

## UNIT 2: Linear population models

# Outline

## Constructing models

- Dynamical models

- Examples

- A simple discrete-time model

- A simple continuous-time model

## Units and scaling

## Key parameters

- Discrete-time model

- Continuous-time model

- Links

## Growth and regulation

# Outline

## Constructing models

### Dynamical models

#### Examples

A simple discrete-time model

A simple continuous-time model

## Units and scaling

## Key parameters

Discrete-time model

Continuous-time model

Links

## Growth and regulation

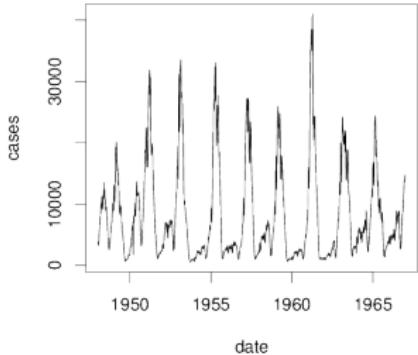
# Dynamical models

Tools to link scales

- Models are what we use to link:



Measles reports from England and Wales



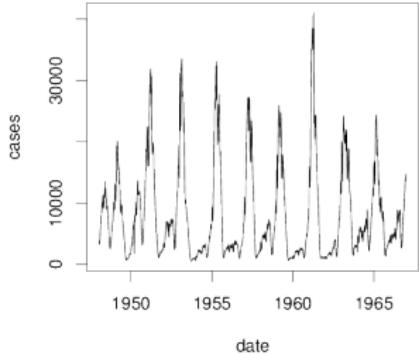
# Dynamical models

Tools to link scales

- ▶ Models are what we use to link:
  - ▶ Individual-level to population-level processes



Measles reports from England and Wales



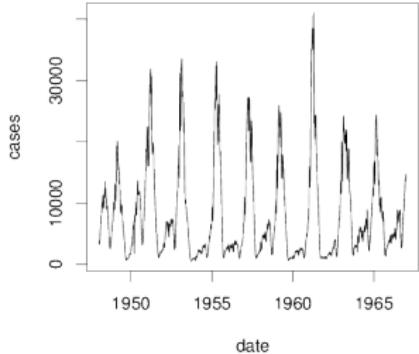
# Dynamical models

Tools to link scales

- ▶ Models are what we use to link:
  - ▶ Individual-level to population-level processes
  - ▶ Short time scales to long time scales



Measles reports from England and Wales



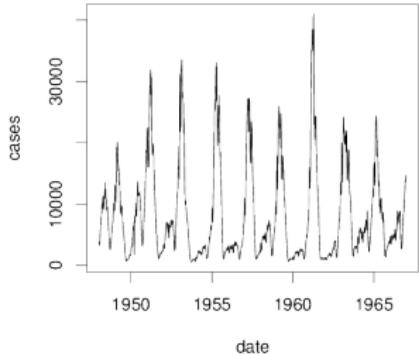
# Dynamical models

## Tools to link scales

- ▶ Models are what we use to link:
  - ▶ Individual-level to population-level processes
  - ▶ Short time scales to long time scales
- ▶ In both directions



Measles reports from England and Wales



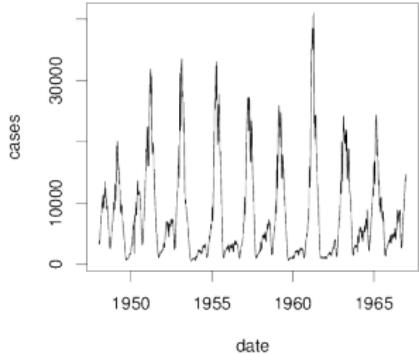
# Dynamical models

Tools to link scales

- ▶ Models are what we use to link:
  - ▶ Individual-level to population-level processes
  - ▶ Short time scales to long time scales
- ▶ In both directions

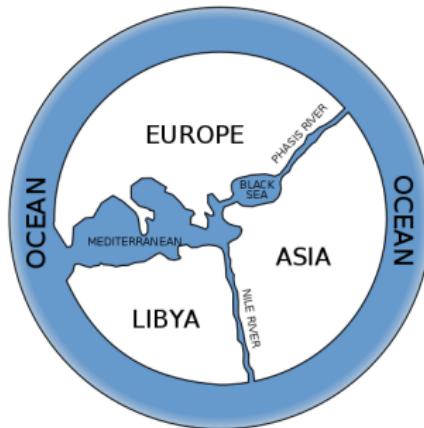


Measles reports from England and Wales



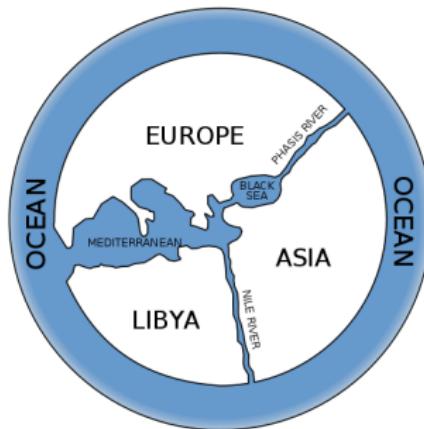
# Assumptions

- Models are always simplifications of reality



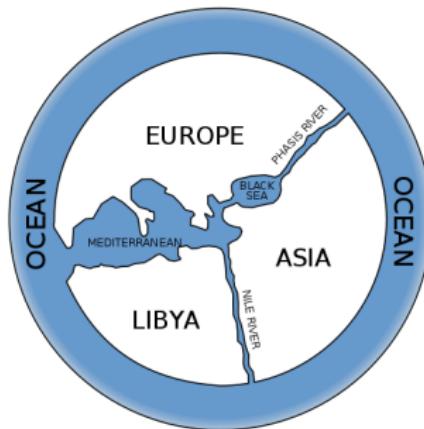
# Assumptions

- ▶ Models are always simplifications of reality
  - ▶ “The map is not the territory”



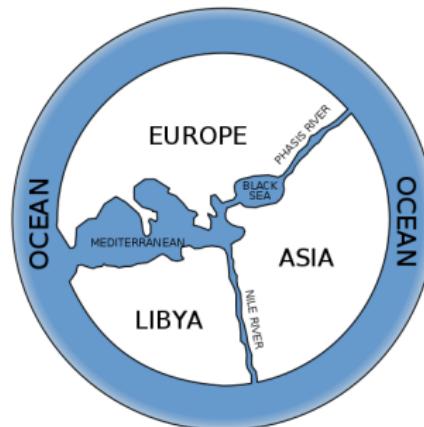
# Assumptions

- ▶ Models are always simplifications of reality
  - ▶ “The map is not the territory”
  - ▶ “All models are wrong, but some are useful”



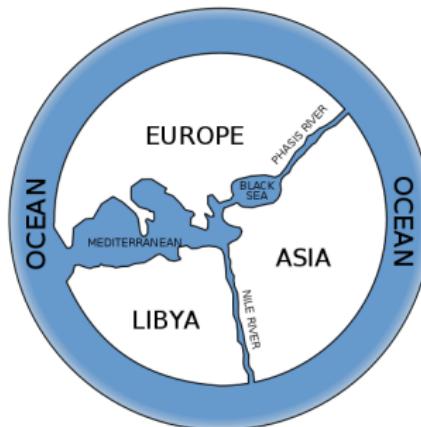
# Assumptions

- ▶ Models are always simplifications of reality
  - ▶ “The map is not the territory”
  - ▶ “All models are wrong, but some are useful”
- ▶ Models are useful for:



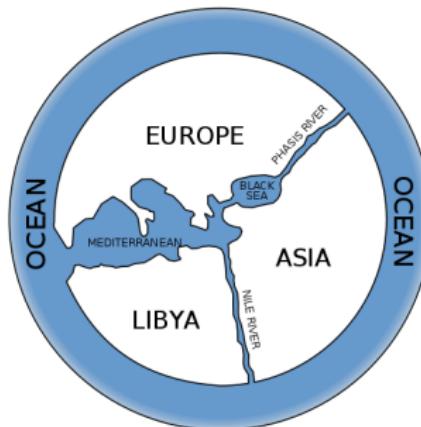
# Assumptions

- ▶ Models are always simplifications of reality
  - ▶ “The map is not the territory”
  - ▶ “All models are wrong, but some are useful”
- ▶ Models are useful for:
  - ▶ linking assumptions to outcomes



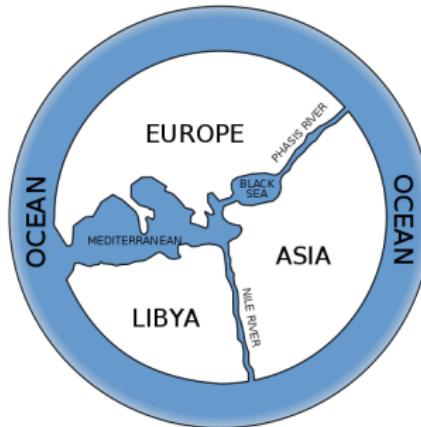
# Assumptions

- ▶ Models are always simplifications of reality
  - ▶ “The map is not the territory”
  - ▶ “All models are wrong, but some are useful”
- ▶ Models are useful for:
  - ▶ linking assumptions to outcomes
  - ▶ identifying where assumptions are broken



# Assumptions

- ▶ Models are always simplifications of reality
  - ▶ “The map is not the territory”
  - ▶ “All models are wrong, but some are useful”
- ▶ Models are useful for:
  - ▶ linking assumptions to outcomes
  - ▶ identifying where assumptions are broken



# Dynamical models

- **Dynamical models** describe rules for how a system changes at each point in time

# Dynamical models

- ▶ **Dynamical models** describe rules for how a system changes at each point in time
- ▶ We will see what these assumptions about how the system *changes* lead to conclusions about what the system *does* over longer time periods

# Dynamical models

- ▶ **Dynamical models** describe rules for how a system changes at each point in time
- ▶ We will see what these assumptions about how the system *changes* lead to conclusions about what the system *does* over longer time periods

## States and state variables

- Our dynamic models imagine that a system has a **state** at any given time, described by one or more **state variables**

## States and state variables

- ▶ Our dynamic models imagine that a system has a **state** at any given time, described by one or more **state variables**
- ▶ These are the things that follow our rules and change

## States and state variables

- ▶ Our dynamic models imagine that a system has a **state** at any given time, described by one or more **state variables**
- ▶ These are the things that follow our rules and change
- ▶ Examples:

## States and state variables

- ▶ Our dynamic models imagine that a system has a **state** at any given time, described by one or more **state variables**
- ▶ These are the things that follow our rules and change
- ▶ Examples:
  - ▶ Dandelions: state is population size, described by one state variable (the number of individuals)

## States and state variables

- ▶ Our dynamic models imagine that a system has a **state** at any given time, described by one or more **state variables**
- ▶ These are the things that follow our rules and change
- ▶ Examples:
  - ▶ Dandelions: state is population size, described by one state variable (the number of individuals)
  - ▶ Bacteria: state is population density, described by one state variable (the number of individuals per ml)

## States and state variables

- ▶ Our dynamic models imagine that a system has a **state** at any given time, described by one or more **state variables**
- ▶ These are the things that follow our rules and change
- ▶ Examples:
  - ▶ Dandelions: state is population size, described by one state variable (the number of individuals)
  - ▶ Bacteria: state is population density, described by one state variable (the number of individuals per ml)
  - ▶ Pine trees: state is amount of wood, described by one state variable (tons per hectare)

## States and state variables

- ▶ Our dynamic models imagine that a system has a **state** at any given time, described by one or more **state variables**
- ▶ These are the things that follow our rules and change
- ▶ Examples:
  - ▶ Dandelions: state is population size, described by one state variable (the number of individuals)
  - ▶ Bacteria: state is population density, described by one state variable (the number of individuals per ml)
  - ▶ Pine trees: state is amount of wood, described by one state variable (tons per hectare)
- ▶ Limiting the number of state variables is key to simple models

## States and state variables

- ▶ Our dynamic models imagine that a system has a **state** at any given time, described by one or more **state variables**
- ▶ These are the things that follow our rules and change
- ▶ Examples:
  - ▶ Dandelions: state is population size, described by one state variable (the number of individuals)
  - ▶ Bacteria: state is population density, described by one state variable (the number of individuals per ml)
  - ▶ Pine trees: state is amount of wood, described by one state variable (tons per hectare)
- ▶ Limiting the number of state variables is key to simple models

# Parameters

- ▶ **Parameters** are the quantities that describe how the rules for our system work

# Parameters

- ▶ **Parameters** are the quantities that describe how the rules for our system work
- ▶ Examples:

# Parameters

- ▶ **Parameters** are the quantities that describe how the rules for our system work
- ▶ Examples:
  - ▶ Birth rate, death rate, fecundity, survival probability

# Parameters

- ▶ **Parameters** are the quantities that describe how the rules for our system work
- ▶ Examples:
  - ▶ Birth rate, death rate, fecundity, survival probability
- ▶ Typically *remain constant* while we are simulating a particular scenario

# Parameters

- ▶ **Parameters** are the quantities that describe how the rules for our system work
- ▶ Examples:
  - ▶ Birth rate, death rate, fecundity, survival probability
- ▶ Typically *remain constant* while we are simulating a particular scenario
- ▶ *Vary when we compare different scenarios*

## Parameters

- ▶ **Parameters** are the quantities that describe how the rules for our system work
- ▶ Examples:
  - ▶ Birth rate, death rate, fecundity, survival probability
- ▶ Typically *remain constant* while we are simulating a particular scenario
- ▶ *Vary* when we compare different scenarios

# How do populations change?

- I survey a population in 2009, and again in 2013. I get a different answer the second time.

# How do populations change?

- ▶ I survey a population in 2009, and again in 2013. I get a different answer the second time.
- ▶ Poll: What are some reasons why this answer might change?

# How do populations change?

- ▶ I survey a population in 2009, and again in 2013. I get a different answer the second time.
- ▶ Poll: What are some reasons why this answer might change?
  - ▶ \*

# How do populations change?

- ▶ I survey a population in 2009, and again in 2013. I get a different answer the second time.
- ▶ Poll: What are some reasons why this answer might change?
  - ▶ \* Birth

# How do populations change?

- ▶ I survey a population in 2009, and again in 2013. I get a different answer the second time.
- ▶ Poll: What are some reasons why this answer might change?
  - ▶ \* Birth
  - ▶ \*

# How do populations change?

- ▶ I survey a population in 2009, and again in 2013. I get a different answer the second time.
- ▶ Poll: What are some reasons why this answer might change?
  - ▶ \* Birth
  - ▶ \* Death

# How do populations change?

- ▶ I survey a population in 2009, and again in 2013. I get a different answer the second time.
- ▶ Poll: What are some reasons why this answer might change?
  - ▶ \* Birth
  - ▶ \* Death
  - ▶ \*

# How do populations change?

- ▶ I survey a population in 2009, and again in 2013. I get a different answer the second time.
- ▶ Poll: What are some reasons why this answer might change?
  - ▶ \* Birth
  - ▶ \* Death
  - ▶ \* Immigration and emigration

# How do populations change?

- ▶ I survey a population in 2009, and again in 2013. I get a different answer the second time.
- ▶ Poll: What are some reasons why this answer might change?
  - ▶ \* Birth
  - ▶ \* Death
  - ▶ \* Immigration and emigration
  - ▶ \*

# How do populations change?

- ▶ I survey a population in 2009, and again in 2013. I get a different answer the second time.
- ▶ Poll: What are some reasons why this answer might change?
  - ▶ \* Birth
  - ▶ \* Death
  - ▶ \* Immigration and emigration
  - ▶ \* Sampling (ie., my counts are not perfectly correct)

# How do populations change?

- ▶ I survey a population in 2009, and again in 2013. I get a different answer the second time.
- ▶ Poll: What are some reasons why this answer might change?
  - ▶ \* Birth
  - ▶ \* Death
  - ▶ \* Immigration and emigration
  - ▶ \* Sampling (ie., my counts are not perfectly correct)

## Censusing and intermediate variables

- ▶ Often, our population models will imagine that the population is **censused** (counted) at particular periods of time

## Censusing and intermediate variables

- ▶ Often, our population models will imagine that the population is **censused** (counted) at particular periods of time
- ▶ Calculations of what happens between census times may be part of how we make our population model, without showing up in the main model itself

## Censusing and intermediate variables

- ▶ Often, our population models will imagine that the population is **censused** (counted) at particular periods of time
- ▶ Calculations of what happens between census times may be part of how we make our population model, without showing up in the main model itself
  - ▶ For example, our moth and dandelion examples

## Censusing and intermediate variables

- ▶ Often, our population models will imagine that the population is **censused** (counted) at particular periods of time
- ▶ Calculations of what happens between census times may be part of how we make our population model, without showing up in the main model itself
  - ▶ For example, our moth and dandelion examples

# Linear population models

- We will focus mostly on births and deaths

# Linear population models

- ▶ We will focus mostly on births and deaths
- ▶ Births and deaths are done by individuals

# Linear population models

- ▶ We will focus mostly on births and deaths
- ▶ Births and deaths are done by individuals
  - ▶ We model the rate of each individual (per capita rates)

# Linear population models

- ▶ We will focus mostly on births and deaths
- ▶ Births and deaths are done by individuals
  - ▶ We model the rate of each individual (per capita rates)
  - ▶ Total rate is the per capita rate multiplied by population size

# Linear population models

- ▶ We will focus mostly on births and deaths
- ▶ Births and deaths are done by individuals
  - ▶ We model the rate of each individual (per capita rates)
  - ▶ Total rate is the per capita rate multiplied by population size
- ▶ If per capita rates are constant, we say that our population *models* are **linear**

# Linear population models

- ▶ We will focus mostly on births and deaths
- ▶ Births and deaths are done by individuals
  - ▶ We model the rate of each individual (per capita rates)
  - ▶ Total rate is the per capita rate multiplied by population size
- ▶ If per capita rates are constant, we say that our population *models* are **linear**
  - ▶ Linear models do not usually correspond to linear growth!

