * Number of susceptibles goes down

Reciprocal control

- ▶ What happens if we remove infectious individuals at a constant rate (find them and cure them or isolate them)?

Reciprocal control

- ▶ What happens if we remove infectious individuals at a constant rate (find them and cure them or isolate them)?

▶ *

Reciprocal control

- ▶ What happens if we remove infectious individuals at a constant rate (find them and cure them or isolate them)?
 - ▶ * We need more susceptibles to balance dl/dt

Reciprocal control

- ▶ What happens if we remove infectious individuals at a constant rate (find them and cure them or isolate them)?
 - ▶ * We need more susceptibles to balance dl/dt
 - ▶ *

Reciprocal control

- ▶ What happens if we remove infectious individuals at a constant rate (find them and cure them or isolate them)?
 - ▶ * We need more susceptibles to balance dl/dt
 - ▶ * If we have more susceptibles, then per capita replenishment goes down

Reciprocal control

- ▶ What happens if we remove infectious individuals at a constant rate (find them and cure them or isolate them)?
 - ▶ * We need more susceptibles to balance dl/dt
 - ▶ * If we have more susceptibles, then per capita replenishment goes down
 - ▶ *

Reciprocal control

- ▶ What happens if we remove infectious individuals at a constant rate (find them and cure them or isolate them)?
 - ▶ * We need more susceptibles to balance dl/dt
 - ▶ * If we have more susceptibles, then per capita replenishment goes down
 - ▶ * So the number of infectious individuals required for balance goes down

Reciprocal control

- ▶ What happens if we remove infectious individuals at a constant rate (find them and cure them or isolate them)?
 - ▶ * We need more susceptibles to balance dl/dt
 - ▶ * If we have more susceptibles, then per capita replenishment goes down
 - ▶ * So the number of infectious individuals required for balance goes down
- ▶ *

Reciprocal control

- ▶ What happens if we remove infectious individuals at a constant rate (find them and cure them or isolate them)?
 - ▶ * We need more susceptibles to balance dl/dt
 - ▶ * If we have more susceptibles, then per capita replenishment goes down
 - ▶ * So the number of infectious individuals required for balance goes down
 - ▶ * If we remove infectious individuals fast enough, the infection could go extinct

Reciprocal control

- ▶ What happens if we remove infectious individuals at a constant rate (find them and cure them or isolate them)?
 - ▶ * We need more susceptibles to balance dl/dt
 - ▶ * If we have more susceptibles, then per capita replenishment goes down
 - ▶ * So the number of infectious individuals required for balance goes down
 - ▶ * If we remove infectious individuals fast enough, the infection could go extinct
- ▶ *

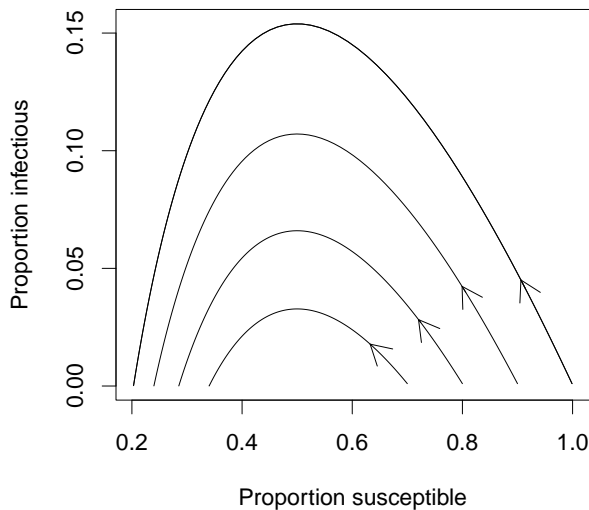
Reciprocal control

- ▶ What happens if we remove infectious individuals at a constant rate (find them and cure them or isolate them)?
 - ▶ * We need more susceptibles to balance dl/dt
 - ▶ * If we have more susceptibles, then per capita replenishment goes down
 - ▶ * So the number of infectious individuals required for balance goes down
 - ▶ * If we remove infectious individuals fast enough, the infection could go extinct
 - ▶ * $\mathcal{R}_c S/N \leq 1$

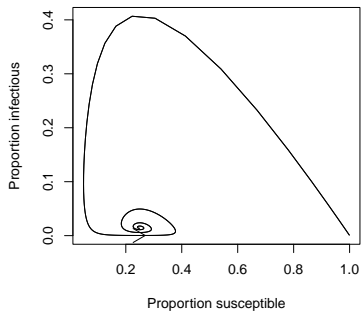
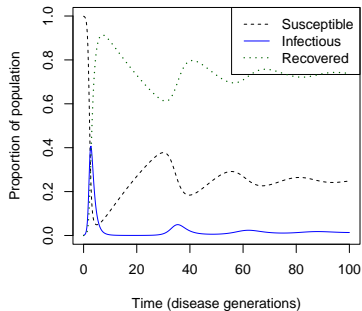
Reciprocal control

- ▶ What happens if we remove infectious individuals at a constant rate (find them and cure them or isolate them)?
 - ▶ * We need more susceptibles to balance dl/dt
 - ▶ * If we have more susceptibles, then per capita replenishment goes down
 - ▶ * So the number of infectious individuals required for balance goes down
 - ▶ * If we remove infectious individuals fast enough, the infection could go extinct
 - ▶ * $\mathcal{R}_c S/N \leq 1$

Single-epidemic model (repeat)



Tendency to oscillate



Tendency to oscillate

- ▶ “Closed-loop” SIR models (ie., with births or loss of immunity):

Tendency to oscillate

- ▶ “Closed-loop” SIR models (ie., with births or loss of immunity):
 - ▶ Tend to oscillate

Tendency to oscillate

- ▶ “Closed-loop” SIR models (ie., with births or loss of immunity):
 - ▶ Tend to oscillate
 - ▶ Oscillations tend to be damped

Tendency to oscillate

- ▶ “Closed-loop” SIR models (ie., with births or loss of immunity):
 - ▶ Tend to oscillate
 - ▶ Oscillations tend to be damped
 - ▶ System reaches an **endemic** equilibrium – disease persists

Tendency to oscillate

- ▶ “Closed-loop” SIR models (ie., with births or loss of immunity):
 - ▶ Tend to oscillate
 - ▶ Oscillations tend to be damped
 - ▶ System reaches an **endemic** equilibrium – disease persists

Source of oscillations

- ▶ Similar to predator-prey systems

Source of oscillations

- ▶ Similar to predator-prey systems
- ▶ What happens if we start with a lot of susceptibles?

Source of oscillations

- ▶ Similar to predator-prey systems
- ▶ What happens if we start with a lot of susceptibles?



