

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

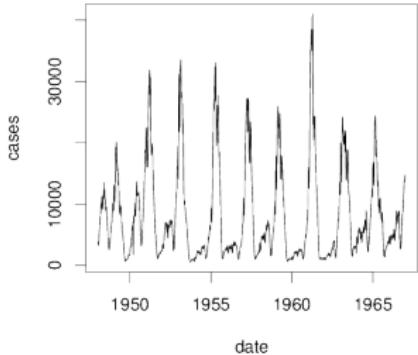
Dynamical models

Tools to link scales

- Models are what we use to link:



Measles reports from England and Wales



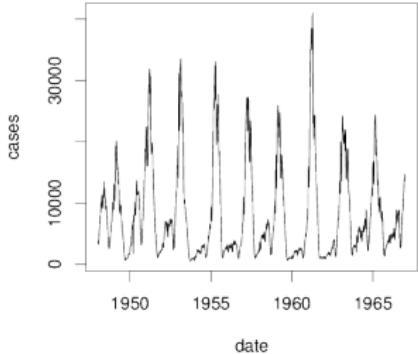
Dynamical models

Tools to link scales

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



Measles reports from England and Wales



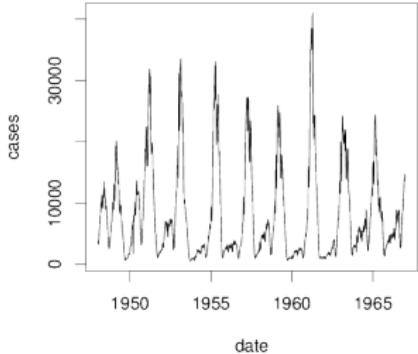
Dynamical models

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



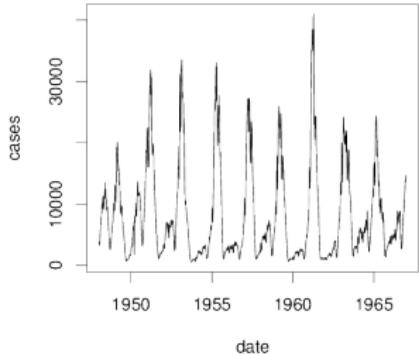
Dynamical models

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



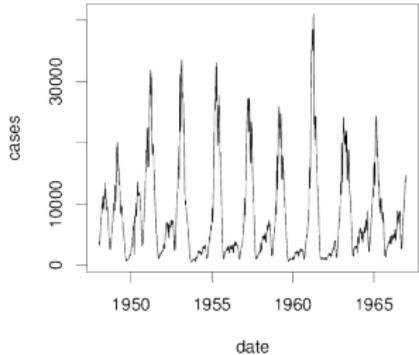
Dynamical models

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

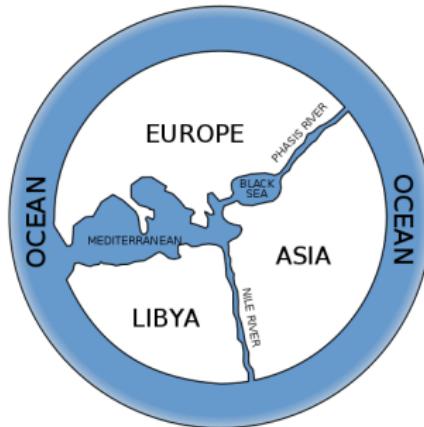


Measles reports from England and Wales



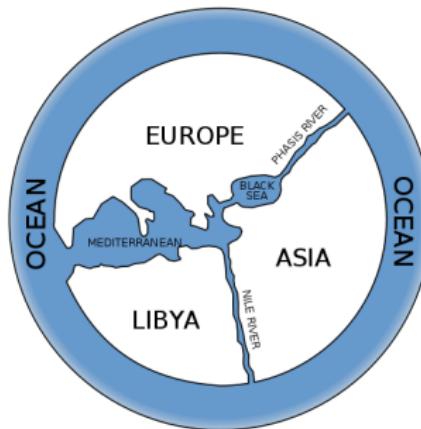
Assumptions

- Models are always simplifications of reality