# Linear population models

- ▶ We will focus mostly on births and deaths
- ▶ Births and deaths are done by individuals
  - ▶ We model the rate of each individual (per capita rates)
  - ▶ Total rate is the per capita rate multiplied by population size
- ▶ If per capita rates are constant, we say that our population *models* are **linear**
  - ▶ Linear models do not usually correspond to linear growth!
  - ▶ \*

# Linear population models

- ▶ We will focus mostly on births and deaths
- ▶ Births and deaths are done by individuals
  - ▶ We model the rate of each individual (per capita rates)
  - ▶ Total rate is the per capita rate multiplied by population size
- ▶ If per capita rates are constant, we say that our population *models* are **linear**
  - ▶ Linear models do not usually correspond to linear growth!
  - ▶ \* They usually correspond to exponential growth

# Linear population models

- ▶ We will focus mostly on births and deaths
- ▶ Births and deaths are done by individuals
  - ▶ We model the rate of each individual (per capita rates)
  - ▶ Total rate is the per capita rate multiplied by population size
- ▶ If per capita rates are constant, we say that our population *models* are **linear**
  - ▶ Linear models do not usually correspond to linear growth!
  - ▶ \* They usually correspond to exponential growth
  - ▶ \*

# Linear population models

- ▶ We will focus mostly on births and deaths
- ▶ Births and deaths are done by individuals
  - ▶ We model the rate of each individual (per capita rates)
  - ▶ Total rate is the per capita rate multiplied by population size
- ▶ If per capita rates are constant, we say that our population *models* are **linear**
  - ▶ Linear models do not usually correspond to linear growth!
  - ▶ \* They usually correspond to exponential growth
    - ▶ \* ...or exponential decline

# Linear population models

- ▶ We will focus mostly on births and deaths
- ▶ Births and deaths are done by individuals
  - ▶ We model the rate of each individual (per capita rates)
  - ▶ Total rate is the per capita rate multiplied by population size
- ▶ If per capita rates are constant, we say that our population *models* are **linear**
  - ▶ Linear models do not usually correspond to linear growth!
  - ▶ \* They usually correspond to exponential growth
    - ▶ \* ...or exponential decline

# Outline

## Constructing models

Dynamical models

### Examples

A simple discrete-time model

A simple continuous-time model

## Units and scaling

## Key parameters

Discrete-time model

Continuous-time model

Links

## Growth and regulation

## *Gypsy moths (repeat)*

- ▶ A pest species that feeds on deciduous trees



## Gypsy moths (repeat)

- ▶ A pest species that feeds on deciduous trees
- ▶ Introduced to N. America from Europe 150 years ago



## *Gypsy moths (repeat)*

- ▶ A pest species that feeds on deciduous trees
- ▶ Introduced to N. America from Europe 150 years ago
- ▶ Capable of wide-scale defoliation

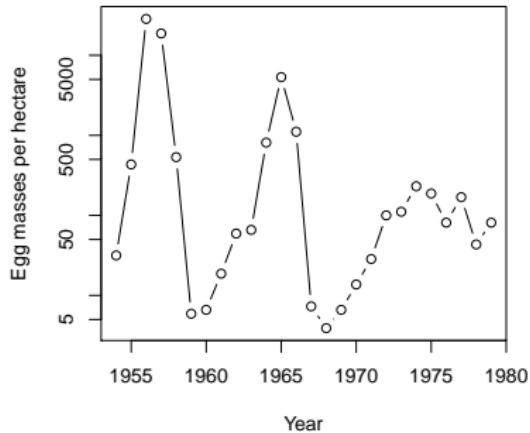
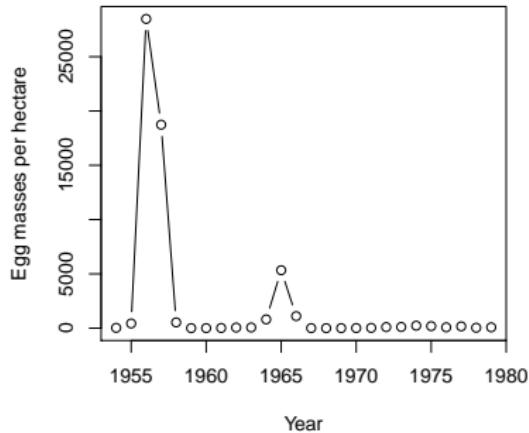


## *Gypsy moths (repeat)*

- ▶ A pest species that feeds on deciduous trees
- ▶ Introduced to N. America from Europe 150 years ago
- ▶ Capable of wide-scale defoliation



## *Gypsy moth populations (repeat)*



# Moth example

- Poll: State variable



# Moth example

- ▶ Poll: State variable

▶ \*



# Moth example

- ▶ Poll: State variable
  - ▶ \* Number of moths/ha



# Moth example

- ▶ Poll: State variable
  - ▶ \* Number of moths/ha
- ▶ Parameters



# Moth example

- ▶ Poll: State variable
  - ▶ \* Number of moths/ha
- ▶ Parameters
  - ▶ \*



# Moth example

- ▶ Poll: State variable
  - ▶ \* Number of moths/ha
- ▶ Parameters
  - ▶ \* Number of eggs



# Moth example

- ▶ Poll: State variable
  - ▶ \* Number of moths/ha
- ▶ Parameters
  - ▶ \* Number of eggs
  - ▶ \*



# Moth example

- ▶ Poll: State variable
  - ▶ \* Number of moths/ha
- ▶ Parameters
  - ▶ \* Number of eggs
  - ▶ \* sex ratio



# Moth example

- ▶ Poll: State variable
  - ▶ \* Number of moths/ha
- ▶ Parameters
  - ▶ \* Number of eggs
  - ▶ \* sex ratio
  - ▶ \*



# Moth example

- ▶ Poll: State variable
  - ▶ \* Number of moths/ha
- ▶ Parameters
  - ▶ \* Number of eggs
  - ▶ \* sex ratio
  - ▶ \* larval survival, pupal survival, adult survival



# Moth example

- ▶ Poll: State variable
  - ▶ \* Number of moths/ha
- ▶ Parameters
  - ▶ \* Number of eggs
  - ▶ \* sex ratio
  - ▶ \* larval survival, pupal survival, adult survival
  - ▶ \*



# Moth example

- ▶ Poll: State variable
  - ▶ \* Number of moths/ha
- ▶ Parameters
  - ▶ \* Number of eggs
  - ▶ \* sex ratio
  - ▶ \* larval survival, pupal survival, adult survival
  - ▶ \* Time step



# Moth example

- ▶ Poll: State variable
  - ▶ \* Number of moths/ha
- ▶ Parameters
  - ▶ \* Number of eggs
  - ▶ \* sex ratio
  - ▶ \* larval survival, pupal survival, adult survival
  - ▶ \* Time step
- ▶ Census time



# Moth example

- ▶ Poll: State variable
  - ▶ \* Number of moths/ha
- ▶ Parameters
  - ▶ \* Number of eggs
  - ▶ \* sex ratio
  - ▶ \* larval survival, pupal survival, adult survival
  - ▶ \* Time step
- ▶ Census time
  - ▶ \*



# Moth example

- ▶ Poll: State variable
  - ▶ \* Number of moths/ha
- ▶ Parameters
  - ▶ \* Number of eggs
  - ▶ \* sex ratio
  - ▶ \* larval survival, pupal survival, adult survival
  - ▶ \* Time step
- ▶ Census time
  - ▶ \* Annually; use the same time (and stage) each year



# Moth example

- ▶ Poll: State variable
  - ▶ \* Number of moths/ha
- ▶ Parameters
  - ▶ \* Number of eggs
  - ▶ \* sex ratio
  - ▶ \* larval survival, pupal survival, adult survival
  - ▶ \* Time step
- ▶ Census time
  - ▶ \* Annually; use the same time (and stage) each year



# Bacteria

## ► State variables



# Bacteria

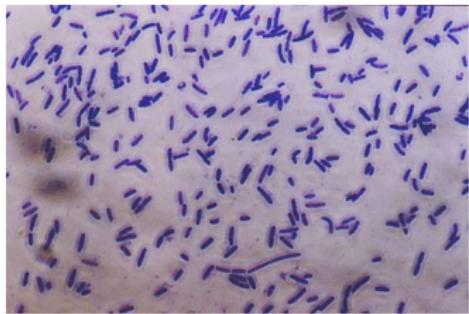
- ▶ State variables

▶ \*



# Bacteria

- ▶ State variables
  - ▶ \* Number of bacteria/ml



# Bacteria

- ▶ State variables
  - ▶ \* Number of bacteria/ml
- ▶ Poll: Parameters



# Bacteria

- ▶ State variables
  - ▶ \* Number of bacteria/ml
- ▶ Poll: Parameters
  - ▶ \*



# Bacteria

- ▶ State variables
  - ▶ \* Number of bacteria/ml
- ▶ Poll: Parameters
  - ▶ \* Division rate, death rate, washout rate



# Bacteria

- ▶ State variables
  - ▶ \* Number of bacteria/ml
- ▶ Poll: Parameters
  - ▶ \* Division rate, death rate, washout rate
- ▶ Census time



# Bacteria

- ▶ State variables
  - ▶ \* Number of bacteria/ml
- ▶ Poll: Parameters
  - ▶ \* Division rate, death rate, washout rate
- ▶ Census time
  - ▶ \*



# Bacteria

- ▶ State variables
  - ▶ \* Number of bacteria/ml
- ▶ Poll: Parameters
  - ▶ \* Division rate, death rate, washout rate
- ▶ Census time
  - ▶ \* Always!



# Bacteria

- ▶ State variables
  - ▶ \* Number of bacteria/ml
- ▶ Poll: Parameters
  - ▶ \* Division rate, death rate, washout rate
- ▶ Census time
  - ▶ \* Always!



# Dandelions

## ► State variables



# Dandelions

- ▶ State variables

▶ \*



# Dandelions

- ▶ State variables
  - ▶ \* Number of dandelions in a field



# Dandelions

- ▶ State variables
  - ▶ \* Number of dandelions in a field
  - ▶ Poll: Are there intermediate variables?



# Dandelions

- ▶ State variables
  - ▶ \* Number of dandelions in a field
  - ▶ Poll: Are there intermediate variables?
    - ▶ \*



# Dandelions

- ▶ State variables
  - ▶ \* Number of dandelions in a field
  - ▶ Poll: Are there intermediate variables?
    - ▶ \* Number of seeds



# Dandelions

- ▶ State variables
  - ▶ \* Number of dandelions in a field
  - ▶ Poll: Are there intermediate variables?
    - ▶ \* Number of seeds
- ▶ Parameters



# Dandelions

- ▶ State variables
  - ▶ \* Number of dandelions in a field
  - ▶ Poll: Are there intermediate variables?
    - ▶ \* Number of seeds
- ▶ Parameters
  - ▶ \*



# Dandelions

- ▶ State variables
  - ▶ \* Number of dandelions in a field
  - ▶ Poll: Are there intermediate variables?
    - ▶ \* Number of seeds
- ▶ Parameters
  - ▶ \* Seed production, survival to adulthood, adult survival



# Dandelions

- ▶ State variables
  - ▶ \* Number of dandelions in a field
  - ▶ Poll: Are there intermediate variables?
    - ▶ \* Number of seeds
- ▶ Parameters
  - ▶ \* Seed production, survival to adulthood, adult survival
- ▶ Census time



# Dandelions

- ▶ State variables
  - ▶ \* Number of dandelions in a field
  - ▶ Poll: Are there intermediate variables?
    - ▶ \* Number of seeds
- ▶ Parameters
  - ▶ \* Seed production, survival to adulthood, adult survival
- ▶ Census time
  - ▶ \*



# Dandelions

- ▶ State variables
  - ▶ \* Number of dandelions in a field
  - ▶ Poll: Are there intermediate variables?
    - ▶ \* Number of seeds
- ▶ Parameters
  - ▶ \* Seed production, survival to adulthood, adult survival
- ▶ Census time
  - ▶ \* Annually, before reproduction



# Dandelions

- ▶ State variables
  - ▶ \* Number of dandelions in a field
  - ▶ Poll: Are there intermediate variables?
    - ▶ \* Number of seeds
- ▶ Parameters
  - ▶ \* Seed production, survival to adulthood, adult survival
- ▶ Census time
  - ▶ \* Annually, before reproduction
  - ▶ \*



# Dandelions

- ▶ State variables
  - ▶ \* Number of dandelions in a field
  - ▶ Poll: Are there intermediate variables?
    - ▶ \* Number of seeds
- ▶ Parameters
  - ▶ \* Seed production, survival to adulthood, adult survival
- ▶ Census time
  - ▶ \* Annually, before reproduction
  - ▶ \* When new and returning individuals are most similar



# Dandelions

- ▶ State variables
  - ▶ \* Number of dandelions in a field
  - ▶ Poll: Are there intermediate variables?
    - ▶ \* Number of seeds
- ▶ Parameters
  - ▶ \* Seed production, survival to adulthood, adult survival
- ▶ Census time
  - ▶ \* Annually, before reproduction
  - ▶ \* When new and returning individuals are most similar



# Outline

## Constructing models

Dynamical models

Examples

A simple discrete-time model

A simple continuous-time model

## Units and scaling

## Key parameters

Discrete-time model

Continuous-time model

Links

## Growth and regulation

## Assumptions

- If we have  $N$  individuals after  $T$  time steps, what determines how many individuals we have after  $T + 1$  time steps?

## Assumptions

- ▶ If we have  $N$  individuals after  $T$  time steps, what determines how many individuals we have after  $T + 1$  time steps?
  - ▶ A fixed proportion  $p$  of the population (on average) survives to be counted at time step  $T + 1$

## Assumptions

- ▶ If we have  $N$  individuals after  $T$  time steps, what determines how many individuals we have after  $T + 1$  time steps?
  - ▶ A fixed proportion  $\rho$  of the population (on average) survives to be counted at time step  $T + 1$
  - ▶ Each individual creates (on average)  $f$  new individuals that will be counted at time step  $T + 1$

## Assumptions

- ▶ If we have  $N$  individuals after  $T$  time steps, what determines how many individuals we have after  $T + 1$  time steps?
  - ▶ A fixed proportion  $\rho$  of the population (on average) survives to be counted at time step  $T + 1$
  - ▶ Each individual creates (on average)  $f$  new individuals that will be counted at time step  $T + 1$
- ▶ How many individuals do we expect in the next time step?

## Assumptions

- ▶ If we have  $N$  individuals after  $T$  time steps, what determines how many individuals we have after  $T + 1$  time steps?
  - ▶ A fixed proportion  $\rho$  of the population (on average) survives to be counted at time step  $T + 1$
  - ▶ Each individual creates (on average)  $f$  new individuals that will be counted at time step  $T + 1$
- ▶ How many individuals do we expect in the next time step?
  - ▶ \*

## Assumptions

- ▶ If we have  $N$  individuals after  $T$  time steps, what determines how many individuals we have after  $T + 1$  time steps?
  - ▶ A fixed proportion  $p$  of the population (on average) survives to be counted at time step  $T + 1$
  - ▶ Each individual creates (on average)  $f$  new individuals that will be counted at time step  $T + 1$
- ▶ How many individuals do we expect in the next time step?
  - ▶ \*  $N_{T+1} = (pN_T + fN_T) = (p + f)N_T$

# Assumptions

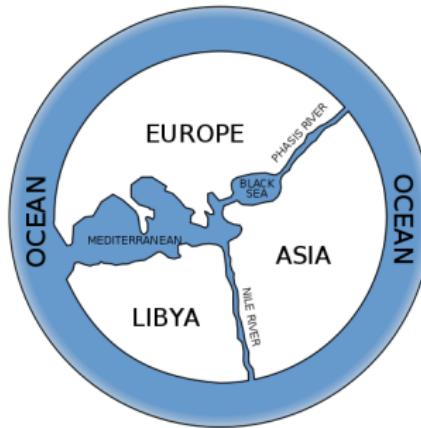
- ▶ If we have  $N$  individuals after  $T$  time steps, what determines how many individuals we have after  $T + 1$  time steps?
  - ▶ A fixed proportion  $p$  of the population (on average) survives to be counted at time step  $T + 1$
  - ▶ Each individual creates (on average)  $f$  new individuals that will be counted at time step  $T + 1$
- ▶ How many individuals do we expect in the next time step?
  - ▶ \*  $N_{T+1} = (pN_T + fN_T) = (p + f)N_T$
- ▶ Diagram

## Assumptions

- ▶ If we have  $N$  individuals after  $T$  time steps, what determines how many individuals we have after  $T + 1$  time steps?
  - ▶ A fixed proportion  $p$  of the population (on average) survives to be counted at time step  $T + 1$
  - ▶ Each individual creates (on average)  $f$  new individuals that will be counted at time step  $T + 1$
- ▶ How many individuals do we expect in the next time step?
  - ▶ \*  $N_{T+1} = (pN_T + fN_T) = (p + f)N_T$
- ▶ Diagram

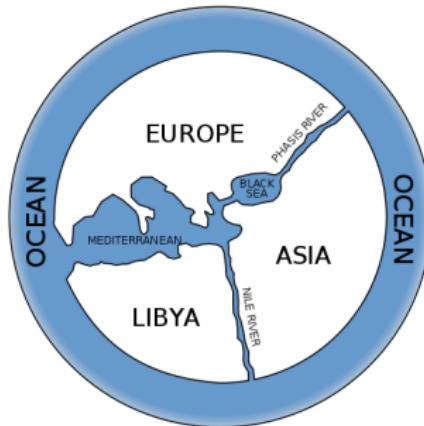
# Assumptions

- ▶ Individuals are **independent**:  
what I do does not depend on how  
many other individuals are around



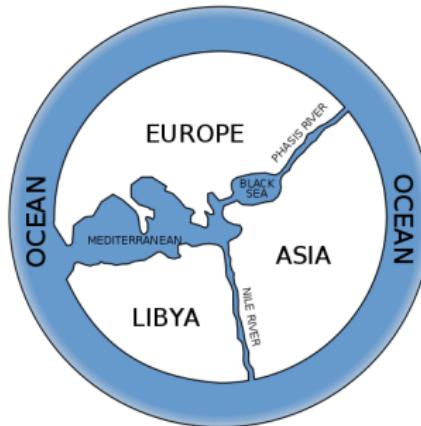
## Assumptions

- ▶ Individuals are **independent**: what I do does not depend on how many other individuals are around
- ▶ The population is censused at regular time intervals  $\Delta t$



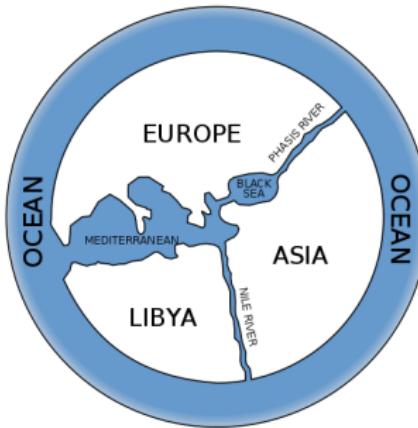
## Assumptions

- ▶ Individuals are **independent**: what I do does not depend on how many other individuals are around
- ▶ The population is censused at regular time intervals  $\Delta t$ 
  - ▶ Usually  $\Delta t = 1 \text{ yr}$



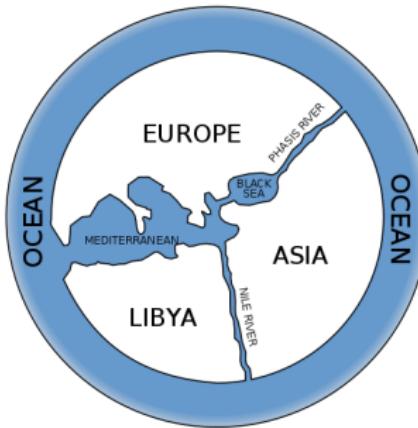
## Assumptions

- ▶ Individuals are **independent**: what I do does not depend on how many other individuals are around
- ▶ The population is censused at regular time intervals  $\Delta t$ 
  - ▶ Usually  $\Delta t = 1$  yr
- ▶ All individuals are the same at the time of census



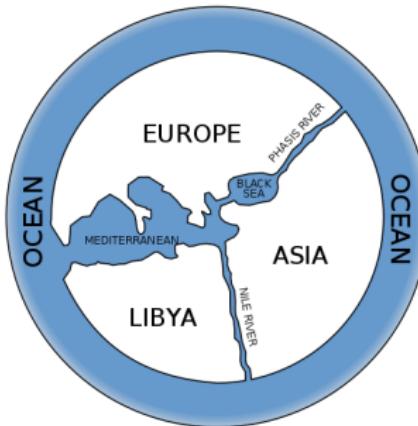
## Assumptions

- ▶ Individuals are **independent**: what I do does not depend on how many other individuals are around
- ▶ The population is censused at regular time intervals  $\Delta t$ 
  - ▶ Usually  $\Delta t = 1 \text{ yr}$
- ▶ All individuals are the same at the time of census
- ▶ Population changes deterministically