Source of oscillations

- ▶ Similar to predator-prey systems
- ▶ What happens if we start with a lot of susceptibles?
 - ▶ * There will be a big epidemic

Source of oscillations

- ▶ Similar to predator-prey systems
- ▶ What happens if we start with a lot of susceptibles?
 - ▶ * There will be a big epidemic
 - ▶ *

Source of oscillations

- ▶ Similar to predator-prey systems
- ▶ What happens if we start with a lot of susceptibles?
 - ▶ * There will be a big epidemic
 - ▶ * ...then a very low number of susceptibles

Source of oscillations

- ▶ Similar to predator-prey systems
- ▶ What happens if we start with a lot of susceptibles?
 - ▶ * There will be a big epidemic
 - ▶ * ... then a very low number of susceptibles
 - ▶ *

Source of oscillations

- ▶ Similar to predator-prey systems
- ▶ What happens if we start with a lot of susceptibles?
 - ▶ * There will be a big epidemic
 - ▶ * ...then a very low number of susceptibles
 - ▶ * ...then a very low level of disease

Source of oscillations

- ▶ Similar to predator-prey systems
- ▶ What happens if we start with a lot of susceptibles?
 - ▶ * There will be a big epidemic
 - ▶ * ...then a very low number of susceptibles
 - ▶ * ...then a very low level of disease
 - ▶ *

Source of oscillations

- ▶ Similar to predator-prey systems
- ▶ What happens if we start with a lot of susceptibles?
 - ▶ * There will be a big epidemic
 - ▶ * ...then a very low number of susceptibles
 - ▶ * ...then a very low level of disease
 - ▶ * ...then an increase in the number of susceptibles

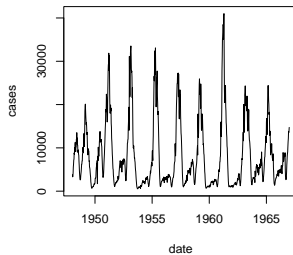
Source of oscillations

- ▶ Similar to predator-prey systems
- ▶ What happens if we start with a lot of susceptibles?
 - ▶ * There will be a big epidemic
 - ▶ * ...then a very low number of susceptibles
 - ▶ * ...then a very low level of disease
 - ▶ * ...then an increase in the number of susceptibles

Persistent oscillations

- If oscillations tend to be damped in simple models, why do they persist in real life?

Measles reports from England and Wales

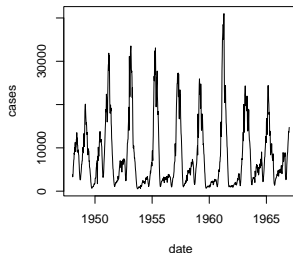


Persistent oscillations

- ▶ If oscillations tend to be damped in simple models, why do they persist in real life?



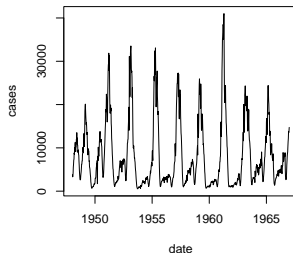
Measles reports from England and Wales



Persistent oscillations

- ▶ If oscillations tend to be damped in simple models, why do they persist in real life?
 - ▶ * Weather

Measles reports from England and Wales



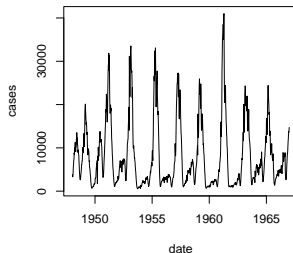
Persistent oscillations

- ▶ If oscillations tend to be damped in simple models, why do they persist in real life?

- ▶ * Weather



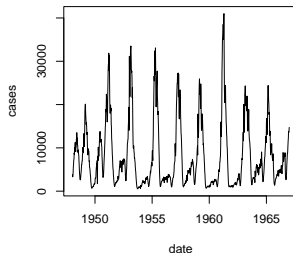
Measles reports from England and Wales



Persistent oscillations

- ▶ If oscillations tend to be damped in simple models, why do they persist in real life?
 - ▶ * Weather
 - ▶ * Seasonality

Measles reports from England and Wales

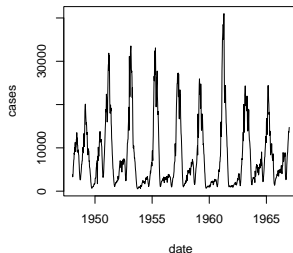


Persistent oscillations

- ▶ If oscillations tend to be damped in simple models, why do they persist in real life?

- ▶ * Weather
 - ▶ * Seasonality
 - ▶ *

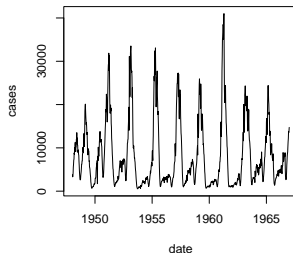
Measles reports from England and Wales



Persistent oscillations

- ▶ If oscillations tend to be damped in simple models, why do they persist in real life?
 - ▶ * Weather
 - ▶ * Seasonality
 - ▶ * Environmental stochasticity

Measles reports from England and Wales



Persistent oscillations

- ▶ If oscillations tend to be damped in simple models, why do they persist in real life?

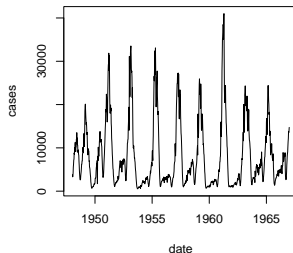
- ▶ * Weather

- ▶ * Seasonality

- ▶ * Environmental stochasticity

- ▶ *

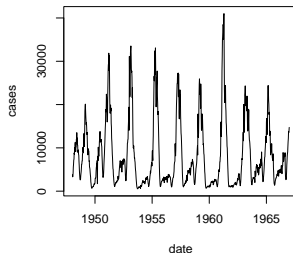
Measles reports from England and Wales



Persistent oscillations

- ▶ If oscillations tend to be damped in simple models, why do they persist in real life?
 - ▶ * Weather
 - ▶ * Seasonality
 - ▶ * Environmental stochasticity
 - ▶ * School terms

Measles reports from England and Wales

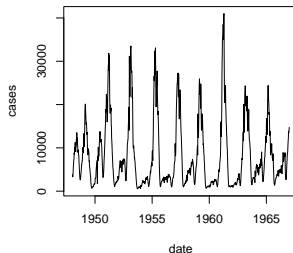


Persistent oscillations

- ▶ If oscillations tend to be damped in simple models, why do they persist in real life?

- ▶ * Weather
 - ▶ * Seasonality
 - ▶ * Environmental stochasticity
- ▶ * School terms
- ▶ *

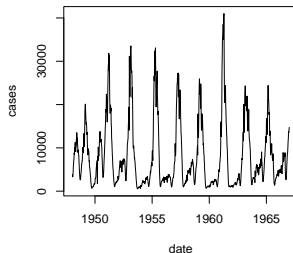
Measles reports from England and Wales



Persistent oscillations

- ▶ If oscillations tend to be damped in simple models, why do they persist in real life?
 - ▶ * Weather
 - ▶ * Seasonality
 - ▶ * Environmental stochasticity
 - ▶ * School terms
 - ▶ * Demographic stochasticity

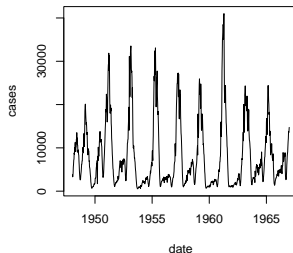
Measles reports from England and Wales



Persistent oscillations

- ▶ If oscillations tend to be damped in simple models, why do they persist in real life?
 - ▶ * Weather
 - ▶ * Seasonality
 - ▶ * Environmental stochasticity
 - ▶ * School terms
 - ▶ * Demographic stochasticity
 - ▶ *