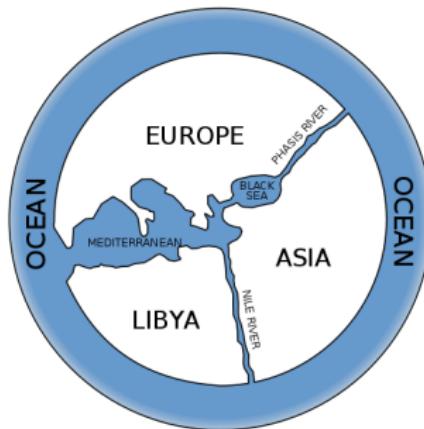
Assumptions

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



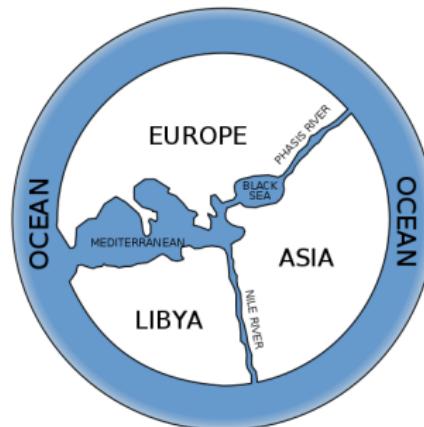
Assumptions

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



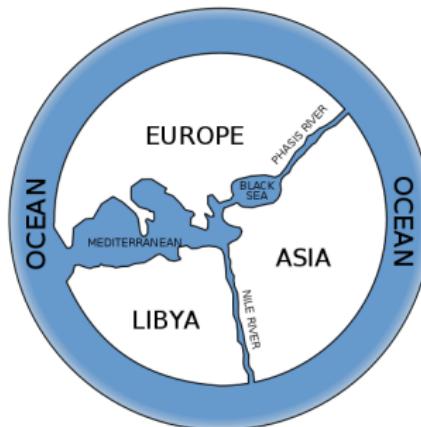
Assumptions

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



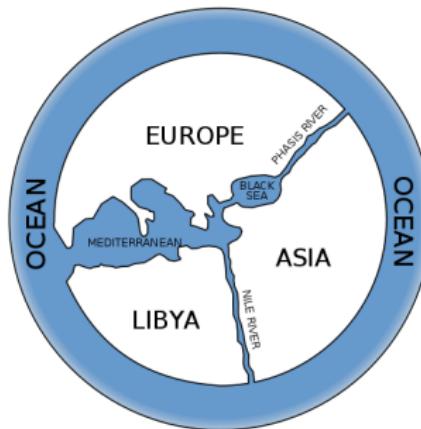
Assumptions

- ▶ 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



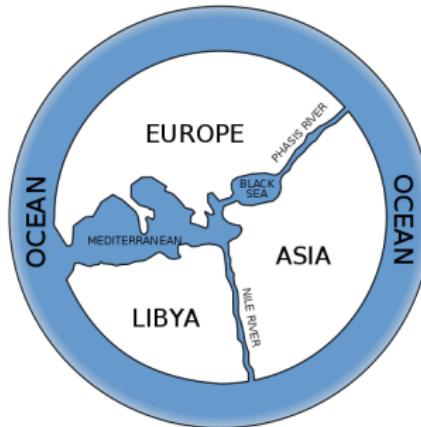
Assumptions

- ▶ 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

Parameters

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

Parameters

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

Parameters

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

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

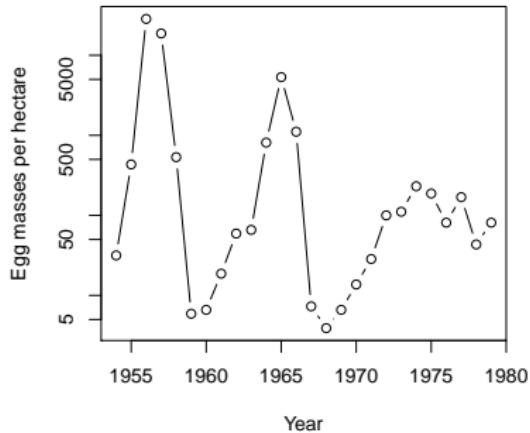
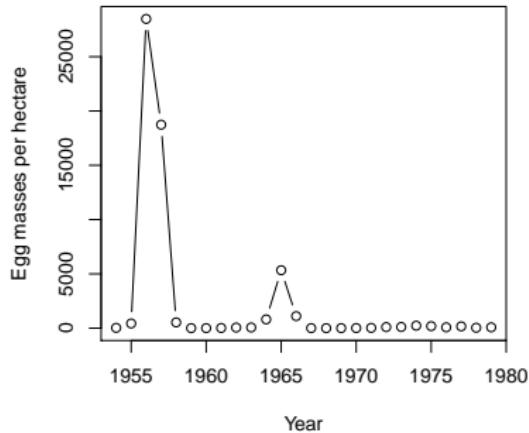