## Assumptions

- ▶ Individuals are **independent**: what I do does not depend on how many other individuals are around
- ▶ The population is censused at regular time intervals  $\Delta t$ 
  - ▶ Usually  $\Delta t = 1 \text{ yr}$
- ▶ All individuals are the same at the time of census
- ▶ Population changes deterministically



# Definitions

- $p$  is the **survival probability**

# Definitions

- ▶  $p$  is the **survival probability**
- ▶  $f$  is the **fecundity**

## Definitions

- ▶  $p$  is the **survival probability**
- ▶  $f$  is the **fecundity**
- ▶  $\lambda \equiv p + f$  is the **finite rate of increase**

# Definitions

- ▶  $p$  is the **survival probability**
- ▶  $f$  is the **fecundity**
- ▶  $\lambda \equiv p + f$  is the **finite rate of increase**
  - ▶ ... associated with the time step  $\Delta t$

# Definitions

- ▶  $p$  is the **survival probability**
- ▶  $f$  is the **fecundity**
- ▶  $\lambda \equiv p + f$  is the **finite rate of increase**
  - ▶ ... associated with the time step  $\Delta t$
  - ▶ ( $\Delta t$  has units of time)

# Definitions

- ▶  $p$  is the **survival probability**
- ▶  $f$  is the **fecundity**
- ▶  $\lambda \equiv p + f$  is the **finite rate of increase**
  - ▶ ... associated with the time step  $\Delta t$
  - ▶ ( $\Delta t$  has units of time)

# Model

- Dynamics:

# Model

- ▶ Dynamics:
  - ▶  $N_{T+1} = \lambda N_T$

# Model

- ▶ Dynamics:

- ▶  $N_{T+1} = \lambda N_T$
- ▶  $t_{T+1} = t_T + \Delta t$

# Model

- ▶ Dynamics:
  - ▶  $N_{T+1} = \lambda N_T$
  - ▶  $t_{T+1} = t_T + \Delta t$
- ▶ Solution:

# Model

- ▶ Dynamics:
  - ▶  $N_{T+1} = \lambda N_T$
  - ▶  $t_{T+1} = t_T + \Delta t$
- ▶ Solution:
  - ▶  $N_T = N_0 \lambda^T$

# Model

- ▶ Dynamics:
  - ▶  $N_{T+1} = \lambda N_T$
  - ▶  $t_{T+1} = t_T + \Delta t$
- ▶ Solution:
  - ▶  $N_T = N_0 \lambda^T$
  - ▶  $t_T = T \Delta t$

# Model

- ▶ Dynamics:
  - ▶  $N_{T+1} = \lambda N_T$
  - ▶  $t_{T+1} = t_T + \Delta t$
- ▶ Solution:
  - ▶  $N_T = N_0 \lambda^T$
  - ▶  $t_T = T \Delta t$
- ▶ Poll: How does  $N$  behave in this model?

# Model

- ▶ Dynamics:
  - ▶  $N_{T+1} = \lambda N_T$
  - ▶  $t_{T+1} = t_T + \Delta t$
- ▶ Solution:
  - ▶  $N_T = N_0 \lambda^T$
  - ▶  $t_T = T \Delta t$
- ▶ Poll: How does  $N$  behave in this model?
  - ▶ \*

# Model

- ▶ Dynamics:
  - ▶  $N_{T+1} = \lambda N_T$
  - ▶  $t_{T+1} = t_T + \Delta t$
- ▶ Solution:
  - ▶  $N_T = N_0 \lambda^T$
  - ▶  $t_T = T \Delta t$
- ▶ Poll: How does  $N$  behave in this model?
  - ▶ \* Increases exponentially (geometrically) when  $\lambda > 1$

# Model

- ▶ Dynamics:
  - ▶  $N_{T+1} = \lambda N_T$
  - ▶  $t_{T+1} = t_T + \Delta t$
- ▶ Solution:
  - ▶  $N_T = N_0 \lambda^T$
  - ▶  $t_T = T \Delta t$
- ▶ Poll: How does  $N$  behave in this model?
  - ▶ \* Increases exponentially (geometrically) when  $\lambda > 1$
  - ▶ \*

# Model

- ▶ Dynamics:
  - ▶  $N_{T+1} = \lambda N_T$
  - ▶  $t_{T+1} = t_T + \Delta t$
- ▶ Solution:
  - ▶  $N_T = N_0 \lambda^T$
  - ▶  $t_T = T \Delta t$
- ▶ Poll: How does  $N$  behave in this model?
  - ▶ \* Increases exponentially (geometrically) when  $\lambda > 1$
  - ▶ \* Decreases exponentially when  $\lambda < 1$

# Model

- ▶ Dynamics:
  - ▶  $N_{T+1} = \lambda N_T$
  - ▶  $t_{T+1} = t_T + \Delta t$
- ▶ Solution:
  - ▶  $N_T = N_0 \lambda^T$
  - ▶  $t_T = T \Delta t$
- ▶ Poll: How does  $N$  behave in this model?
  - ▶ \* Increases exponentially (geometrically) when  $\lambda > 1$
  - ▶ \* Decreases exponentially when  $\lambda < 1$

# Example



	A	B	C	D
1	Date	Income	Expenses	Profit
2	2005-12-17	235 €	128 €	107 €
3	2005-12-18	311 €	124 €	187 €
4	2005-12-19	457 €	466 €	-9 €
5	2005-12-20	232 €	132 €	100 €
6	2005-12-21	122 €	134 €	-12 €
7	2005-12-22	128 €	223 €	-95 €
8	2005-12-23	432 €	218 €	214 €
9	2005-12-24	256 €	121 €	135 €
10		2.173 €	1.546 €	627 €
11				
12	Avg. Profit	=AVERAGE(D2:D9)		

► Spreadsheet (see resource page)

# Example



	A	B	C	D
1	Date	Income	Expenses	Profit
2	2005-12-17	235 €	128 €	107 €
3	2005-12-18	311 €	124 €	187 €
4	2005-12-19	457 €	466 €	-9 €
5	2005-12-20	232 €	132 €	100 €
6	2005-12-21	122 €	134 €	-12 €
7	2005-12-22	128 €	223 €	-95 €
8	2005-12-23	432 €	218 €	214 €
9	2005-12-24	256 €	121 €	135 €
10		2.173 €	1.546 €	627 €
11				
12	Avg. Profit	=AVERAGE(D2:D9)		

- ▶ Spreadsheet (see resource page)

# Interpretation

- ▶ Assumptions are simplifications based on reality

# Interpretation

- ▶ Assumptions are simplifications based on reality
- ▶ We can understand why populations change exponentially sometimes

# Interpretation

- ▶ Assumptions are simplifications based on reality
- ▶ We can understand why populations change exponentially sometimes
- ▶ We can look for *reasons* when they don't

# Interpretation

- ▶ Assumptions are simplifications based on reality
- ▶ We can understand why populations change exponentially sometimes
- ▶ We can look for *reasons* when they don't

# Examples

## ► Moths



# Examples

- ▶ Moths
  - ▶  $p = 0$ , so  $\lambda = f$ .



# Examples

- ▶ Moths
  - ▶  $p = 0$ , so  $\lambda = f$ .
    - ▶ Moths are **semelparous** (reproduce once); they have an **annual** population



# Examples

- ▶ Moths
  - ▶  $p = 0$ , so  $\lambda = f$ .
    - ▶ Moths are **semelparous** (reproduce once); they have an **annual** population
- ▶ Dandelions



# Examples

- ▶ Moths
  - ▶  $p = 0$ , so  $\lambda = f$ .
    - ▶ Moths are **semelparous** (reproduce once); they have an **annual** population
  
- ▶ Dandelions
  - ▶ If  $p > 0$ , then the dandelions are **iteroparous**; they are a **perennial** population



# Examples

- ▶ Moths
  - ▶  $p = 0$ , so  $\lambda = f$ .
    - ▶ Moths are **semelparous** (reproduce once); they have an **annual** population
  
- ▶ Dandelions
  - ▶ If  $p > 0$ , then the dandelions are **iteroparous**; they are a **perennial** population



# Outline

## Constructing models

Dynamical models

Examples

A simple discrete-time model

**A simple continuous-time model**

## Units and scaling

## Key parameters

Discrete-time model

Continuous-time model

Links

## Growth and regulation

# Assumptions

- If we have  $N$  individuals at time  $t$ , how does the population change?

## Assumptions

- ▶ If we have  $N$  individuals at time  $t$ , how does the population change?
  - ▶ Individuals are giving birth at per-capita rate  $b$

## Assumptions

- ▶ If we have  $N$  individuals at time  $t$ , how does the population change?
  - ▶ Individuals are giving birth at per-capita rate  $b$
  - ▶ Individuals are dying at per-capita rate  $d$

# Assumptions

- ▶ If we have  $N$  individuals at time  $t$ , how does the population change?
  - ▶ Individuals are giving birth at per-capita rate  $b$
  - ▶ Individuals are dying at per-capita rate  $d$
- ▶ How we describe the population dynamics?

## Assumptions

- ▶ If we have  $N$  individuals at time  $t$ , how does the population change?
  - ▶ Individuals are giving birth at per-capita rate  $b$
  - ▶ Individuals are dying at per-capita rate  $d$
- ▶ How we describe the population dynamics?
  - ▶ \*

# Assumptions

- ▶ If we have  $N$  individuals at time  $t$ , how does the population change?
  - ▶ Individuals are giving birth at per-capita rate  $b$
  - ▶ Individuals are dying at per-capita rate  $d$
- ▶ How we describe the population dynamics?
  - ▶ \*  $\frac{dN}{dt} = (b - d)N$

# Assumptions

- ▶ If we have  $N$  individuals at time  $t$ , how does the population change?
  - ▶ Individuals are giving birth at per-capita rate  $b$
  - ▶ Individuals are dying at per-capita rate  $d$
- ▶ How we describe the population dynamics?
  - ▶ \*  $\frac{dN}{dt} = (b - d)N$
  - ▶ \*

# Assumptions

- ▶ If we have  $N$  individuals at time  $t$ , how does the population change?
  - ▶ Individuals are giving birth at per-capita rate  $b$
  - ▶ Individuals are dying at per-capita rate  $d$
- ▶ How we describe the population dynamics?
  - ▶ \*  $\frac{dN}{dt} = (b - d)N$
  - ▶ \* That's what calculus is *for* – describing instantaneous rates of change

# Assumptions

- ▶ If we have  $N$  individuals at time  $t$ , how does the population change?
  - ▶ Individuals are giving birth at per-capita rate  $b$
  - ▶ Individuals are dying at per-capita rate  $d$
- ▶ How we describe the population dynamics?
  - ▶ \*  $\frac{dN}{dt} = (b - d)N$
  - ▶ \* That's what calculus is *for* – describing instantaneous rates of change

## *Assumptions*

- ▶ Individuals are **independent**: what I do does not depend on how many other individuals are around

## *Assumptions*

- ▶ Individuals are **independent**: what I do does not depend on how many other individuals are around
- ▶ The population can be censused at any time

## *Assumptions*

- ▶ Individuals are **independent**: what I do does not depend on how many other individuals are around
- ▶ The population can be censused at any time
- ▶ Population size changes continuously

## *Assumptions*

- ▶ Individuals are **independent**: what I do does not depend on how many other individuals are around
- ▶ The population can be censused at any time
- ▶ Population size changes continuously
- ▶ All individuals are the same all the time

## *Assumptions*

- ▶ Individuals are **independent**: what I do does not depend on how many other individuals are around
- ▶ The population can be censused at any time
- ▶ Population size changes continuously
- ▶ All individuals are the same all the time

# Definitions

- $b$  is the **birth rate**

# Definitions

- ▶  $b$  is the **birth rate**
- ▶  $d$  is the **death rate**

## Definitions

- ▶  $b$  is the **birth rate**
- ▶  $d$  is the **death rate**
- ▶  $r \equiv b - d$  is the **instantaneous rate of increase**.

## Definitions

- ▶  $b$  is the **birth rate**
- ▶  $d$  is the **death rate**
- ▶  $r \equiv b - d$  is the **instantaneous rate of increase**.
- ▶ These quantities are not associated with a time period, but they have units:

## Definitions

- ▶  $b$  is the **birth rate**
- ▶  $d$  is the **death rate**
- ▶  $r \equiv b - d$  is the **instantaneous rate of increase**.
- ▶ These quantities are not associated with a time period, but they have units:
  - ▶ \*

## Definitions

- ▶  $b$  is the **birth rate**
- ▶  $d$  is the **death rate**
- ▶  $r \equiv b - d$  is the **instantaneous rate of increase**.
- ▶ These quantities are not associated with a time period, but they have units:
  - ▶ \*  $1/\text{[time]}$

## Definitions

- ▶  $b$  is the **birth rate**
- ▶  $d$  is the **death rate**
- ▶  $r \equiv b - d$  is the **instantaneous rate of increase**.
- ▶ These quantities are not associated with a time period, but they have units:
  - ▶ \*  $1/\text{[time]}$
  - ▶ \*

## Definitions

- ▶  $b$  is the **birth rate**
- ▶  $d$  is the **death rate**
- ▶  $r \equiv b - d$  is the **instantaneous rate of increase**.
- ▶ These quantities are not associated with a time period, but they have units:
  - ▶ \*  $1/\text{[time]}$
  - ▶ \*  $\equiv (\text{indiv}/\text{[time]}))/\text{indiv}$

## Definitions

- ▶  $b$  is the **birth rate**
- ▶  $d$  is the **death rate**
- ▶  $r \equiv b - d$  is the **instantaneous rate of increase**.
- ▶ These quantities are not associated with a time period, but they have units:
  - ▶ \*  $1/\text{[time]}$
  - ▶ \*  $\equiv (\text{indiv}/\text{[time]}))/\text{indiv}$

# Model

- ▶ Dynamics:

# Model

- ▶ Dynamics:

- ▶  $\frac{dN}{dt} = rN$

# Model

- ▶ Dynamics:

- ▶  $\frac{dN}{dt} = rN$

- ▶ Solution:

# Model

- ▶ Dynamics:

- ▶  $\frac{dN}{dt} = rN$

- ▶ Solution:

- ▶  $N(t) = N_0 \exp(rt)$

# Model

- ▶ Dynamics:

- ▶  $\frac{dN}{dt} = rN$

- ▶ Solution:

- ▶  $N(t) = N_0 \exp(rt)$

- ▶ Behaviour

# Model

- ▶ Dynamics:

- ▶  $\frac{dN}{dt} = rN$

- ▶ Solution:

- ▶  $N(t) = N_0 \exp(rt)$

- ▶ Behaviour

- ▶ \*

# Model

- ▶ Dynamics:
  - ▶  $\frac{dN}{dt} = rN$
- ▶ Solution:
  - ▶  $N(t) = N_0 \exp(rt)$
- ▶ Behaviour
  - ▶ \* Increases exponentially when  $r > 0$

# Model

- ▶ Dynamics:
  - ▶  $\frac{dN}{dt} = rN$
- ▶ Solution:
  - ▶  $N(t) = N_0 \exp(rt)$
- ▶ Behaviour
  - ▶ \* Increases exponentially when  $r > 0$
  - ▶ \*

# Model

- ▶ Dynamics:

- ▶ 
$$\frac{dN}{dt} = rN$$

- ▶ Solution:

- ▶ 
$$N(t) = N_0 \exp(rt)$$

- ▶ Behaviour

- ▶ \* Increases exponentially when  $r > 0$
- ▶ \* Decreases exponentially when  $r < 0$

# Model

- ▶ Dynamics:

- ▶ 
$$\frac{dN}{dt} = rN$$

- ▶ Solution:

- ▶ 
$$N(t) = N_0 \exp(rt)$$

- ▶ Behaviour

- ▶ \* Increases exponentially when  $r > 0$
- ▶ \* Decreases exponentially when  $r < 0$

# Bacteria

- ▶ Conceptually, this is just as simple as the dandelions or the moths

# Bacteria

- ▶ Conceptually, this is just as simple as the dandelions or the moths
  - ▶ In fact, simpler

# Bacteria

- ▶ Conceptually, this is just as simple as the dandelions or the moths
  - ▶ In fact, simpler
- ▶ But we can't do an infinite number of simulation steps on the computer

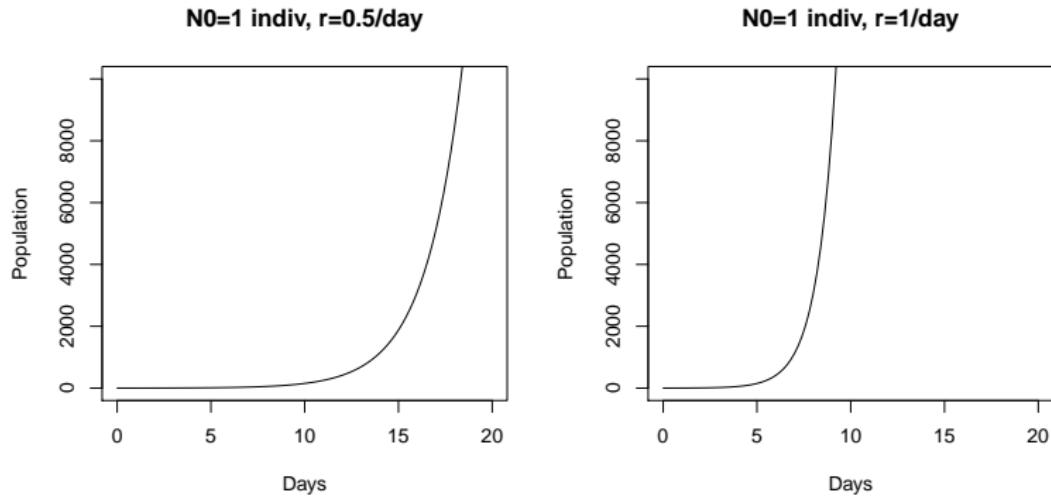
# Bacteria

- ▶ Conceptually, this is just as simple as the dandelions or the moths
  - ▶ In fact, simpler
- ▶ But we can't do an infinite number of simulation steps on the computer
  - ▶ We need fancier methods

# Bacteria

- ▶ Conceptually, this is just as simple as the dandelions or the moths
  - ▶ In fact, simpler
- ▶ But we can't do an infinite number of simulation steps on the computer
  - ▶ We need fancier methods

# Bacteria



# Summary

- We can construct simple, conceptual models and make them into dynamic models

# Summary

- ▶ We can construct simple, conceptual models and make them into dynamic models
- ▶ If we assume that *individuals* behave independently, then

# Summary

- ▶ We can construct simple, conceptual models and make them into dynamic models
- ▶ If we assume that *individuals* behave independently, then
  - ▶ we expect *populations* to grow (or decline) exponentially

# Summary

- ▶ We can construct simple, conceptual models and make them into dynamic models
- ▶ If we assume that *individuals* behave independently, then
  - ▶ we expect *populations* to grow (or decline) exponentially

# Outline

Constructing models

Dynamical models

Examples

A simple discrete-time model

A simple continuous-time model

## Units and scaling

Key parameters

Discrete-time model

Continuous-time model

Links

## Growth and regulation

# Units are our friends

- Keep track of units at all times



# Units are our friends

- ▶ Keep track of units at all times
- ▶ Use units to confirm that your answers make sense



# Units are our friends

- ▶ Keep track of units at all times
- ▶ Use units to confirm that your answers make sense
  - ▶ Or to find quick ways of getting the answer



# Units are our friends

- ▶ Keep track of units at all times
- ▶ Use units to confirm that your answers make sense
  - ▶ Or to find quick ways of getting the answer
- ▶ What is  $3 \text{ day} \cdot 4 \text{ espressos/day}$ ?