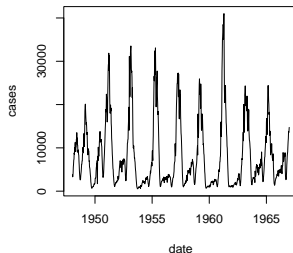
Measles reports from England and Wales



Persistent oscillations

- ▶ If oscillations tend to be damped in simple models, why do they persist in real life?
 - ▶ * Weather
 - ▶ * Seasonality
 - ▶ * Environmental stochasticity
 - ▶ * School terms
 - ▶ * Demographic stochasticity
 - ▶ * Changes in Behaviour

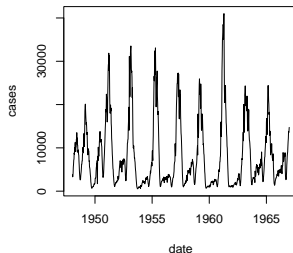
Measles reports from England and Wales



Persistent oscillations

- ▶ If oscillations tend to be damped in simple models, why do they persist in real life?
 - ▶ * Weather
 - ▶ * Seasonality
 - ▶ * Environmental stochasticity
 - ▶ * School terms
 - ▶ * Demographic stochasticity
 - ▶ * Changes in Behaviour
 - ▶ *

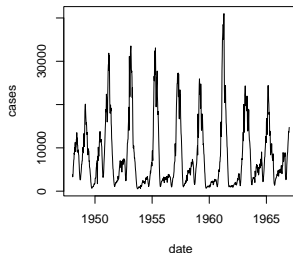
Measles reports from England and Wales



Persistent oscillations

- ▶ If oscillations tend to be damped in simple models, why do they persist in real life?
 - ▶ * Weather
 - ▶ * Seasonality
 - ▶ * Environmental stochasticity
 - ▶ * School terms
 - ▶ * Demographic stochasticity
 - ▶ * Changes in Behaviour
 - ▶ * People are more careful when disease levels are high

Measles reports from England and Wales

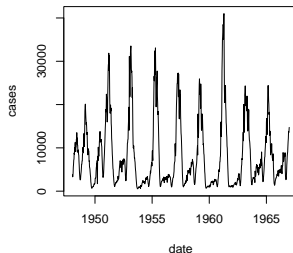


Persistent oscillations

- ▶ If oscillations tend to be damped in simple models, why do they persist in real life?
 - ▶ * Weather
 - ▶ * Seasonality
 - ▶ * Environmental stochasticity
 - ▶ * School terms
 - ▶ * Demographic stochasticity
 - ▶ * Changes in Behaviour
 - ▶ * People are more careful when disease levels are high

▶ *

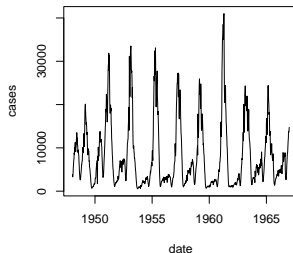
Measles reports from England and Wales



Persistent oscillations

- ▶ If oscillations tend to be damped in simple models, why do they persist in real life?
 - ▶ * Weather
 - ▶ * Seasonality
 - ▶ * Environmental stochasticity
 - ▶ * School terms
 - ▶ * Demographic stochasticity
 - ▶ * Changes in Behaviour
 - ▶ * People are more careful when disease levels are high
 - ▶ * Pathogen mutations

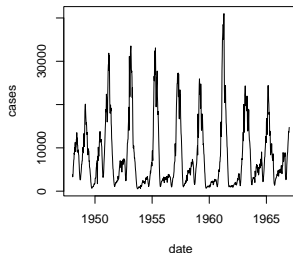
Measles reports from England and Wales



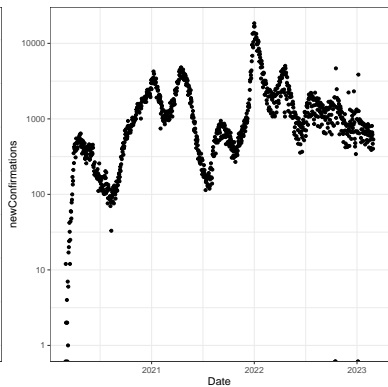
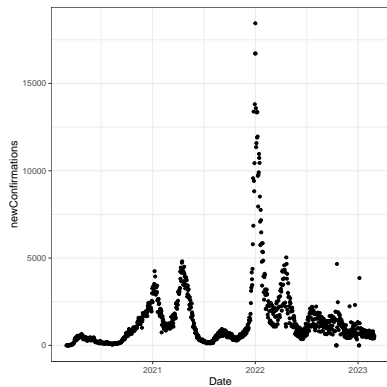
Persistent oscillations

- ▶ If oscillations tend to be damped in simple models, why do they persist in real life?
 - ▶ * Weather
 - ▶ * Seasonality
 - ▶ * Environmental stochasticity
 - ▶ * School terms
 - ▶ * Demographic stochasticity
 - ▶ * Changes in Behaviour
 - ▶ * People are more careful when disease levels are high
 - ▶ * Pathogen mutations

Measles reports from England and Wales



COVID in Ontario



Behaviour and policy change

- ▶ Why did SARS-CoV-2 not follow this pattern?

Behaviour and policy change

- ▶ Why did SARS-CoV-2 not follow this pattern?



Behaviour and policy change

- ▶ Why did SARS-CoV-2 not follow this pattern?
 - ▶ * People and governments changed behaviour

Behaviour and policy change

- ▶ Why did SARS-CoV-2 not follow this pattern?
 - ▶ * People and governments changed behaviour
 - ▶ *

Behaviour and policy change

- ▶ Why did SARS-CoV-2 not follow this pattern?
 - ▶ * People and governments changed behaviour
 - ▶ * Fear of overflowing hospitals and chaos in general

Behaviour and policy change

- ▶ Why did SARS-CoV-2 not follow this pattern?
 - ▶ * People and governments changed behaviour
 - ▶ * Fear of overflowing hospitals and chaos in general
 - ▶ *

Behaviour and policy change

- ▶ Why did SARS-CoV-2 not follow this pattern?
 - ▶ * People and governments changed behaviour
 - ▶ * Fear of overflowing hospitals and chaos in general
 - ▶ * Population heterogeneity

Behaviour and policy change

- ▶ Why did SARS-CoV-2 not follow this pattern?
 - ▶ * People and governments changed behaviour
 - ▶ * Fear of overflowing hospitals and chaos in general
 - ▶ * Population heterogeneity
 - ▶ *

Behaviour and policy change

- ▶ Why did SARS-CoV-2 not follow this pattern?
 - ▶ * People and governments changed behaviour
 - ▶ * Fear of overflowing hospitals and chaos in general
 - ▶ * Population heterogeneity
 - ▶ * Not everyone mixes the same, or at the same time

Behaviour and policy change

- ▶ Why did SARS-CoV-2 not follow this pattern?
 - ▶ * People and governments changed behaviour
 - ▶ * Fear of overflowing hospitals and chaos in general
 - ▶ * Population heterogeneity
 - ▶ * Not everyone mixes the same, or at the same time
 - ▶ *