Gypsy moths (repeat)

- ▶ 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

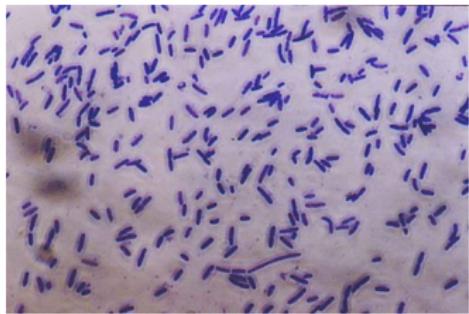
► State variables



Bacteria

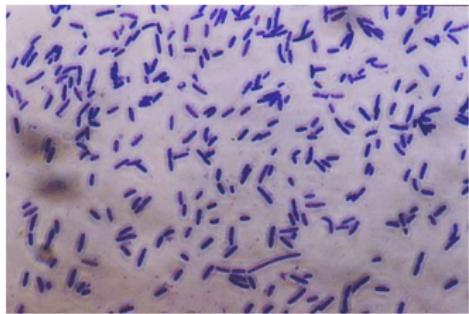
- ▶ State variables

▶ *



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?
- ▶ Parameters



Dandelions

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



Dandelions

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



Dandelions

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



Dandelions

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



Dandelions

- ▶ State variables
 - ▶ * Number of dandelions in a field
 - ▶ Poll: Are there intermediate variables?
- ▶ 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?
- ▶ 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?
- ▶ 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?
- ▶ 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 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 $T + 1$

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?

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?
 - ▶ *

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

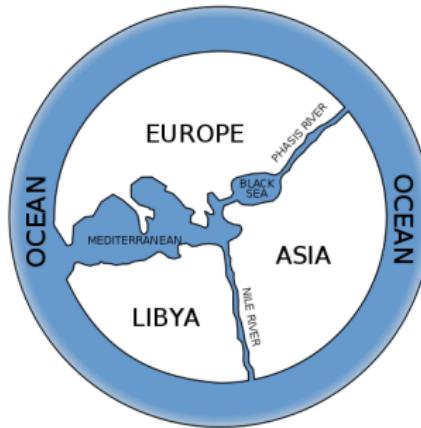
- ▶ If we have N individuals after T time steps, what determines how many individuals we have after $T + 1$ time steps?
 - ▶ A fixed proportion p of the population (on average) survives to be counted at time step $T + 1$
 - ▶ Each individual creates (on average) f new individuals that will be counted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