# Units are our friends

- ▶ Keep track of units at all times
- ▶ Use units to confirm that your answers make sense
  - ▶ Or to find quick ways of getting the answer
- ▶ What is  $3 \text{ day} \cdot 4 \text{ espressos/day}$ ?
  - ▶ \*



# Units are our friends

- ▶ Keep track of units at all times
- ▶ Use units to confirm that your answers make sense
  - ▶ Or to find quick ways of getting the answer
- ▶ What is  $3 \text{ day} \cdot 4 \text{ espressos/day}$ ?
  - ▶ \* [12 espressos](#)



# Units are our friends

- ▶ Keep track of units at all times
- ▶ Use units to confirm that your answers make sense
  - ▶ Or to find quick ways of getting the answer
- ▶ What is  $3 \text{ day} \cdot 4 \text{ espressos/day}$ ?
  - ▶ \* 12 espressos
- ▶ What is  $1 \text{ hr} \cdot 0.2 \text{ cm/day}$ ?



# Units are our friends

- ▶ Keep track of units at all times
- ▶ Use units to confirm that your answers make sense
  - ▶ Or to find quick ways of getting the answer
- ▶ What is  $3 \text{ day} \cdot 4 \text{ espressos/day}$ ?
  - ▶ \* 12 espressos
- ▶ What is  $1 \text{ hr} \cdot 0.2 \text{ cm/day}$ ?
  - ▶ \*



# Units are our friends

- ▶ Keep track of units at all times
- ▶ Use units to confirm that your answers make sense
  - ▶ Or to find quick ways of getting the answer
- ▶ What is  $3 \text{ day} \cdot 4 \text{ espressos/day}$ ?
  - ▶ \* 12 espressos
- ▶ What is  $1 \text{ hr} \cdot 0.2 \text{ cm/day}$ ?
  - ▶ \* 1 hr · 0.2 cm / day



# Units are our friends

- ▶ Keep track of units at all times
- ▶ Use units to confirm that your answers make sense
  - ▶ Or to find quick ways of getting the answer
- ▶ What is  $3 \text{ day} \cdot 4 \text{ espressos/day}$ ?
  - ▶ \* 12 espressos
- ▶ What is  $1 \text{ hr} \cdot 0.2 \text{ cm/day}$ ?
  - ▶ \* 1 hr · 0.2 cm / day
  - ▶ \*



# Units are our friends

- ▶ Keep track of units at all times
- ▶ Use units to confirm that your answers make sense
  - ▶ Or to find quick ways of getting the answer
- ▶ What is  $3 \text{ day} \cdot 4 \text{ espressos/day}$ ?
  - ▶ \*  $12 \text{ espressos}$
- ▶ What is  $1 \text{ hr} \cdot 0.2 \text{ cm/day}$ ?
  - ▶ \*  $1 \text{ hr} \cdot 0.2 \text{ cm/day}$
  - ▶ \*  $1 \text{ hr} \cdot 0.2 \text{ cm/day} \cdot \frac{1 \text{ day}}{24 \text{ hr}}$



# Units are our friends

- ▶ Keep track of units at all times
- ▶ Use units to confirm that your answers make sense
  - ▶ Or to find quick ways of getting the answer
- ▶ What is  $3 \text{ day} \cdot 4 \text{ espressos/day}$ ?
  - ▶ \* 12 espressos
- ▶ What is  $1 \text{ hr} \cdot 0.2 \text{ cm/day}$ ?
  - ▶ \*  $1 \text{ hr} \cdot 0.2 \text{ cm/day}$
  - ▶ \*  $1 \text{ hr} \cdot 0.2 \text{ cm/day} \cdot \frac{1 \text{ day}}{24 \text{ hr}}$
  - ▶ \*



# Units are our friends

- ▶ Keep track of units at all times
- ▶ Use units to confirm that your answers make sense
  - ▶ Or to find quick ways of getting the answer
- ▶ What is  $3 \text{ day} \cdot 4 \text{ espressos/day}$ ?
  - ▶ \* 12 espressos
- ▶ What is  $1 \text{ hr} \cdot 0.2 \text{ cm/day}$ ?
  - ▶ \*  $1 \text{ hr} \cdot 0.2 \text{ cm/day}$
  - ▶ \*  $1 \text{ hr} \cdot 0.2 \text{ cm/day} \cdot \frac{1 \text{ day}}{24 \text{ hr}}$
  - ▶ \* 0.0083 cm



# Units are our friends

- ▶ Keep track of units at all times
- ▶ Use units to confirm that your answers make sense
  - ▶ Or to find quick ways of getting the answer
- ▶ What is  $3 \text{ day} \cdot 4 \text{ espressos/day}$ ?
  - ▶ \* 12 espressos
- ▶ What is  $1 \text{ hr} \cdot 0.2 \text{ cm/day}$ ?
  - ▶ \*  $1 \text{ hr} \cdot 0.2 \text{ cm/day}$
  - ▶ \*  $1 \text{ hr} \cdot 0.2 \text{ cm/day} \cdot \frac{1 \text{ day}}{24 \text{ hr}}$
  - ▶ \* 0.0083 cm



# Manipulating units

- We can multiply quantities with different units by keeping track of the units



# Manipulating units

- ▶ We can multiply quantities with different units by keeping track of the units
- ▶ We *cannot* add quantities with different units (unless they can be converted to the same units)



# Manipulating units

- ▶ We can multiply quantities with different units by keeping track of the units
- ▶ We *cannot* add quantities with different units (unless they can be converted to the same units)
- ▶ Poll: How many seconds are there in a day?



# Manipulating units

- ▶ We can multiply quantities with different units by keeping track of the units
- ▶ We *cannot* add quantities with different units (unless they can be converted to the same units)
- ▶ Poll: How many seconds are there in a day?

▶ \*



# Manipulating units

- ▶ We can multiply quantities with different units by keeping track of the units
- ▶ We *cannot* add quantities with different units (unless they can be converted to the same units)
- ▶ Poll: How many seconds are there in a day?
  - ▶ \*  $\frac{60 \text{ sec}}{\text{min}} \cdot \frac{60 \text{ min}}{\text{hr}} \cdot \frac{24 \text{ hr}}{\text{day}}$



# Manipulating units

- ▶ We can multiply quantities with different units by keeping track of the units
- ▶ We *cannot* add quantities with different units (unless they can be converted to the same units)
- ▶ Poll: How many seconds are there in a day?

- ▶ \*  $\frac{60 \text{ sec}}{\text{min}} \cdot \frac{60 \text{ min}}{\text{hr}} \cdot \frac{24 \text{ hr}}{\text{day}}$

- ▶ \*



# Manipulating units

- ▶ We can multiply quantities with different units by keeping track of the units
- ▶ We *cannot* add quantities with different units (unless they can be converted to the same units)
- ▶ Poll: How many seconds are there in a day?
  - ▶ \*  $\frac{60 \text{ sec}}{\text{min}} \cdot \frac{60 \text{ min}}{\text{hr}} \cdot \frac{24 \text{ hr}}{\text{day}}$
  - ▶ \*  $86400 \text{ sec/day}$



# Manipulating units

- ▶ We can multiply quantities with different units by keeping track of the units
- ▶ We *cannot* add quantities with different units (unless they can be converted to the same units)
- ▶ Poll: How many seconds are there in a day?
  - ▶ \*  $\frac{60 \text{ sec}}{\text{min}} \cdot \frac{60 \text{ min}}{\text{hr}} \cdot \frac{24 \text{ hr}}{\text{day}}$
  - ▶ \*  $86400 \text{ sec/day}$



# Scaling

- Quantities with units set scales, which can be changed

# Scaling

- ▶ Quantities with units set scales, which can be changed
  - ▶ If I multiply all the quantities with units of time in my model by 10, I should get an answer that looks the same, but with a different time scale

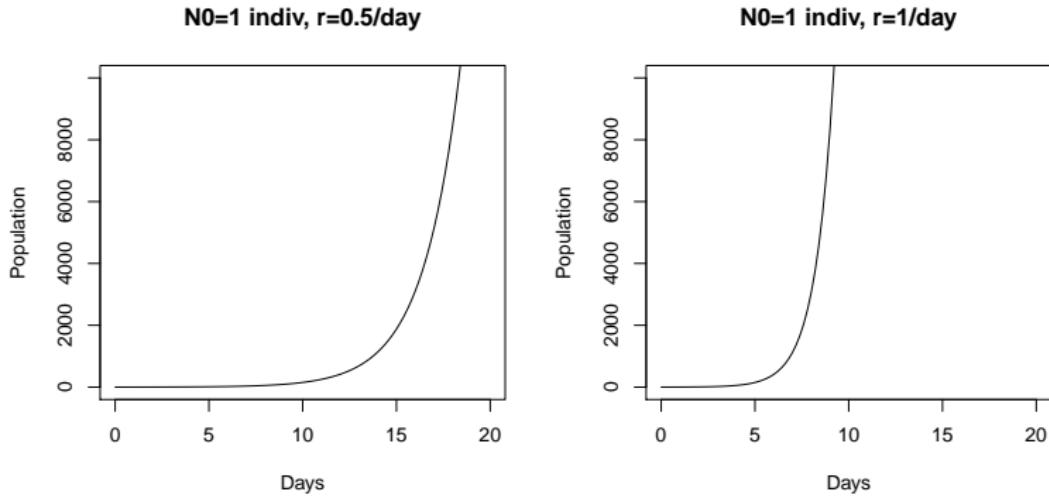
# Scaling

- ▶ Quantities with units set scales, which can be changed
  - ▶ If I multiply all the quantities with units of time in my model by 10, I should get an answer that looks the same, but with a different time scale
  - ▶ If I multiply all the quantities with units of dandelions in my model by 10, I should get an answer that looks the same, but with a different number of dandelions

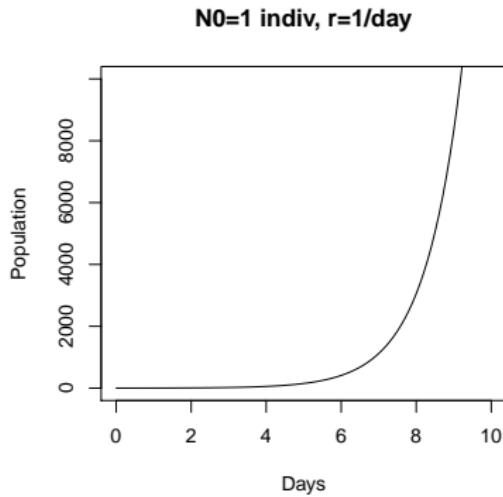
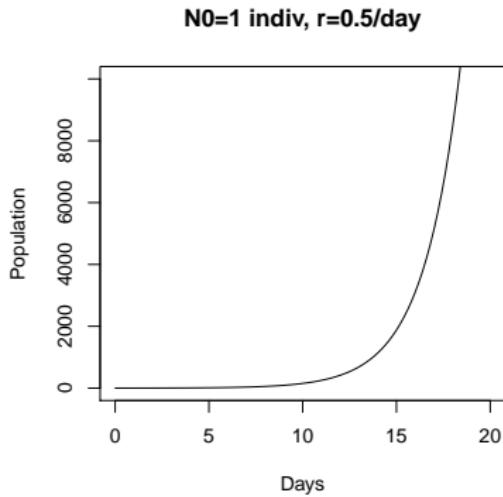
# Scaling

- ▶ Quantities with units set scales, which can be changed
  - ▶ If I multiply all the quantities with units of time in my model by 10, I should get an answer that looks the same, but with a different time scale
  - ▶ If I multiply all the quantities with units of dandelions in my model by 10, I should get an answer that looks the same, but with a different number of dandelions

# Scaling time in bacteria

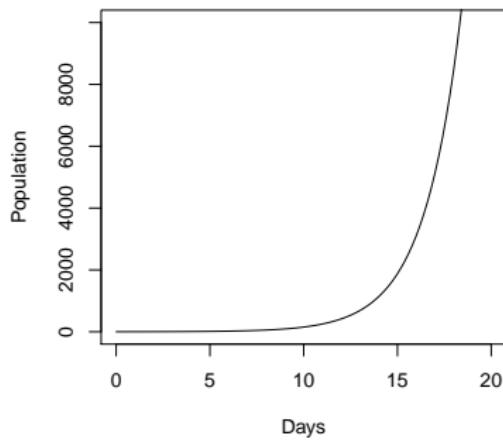


# Scaling time in bacteria

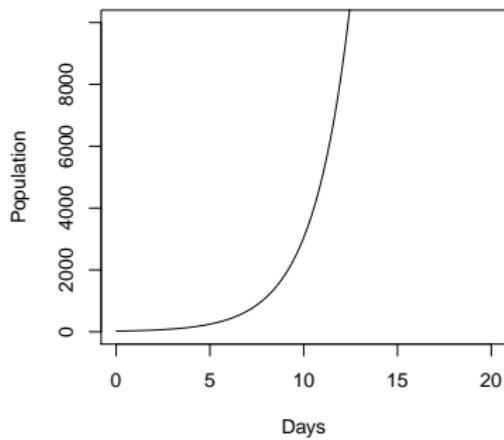


## Scaling population

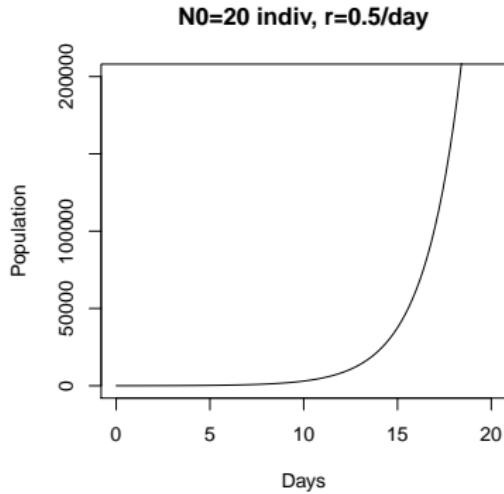
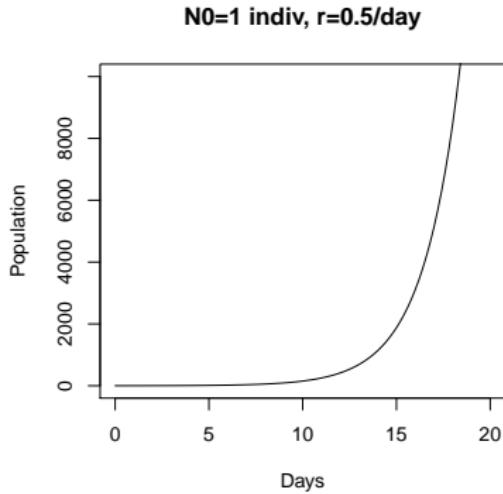
$N_0=1$  indiv,  $r=0.5/\text{day}$



$N_0=20$  indiv,  $r=0.5/\text{day}$



## Scaling population



# Thinking about units

- ▶ Poll: What is  $10^3$  day?

# Thinking about units

- ▶ Poll: What is  $10^3$  day?
- ▶ \*

# Thinking about units

- ▶ Poll: What is  $10^3$  day?
- ▶ \*

# Thinking about units

- ▶ Poll: What is  $10^3$  day?

- ▶ \*

- ▶ What is  $10^{72}$  hr?

# Thinking about units

- ▶ Poll: What is  $10^3$  day?
- ▶ \*
  
- ▶ What is  $10^{72}$  hr?
- ▶ \*

# Thinking about units

- ▶ Poll: What is  $10^3$  day?
- ▶ \*
  
- ▶ What is  $10^{72}$  hr?
- ▶ \* Nonsense! 72 hr means *exactly* the same thing as 3 day – there is no way to resolve this to make sense.

# Thinking about units

- ▶ Poll: What is  $10^3$  day?
  - ▶ \*
- ▶ What is  $10^{72}$  hr?
  - ▶ \* Nonsense! 72 hr means *exactly* the same thing as 3 day – there is no way to resolve this to make sense.
- ▶ What is 3 day · 3 day?

# Thinking about units

- ▶ Poll: What is  $10^3$  day?
  - ▶ \*
- ▶ What is  $10^{72}$  hr?
  - ▶ \* Nonsense! 72 hr means *exactly* the same thing as 3 day – there is no way to resolve this to make sense.
- ▶ What is 3 day · 3 day?
  - ▶ \*

# Thinking about units

- ▶ Poll: What is  $10^3$  day?
  - ▶ \*
- ▶ What is  $10^{72}$  hr?
  - ▶ \* Nonsense! 72 hr means *exactly* the same thing as 3 day – there is no way to resolve this to make sense.
- ▶ What is 3 day · 3 day?
  - ▶ \*  $9 \text{ day}^2$  – this *could* make sense, but it's probably wrong

# Thinking about units

- ▶ Poll: What is  $10^3$  day?
  - ▶ \*
- ▶ What is  $10^{72}$  hr?
  - ▶ \* Nonsense! 72 hr means *exactly* the same thing as 3 day – there is no way to resolve this to make sense.
- ▶ What is 3 day · 3 day?
  - ▶ \*  $9 \text{ day}^2$  – this *could* make sense, but it's probably wrong
  - ▶ \*

# Thinking about units

- ▶ Poll: What is  $10^3$  day?
  - ▶ \*
- ▶ What is  $10^{72}$  hr?
  - ▶ \* Nonsense! 72 hr means *exactly* the same thing as 3 day – there is no way to resolve this to make sense.
- ▶ What is 3 day · 3 day?
  - ▶ \*  $9 \text{ day}^2$  – this *could* make sense, but it's probably wrong
  - ▶ \* ... very different from 9 day.

# Thinking about units

- ▶ Poll: What is  $10^3$  day?
  - ▶ \*
- ▶ What is  $10^{72}$  hr?
  - ▶ \* Nonsense! 72 hr means *exactly* the same thing as 3 day – there is no way to resolve this to make sense.
- ▶ What is 3 day · 3 day?
  - ▶ \*  $9 \text{ day}^2$  – this *could* make sense, but it's probably wrong
  - ▶ \* ... very different from 9 day.