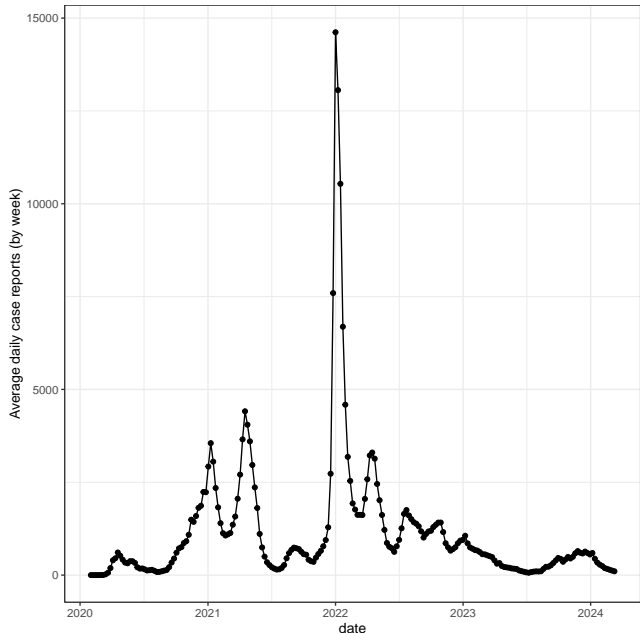
Behaviour and policy change

- ▶ Why did SARS-CoV-2 not follow this pattern?
 - ▶ * People and governments changed behaviour
 - ▶ * Fear of overflowing hospitals and chaos in general
 - ▶ * Population heterogeneity
 - ▶ * Not everyone mixes the same, or at the same time
 - ▶ * Is SARS-CoV-2 following a similar pattern now?

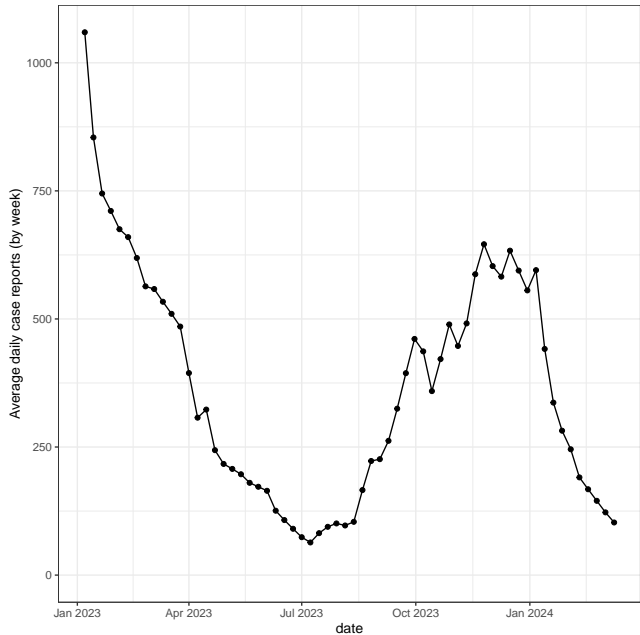
Behaviour and policy change

- ▶ Why did SARS-CoV-2 not follow this pattern?
 - ▶ * People and governments changed behaviour
 - ▶ * Fear of overflowing hospitals and chaos in general
 - ▶ * Population heterogeneity
 - ▶ * Not everyone mixes the same, or at the same time
 - ▶ * Is SARS-CoV-2 following a similar pattern now?

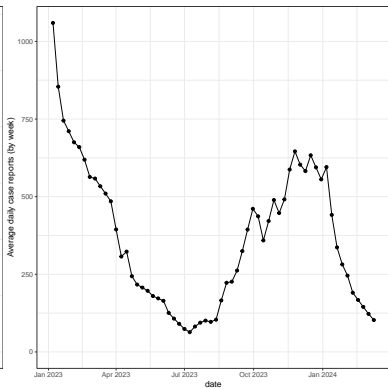
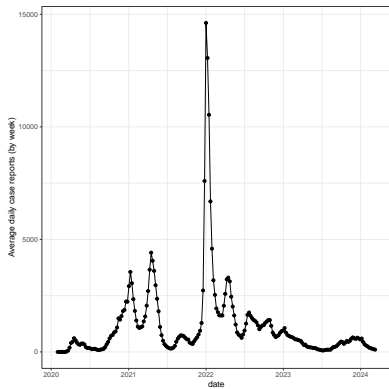
Post-pandemic COVID (preview)



Post-pandemic COVID (preview)



Post-pandemic COVID



Outline

Introduction

Rate of spread

Single-epidemic model

Epidemic size

Recurrent epidemic models

Dynamics

Reproductive numbers and risk

Pathogen aggressiveness

Reproductive numbers and risk

- ▶ At equilibrium, the proportion of people who are susceptible to disease should be approximately $S/N = 1/\mathcal{R}_0$

Reproductive numbers and risk

- ▶ At equilibrium, the proportion of people who are susceptible to disease should be approximately $S/N = 1/\mathcal{R}_0$
- ▶ Proportion “affected” (infectious or immune) should be approximately $V/N = 1 - 1/\mathcal{R}_0$

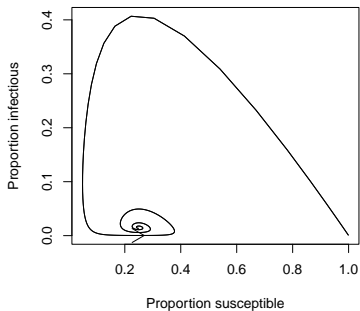
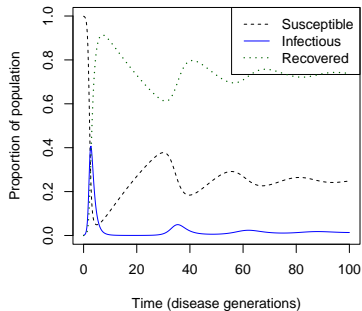
Reproductive numbers and risk

- ▶ At equilibrium, the proportion of people who are susceptible to disease should be approximately $S/N = 1/\mathcal{R}_0$
- ▶ Proportion “affected” (infectious or immune) should be approximately $V/N = 1 - 1/\mathcal{R}_0$
- ▶ If you have a single, fast epidemic, the size is also predicted by \mathcal{R}_0 .

Reproductive numbers and risk

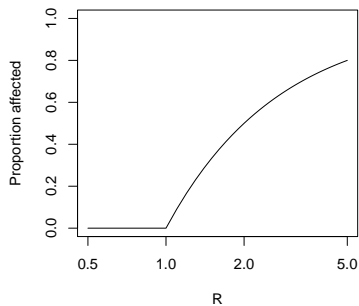
- ▶ At equilibrium, the proportion of people who are susceptible to disease should be approximately $S/N = 1/\mathcal{R}_0$
- ▶ Proportion “affected” (infectious or immune) should be approximately $V/N = 1 - 1/\mathcal{R}_0$
- ▶ If you have a single, fast epidemic, the size is also predicted by \mathcal{R}_0 .

Reproductive numbers and risk (repeat)

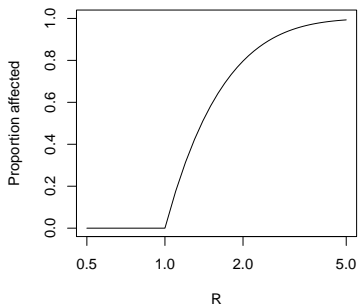


Reproductive numbers and risk

Equilibrium



Single epidemic



Examples

- ▶ Ronald Ross predicted 100 years ago that reducing mosquito densities by a factor of 5 or so would *eliminate* malaria

Examples

- ▶ Ronald Ross predicted 100 years ago that reducing mosquito densities by a factor of 5 or so would *eliminate* malaria
- ▶ Gradual disappearance of polio, typhoid, etc., without risk factors going to zero

Examples

- ▶ Ronald Ross predicted 100 years ago that reducing mosquito densities by a factor of 5 or so would *eliminate* malaria
- ▶ Gradual disappearance of polio, typhoid, etc., without risk factors going to zero
- ▶ Eradication of smallpox!

Examples

- ▶ Ronald Ross predicted 100 years ago that reducing mosquito densities by a factor of 5 or so would *eliminate* malaria
- ▶ Gradual disappearance of polio, typhoid, etc., without risk factors going to zero
- ▶ Eradication of smallpox!

Threshold for elimination

- ▶ What proportion of the population should be vaccinated to eliminate a disease?

Threshold for elimination

- ▶ What proportion of the population should be vaccinated to eliminate a disease?



Threshold for elimination

- ▶ What proportion of the population should be vaccinated to eliminate a disease?
 - ▶ * Transmission should be reduced by a factor of \mathcal{R} , so at least fraction $1 - 1/\mathcal{R}$ should be vaccinated (effectively)

Threshold for elimination

- ▶ What proportion of the population should be vaccinated to eliminate a disease?
 - ▶ * Transmission should be reduced by a factor of \mathcal{R} , so at least fraction $1 - 1/\mathcal{R}$ should be vaccinated (effectively)
 - ▶ *

Threshold for elimination

- ▶ What proportion of the population should be vaccinated to eliminate a disease?
 - ▶ * Transmission should be reduced by a factor of \mathcal{R} , so at least fraction $1 - 1/\mathcal{R}$ should be vaccinated (effectively)
 - ▶ * You may need to give vaccines to a larger fraction, since they don't always work

Threshold for elimination

- ▶ What proportion of the population should be vaccinated to eliminate a disease?
 - ▶ * Transmission should be reduced by a factor of \mathcal{R} , so at least fraction $1 - 1/\mathcal{R}$ should be vaccinated (effectively)
 - ▶ * You may need to give vaccines to a larger fraction, since they don't always work

Examples:

- ▶ Polio has an \mathcal{R}_0 of about 5.

Examples:

- ▶ Polio has an \mathcal{R}_0 of about 5.
- ▶ What proportion of the population should be vaccinated to eliminate polio?

Examples:

- ▶ Polio has an \mathcal{R}_0 of about 5.
- ▶ What proportion of the population should be vaccinated to eliminate polio?
 - ▶ *

Examples:

- ▶ Polio has an \mathcal{R}_0 of about 5.
- ▶ What proportion of the population should be vaccinated to eliminate polio?
 - ▶ * At least $1 - 1/5 = 80\%$

Examples:

- ▶ Polio has an \mathcal{R}_0 of about 5.
- ▶ What proportion of the population should be vaccinated to eliminate polio?
 - ▶ * At least $1 - 1/5 = 80\%$
 - ▶ *

Examples:

- ▶ Polio has an \mathcal{R}_0 of about 5.
- ▶ What proportion of the population should be vaccinated to eliminate polio?
 - ▶ * At least $1 - 1/5 = 80\%$
 - ▶ * Kind of worked in much of the world

Examples:

- ▶ Polio has an \mathcal{R}_0 of about 5.
- ▶ What proportion of the population should be vaccinated to eliminate polio?
 - ▶ * At least $1 - 1/5 = 80\%$
 - ▶ * Kind of worked in much of the world
- ▶ Measles has an \mathcal{R}_0 of about 20. What proportion of the population should be vaccinated to eliminate measles?

Examples:

- ▶ Polio has an \mathcal{R}_0 of about 5.
- ▶ What proportion of the population should be vaccinated to eliminate polio?
 - ▶ * At least $1 - 1/5 = 80\%$
 - ▶ * Kind of worked in much of the world
- ▶ Measles has an \mathcal{R}_0 of about 20. What proportion of the population should be vaccinated to eliminate measles?
 - ▶ *

Examples:

- ▶ Polio has an \mathcal{R}_0 of about 5.
- ▶ What proportion of the population should be vaccinated to eliminate polio?
 - ▶ * At least $1 - 1/5 = 80\%$
 - ▶ * Kind of worked in much of the world
- ▶ Measles has an \mathcal{R}_0 of about 20. What proportion of the population should be vaccinated to eliminate measles?
 - ▶ * At least $1 - 1/20 = 95\%$

Examples:

- ▶ Polio has an \mathcal{R}_0 of about 5.
- ▶ What proportion of the population should be vaccinated to eliminate polio?
 - ▶ * At least $1 - 1/5 = 80\%$
 - ▶ * Kind of worked in much of the world
- ▶ Measles has an \mathcal{R}_0 of about 20. What proportion of the population should be vaccinated to eliminate measles?
 - ▶ * At least $1 - 1/20 = 95\%$
- ▶ If gonorrhea has an \mathcal{R}_0 of about 2, what proportion of unprotected sexual encounters should be protected to eliminate gonorrhea?

Examples:

- ▶ Polio has an \mathcal{R}_0 of about 5.
- ▶ What proportion of the population should be vaccinated to eliminate polio?
 - ▶ * At least $1 - 1/5 = 80\%$
 - ▶ * Kind of worked in much of the world
- ▶ Measles has an \mathcal{R}_0 of about 20. What proportion of the population should be vaccinated to eliminate measles?
 - ▶ * At least $1 - 1/20 = 95\%$
- ▶ If gonorrhea has an \mathcal{R}_0 of about 2, what proportion of unprotected sexual encounters should be protected to eliminate gonorrhea?
 - ▶ *

Examples:

- ▶ Polio has an \mathcal{R}_0 of about 5.
- ▶ What proportion of the population should be vaccinated to eliminate polio?
 - ▶ * At least $1 - 1/5 = 80\%$
 - ▶ * Kind of worked in much of the world
- ▶ Measles has an \mathcal{R}_0 of about 20. What proportion of the population should be vaccinated to eliminate measles?
 - ▶ * At least $1 - 1/20 = 95\%$
- ▶ If gonorrhea has an \mathcal{R}_0 of about 2, what proportion of unprotected sexual encounters should be protected to eliminate gonorrhea?
 - ▶ * At least $1 - 1/2 = 50\%$

Examples:

- ▶ Polio has an \mathcal{R}_0 of about 5.
- ▶ What proportion of the population should be vaccinated to eliminate polio?
 - ▶ * At least $1 - 1/5 = 80\%$
 - ▶ * Kind of worked in much of the world
- ▶ Measles has an \mathcal{R}_0 of about 20. What proportion of the population should be vaccinated to eliminate measles?
 - ▶ * At least $1 - 1/20 = 95\%$
- ▶ If gonorrhea has an \mathcal{R}_0 of about 2, what proportion of unprotected sexual encounters should be protected to eliminate gonorrhea?
 - ▶ * At least $1 - 1/2 = 50\%$
 - ▶ *

Examples:

- ▶ Polio has an \mathcal{R}_0 of about 5.
 - ▶ * At least $1 - 1/5 = 80\%$
 - ▶ * Kind of worked in much of the world
- ▶ Measles has an \mathcal{R}_0 of about 20. What proportion of the population should be vaccinated to eliminate measles?
 - ▶ * At least $1 - 1/20 = 95\%$
- ▶ If gonorrhea has an \mathcal{R}_0 of about 2, what proportion of unprotected sexual encounters should be protected to eliminate gonorrhea?
 - ▶ * At least $1 - 1/2 = 50\%$
 - ▶ * Does not actually work ...