# Unit-ed quantities

- Quantities with units *scale*

# Unit-ed quantities

- ▶ Quantities with units *scale*
  - ▶ If you change everything with the same units by the same factor, you should not change the behaviour of your system

# Unit-ed quantities

- ▶ Quantities with units *scale*
  - ▶ If you change everything with the same units by the same factor, you should not change the behaviour of your system
- ▶ We typically make sense of quantities with units by comparing them to other quantities with the same units, e.g.:

# Unit-ed quantities

- ▶ Quantities with units *scale*
  - ▶ If you change everything with the same units by the same factor, you should not change the behaviour of your system
- ▶ We typically make sense of quantities with units by comparing them to other quantities with the same units, e.g.:
  - ▶ birth rate vs. death rate

# Unit-ed quantities

- ▶ Quantities with units *scale*
  - ▶ If you change everything with the same units by the same factor, you should not change the behaviour of your system
- ▶ We typically make sense of quantities with units by comparing them to other quantities with the same units, e.g.:
  - ▶ birth rate vs. death rate
  - ▶ characteristic time of exponential growth vs. observation time

# Unit-ed quantities

- ▶ Quantities with units *scale*
  - ▶ If you change everything with the same units by the same factor, you should not change the behaviour of your system
- ▶ We typically make sense of quantities with units by comparing them to other quantities with the same units, e.g.:
  - ▶ birth rate vs. death rate
  - ▶ characteristic time of exponential growth vs. observation time

# Unitless quantities

- Quantities in exponents must be unitless

## Unitless quantities

- ▶ Quantities in exponents must be unitless
- ▶ Quantities with variable exponents (quantities that can be multiplied by themselves over and over) must be unitless

## Unitless quantities

- ▶ Quantities in exponents must be unitless
- ▶ Quantities with variable exponents (quantities that can be multiplied by themselves over and over) must be unitless
- ▶ Quantities that determine *how* a system behaves must have a unitless form

## Unitless quantities

- ▶ Quantities in exponents must be unitless
- ▶ Quantities with variable exponents (quantities that can be multiplied by themselves over and over) must be unitless
- ▶ Quantities that determine *how* a system behaves must have a unitless form
  - ▶ Otherwise, they could be scaled

# Unitless quantities

- ▶ Quantities in exponents must be unitless
- ▶ Quantities with variable exponents (quantities that can be multiplied by themselves over and over) must be unitless
- ▶ Quantities that determine *how* a system behaves must have a unitless form
  - ▶ Otherwise, they could be scaled
  - ▶ Zero works as a unitless quantity:

# Unitless quantities

- ▶ Quantities in exponents must be unitless
- ▶ Quantities with variable exponents (quantities that can be multiplied by themselves over and over) must be unitless
- ▶ Quantities that determine *how* a system behaves must have a unitless form
  - ▶ Otherwise, they could be scaled
  - ▶ Zero works as a unitless quantity:
    - ▶  $0\text{km} = 0\text{cm}$

# Unitless quantities

- ▶ Quantities in exponents must be unitless
- ▶ Quantities with variable exponents (quantities that can be multiplied by themselves over and over) must be unitless
- ▶ Quantities that determine *how* a system behaves must have a unitless form
  - ▶ Otherwise, they could be scaled
  - ▶ Zero works as a unitless quantity:
    - ▶  $0\text{km} = 0\text{cm}$
- ▶ What unitless quantities have we already talked about?

# Unitless quantities

- ▶ Quantities in exponents must be unitless
- ▶ Quantities with variable exponents (quantities that can be multiplied by themselves over and over) must be unitless
- ▶ Quantities that determine *how* a system behaves must have a unitless form
  - ▶ Otherwise, they could be scaled
  - ▶ Zero works as a unitless quantity:
    - ▶  $0\text{km} = 0\text{cm}$
- ▶ What unitless quantities have we already talked about?
  - ▶ \*

# Unitless quantities

- ▶ Quantities in exponents must be unitless
- ▶ Quantities with variable exponents (quantities that can be multiplied by themselves over and over) must be unitless
- ▶ Quantities that determine *how* a system behaves must have a unitless form
  - ▶ Otherwise, they could be scaled
  - ▶ Zero works as a unitless quantity:
    - ▶  $0\text{km} = 0\text{cm}$
- ▶ What unitless quantities have we already talked about?
  - ▶ \*  $\lambda$ ,  $f$  and  $p$ .

# Unitless quantities

- ▶ Quantities in exponents must be unitless
- ▶ Quantities with variable exponents (quantities that can be multiplied by themselves over and over) must be unitless
- ▶ Quantities that determine *how* a system behaves must have a unitless form
  - ▶ Otherwise, they could be scaled
  - ▶ Zero works as a unitless quantity:
    - ▶  $0\text{km} = 0\text{cm}$
- ▶ What unitless quantities have we already talked about?
  - ▶ \*  $\lambda$ ,  $f$  and  $p$ .

## *Moth calculation (repeat)*

- Researchers studying a gypsy moth population make the following estimates:

## *Moth calculation (repeat)*

- ▶ Researchers studying a gypsy moth population make the following estimates:
  - ▶ The average reproductive female lays 600 eggs

## *Moth calculation (repeat)*

- ▶ Researchers studying a gypsy moth population make the following estimates:
  - ▶ The average reproductive female lays 600 eggs
  - ▶ 10% of eggs hatch into larvae

## *Moth calculation (repeat)*

- ▶ Researchers studying a gypsy moth population make the following estimates:
  - ▶ The average reproductive female lays 600 eggs
  - ▶ 10% of eggs hatch into larvae
  - ▶ **10% of larvae mature into pupae**

## *Moth calculation (repeat)*

- ▶ Researchers studying a gypsy moth population make the following estimates:
  - ▶ The average reproductive female lays 600 eggs
  - ▶ 10% of eggs hatch into larvae
  - ▶ 10% of larvae mature into pupae
  - ▶ 50% of pupae mature into adults

## *Moth calculation (repeat)*

- ▶ Researchers studying a gypsy moth population make the following estimates:
  - ▶ The average reproductive female lays 600 eggs
  - ▶ 10% of eggs hatch into larvae
  - ▶ 10% of larvae mature into pupae
  - ▶ 50% of pupae mature into adults
  - ▶ **50% of adults survive to reproduce**

## *Moth calculation (repeat)*

- ▶ Researchers studying a gypsy moth population make the following estimates:
  - ▶ The average reproductive female lays 600 eggs
  - ▶ 10% of eggs hatch into larvae
  - ▶ 10% of larvae mature into pupae
  - ▶ 50% of pupae mature into adults
  - ▶ 50% of adults survive to reproduce
  - ▶ All adults die after reproduction

## *Moth calculation (repeat)*

- ▶ Researchers studying a gypsy moth population make the following estimates:
  - ▶ The average reproductive female lays 600 eggs
  - ▶ 10% of eggs hatch into larvae
  - ▶ 10% of larvae mature into pupae
  - ▶ 50% of pupae mature into adults
  - ▶ 50% of adults survive to reproduce
  - ▶ All adults die after reproduction

# Moths

- 600 egg/ rF

## Moths

- ▶ 600 egg/ rF
- ▶ .0.1 larva/ egg

# Moths

- ▶ 600 egg/ rF
- ▶ ·0.1 larva/ egg
- ▶ ·0.1 pupa/ larva

# Moths

- ▶ 600 egg/ rF
- ▶ ·0.1 larva/ egg
- ▶ ·0.1 pupa/ larva
- ▶ ·0.5 A/ pupa

## Moths

- ▶ 600 egg/ rF
- ▶ ·0.1 larva/ egg
- ▶ ·0.1 pupa/ larva
- ▶ ·0.5 A/ pupa
- ▶ ·0.5 rA/ A

# Moths

- ▶ 600 egg/ rF
- ▶ ·0.1 larva/ egg
- ▶ ·0.1 pupa/ larva
- ▶ ·0.5 A/ pupa
- ▶ ·0.5 rA/ A
- ▶ Poll: What's the product?

# Moths

- ▶ 600 egg/ rF
- ▶ ·0.1 larva/ egg
- ▶ ·0.1 pupa/ larva
- ▶ ·0.5 A/ pupa
- ▶ ·0.5 rA/ A
- ▶ Poll: What's the product?
  - ▶ \*

## Moths

- ▶ 600 egg/ rF
- ▶ ·0.1 larva/ egg
- ▶ ·0.1 pupa/ larva
- ▶ ·0.5 A/ pupa
- ▶ ·0.5 rA/ A
- ▶ Poll: What's the product?
  - ▶ \* 1.5 rA/ rF

# Moths

- ▶ 600 egg/ rF
- ▶ ·0.1 larva/ egg
- ▶ ·0.1 pupa/ larva
- ▶ ·0.5 A/ pupa
- ▶ ·0.5 rA/ A
- ▶ Poll: What's the product?
  - ▶ \* 1.5 rA/ rF
  - ▶ \*

# Moths

- ▶ 600 egg/ rF
- ▶ ·0.1 larva/ egg
- ▶ ·0.1 pupa/ larva
- ▶ ·0.5 A/ pupa
- ▶ ·0.5 rA/ A
- ▶ Poll: What's the product?
  - ▶ \* 1.5 rA/ rF
  - ▶ \* Not enough information to make a prediction!

# Moths

- ▶ 600 egg/ rF
- ▶ ·0.1 larva/ egg
- ▶ ·0.1 pupa/ larva
- ▶ ·0.5 A/ pupa
- ▶ ·0.5 rA/ A
- ▶ Poll: What's the product?
  - ▶ \* 1.5 rA/ rF
  - ▶ \* Not enough information to make a prediction!
  - ▶ \*

## Moths

- ▶ 600 egg/ rF
- ▶ ·0.1 larva/ egg
- ▶ ·0.1 pupa/ larva
- ▶ ·0.5 A/ pupa
- ▶ ·0.5 rA/ A
- ▶ Poll: What's the product?
  - ▶ \* 1.5 rA/ rF
  - ▶ \* Not enough information to make a prediction!
  - ▶ \* Need to multiply by something with units rF/rA to close the loop

# Moths

- ▶ 600 egg/ rF
- ▶ ·0.1 larva/ egg
- ▶ ·0.1 pupa/ larva
- ▶ ·0.5 A/ pupa
- ▶ ·0.5 rA/ A
- ▶ Poll: What's the product?
  - ▶ \*  $1.5 \text{ rA} / \text{rF}$
  - ▶ \* Not enough information to make a prediction!
  - ▶ \* Need to multiply by something with units  $\text{rF}/\text{rA}$  to close the loop

## Closing the loop

- Once we close the loop, it doesn't matter where we start:

## Closing the loop

- ▶ Once we close the loop, it doesn't matter where we start:
  - ▶ Reproductive adults to reproductive adults

## Closing the loop

- ▶ Once we close the loop, it doesn't matter where we start:
  - ▶ Reproductive adults to reproductive adults
  - ▶ **Larvae to larvae**

## Closing the loop

- ▶ Once we close the loop, it doesn't matter where we start:
  - ▶ Reproductive adults to reproductive adults
  - ▶ Larvae to larvae
  - ▶ Pupae to pupae is common in real studies

## Closing the loop

- ▶ Once we close the loop, it doesn't matter where we start:
  - ▶ Reproductive adults to reproductive adults
  - ▶ Larvae to larvae
  - ▶ Pupae to pupae is common in real studies
    - ▶ \*

## Closing the loop

- ▶ Once we close the loop, it doesn't matter where we start:
  - ▶ Reproductive adults to reproductive adults
  - ▶ Larvae to larvae
  - ▶ Pupae to pupae is common in real studies
    - ▶ \* **Pupae are easy to count**

## Closing the loop

- ▶ Once we close the loop, it doesn't matter where we start:
  - ▶ Reproductive adults to reproductive adults
  - ▶ Larvae to larvae
  - ▶ Pupae to pupae is common in real studies
    - ▶ \* Pupae are easy to count
- ▶ If we don't close the loop, we can't correctly move from step to step

## Closing the loop

- ▶ Once we close the loop, it doesn't matter where we start:
  - ▶ Reproductive adults to reproductive adults
  - ▶ Larvae to larvae
  - ▶ Pupae to pupae is common in real studies
    - ▶ \* **Pupae are easy to count**
- ▶ If we don't close the loop, we can't correctly move from step to step

# Calculating $\lambda$

- $\lambda \equiv p + f$  is the **finite rate of increase**

# Calculating $\lambda$

- ▶  $\lambda \equiv p + f$  is the **finite rate of increase**
- ▶ If  $N_{T+1} = \lambda N_T$ , what are the units of  $\lambda$ ?

# Calculating $\lambda$

- ▶  $\lambda \equiv p + f$  is the **finite rate of increase**
- ▶ If  $N_{T+1} = \lambda N_T$ , what are the units of  $\lambda$ ?
  - ▶ \*

# Calculating $\lambda$

- ▶  $\lambda \equiv p + f$  is the **finite rate of increase**
- ▶ If  $N_{T+1} = \lambda N_T$ , what are the units of  $\lambda$ ?
  - ▶ \* We multiply by  $\lambda$  over and over

# Calculating $\lambda$

- ▶  $\lambda \equiv p + f$  is the **finite rate of increase**
- ▶ If  $N_{T+1} = \lambda N_T$ , what are the units of  $\lambda$ ?
  - ▶ \* We multiply by  $\lambda$  over and over
  - ▶ \*

# Calculating $\lambda$

- ▶  $\lambda \equiv p + f$  is the **finite rate of increase**
- ▶ If  $N_{T+1} = \lambda N_T$ , what are the units of  $\lambda$ ?
  - ▶ \* We multiply by  $\lambda$  over and over
  - ▶ \* Therefore  $\lambda$  must be unitless

# Calculating $\lambda$

- ▶  $\lambda \equiv p + f$  is the **finite rate of increase**
- ▶ If  $N_{T+1} = \lambda N_T$ , what are the units of  $\lambda$ ?
  - ▶ \* We multiply by  $\lambda$  over and over
  - ▶ \* Therefore  $\lambda$  must be unitless
- ▶ Therefore  $p$  and  $f$  must be unitless

# Calculating $\lambda$

- ▶  $\lambda \equiv p + f$  is the **finite rate of increase**
- ▶ If  $N_{T+1} = \lambda N_T$ , what are the units of  $\lambda$ ?
  - ▶ \* We multiply by  $\lambda$  over and over
  - ▶ \* Therefore  $\lambda$  must be unitless
- ▶ Therefore  $p$  and  $f$  must be unitless
  - ▶ example, rA/rA; seed/seed

# Calculating $\lambda$

- ▶  $\lambda \equiv p + f$  is the **finite rate of increase**
- ▶ If  $N_{T+1} = \lambda N_T$ , what are the units of  $\lambda$ ?
  - ▶ \* We multiply by  $\lambda$  over and over
  - ▶ \* Therefore  $\lambda$  must be unitless
- ▶ Therefore  $p$  and  $f$  must be unitless
  - ▶ example, rA/rA; seed/seed
  - ▶ to do it right, we close the loop

# Calculating $\lambda$

- ▶  $\lambda \equiv p + f$  is the **finite rate of increase**
- ▶ If  $N_{T+1} = \lambda N_T$ , what are the units of  $\lambda$ ?
  - ▶ \* We multiply by  $\lambda$  over and over
  - ▶ \* Therefore  $\lambda$  must be unitless
- ▶ Therefore  $p$  and  $f$  must be unitless
  - ▶ example, rA/rA; seed/seed
  - ▶ to do it right, we close the loop

# Outline

Constructing models

Dynamical models

Examples

A simple discrete-time model

A simple continuous-time model

Units and scaling

Key parameters

Discrete-time model

Continuous-time model

Links

Growth and regulation

# Outline

Constructing models

Dynamical models

Examples

A simple discrete-time model

A simple continuous-time model

Units and scaling

**Key parameters**

Discrete-time model

Continuous-time model

Links

Growth and regulation

## Discrete-time model

►  $N_{T+1} = \lambda N_T$

## Discrete-time model

- ▶  $N_{T+1} = \lambda N_T$
- ▶  $\lambda \equiv p + f$

## Discrete-time model

- ▶  $N_{T+1} = \lambda N_T$
- ▶  $\lambda \equiv p + f$

# Calculating fecundity

- Fecundity  $f$  in our model must be unitless

# Calculating fecundity

- ▶ Fecundity  $f$  in our model must be unitless
- ▶ Multiply:

# Calculating fecundity

- ▶ Fecundity  $f$  in our model must be unitless
- ▶ Multiply:
  - ▶ Probability of surviving from census to reproduction

## Calculating fecundity

- ▶ Fecundity  $f$  in our model must be unitless
- ▶ Multiply:
  - ▶ Probability of surviving from census to reproduction
  - ▶ Expected number of offspring when reproducing (maternity)

## Calculating fecundity

- ▶ Fecundity  $f$  in our model must be unitless
- ▶ Multiply:
  - ▶ Probability of surviving from census to reproduction
  - ▶ Expected number of offspring when reproducing (maternity)
  - ▶ **Probability of offspring surviving to census**

# Calculating fecundity

- ▶ Fecundity  $f$  in our model must be unitless
- ▶ Multiply:
  - ▶ Probability of surviving from census to reproduction
  - ▶ Expected number of offspring when reproducing (maternity)
  - ▶ Probability of offspring surviving to census
- ▶ Need to end where we started

# Calculating fecundity

- ▶ Fecundity  $f$  in our model must be unitless
- ▶ Multiply:
  - ▶ Probability of surviving from census to reproduction
  - ▶ Expected number of offspring when reproducing (maternity)
  - ▶ Probability of offspring surviving to census
- ▶ Need to end where we started
- ▶ Diagram

# Calculating fecundity

- ▶ Fecundity  $f$  in our model must be unitless
- ▶ Multiply:
  - ▶ Probability of surviving from census to reproduction
  - ▶ Expected number of offspring when reproducing (maternity)
  - ▶ Probability of offspring surviving to census
- ▶ Need to end where we started
- ▶ Diagram

# Calculating survival

- Survival  $p$  must be unitless

# Calculating survival

- ▶ Survival  $p$  must be unitless
- ▶ Multiply:

# Calculating survival

- ▶ Survival  $p$  must be unitless
- ▶ Multiply:
  - ▶ Probability of surviving from census to reproduction

# Calculating survival

- ▶ Survival  $p$  must be unitless
- ▶ Multiply:
  - ▶ Probability of surviving from census to reproduction
  - ▶ Probability of surviving the reproduction period

# Calculating survival

- ▶ Survival  $p$  must be unitless
- ▶ Multiply:
  - ▶ Probability of surviving from census to reproduction
  - ▶ Probability of surviving the reproduction period
  - ▶ Probability of surviving until the next census

## Calculating survival

- ▶ Survival  $p$  must be unitless
- ▶ Multiply:
  - ▶ Probability of surviving from census to reproduction
  - ▶ Probability of surviving the reproduction period
  - ▶ Probability of surviving until the next census

## Finite rate of increase

- ▶ Population increases when  $\lambda > 1$

## Finite rate of increase

- ▶ Population increases when  $\lambda > 1$
- ▶ So  $\lambda$  must be unitless

## Finite rate of increase

- ▶ Population increases when  $\lambda > 1$
- ▶ So  $\lambda$  must be unitless
- ▶ But it is *associated with* the time step  $\Delta t$

## Finite rate of increase

- ▶ Population increases when  $\lambda > 1$
- ▶ So  $\lambda$  must be unitless
- ▶ But it is *associated with* the time step  $\Delta t$ 
  - ▶ This means it is potentially confusing. It is often better to use  $\mathcal{R}$  or  $r$  (see below).

## Finite rate of increase

- ▶ Population increases when  $\lambda > 1$
- ▶ So  $\lambda$  must be unitless
- ▶ But it is *associated with* the time step  $\Delta t$ 
  - ▶ This means it is potentially confusing. It is often better to use  $\mathcal{R}$  or  $r$  (see below).