Examples:

- ▶ Polio has an \mathcal{R}_0 of about 5.
 - ▶ * At least $1 - 1/5 = 80\%$
 - ▶ * Kind of worked in much of the world
- ▶ Measles has an \mathcal{R}_0 of about 20. What proportion of the population should be vaccinated to eliminate measles?
 - ▶ * At least $1 - 1/20 = 95\%$
- ▶ If gonorrhea has an \mathcal{R}_0 of about 2, what proportion of unprotected sexual encounters should be protected to eliminate gonorrhea?
 - ▶ * At least $1 - 1/2 = 50\%$
 - ▶ * Does not actually work ...

Persistence of infectious disease

- ▶ Why have infectious diseases persisted?

Persistence of infectious disease

- ▶ Why have infectious diseases persisted?
 - ▶ The pathogens *evolve*

Persistence of infectious disease

- ▶ Why have infectious diseases persisted?
 - ▶ The pathogens *evolve*
 - ▶ Human populations are **heterogeneous**

Persistence of infectious disease

- ▶ Why have infectious diseases persisted?
 - ▶ The pathogens *evolve*
 - ▶ Human populations are **heterogeneous**
 - ▶ People differ in: nutrition, exposure, access to care

Persistence of infectious disease

- ▶ Why have infectious diseases persisted?
 - ▶ The pathogens *evolve*
 - ▶ Human populations are **heterogeneous**
 - ▶ People differ in: nutrition, exposure, access to care
 - ▶ Information and misinformation

Persistence of infectious disease

- ▶ Why have infectious diseases persisted?
 - ▶ The pathogens *evolve*
 - ▶ Human populations are **heterogeneous**
 - ▶ People differ in: nutrition, exposure, access to care
 - ▶ Information and misinformation
 - ▶ Vaccine scares, trust in health care in general

Persistence of infectious disease

- ▶ Why have infectious diseases persisted?
 - ▶ The pathogens *evolve*
 - ▶ Human populations are **heterogeneous**
 - ▶ People differ in: nutrition, exposure, access to care
 - ▶ Information and misinformation
 - ▶ Vaccine scares, trust in health care in general

Heterogeneity and persistence

- ▶ Heterogeneity *increases* \mathcal{R}_0

Heterogeneity and persistence

- ▶ Heterogeneity *increases* \mathcal{R}_0
 - ▶ When disease is rare, it is concentrated in the most vulnerable populations

Heterogeneity and persistence

- ▶ Heterogeneity *increases* \mathcal{R}_0
 - ▶ When disease is rare, it is concentrated in the most vulnerable populations
 - ▶ Cases per case is high

Heterogeneity and persistence

- ▶ Heterogeneity *increases* \mathcal{R}_0
 - ▶ When disease is rare, it is concentrated in the most vulnerable populations
 - ▶ Cases per case is high
 - ▶ Elimination is harder

Heterogeneity and persistence

- ▶ Heterogeneity *increases* \mathcal{R}_0
 - ▶ When disease is rare, it is concentrated in the most vulnerable populations
 - ▶ Cases per case is high
 - ▶ Elimination is harder
- ▶ Marginal populations

Heterogeneity and persistence

- ▶ Heterogeneity *increases* \mathcal{R}_0
 - ▶ When disease is rare, it is concentrated in the most vulnerable populations
 - ▶ Cases per case is high
 - ▶ Elimination is harder
- ▶ Marginal populations
 - ▶ Heterogeneity could make it easier to concentrate on the most vulnerable populations and eliminate disease

Heterogeneity and persistence

- ▶ Heterogeneity *increases* \mathcal{R}_0
 - ▶ When disease is rare, it is concentrated in the most vulnerable populations
 - ▶ Cases per case is high
 - ▶ Elimination is harder
- ▶ Marginal populations
 - ▶ Heterogeneity could make it easier to concentrate on the most vulnerable populations and eliminate disease
 - ▶ Humans rarely do this, however: the populations that need the most support typically have the least access

Heterogeneity and persistence

- ▶ Heterogeneity *increases* \mathcal{R}_0
 - ▶ When disease is rare, it is concentrated in the most vulnerable populations
 - ▶ Cases per case is high
 - ▶ Elimination is harder
- ▶ Marginal populations
 - ▶ Heterogeneity could make it easier to concentrate on the most vulnerable populations and eliminate disease
 - ▶ Humans rarely do this, however: the populations that need the most support typically have the least access

Outline

Introduction

Rate of spread

Single-epidemic model

Epidemic size

Recurrent epidemic models

Dynamics

Reproductive numbers and risk

Pathogen aggressiveness

Pathogen aggressiveness

- ▶ Should viruses evolve to become more or less dangerous?

Pathogen aggressiveness

- ▶ Should viruses evolve to become more or less dangerous?



Pathogen aggressiveness

- ▶ Should viruses evolve to become more or less dangerous?
 - ▶ * It depends

Pathogen aggressiveness

- ▶ Should viruses evolve to become more or less dangerous?
 - ▶ * It depends
 - ▶ *

Pathogen aggressiveness

- ▶ Should viruses evolve to become more or less dangerous?
 - ▶ * It depends
 - ▶ * The virus evolves in the way that's best for the virus

Pathogen aggressiveness

- ▶ Should viruses evolve to become more or less dangerous?
 - ▶ * It depends
 - ▶ * The virus evolves in the way that's best for the virus
 - ▶ *

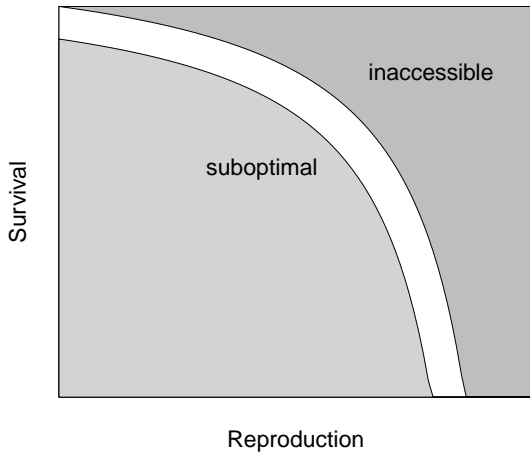
Pathogen aggressiveness

- ▶ Should viruses evolve to become more or less dangerous?
 - ▶ * It depends
 - ▶ * The virus evolves in the way that's best for the virus
 - ▶ * Host death and host recovery are equally bad!

Pathogen aggressiveness

- ▶ Should viruses evolve to become more or less dangerous?
 - ▶ * It depends
 - ▶ * The virus evolves in the way that's best for the virus
 - ▶ * Host death and host recovery are equally bad!