# Reproductive number

- The reproductive number  $\mathcal{R}$  measures the average number of offspring produced by a single individual over the course of its lifetime

# Reproductive number

- ▶ The reproductive number  $\mathcal{R}$  measures the average number of offspring produced by a single individual over the course of its lifetime
- ▶ Poll: The population will increase when  $\mathcal{R} \dots$ :

## Reproductive number

- ▶ The reproductive number  $\mathcal{R}$  measures the average number of offspring produced by a single individual over the course of its lifetime
- ▶ Poll: The population will increase when  $\mathcal{R} \dots$ :
  - ▶ \*

## Reproductive number

- ▶ The reproductive number  $\mathcal{R}$  measures the average number of offspring produced by a single individual over the course of its lifetime
- ▶ Poll: The population will increase when  $\mathcal{R} \dots$ :
  - ▶ \*  $\mathcal{R} > 1$

## Reproductive number

- ▶ The reproductive number  $\mathcal{R}$  measures the average number of offspring produced by a single individual over the course of its lifetime
- ▶ Poll: The population will increase when  $\mathcal{R} \dots$ :
  - ▶ \*  $\mathcal{R} > 1$
- ▶ Poll: What are the units of  $\mathcal{R}$ ?

# Reproductive number

- ▶ The reproductive number  $\mathcal{R}$  measures the average number of offspring produced by a single individual over the course of its lifetime
- ▶ Poll: The population will increase when  $\mathcal{R} \dots$ :
  - ▶ \*  $\mathcal{R} > 1$
- ▶ Poll: What are the units of  $\mathcal{R}$ ?
  - ▶ \*

## Reproductive number

- ▶ The reproductive number  $\mathcal{R}$  measures the average number of offspring produced by a single individual over the course of its lifetime
- ▶ Poll: The population will increase when  $\mathcal{R} \dots$ :
  - ▶ \*  $\mathcal{R} > 1$
- ▶ Poll: What are the units of  $\mathcal{R}$ ?
  - ▶ \*  $\mathcal{R}$  must be unitless

## Reproductive number

- ▶ The reproductive number  $\mathcal{R}$  measures the average number of offspring produced by a single individual over the course of its lifetime
- ▶ Poll: The population will increase when  $\mathcal{R} \dots$ :
  - ▶ \*  $\mathcal{R} > 1$
- ▶ Poll: What are the units of  $\mathcal{R}$ ?
  - ▶ \*  $\mathcal{R}$  must be unitless

# Lifespan

- In this model world, how long do individuals live, on average in this model?

# Lifespan

- ▶ In this model world, how long do individuals live, on average in this model?
- ▶ If  $p$  is the proportion of individuals that survive, then the proportion that die is:

# Lifespan

- ▶ In this model world, how long do individuals live, on average in this model?
- ▶ If  $p$  is the proportion of individuals that survive, then the proportion that die is:
  - ▶ \*

## Lifespan

- ▶ In this model world, how long do individuals live, on average in this model?
- ▶ If  $p$  is the proportion of individuals that survive, then the proportion that die is:
  - ▶ \*  $\mu = 1 - p$

## Lifespan

- ▶ In this model world, how long do individuals live, on average in this model?
- ▶ If  $p$  is the proportion of individuals that survive, then the proportion that die is:
  - ▶ \*  $\mu = 1 - p$
- ▶ How many time steps do you expect to survive, on average?

## Lifespan

- ▶ In this model world, how long do individuals live, on average in this model?
- ▶ If  $p$  is the proportion of individuals that survive, then the proportion that die is:
  - ▶ \*  $\mu = 1 - p$
- ▶ How many time steps do you expect to survive, on average?
  - ▶ \*

## Lifespan

- ▶ In this model world, how long do individuals live, on average in this model?
- ▶ If  $p$  is the proportion of individuals that survive, then the proportion that die is:
  - ▶ \*  $\mu = 1 - p$
- ▶ How many time steps do you expect to survive, on average?
  - ▶ \*  $1/\mu$

# Lifespan

- ▶ In this model world, how long do individuals live, on average in this model?
- ▶ If  $p$  is the proportion of individuals that survive, then the proportion that die is:
  - ▶ \*  $\mu = 1 - p$
- ▶ How many time steps do you expect to survive, on average?
  - ▶ \*  $1/\mu$
  - ▶ \*

## Lifespan

- ▶ In this model world, how long do individuals live, on average in this model?
- ▶ If  $p$  is the proportion of individuals that survive, then the proportion that die is:
  - ▶ \*  $\mu = 1 - p$
- ▶ How many time steps do you expect to survive, on average?
  - ▶ \*  $1/\mu$
  - ▶ \* Roughly makes sense, and is also right

# Lifespan

- ▶ In this model world, how long do individuals live, on average in this model?
- ▶ If  $p$  is the proportion of individuals that survive, then the proportion that die is:
  - ▶ \*  $\mu = 1 - p$
- ▶ How many time steps do you expect to survive, on average?
  - ▶ \*  $1/\mu$
  - ▶ \* Roughly makes sense, and is also right
  - ▶ \*

# Lifespan

- ▶ In this model world, how long do individuals live, on average in this model?
- ▶ If  $p$  is the proportion of individuals that survive, then the proportion that die is:
  - ▶ \*  $\mu = 1 - p$
- ▶ How many time steps do you expect to survive, on average?
  - ▶ \*  $1/\mu$
  - ▶ \* Roughly makes sense, and is also right
  - ▶ \* Average lifetime is  $1/\mu * \Delta t$

# Lifespan

- ▶ In this model world, how long do individuals live, on average in this model?
- ▶ If  $p$  is the proportion of individuals that survive, then the proportion that die is:
  - ▶ \*  $\mu = 1 - p$
- ▶ How many time steps do you expect to survive, on average?
  - ▶ \*  $1/\mu$
  - ▶ \* Roughly makes sense, and is also right
  - ▶ \* Average lifetime is  $1/\mu * \Delta t$

# Calculating $\mathcal{R}$

- $\mathcal{R}$  is fecundity multiplied by lifespan

# Calculating $\mathcal{R}$

- ▶  $\mathcal{R}$  is fecundity multiplied by lifespan
- ▶  $\mathcal{R} = f/\mu = f/(1 - p)$

# Calculating $\mathcal{R}$

- ▶  $\mathcal{R}$  is fecundity multiplied by lifespan
- ▶  $\mathcal{R} = f/\mu = f/(1 - p)$
- ▶ Why do we multiply by time *steps* instead of lifetime?

# Calculating $\mathcal{R}$

- ▶  $\mathcal{R}$  is fecundity multiplied by lifespan
- ▶  $\mathcal{R} = f/\mu = f/(1 - p)$
- ▶ Why do we multiply by time *steps* instead of lifetime?
  - ▶ \*

# Calculating $\mathcal{R}$

- ▶  $\mathcal{R}$  is fecundity multiplied by lifespan
- ▶  $\mathcal{R} = f/\mu = f/(1 - p)$
- ▶ Why do we multiply by time *steps* instead of lifetime?
  - ▶ \* Because  $f$  is also measured per time step

# Calculating $\mathcal{R}$

- ▶  $\mathcal{R}$  is fecundity multiplied by lifespan
- ▶  $\mathcal{R} = f/\mu = f/(1 - p)$
- ▶ Why do we multiply by time *steps* instead of lifetime?
  - ▶ \* Because  $f$  is also measured per time step
  - ▶ \*

## Calculating $\mathcal{R}$

- ▶  $\mathcal{R}$  is fecundity multiplied by lifespan
- ▶ 
$$\mathcal{R} = f/\mu = f/(1 - p)$$
- ▶ Why do we multiply by time *steps* instead of lifetime?
  - ▶ \* Because  $f$  is also measured per time step
  - ▶ \*  $\mathcal{R}$  must be unitless

# Calculating $\mathcal{R}$

- ▶  $\mathcal{R}$  is fecundity multiplied by lifespan
- ▶ 
$$\mathcal{R} = f/\mu = f/(1 - p)$$
- ▶ Why do we multiply by time *steps* instead of lifetime?
  - ▶ \* Because  $f$  is also measured per time step
  - ▶ \*  $\mathcal{R}$  must be unitless

# Comparison

*Lifetime reproduction*

►  $\mathcal{R} = f/\mu = f/(1 - p)$

*Reproduction over one time step*

# Comparison

*Lifetime reproduction*

- ▶  $\mathcal{R} = f/\mu = f/(1 - p)$
- ▶ Unitless

*Reproduction over one time step*

# Comparison

*Lifetime reproduction*

*Reproduction over one time step*

- ▶  $\mathcal{R} = f/\mu = f/(1 - p)$
- ▶ Unitless
- ▶ Population behaviour depends on the **comparison**  
 $\mathcal{R} : 1$

# Comparison

*Lifetime reproduction*

*Reproduction over one time step*

- ▶  $\mathcal{R} = f/\mu = f/(1 - p)$
- ▶ Unitless
- ▶ Population behaviour depends on the **comparison**  
 $\mathcal{R} : 1$ 
  - ▶ Equivalent to  $f : \mu$

# Comparison

*Lifetime reproduction*

- ▶  $\mathcal{R} = f/\mu = f/(1 - p)$
- ▶ Unitless
- ▶ Population behaviour depends on the **comparison**  
 $\mathcal{R} : 1$ 
  - ▶ Equivalent to  $f : \mu$

*Reproduction over one time step*

- ▶  $\lambda = f + p = f + (1 - \mu)$

# Comparison

## *Lifetime reproduction*

- ▶  $\mathcal{R} = f/\mu = f/(1 - p)$
- ▶ Unitless
- ▶ Population behaviour depends on the **comparison**  
 $\mathcal{R} : 1$ 
  - ▶ Equivalent to  $f : \mu$

## *Reproduction over one time step*

- ▶  $\lambda = f + p = f + (1 - \mu)$
- ▶ Unitless

# Comparison

## *Lifetime reproduction*

- ▶  $\mathcal{R} = f/\mu = f/(1 - p)$
- ▶ Unitless
- ▶ Population behaviour depends on the **comparison**  $\mathcal{R} : 1$ 
  - ▶ Equivalent to  $f : \mu$

## *Reproduction over one time step*

- ▶  $\lambda = f + p = f + (1 - \mu)$
- ▶ Unitless
- ▶ Population behaviour depends on the comparison  $\lambda : 1$

# Comparison

## *Lifetime reproduction*

- ▶  $\mathcal{R} = f/\mu = f/(1 - p)$
- ▶ Unitless
- ▶ Population behaviour depends on the **comparison**  $\mathcal{R} : 1$ 
  - ▶ Equivalent to  $f : \mu$

## *Reproduction over one time step*

- ▶  $\lambda = f + p = f + (1 - \mu)$
- ▶ Unitless
- ▶ Population behaviour depends on the comparison  $\lambda : 1$ 
  - ▶ Equivalent to  $f : \mu$

# Comparison

## *Lifetime reproduction*

- ▶  $\mathcal{R} = f/\mu = f/(1 - p)$
- ▶ Unitless
- ▶ Population behaviour depends on the **comparison**  $\mathcal{R} : 1$ 
  - ▶ Equivalent to  $f : \mu$

## *Reproduction over one time step*

- ▶  $\lambda = f + p = f + (1 - \mu)$
- ▶ Unitless
- ▶ Population behaviour depends on the comparison  $\lambda : 1$ 
  - ▶ Equivalent to  $f : \mu$

# Is the population increasing?

- What does  $\lambda$  tell us about whether the population is increasing?

# Is the population increasing?

- ▶ What does  $\lambda$  tell us about whether the population is increasing?
  - ▶ \*

# Is the population increasing?

- ▶ What does  $\lambda$  tell us about whether the population is increasing?
  - ▶ \* Population is increasing each time step when  $\lambda > 1$

# Is the population increasing?

- ▶ What does  $\lambda$  tell us about whether the population is increasing?
  - ▶ \* Population is increasing each time step when  $\lambda > 1$
- ▶ What does  $\mathcal{R}$  tell us about whether the population is increasing?

# Is the population increasing?

- ▶ What does  $\lambda$  tell us about whether the population is increasing?
  - ▶ \* Population is increasing each time step when  $\lambda > 1$
- ▶ What does  $\mathcal{R}$  tell us about whether the population is increasing?
  - ▶ \*

# Is the population increasing?

- ▶ What does  $\lambda$  tell us about whether the population is increasing?
  - ▶ \* Population is increasing each time step when  $\lambda > 1$
- ▶ What does  $\mathcal{R}$  tell us about whether the population is increasing?
  - ▶ \* Population is increasing when  $\mathcal{R} > 1$ . Each individual is (on average) more than replacing itself over its lifetime

# Is the population increasing?

- ▶ What does  $\lambda$  tell us about whether the population is increasing?
  - ▶ \* Population is increasing each time step when  $\lambda > 1$
- ▶ What does  $\mathcal{R}$  tell us about whether the population is increasing?
  - ▶ \* Population is increasing when  $\mathcal{R} > 1$ . Each individual is (on average) more than replacing itself over its lifetime
- ▶ Therefore, these two criteria must be the same!

# Is the population increasing?

- ▶ What does  $\lambda$  tell us about whether the population is increasing?
  - ▶ \* Population is increasing each time step when  $\lambda > 1$
- ▶ What does  $\mathcal{R}$  tell us about whether the population is increasing?
  - ▶ \* Population is increasing when  $\mathcal{R} > 1$ . Each individual is (on average) more than replacing itself over its lifetime
- ▶ Therefore, these two criteria must be the same!
  - ▶ \*

# Is the population increasing?

- ▶ What does  $\lambda$  tell us about whether the population is increasing?
  - ▶ \* Population is increasing each time step when  $\lambda > 1$
- ▶ What does  $\mathcal{R}$  tell us about whether the population is increasing?
  - ▶ \* Population is increasing when  $\mathcal{R} > 1$ . Each individual is (on average) more than replacing itself over its lifetime
- ▶ Therefore, these two criteria must be the same!
  - ▶ \* Both come down to  $f > \mu$ .

# Is the population increasing?

- ▶ What does  $\lambda$  tell us about whether the population is increasing?
  - ▶ \* Population is increasing each time step when  $\lambda > 1$
- ▶ What does  $\mathcal{R}$  tell us about whether the population is increasing?
  - ▶ \* Population is increasing when  $\mathcal{R} > 1$ . Each individual is (on average) more than replacing itself over its lifetime
- ▶ Therefore, these two criteria must be the same!
  - ▶ \* Both come down to  $f > \mu$ .

# Outline

Constructing models

Dynamical models

Examples

A simple discrete-time model

A simple continuous-time model

Units and scaling

**Key parameters**

Discrete-time model

**Continuous-time model**

Links

Growth and regulation

## Calculating birth rate

- The birth rate  $b$  in the continuous-time model is new individuals per individual per unit time

## Calculating birth rate

- ▶ The birth rate  $b$  in the continuous-time model is new individuals per individual per unit time
  - ▶ An instantaneous rate

## Calculating birth rate

- ▶ The birth rate  $b$  in the continuous-time model is new individuals per individual per unit time
  - ▶ An instantaneous rate
  - ▶ Units of [1/time] – implies what assumption?

## Calculating birth rate

- ▶ The birth rate  $b$  in the continuous-time model is new individuals per individual per unit time
  - ▶ An instantaneous rate
  - ▶ Units of [1/time] – implies what assumption?
    - ▶ \*

## Calculating birth rate

- ▶ The birth rate  $b$  in the continuous-time model is new individuals per individual per unit time
  - ▶ An instantaneous rate
  - ▶ Units of [1/time] – implies what assumption?
    - ▶ \* New individuals are cancelling with old individuals in the equation

## Calculating birth rate

- ▶ The birth rate  $b$  in the continuous-time model is new individuals per individual per unit time
  - ▶ An instantaneous rate
  - ▶ Units of [1/time] – implies what assumption?
    - ▶ \* New individuals are cancelling with old individuals in the equation
    - ▶ \*

## Calculating birth rate

- ▶ The birth rate  $b$  in the continuous-time model is new individuals per individual per unit time
  - ▶ An instantaneous rate
  - ▶ Units of [1/time] – implies what assumption?
    - ▶ \* New individuals are cancelling with old individuals in the equation
    - ▶ \* New individuals are being treated the same as old individuals

## Calculating birth rate

- ▶ The birth rate  $b$  in the continuous-time model is new individuals per individual per unit time
  - ▶ An instantaneous rate
  - ▶ Units of [1/time] – implies what assumption?
    - ▶ \* New individuals are cancelling with old individuals in the equation
    - ▶ \* New individuals are being treated the same as old individuals
    - ▶ \*

## Calculating birth rate

- ▶ The birth rate  $b$  in the continuous-time model is new individuals per individual per unit time
  - ▶ An instantaneous rate
  - ▶ Units of [1/time] – implies what assumption?
    - ▶ \* New individuals are cancelling with old individuals in the equation
    - ▶ \* New individuals are being treated the same as old individuals
    - ▶ \* Not very realistic – a potential problem with our model world

## Calculating birth rate

- ▶ The birth rate  $b$  in the continuous-time model is new individuals per individual per unit time
  - ▶ An instantaneous rate
  - ▶ Units of [1/time] – implies what assumption?
    - ▶ \* New individuals are cancelling with old individuals in the equation
    - ▶ \* New individuals are being treated the same as old individuals
    - ▶ \* Not very realistic – a potential problem with our model world

## Calculating death rate

- The death rate  $d$  in the continuous-time model is deaths per individual per unit time

## Calculating death rate

- ▶ The death rate  $d$  in the continuous-time model is deaths per individual per unit time
  - ▶ An instantaneous rate

## Calculating death rate

- ▶ The death rate  $d$  in the continuous-time model is deaths per individual per unit time
  - ▶ An instantaneous rate
  - ▶ Units of [1/time]

## Calculating death rate

- ▶ The death rate  $d$  in the continuous-time model is deaths per individual per unit time
  - ▶ An instantaneous rate
  - ▶ Units of [1/time]
- ▶ Is there a concern with these units?

## Calculating death rate

- ▶ The death rate  $d$  in the continuous-time model is deaths per individual per unit time
  - ▶ An instantaneous rate
  - ▶ Units of [1/time]
- ▶ Is there a concern with these units?
  - ▶ \*

## Calculating death rate

- ▶ The death rate  $d$  in the continuous-time model is deaths per individual per unit time
  - ▶ An instantaneous rate
  - ▶ Units of [1/time]
- ▶ Is there a concern with these units?
  - ▶ \* Not really. The individuals dying are exactly the same ones we're counting.

## Calculating death rate

- ▶ The death rate  $d$  in the continuous-time model is deaths per individual per unit time
  - ▶ An instantaneous rate
  - ▶ Units of [1/time]
- ▶ Is there a concern with these units?
  - ▶ \* Not really. The individuals dying are exactly the same ones we're counting.

## Instantaneous rate of increase

- ▶ Population increases when  $r = b - d > 0$

## Instantaneous rate of increase

- ▶ Population increases when  $r = b - d > 0$
- ▶  $r$  is not unitless, units are:

## Instantaneous rate of increase

- ▶ Population increases when  $r = b - d > 0$
- ▶  $r$  is not unitless, units are:
  - ▶ \*

## Instantaneous rate of increase

- ▶ Population increases when  $r = b - d > 0$
- ▶  $r$  is not unitless, units are:
  - ▶ \* [1/time]

## Instantaneous rate of increase

- ▶ Population increases when  $r = b - d > 0$
- ▶  $r$  is not unitless, units are:
  - ▶ \* [1/time]
- ▶ So how can  $r = 0$  be a criterion?