Tradeoffs (repeat)



Which strain will win?

- ▶ If the competing strains produce similar immune responses, this is exactly like equal competition: infections are competing for a single resource:

Which strain will win?

- ▶ If the competing strains produce similar immune responses, this is exactly like equal competition: infections are competing for a single resource:



Which strain will win?

- ▶ If the competing strains produce similar immune responses, this is exactly like equal competition: infections are competing for a single resource:
 - ▶ * Susceptible humans

Which strain will win?

- ▶ If the competing strains produce similar immune responses, this is exactly like equal competition: infections are competing for a single resource:
 - ▶ * Susceptible humans
- ▶ The winner will be the strain that has the highest “carrying capacity”:

Which strain will win?

- ▶ If the competing strains produce similar immune responses, this is exactly like equal competition: infections are competing for a single resource:
 - ▶ * Susceptible humans
- ▶ The winner will be the strain that has the highest “carrying capacity”:
 - ▶ *

Which strain will win?

- ▶ If the competing strains produce similar immune responses, this is exactly like equal competition: infections are competing for a single resource:
 - ▶ * Susceptible humans
- ▶ The winner will be the strain that has the highest “carrying capacity”:
 - ▶ * Removes the largest number from susceptible pool

Which strain will win?

- ▶ If the competing strains produce similar immune responses, this is exactly like equal competition: infections are competing for a single resource:
 - ▶ * Susceptible humans
- ▶ The winner will be the strain that has the highest “carrying capacity”:
 - ▶ * Removes the largest number from susceptible pool
 - ▶ *

Which strain will win?

- ▶ If the competing strains produce similar immune responses, this is exactly like equal competition: infections are competing for a single resource:
 - ▶ * Susceptible humans
- ▶ The winner will be the strain that has the highest “carrying capacity”:
 - ▶ * Removes the largest number from susceptible pool
 - ▶ * Highest \mathcal{R}_0

Which strain will win?

- ▶ If the competing strains produce similar immune responses, this is exactly like equal competition: infections are competing for a single resource:
 - ▶ * Susceptible humans
- ▶ The winner will be the strain that has the highest “carrying capacity”:
 - ▶ * Removes the largest number from susceptible pool
 - ▶ * Highest \mathcal{R}_0
 - ▶ *

Which strain will win?

- ▶ If the competing strains produce similar immune responses, this is exactly like equal competition: infections are competing for a single resource:
 - ▶ * Susceptible humans
- ▶ The winner will be the strain that has the highest “carrying capacity”:
 - ▶ * Removes the largest number from susceptible pool
 - ▶ * Highest \mathcal{R}_0
 - ▶ * This could be more or less deadly

Which strain will win?

- ▶ If the competing strains produce similar immune responses, this is exactly like equal competition: infections are competing for a single resource:
 - ▶ * Susceptible humans
- ▶ The winner will be the strain that has the highest “carrying capacity”:
 - ▶ * Removes the largest number from susceptible pool
 - ▶ * Highest \mathcal{R}_0
 - ▶ * This could be more or less deadly
 - ▶ *

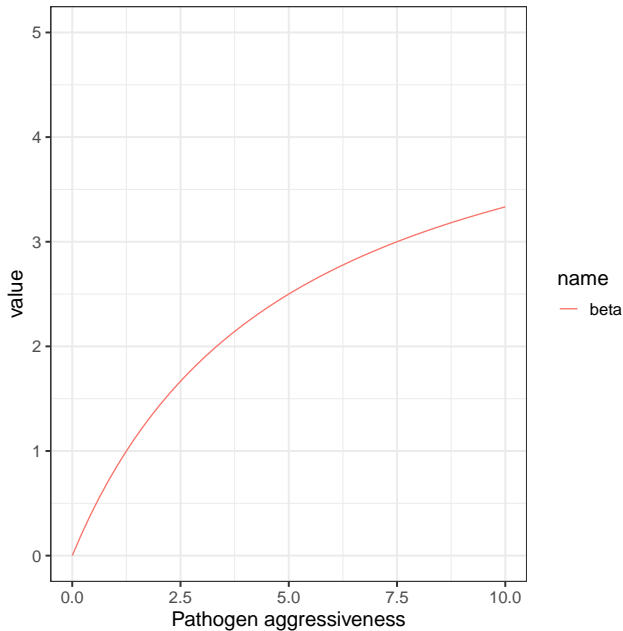
Which strain will win?

- ▶ If the competing strains produce similar immune responses, this is exactly like equal competition: infections are competing for a single resource:
 - ▶ * Susceptible humans
- ▶ The winner will be the strain that has the highest “carrying capacity”:
 - ▶ * Removes the largest number from susceptible pool
 - ▶ * Highest \mathcal{R}_0
 - ▶ * This could be more or less deadly
 - ▶ * Removal by killing and removal by recovery have similar effects on the virus

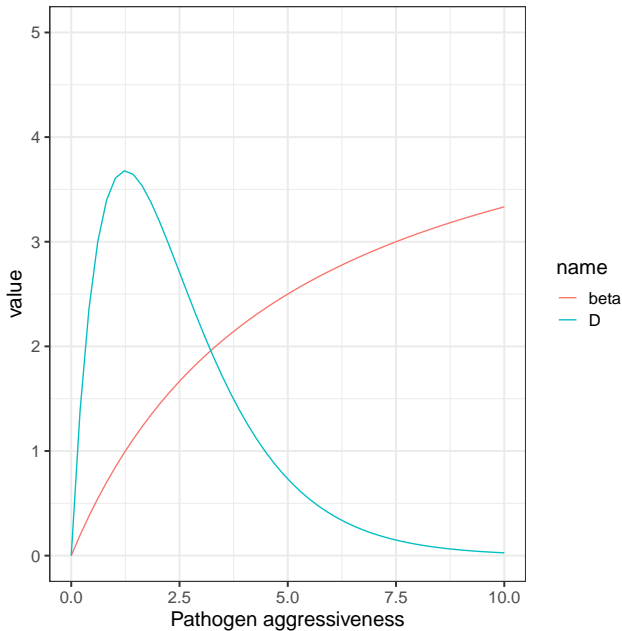
Which strain will win?

- ▶ If the competing strains produce similar immune responses, this is exactly like equal competition: infections are competing for a single resource:
 - ▶ * Susceptible humans
- ▶ The winner will be the strain that has the highest “carrying capacity”:
 - ▶ * Removes the largest number from susceptible pool
 - ▶ * Highest \mathcal{R}_0
 - ▶ * This could be more or less deadly
 - ▶ * Removal by killing and removal by recovery have similar effects on the virus

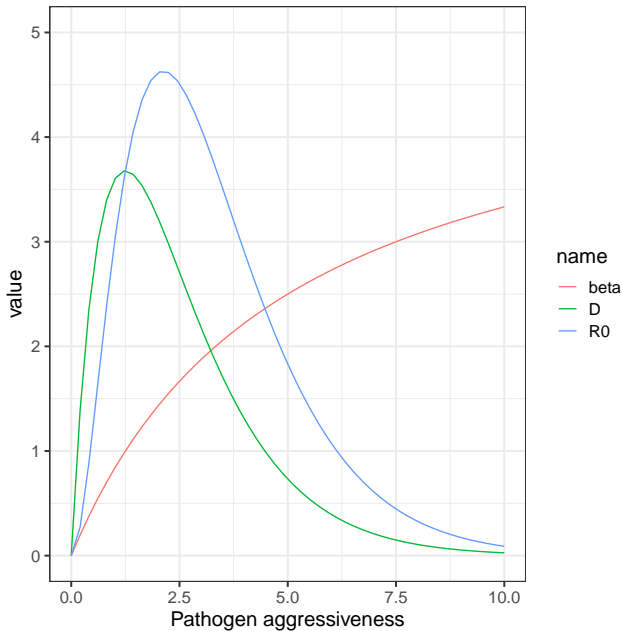
Pathogen aggressiveness (repeat)



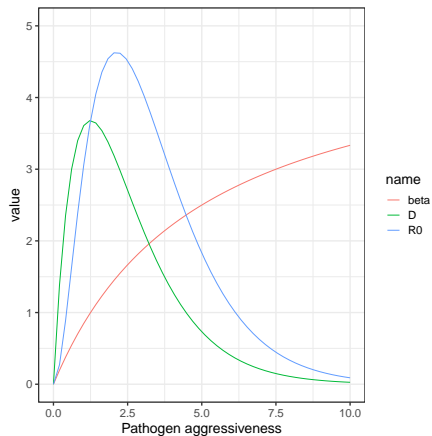
Pathogen aggressiveness (repeat)



Pathogen aggressiveness (repeat)

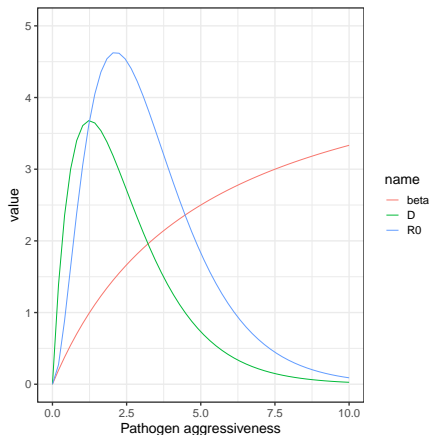


Pathogen aggressiveness



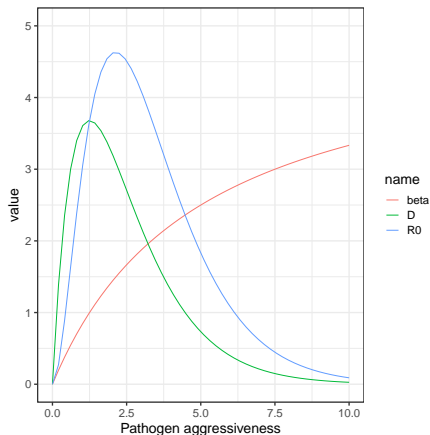
► Pathogen will evolve to maximize R_0 .

Pathogen aggressiveness



- ▶ Pathogen will evolve to maximize \mathcal{R}_0 .
- ▶ Pattern does not depend on whether duration D is ended by host death, or by immune system clearing the pathogen

Pathogen aggressiveness



- ▶ Pathogen will evolve to maximize \mathcal{R}_0 .
- ▶ Pattern does not depend on whether duration D is ended by host death, or by immune system clearing the pathogen

Human evolution

- ▶ We have evolved very good immune systems, but we can't always stay ahead of the viruses

Human evolution

- ▶ We have evolved very good immune systems, but we can't always stay ahead of the viruses
- ▶ Should people evolve to favor the spread of more or less dangerous viruses?

Human evolution

- ▶ We have evolved very good immune systems, but we can't always stay ahead of the viruses
- ▶ Should people evolve to favor the spread of more or less dangerous viruses?



Human evolution

- ▶ We have evolved very good immune systems, but we can't always stay ahead of the viruses
- ▶ Should people evolve to favor the spread of more or less dangerous viruses?
 - ▶ * Less dangerous!

Human evolution

- ▶ We have evolved very good immune systems, but we can't always stay ahead of the viruses
- ▶ Should people evolve to favor the spread of more or less dangerous viruses?
 - ▶ * Less dangerous!
 - ▶ *

Human evolution

- ▶ We have evolved very good immune systems, but we can't always stay ahead of the viruses
- ▶ Should people evolve to favor the spread of more or less dangerous viruses?
 - ▶ * Less dangerous!
 - ▶ * Viruses that do well in the upper respiratory tract may spread better

Human evolution

- ▶ We have evolved very good immune systems, but we can't always stay ahead of the viruses
- ▶ Should people evolve to favor the spread of more or less dangerous viruses?
 - ▶ * Less dangerous!
 - ▶ * Viruses that do well in the upper respiratory tract may spread better
 - ▶ *

Human evolution

- ▶ We have evolved very good immune systems, but we can't always stay ahead of the viruses
- ▶ Should people evolve to favor the spread of more or less dangerous viruses?
 - ▶ * Less dangerous!
 - ▶ * Viruses that do well in the upper respiratory tract may spread better
 - ▶ * Viruses that do well in the lower respiratory tract are more dangerous

Human evolution

- ▶ We have evolved very good immune systems, but we can't always stay ahead of the viruses
- ▶ Should people evolve to favor the spread of more or less dangerous viruses?
 - ▶ * Less dangerous!
 - ▶ * Viruses that do well in the upper respiratory tract may spread better
 - ▶ * Viruses that do well in the lower respiratory tract are more dangerous
 - ▶ *

Human evolution

- ▶ We have evolved very good immune systems, but we can't always stay ahead of the viruses
- ▶ Should people evolve to favor the spread of more or less dangerous viruses?
 - ▶ * Less dangerous!
 - ▶ * Viruses that do well in the upper respiratory tract may spread better
 - ▶ * Viruses that do well in the lower respiratory tract are more dangerous
 - ▶ * Have we evolved to make this a tradeoff for viruses?

Human evolution

- ▶ We have evolved very good immune systems, but we can't always stay ahead of the viruses
- ▶ Should people evolve to favor the spread of more or less dangerous viruses?
 - ▶ * Less dangerous!
 - ▶ * Viruses that do well in the upper respiratory tract may spread better
 - ▶ * Viruses that do well in the lower respiratory tract are more dangerous
 - ▶ * Have we evolved to make this a tradeoff for viruses?

Omicron example

- ▶ Omicron spreads *much* better than earlier SARS-CoV-2 viruses

Omicron example

- ▶ Omicron spreads *much* better than earlier SARS-CoV-2 viruses
- ▶ It does less well in the lungs and better in the upper airways

Omicron example

- ▶ Omicron spreads *much* better than earlier SARS-CoV-2 viruses
- ▶ It does less well in the lungs and better in the upper airways
- ▶ SARS-CoV-2 apparently evolved to be less dangerous

Omicron example

- ▶ Omicron spreads *much* better than earlier SARS-CoV-2 viruses
- ▶ It does less well in the lungs and better in the upper airways
- ▶ SARS-CoV-2 apparently evolved to be less dangerous
 - ▶ This is a pattern, but not a guarantee

Omicron example

- ▶ Omicron spreads *much* better than earlier SARS-CoV-2 viruses
- ▶ It does less well in the lungs and better in the upper airways
- ▶ SARS-CoV-2 apparently evolved to be less dangerous
 - ▶ This is a pattern, but not a guarantee