## Instantaneous rate of increase

- ▶ Population increases when  $r = b - d > 0$
- ▶  $r$  is not unitless, units are:
  - ▶ \* [1/time]
- ▶ So how can  $r = 0$  be a criterion?
  - ▶ \*

## Instantaneous rate of increase

- ▶ Population increases when  $r = b - d > 0$
- ▶  $r$  is not unitless, units are:
  - ▶ \* [1/time]
- ▶ So how can  $r = 0$  be a criterion?
  - ▶ \* Because 0 anything is unitless!

## Instantaneous rate of increase

- ▶ Population increases when  $r = b - d > 0$
- ▶  $r$  is not unitless, units are:
  - ▶ \* [1/time]
- ▶ So how can  $r = 0$  be a criterion?
  - ▶ \* Because 0 anything is unitless!
  - ▶ \*

## Instantaneous rate of increase

- ▶ Population increases when  $r = b - d > 0$
- ▶  $r$  is not unitless, units are:
  - ▶ \* [1/time]
- ▶ So how can  $r = 0$  be a criterion?
  - ▶ \* Because 0 anything is unitless!
  - ▶ \* Does  $0\text{km} = 0\text{cm}$ ?

## Instantaneous rate of increase

- ▶ Population increases when  $r = b - d > 0$
- ▶  $r$  is not unitless, units are:
  - ▶ \* [1/time]
- ▶ So how can  $r = 0$  be a criterion?
  - ▶ \* Because 0 anything is unitless!
  - ▶ \* Does  $0\text{km} = 0\text{cm}$ ?

# Calculating $\mathcal{R}$

- The mean lifespan is  $L = 1/d$

# Calculating $\mathcal{R}$

- ▶ The mean lifespan is  $L = 1/d$ 
  - ▶ Equivalent to the characteristic time for the death process

# Calculating $\mathcal{R}$

- ▶ The mean lifespan is  $L = 1/d$ 
  - ▶ Equivalent to the characteristic time for the death process
- ▶  $\mathcal{R}$  is the average number of births expected over that time frame:

# Calculating $\mathcal{R}$

- ▶ The mean lifespan is  $L = 1/d$ 
  - ▶ Equivalent to the characteristic time for the death process
- ▶  $\mathcal{R}$  is the average number of births expected over that time frame:
  - ▶  $\mathcal{R} = bL = b/d$

# Calculating $\mathcal{R}$

- ▶ The mean lifespan is  $L = 1/d$ 
  - ▶ Equivalent to the characteristic time for the death process
- ▶  $\mathcal{R}$  is the average number of births expected over that time frame:
  - ▶  $\mathcal{R} = bL = b/d$

# Comparison

*Lifetime reproduction*

►  $\mathcal{R} = bL = b/d$

*Instantaneous change*

# Comparison

*Lifetime reproduction*

- ▶  $\mathcal{R} = bL = b/d$

- ▶ Unitless

*Instantaneous change*

# Comparison

*Lifetime reproduction*

*Instantaneous change*

- ▶  $\mathcal{R} = bL = b/d$
- ▶ Unitless
- ▶ Population behaviour  
depends on the comparison  
 $\mathcal{R} : 1$

# Comparison

*Lifetime reproduction*

*Instantaneous change*

- ▶  $\mathcal{R} = bL = b/d$
- ▶ Unitless
- ▶ Population behaviour depends on the comparison  
 $\mathcal{R} : 1$ 
  - ▶ Equivalent to  $b : d$

# Comparison

*Lifetime reproduction*

- ▶  $\mathcal{R} = bL = b/d$
- ▶ Unitless
- ▶ Population behaviour depends on the comparison  
 $\mathcal{R} : 1$ 
  - ▶ Equivalent to  $b : d$

*Instantaneous change*

▶  $r = b - d$

# Comparison

## *Lifetime reproduction*

- ▶  $\mathcal{R} = bL = b/d$
- ▶ Unitless
- ▶ Population behaviour depends on the comparison  
 $\mathcal{R} : 1$ 
  - ▶ Equivalent to  $b : d$

## *Instantaneous change*

- ▶  $r = b - d$
- ▶ Units [1/t] (a rate)

# Comparison

## *Lifetime reproduction*

- ▶  $\mathcal{R} = bL = b/d$
- ▶ Unitless
- ▶ Population behaviour depends on the comparison  $\mathcal{R} : 1$ 
  - ▶ Equivalent to  $b : d$

## *Instantaneous change*

- ▶  $r = b - d$
- ▶ Units  $[1/t]$  (a rate)
- ▶ Population behaviour depends on the comparison  $r : 0$

# Comparison

## *Lifetime reproduction*

- ▶  $\mathcal{R} = bL = b/d$
- ▶ Unitless
- ▶ Population behaviour depends on the comparison  $\mathcal{R} : 1$ 
  - ▶ Equivalent to  $b : d$

## *Instantaneous change*

- ▶  $r = b - d$
- ▶ Units  $[1/t]$  (a rate)
- ▶ Population behaviour depends on the comparison  $r : 0$ 
  - ▶ Equivalent to  $b : d$

# Comparison

## *Lifetime reproduction*

- ▶  $\mathcal{R} = bL = b/d$
- ▶ Unitless
- ▶ Population behaviour depends on the comparison  $\mathcal{R} : 1$ 
  - ▶ Equivalent to  $b : d$

## *Instantaneous change*

- ▶  $r = b - d$
- ▶ Units  $[1/t]$  (a rate)
- ▶ Population behaviour depends on the comparison  $r : 0$ 
  - ▶ Equivalent to  $b : d$

# Is the population increasing?

- What does  $r$  tell us about whether the population is increasing?

# Is the population increasing?

- ▶ What does  $r$  tell us about whether the population is increasing?
  - ▶ \*

# Is the population increasing?

- ▶ What does  $r$  tell us about whether the population is increasing?
  - ▶ \* Population is increasing at any particular time step when  $r > 0$

# Is the population increasing?

- ▶ What does  $r$  tell us about whether the population is increasing?
  - ▶ \* Population is increasing at any particular time step when  $r > 0$
- ▶ What does  $\mathcal{R}$  tell us about whether the population is increasing?

# Is the population increasing?

- ▶ What does  $r$  tell us about whether the population is increasing?
  - ▶ \* Population is increasing at any particular time step when  $r > 0$
- ▶ What does  $\mathcal{R}$  tell us about whether the population is increasing?
  - ▶ \*

# Is the population increasing?

- ▶ What does  $r$  tell us about whether the population is increasing?
  - ▶ \* Population is increasing at any particular time step when  $r > 0$
- ▶ What does  $\mathcal{R}$  tell us about whether the population is increasing?
  - ▶ \* Population is increasing when  $\mathcal{R} > 1$ . Each individual is (on average) more than replacing itself over its lifetime

# Is the population increasing?

- ▶ What does  $r$  tell us about whether the population is increasing?
  - ▶ \* Population is increasing at any particular time step when  $r > 0$
- ▶ What does  $\mathcal{R}$  tell us about whether the population is increasing?
  - ▶ \* Population is increasing when  $\mathcal{R} > 1$ . Each individual is (on average) more than replacing itself over its lifetime
- ▶ Therefore, these two criteria must be the same!

# Is the population increasing?

- ▶ What does  $r$  tell us about whether the population is increasing?
  - ▶ \* Population is increasing at any particular time step when  $r > 0$
- ▶ What does  $\mathcal{R}$  tell us about whether the population is increasing?
  - ▶ \* Population is increasing when  $\mathcal{R} > 1$ . Each individual is (on average) more than replacing itself over its lifetime
- ▶ Therefore, these two criteria must be the same!
  - ▶ \*

# Is the population increasing?

- ▶ What does  $r$  tell us about whether the population is increasing?
  - ▶ \* Population is increasing at any particular time step when  $r > 0$
- ▶ What does  $\mathcal{R}$  tell us about whether the population is increasing?
  - ▶ \* Population is increasing when  $\mathcal{R} > 1$ . Each individual is (on average) more than replacing itself over its lifetime
- ▶ Therefore, these two criteria must be the same!
  - ▶ \* Both come down to  $b > d$ .

# Is the population increasing?

- ▶ What does  $r$  tell us about whether the population is increasing?
  - ▶ \* Population is increasing at any particular time step when  $r > 0$
- ▶ What does  $\mathcal{R}$  tell us about whether the population is increasing?
  - ▶ \* Population is increasing when  $\mathcal{R} > 1$ . Each individual is (on average) more than replacing itself over its lifetime
- ▶ Therefore, these two criteria must be the same!
  - ▶ \* Both come down to  $b > d$ .

# Outline

Constructing models

Dynamical models

Examples

A simple discrete-time model

A simple continuous-time model

Units and scaling

**Key parameters**

Discrete-time model

Continuous-time model

Links

Growth and regulation

# Links

- ▶ After one time step in a discrete-time model

# Links

- ▶ After one time step in a discrete-time model
  - ▶  $N_0 \rightarrow N_0\lambda$

# Links

- ▶ After one time step in a discrete-time model
  - ▶  $N_0 \rightarrow N_0\lambda$
  - ▶  $t \rightarrow t + \Delta t$

# Links

- ▶ After one time step in a discrete-time model
  - ▶  $N_0 \rightarrow N_0\lambda$
  - ▶  $t \rightarrow t + \Delta t$
- ▶ In a continuous model

# Links

- ▶ After one time step in a discrete-time model
  - ▶  $N_0 \rightarrow N_0\lambda$
  - ▶  $t \rightarrow t + \Delta t$
- ▶ In a continuous model
  - ▶  $N_0 \rightarrow N_0 \exp(r\Delta t)$  in the same time period

# Links

- ▶ After one time step in a discrete-time model
  - ▶  $N_0 \rightarrow N_0\lambda$
  - ▶  $t \rightarrow t + \Delta t$
- ▶ In a continuous model
  - ▶  $N_0 \rightarrow N_0 \exp(r\Delta t)$  in the same time period
- ▶ To link them, we set:

# Links

- ▶ After one time step in a discrete-time model
  - ▶  $N_0 \rightarrow N_0\lambda$
  - ▶  $t \rightarrow t + \Delta t$
- ▶ In a continuous model
  - ▶  $N_0 \rightarrow N_0 \exp(r\Delta t)$  in the same time period
- ▶ To link them, we set:
  - ▶  $\lambda = \exp(r\Delta t)$

# Links

- ▶ After one time step in a discrete-time model
  - ▶  $N_0 \rightarrow N_0\lambda$
  - ▶  $t \rightarrow t + \Delta t$
- ▶ In a continuous model
  - ▶  $N_0 \rightarrow N_0 \exp(r\Delta t)$  in the same time period
- ▶ To link them, we set:
  - ▶  $\lambda = \exp(r\Delta t)$
- ▶ In the other direction:

# Links

- ▶ After one time step in a discrete-time model
  - ▶  $N_0 \rightarrow N_0\lambda$
  - ▶  $t \rightarrow t + \Delta t$
- ▶ In a continuous model
  - ▶  $N_0 \rightarrow N_0 \exp(r\Delta t)$  in the same time period
- ▶ To link them, we set:
  - ▶  $\lambda = \exp(r\Delta t)$
- ▶ In the other direction:
  - ▶ \*

# Links

- ▶ After one time step in a discrete-time model
  - ▶  $N_0 \rightarrow N_0\lambda$
  - ▶  $t \rightarrow t + \Delta t$
- ▶ In a continuous model
  - ▶  $N_0 \rightarrow N_0 \exp(r\Delta t)$  in the same time period
- ▶ To link them, we set:
  - ▶  $\lambda = \exp(r\Delta t)$
- ▶ In the other direction:
  - ▶ \*  $r = \log_e(\lambda)/\Delta t$

# Links

- ▶ After one time step in a discrete-time model
  - ▶  $N_0 \rightarrow N_0\lambda$
  - ▶  $t \rightarrow t + \Delta t$
- ▶ In a continuous model
  - ▶  $N_0 \rightarrow N_0 \exp(r\Delta t)$  in the same time period
- ▶ To link them, we set:
  - ▶  $\lambda = \exp(r\Delta t)$
- ▶ In the other direction:
  - ▶ \*  $r = \log_e(\lambda)/\Delta t$

# Characteristic time

- We can now find characteristic times of exponential change:

## Characteristic time

- ▶ We can now find characteristic times of exponential change:
  - ▶  $T_c = 1/r$  for exponential growth when  $r > 0$

## Characteristic time

- ▶ We can now find characteristic times of exponential change:
  - ▶  $T_c = 1/r$  for exponential growth when  $r > 0$
  - ▶  $T_c = -1/r$  for exponential decline when  $r < 0$

## Characteristic time

- ▶ We can now find characteristic times of exponential change:
  - ▶  $T_c = 1/r$  for exponential growth when  $r > 0$
  - ▶  $T_c = -1/r$  for exponential decline when  $r < 0$
- ▶ Rule of thumb: population changes by a factor of 20 after 3 characteristic times

## Characteristic time

- ▶ We can now find characteristic times of exponential change:
  - ▶  $T_c = 1/r$  for exponential growth when  $r > 0$
  - ▶  $T_c = -1/r$  for exponential decline when  $r < 0$
- ▶ Rule of thumb: population changes by a factor of 20 after 3 characteristic times
  - ▶  $\exp(3) = 20.1$

## Characteristic time

- ▶ We can now find characteristic times of exponential change:
  - ▶  $T_c = 1/r$  for exponential growth when  $r > 0$
  - ▶  $T_c = -1/r$  for exponential decline when  $r < 0$
- ▶ Rule of thumb: population changes by a factor of 20 after 3 characteristic times
  - ▶  $\exp(3) = 20.1$

# Outline

Constructing models

Dynamical models

Examples

A simple discrete-time model

A simple continuous-time model

Units and scaling

Key parameters

Discrete-time model

Continuous-time model

Links

Growth and regulation

## *Long-term growth rate (preview)*

- ▶ What is the long-term average exponential growth rate (using either  $r$  or  $\lambda$ ) of:



## *Long-term growth rate (preview)*

- ▶ What is the long-term average exponential growth rate (using either  $r$  or  $\lambda$ ) of:
  - ▶ A successful population?



## *Long-term growth rate (preview)*

- ▶ What is the long-term average exponential growth rate (using either  $r$  or  $\lambda$ ) of:
  - ▶ A successful population?
    - ▶ \*



## *Long-term growth rate (preview)*

- ▶ What is the long-term average exponential growth rate (using either  $r$  or  $\lambda$ ) of:
  - ▶ A successful population?
    - ▶ \*



## *Long-term growth rate (preview)*

- ▶ What is the long-term average exponential growth rate (using either  $r$  or  $\lambda$ ) of:
  - ▶ A successful population?
    - ▶ \*
  - ▶ An unsuccessful population?



## *Long-term growth rate (preview)*

- ▶ What is the long-term average exponential growth rate (using either  $r$  or  $\lambda$ ) of:
  - ▶ A successful population?
    - ▶ \*
  - ▶ An unsuccessful population?
    - ▶ \*



## *Long-term growth rate (preview)*

- ▶ What is the long-term average exponential growth rate (using either  $r$  or  $\lambda$ ) of:
  - ▶ A successful population?
    - ▶ \*
  - ▶ An unsuccessful population?
    - ▶ \*



## *Long-term growth rate (preview)*

- ▶ What is the long-term average exponential growth rate (using either  $r$  or  $\lambda$ ) of:
  - ▶ A successful population?
    - ▶ \*
  - ▶ An unsuccessful population?
    - ▶ \*



## Example: Human population growth

- In the last 50,000 years, the population of **modern humans** has increased from about 1000 to about 7 billion

## Example: Human population growth

- ▶ In the last 50,000 years, the population of **modern humans** has increased from about 1000 to about 7 billion
- ▶ What value of  $r$  does this correspond to? If we use a time step of 20-year generations, what value of  $\lambda$  does it correspond to?

## Example: Human population growth

- ▶ In the last 50,000 years, the population of **modern humans** has increased from about 1000 to about 7 billion
- ▶ What value of  $r$  does this correspond to? If we use a time step of 20-year generations, what value of  $\lambda$  does it correspond to?
  - ▶ \*

## Example: Human population growth

- ▶ In the last 50,000 years, the population of **modern humans** has increased from about 1000 to about 7 billion
- ▶ What value of  $r$  does this correspond to? If we use a time step of 20-year generations, what value of  $\lambda$  does it correspond to?
  - ▶ \*  $N(t) = N(0) \exp(rt)$

## Example: Human population growth

- ▶ In the last 50,000 years, the population of **modern humans** has increased from about 1000 to about 7 billion
- ▶ What value of  $r$  does this correspond to? If we use a time step of 20-year generations, what value of  $\lambda$  does it correspond to?
  - ▶ \*  $N(t) = N(0) \exp(rt)$
  - ▶ \*

## Example: Human population growth

- ▶ In the last 50,000 years, the population of **modern humans** has increased from about 1000 to about 7 billion
- ▶ What value of  $r$  does this correspond to? If we use a time step of 20-year generations, what value of  $\lambda$  does it correspond to?
  - ▶ \*  $N(t) = N(0) \exp(rt)$
  - ▶ \*  $r = \log_e(N/N(0))/t$

## Example: Human population growth

- ▶ In the last 50,000 years, the population of **modern humans** has increased from about 1000 to about 7 billion
- ▶ What value of  $r$  does this correspond to? If we use a time step of 20-year generations, what value of  $\lambda$  does it correspond to?
  - ▶ \*  $N(t) = N(0) \exp(rt)$
  - ▶ \*  $r = \log_e(N/N(0))/t$
  - ▶ \*

## Example: Human population growth

- ▶ In the last 50,000 years, the population of **modern humans** has increased from about 1000 to about 7 billion
- ▶ What value of  $r$  does this correspond to? If we use a time step of 20-year generations, what value of  $\lambda$  does it correspond to?
  - ▶ \*  $N(t) = N(0) \exp(rt)$ 
    - ▶ \*  $r = \log_e(N/N(0))/t$
    - ▶ \*  $r = \log_e(7000000000/1000)/50000 \text{ yr} = 0.0003/\text{yr}$

## Example: Human population growth

- ▶ In the last 50,000 years, the population of **modern humans** has increased from about 1000 to about 7 billion
- ▶ What value of  $r$  does this correspond to? If we use a time step of 20-year generations, what value of  $\lambda$  does it correspond to?
  - ▶ \*  $N(t) = N(0) \exp(rt)$ 
    - ▶ \*  $r = \log_e(N/N(0))/t$
    - ▶ \*  $r = \log_e(7000000000/1000)/50000 \text{ yr} = 0.0003/\text{yr}$
  - ▶ \*

## Example: Human population growth

- ▶ In the last 50,000 years, the population of **modern humans** has increased from about 1000 to about 7 billion
- ▶ What value of  $r$  does this correspond to? If we use a time step of 20-year generations, what value of  $\lambda$  does it correspond to?
  - ▶ \*  $N(t) = N(0) \exp(rt)$ 
    - ▶ \*  $r = \log_e(N/N(0))/t$
    - ▶ \*  $r = \log_e(7000000000/1000)/50000 \text{ yr} = 0.0003/\text{yr}$
  - ▶ \*  $N_T = N_0 \lambda^T$

## Example: Human population growth

- ▶ In the last 50,000 years, the population of **modern humans** has increased from about 1000 to about 7 billion
- ▶ What value of  $r$  does this correspond to? If we use a time step of 20-year generations, what value of  $\lambda$  does it correspond to?
  - ▶ \*  $N(t) = N(0) \exp(rt)$ 
    - ▶ \*  $r = \log_e(N/N(0))/t$
    - ▶ \*  $r = \log_e(7000000000/1000)/50000 \text{ yr} = 0.0003/\text{yr}$
  - ▶ \*  $N_T = N_0 \lambda^T$ 
    - ▶ \*

## Example: Human population growth

- ▶ In the last 50,000 years, the population of **modern humans** has increased from about 1000 to about 7 billion
- ▶ What value of  $r$  does this correspond to? If we use a time step of 20-year generations, what value of  $\lambda$  does it correspond to?
  - ▶ \*  $N(t) = N(0) \exp(rt)$ 
    - ▶ \*  $r = \log_e(N/N(0))/t$
    - ▶ \*  $r = \log_e(7000000000/1000)/50000 \text{ yr} = 0.0003/\text{yr}$
  - ▶ \*  $N_T = N_0 \lambda^T$ 
    - ▶ \*  $T = t/\Delta t = 50000 \text{ yr}/20 \text{ yr} = 2500$

## Example: Human population growth

- ▶ In the last 50,000 years, the population of **modern humans** has increased from about 1000 to about 7 billion
- ▶ What value of  $r$  does this correspond to? If we use a time step of 20-year generations, what value of  $\lambda$  does it correspond to?
  - ▶ \*  $N(t) = N(0) \exp(rt)$ 
    - ▶ \*  $r = \log_e(N/N(0))/t$
    - ▶ \*  $r = \log_e(7000000000/1000)/50000 \text{ yr} = 0.0003/\text{yr}$
  - ▶ \*  $N_T = N_0 \lambda^T$ 
    - ▶ \*  $T = t/\Delta t = 50000 \text{ yr}/20 \text{ yr} = 2500$
    - ▶ \*

## Example: Human population growth

- ▶ In the last 50,000 years, the population of **modern humans** has increased from about 1000 to about 7 billion
- ▶ What value of  $r$  does this correspond to? If we use a time step of 20-year generations, what value of  $\lambda$  does it correspond to?
  - ▶ \*  $N(t) = N(0) \exp(rt)$ 
    - ▶ \*  $r = \log_e(N/N(0))/t$
    - ▶ \*  $r = \log_e(7000000000/1000)/50000 \text{ yr} = 0.0003/\text{yr}$
  - ▶ \*  $N_T = N_0 \lambda^T$ 
    - ▶ \*  $T = t/\Delta t = 50000 \text{ yr}/20 \text{ yr} = 2500$
    - ▶ \*  $\lambda = (N_T/N_0)^{1/T}$

## Example: Human population growth

- ▶ In the last 50,000 years, the population of **modern humans** has increased from about 1000 to about 7 billion
- ▶ What value of  $r$  does this correspond to? If we use a time step of 20-year generations, what value of  $\lambda$  does it correspond to?
  - ▶ \*  $N(t) = N(0) \exp(rt)$ 
    - ▶ \*  $r = \log_e(N/N(0))/t$
    - ▶ \*  $r = \log_e(7000000000/1000)/50000 \text{ yr} = 0.0003/\text{yr}$
  - ▶ \*  $N_T = N_0 \lambda^T$ 
    - ▶ \*  $T = t/\Delta t = 50000 \text{ yr}/20 \text{ yr} = 2500$
    - ▶ \*  $\lambda = (N_T/N_0)^{1/T}$
    - ▶ \*

## Example: Human population growth

- ▶ In the last 50,000 years, the population of **modern humans** has increased from about 1000 to about 7 billion
- ▶ What value of  $r$  does this correspond to? If we use a time step of 20-year generations, what value of  $\lambda$  does it correspond to?
  - ▶ \*  $N(t) = N(0) \exp(rt)$ 
    - ▶ \*  $r = \log_e(N/N(0))/t$
    - ▶ \*  $r = \log_e(7000000000/1000)/50000 \text{ yr} = 0.0003/\text{yr}$
  - ▶ \*  $N_T = N_0 \lambda^T$ 
    - ▶ \*  $T = t/\Delta t = 50000 \text{ yr}/20 \text{ yr} = 2500$
    - ▶ \*  $\lambda = (N_T/N_0)^{1/T}$
    - ▶ \*  $\lambda = (7000000000/1000)^{1/2500} = 1.006$

## Example: Human population growth

- ▶ In the last 50,000 years, the population of **modern humans** has increased from about 1000 to about 7 billion
- ▶ What value of  $r$  does this correspond to? If we use a time step of 20-year generations, what value of  $\lambda$  does it correspond to?
  - ▶ \*  $N(t) = N(0) \exp(rt)$ 
    - ▶ \*  $r = \log_e(N/N(0))/t$
    - ▶ \*  $r = \log_e(7000000000/1000)/50000 \text{ yr} = 0.0003/\text{yr}$
  - ▶ \*  $N_T = N_0 \lambda^T$ 
    - ▶ \*  $T = t/\Delta t = 50000 \text{ yr}/20 \text{ yr} = 2500$
    - ▶ \*  $\lambda = (N_T/N_0)^{1/T}$
    - ▶ \*  $\lambda = (7000000000/1000)^{1/2500} = 1.006$

## Long-term growth rate

- What is the long-term average exponential growth rate (using either  $r$  or  $\lambda$ ) of:

## Long-term growth rate

- ▶ What is the long-term average exponential growth rate (using either  $r$  or  $\lambda$ ) of:
  - ▶ A successful population?

## Long-term growth rate

- ▶ What is the long-term average exponential growth rate (using either  $r$  or  $\lambda$ ) of:
  - ▶ A successful population?
    - ▶ \*

## Long-term growth rate

- ▶ What is the long-term average exponential growth rate (using either  $r$  or  $\lambda$ ) of:
  - ▶ A successful population?
    - ▶ \* Very close to  $r = 0$  or  $\lambda = 1$

## Long-term growth rate

- ▶ What is the long-term average exponential growth rate (using either  $r$  or  $\lambda$ ) of:
  - ▶ A successful population?
    - ▶ \* Very close to  $r = 0$  or  $\lambda = 1$
    - ▶ \*

## Long-term growth rate

- ▶ What is the long-term average exponential growth rate (using either  $r$  or  $\lambda$ ) of:
  - ▶ A successful population?
    - ▶ \* Very close to  $r = 0$  or  $\lambda = 1$
    - ▶ \* But a little larger

## Long-term growth rate

- ▶ What is the long-term average exponential growth rate (using either  $r$  or  $\lambda$ ) of:
  - ▶ A successful population?
    - ▶ \* Very close to  $r = 0$  or  $\lambda = 1$
    - ▶ \* But a little larger
  - ▶ An unsuccessful population?

## Long-term growth rate

- ▶ What is the long-term average exponential growth rate (using either  $r$  or  $\lambda$ ) of:
  - ▶ A successful population?
    - ▶ \* Very close to  $r = 0$  or  $\lambda = 1$
    - ▶ \* But a little larger
  - ▶ An unsuccessful population?
    - ▶ \*

## Long-term growth rate

- ▶ What is the long-term average exponential growth rate (using either  $r$  or  $\lambda$ ) of:
  - ▶ A successful population?
    - ▶ \* Very close to  $r = 0$  or  $\lambda = 1$
    - ▶ \* But a little larger
  - ▶ An unsuccessful population?
    - ▶ \* *Probably* very close to  $r = 0$  or  $\lambda = 1$

## Long-term growth rate

- ▶ What is the long-term average exponential growth rate (using either  $r$  or  $\lambda$ ) of:
  - ▶ A successful population?
    - ▶ \* Very close to  $r = 0$  or  $\lambda = 1$
    - ▶ \* But a little larger
  - ▶ An unsuccessful population?
    - ▶ \* *Probably* very close to  $r = 0$  or  $\lambda = 1$
    - ▶ \*

## Long-term growth rate

- ▶ What is the long-term average exponential growth rate (using either  $r$  or  $\lambda$ ) of:
  - ▶ A successful population?
    - ▶ \* *Very close to  $r = 0$  or  $\lambda = 1$*
    - ▶ \* *But a little larger*
  - ▶ An unsuccessful population?
    - ▶ \* *Probably very close to  $r = 0$  or  $\lambda = 1$*
    - ▶ \* *But a little smaller*

## Long-term growth rate

- ▶ What is the long-term average exponential growth rate (using either  $r$  or  $\lambda$ ) of:
  - ▶ A successful population?
    - ▶ \* Very close to  $r = 0$  or  $\lambda = 1$
    - ▶ \* But a little larger
  - ▶ An unsuccessful population?
    - ▶ \* *Probably* very close to  $r = 0$  or  $\lambda = 1$
    - ▶ \* But a little smaller
    - ▶ \*

## Long-term growth rate

- ▶ What is the long-term average exponential growth rate (using either  $r$  or  $\lambda$ ) of:
  - ▶ A successful population?
    - ▶ \* *Very close to  $r = 0$  or  $\lambda = 1$*
    - ▶ \* *But a little larger*
  - ▶ An unsuccessful population?
    - ▶ \* *Probably very close to  $r = 0$  or  $\lambda = 1$*
    - ▶ \* *But a little smaller*
    - ▶ \* *If more than a little, it would probably be gone by now!*

## Long-term growth rate

- ▶ What is the long-term average exponential growth rate (using either  $r$  or  $\lambda$ ) of:
  - ▶ A successful population?
    - ▶ \* *Very close to  $r = 0$  or  $\lambda = 1$*
    - ▶ \* *But a little larger*
  - ▶ An unsuccessful population?
    - ▶ \* *Probably very close to  $r = 0$  or  $\lambda = 1$*
    - ▶ \* *But a little smaller*
    - ▶ \* *If more than a little, it would probably be gone by now!*

## Time scales

- ▶ Estimated characteristic time scales for exponential growth or decay are usually a few (or a few tens) of generations

# Time scales

- ▶ Estimated characteristic time scales for exponential growth or decay are usually a few (or a few tens) of generations
  - ▶ years to a few kiloyears

## Time scales

- ▶ Estimated characteristic time scales for exponential growth or decay are usually a few (or a few tens) of generations
  - ▶ years to a few kiloyears
- ▶ Species typically persist for far longer

## Time scales

- ▶ Estimated characteristic time scales for exponential growth or decay are usually a few (or a few tens) of generations
  - ▶ years to a few kiloyears
- ▶ Species typically persist for far longer
  - ▶ many kiloyears to megayears

## Time scales

- ▶ Estimated characteristic time scales for exponential growth or decay are usually a few (or a few tens) of generations
  - ▶ years to a few kiloyears
- ▶ Species typically persist for far longer
  - ▶ many kiloyears to megayears

# Balance

- If populations grow and shrink proportionally to their size, why don't they go exponentially to zero or infinity?

# Balance

- ▶ If populations grow and shrink proportionally to their size, why don't they go exponentially to zero or infinity?
  - ▶ \*

# Balance

- ▶ If populations grow and shrink proportionally to their size, why don't they go exponentially to zero or infinity?
  - ▶ \*  $\mathcal{R}$  is extremely close to 1 for every species

# Balance

- ▶ If populations grow and shrink proportionally to their size, why don't they go exponentially to zero or infinity?
  - ▶ \*  $\mathcal{R}$  is extremely close to 1 for every species
- ▶ How is this possible?

# Balance

- ▶ If populations grow and shrink proportionally to their size, why don't they go exponentially to zero or infinity?
  - ▶ \*  $\mathcal{R}$  is extremely close to 1 for every species
- ▶ How is this possible?
  - ▶ \*

# Balance

- ▶ If populations grow and shrink proportionally to their size, why don't they go exponentially to zero or infinity?
  - ▶ \*  $\mathcal{R}$  is extremely close to 1 for every species
- ▶ How is this possible?
  - ▶ \* Growth rates change through time

# Balance

- ▶ If populations grow and shrink proportionally to their size, why don't they go exponentially to zero or infinity?
  - ▶ \*  $\mathcal{R}$  is extremely close to 1 for every species
- ▶ How is this possible?
  - ▶ \* Growth rates change through time

# Changing growth rates

- ▶ Poll: What sort of factors can make species growth rates change?

## Changing growth rates

- ▶ Poll: What sort of factors can make species growth rates change?
  - ▶ \*

# Changing growth rates

- ▶ Poll: What sort of factors can make species growth rates change?
  - ▶ \* Seasonality

# Changing growth rates

- ▶ Poll: What sort of factors can make species growth rates change?
  - ▶ \* Seasonality
  - ▶ \*

# Changing growth rates

- ▶ Poll: What sort of factors can make species growth rates change?
  - ▶ \* Seasonality
  - ▶ \* Environmental changes (gradual or dramatic)

# Changing growth rates

- ▶ Poll: What sort of factors can make species growth rates change?
  - ▶ \* Seasonality
  - ▶ \* Environmental changes (gradual or dramatic)
  - ▶ \*

# Changing growth rates

- ▶ Poll: What sort of factors can make species growth rates change?
  - ▶ \* Seasonality
  - ▶ \* Environmental changes (gradual or dramatic)
  - ▶ \* Competition within species

# Changing growth rates

- ▶ Poll: What sort of factors can make species growth rates change?
  - ▶ \* Seasonality
  - ▶ \* Environmental changes (gradual or dramatic)
  - ▶ \* Competition within species
  - ▶ \*

# Changing growth rates

- ▶ Poll: What sort of factors can make species growth rates change?
  - ▶ \* Seasonality
  - ▶ \* Environmental changes (gradual or dramatic)
  - ▶ \* Competition within species
  - ▶ \* Competition between species

# Changing growth rates

- ▶ Poll: What sort of factors can make species growth rates change?
  - ▶ \* Seasonality
  - ▶ \* Environmental changes (gradual or dramatic)
  - ▶ \* Competition within species
  - ▶ \* Competition between species
  - ▶ \*

# Changing growth rates

- ▶ Poll: What sort of factors can make species growth rates change?
  - ▶ \* Seasonality
  - ▶ \* Environmental changes (gradual or dramatic)
  - ▶ \* Competition within species
  - ▶ \* Competition between species
  - ▶ \* Predators and diseases

# Changing growth rates

- ▶ Poll: What sort of factors can make species growth rates change?
  - ▶ \* Seasonality
  - ▶ \* Environmental changes (gradual or dramatic)
  - ▶ \* Competition within species
  - ▶ \* Competition between species
  - ▶ \* Predators and diseases
  - ▶ \*

# Changing growth rates

- ▶ Poll: What sort of factors can make species growth rates change?
  - ▶ \* Seasonality
  - ▶ \* Environmental changes (gradual or dramatic)
  - ▶ \* Competition within species
  - ▶ \* Competition between species
  - ▶ \* Predators and diseases
  - ▶ \* Resources (food and space)

# Changing growth rates

- ▶ Poll: What sort of factors can make species growth rates change?
  - ▶ \* Seasonality
  - ▶ \* Environmental changes (gradual or dramatic)
  - ▶ \* Competition within species
  - ▶ \* Competition between species
  - ▶ \* Predators and diseases
  - ▶ \* Resources (food and space)

# Regulation

- What do we expect to happen if a population's growth rate is affected only by seasons and climate?

# Regulation

- ▶ What do we expect to happen if a population's growth rate is affected only by seasons and climate?
  - ▶ \*

# Regulation

- ▶ What do we expect to happen if a population's growth rate is affected only by seasons and climate?
  - ▶ \* In the long-term, it will grow or shrink according to some average value

# Regulation

- ▶ What do we expect to happen if a population's growth rate is affected only by seasons and climate?
  - ▶ \* In the long-term, it will grow or shrink according to some average value
  - ▶ \*

# Regulation

- ▶ What do we expect to happen if a population's growth rate is affected only by seasons and climate?
  - ▶ \* In the long-term, it will grow or shrink according to some average value
  - ▶ \* We don't expect perfect balance, so we don't expect population to stay under control

# Regulation

- ▶ What do we expect to happen if a population's growth rate is affected only by seasons and climate?
  - ▶ \* In the long-term, it will grow or shrink according to some average value
  - ▶ \* We don't expect perfect balance, so we don't expect population to stay under control
- ▶ What sort of mechanism could keep a population in a reasonable range for a long time?

# Regulation

- ▶ What do we expect to happen if a population's growth rate is affected only by seasons and climate?
  - ▶ \* In the long-term, it will grow or shrink according to some average value
  - ▶ \* We don't expect perfect balance, so we don't expect population to stay under control
- ▶ What sort of mechanism could keep a population in a reasonable range for a long time?
  - ▶ \*

# Regulation

- ▶ What do we expect to happen if a population's growth rate is affected only by seasons and climate?
  - ▶ \* In the long-term, it will grow or shrink according to some average value
  - ▶ \* We don't expect perfect balance, so we don't expect population to stay under control
- ▶ What sort of mechanism could keep a population in a reasonable range for a long time?
  - ▶ \* If the growth rate is directly or indirectly affected by the size of the population

# Regulation

- ▶ What do we expect to happen if a population's growth rate is affected only by seasons and climate?
  - ▶ \* In the long-term, it will grow or shrink according to some average value
  - ▶ \* We don't expect perfect balance, so we don't expect population to stay under control
- ▶ What sort of mechanism could keep a population in a reasonable range for a long time?
  - ▶ \* If the growth rate is directly or indirectly affected by the size of the population
  - ▶ \*

# Regulation

- ▶ What do we expect to happen if a population's growth rate is affected only by seasons and climate?
  - ▶ \* In the long-term, it will grow or shrink according to some average value
  - ▶ \* We don't expect perfect balance, so we don't expect population to stay under control
- ▶ What sort of mechanism could keep a population in a reasonable range for a long time?
  - ▶ \* If the growth rate is directly or indirectly affected by the size of the population
  - ▶ \* There should be some mechanism that decreases population growth rate when population is large

# Regulation

- ▶ What do we expect to happen if a population's growth rate is affected only by seasons and climate?
  - ▶ \* In the long-term, it will grow or shrink according to some average value
  - ▶ \* We don't expect perfect balance, so we don't expect population to stay under control
- ▶ What sort of mechanism could keep a population in a reasonable range for a long time?
  - ▶ \* If the growth rate is directly or indirectly affected by the size of the population
  - ▶ \* There should be some mechanism that decreases population growth rate when population is large
- ▶ This is even true for modern humans!

# Regulation

- ▶ What do we expect to happen if a population's growth rate is affected only by seasons and climate?
  - ▶ \* In the long-term, it will grow or shrink according to some average value
  - ▶ \* We don't expect perfect balance, so we don't expect population to stay under control
- ▶ What sort of mechanism could keep a population in a reasonable range for a long time?
  - ▶ \* If the growth rate is directly or indirectly affected by the size of the population
  - ▶ \* There should be some mechanism that decreases population growth rate when population is large
- ▶ This is even true for modern humans!