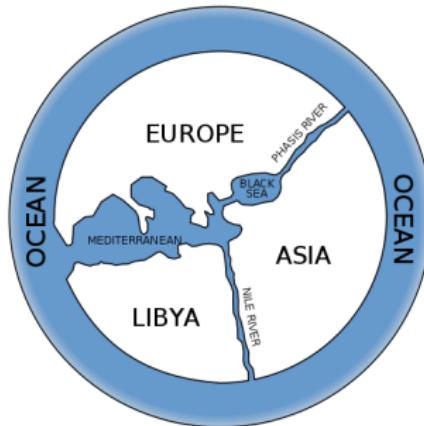
Assumptions

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



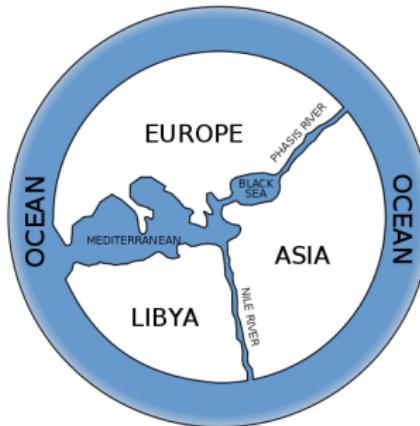
Assumptions

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



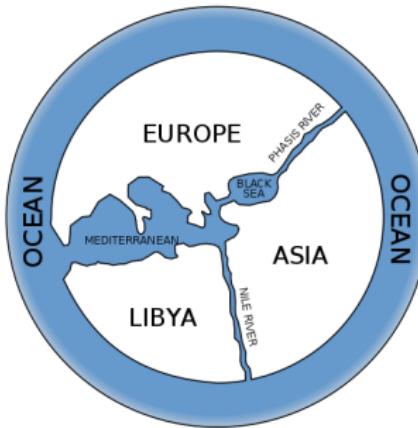
Assumptions

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



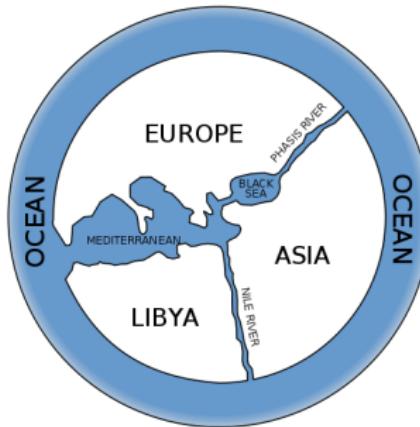
Assumptions

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



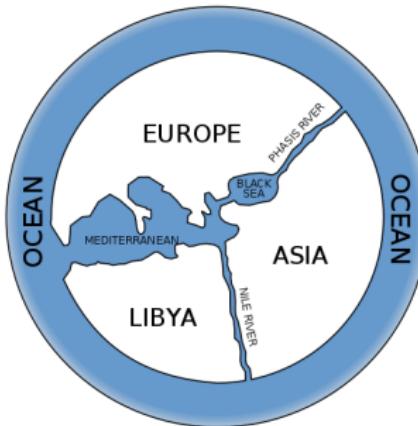
Assumptions

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

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 Δt
 - ▶ (Δt 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 Δt
 - ▶ (Δt 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

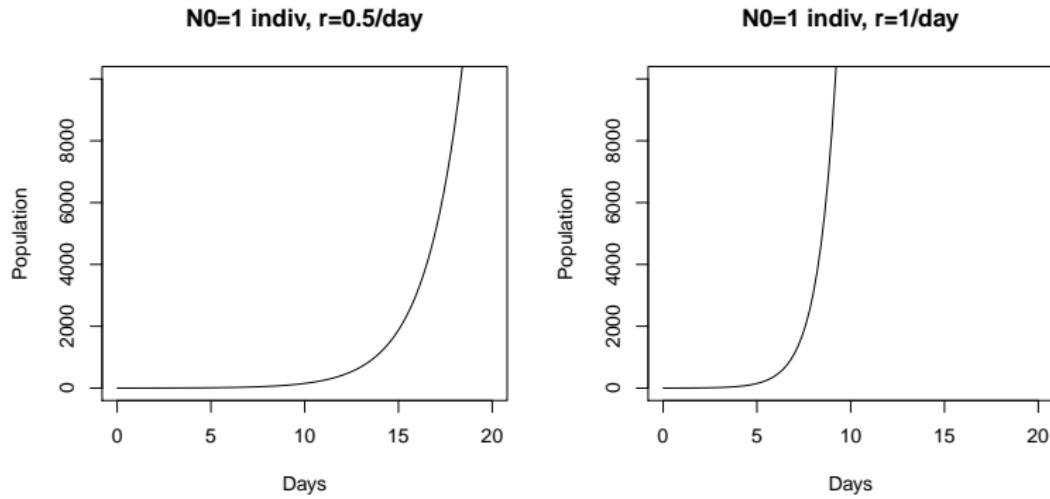
Bacteria

- ▶ 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 $1 \text{ wk} \cdot 0.02/\text{day}$?



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 $1 \text{ wk} \cdot 0.02/\text{day}$?
 - ▶ *



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 $1 \text{ wk} \cdot 0.02/\text{day}$?
 - ▶ * 1 wk · 0.02 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 $1 \text{ wk} \cdot 0.02/\text{day}$?
 - ▶ * 1 wk · 0.02 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 $1 \text{ wk} \cdot 0.02/\text{day}$?
 - ▶ * $1 \text{ wk} \cdot 0.02 \text{ day}$
 - ▶ * $1 \text{ wk} \cdot 0.02 \text{ day} \cdot \frac{7 \text{ day}}{\text{wk}}$



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 $1 \text{ wk} \cdot 0.02/\text{day}$?
 - ▶ * $1 \text{ wk} \cdot 0.02 \text{ day}$
 - ▶ * $1 \text{ wk} \cdot 0.02 \text{ day} \cdot \frac{7 \text{ day}}{\text{wk}}$
 - ▶ *



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 $1 \text{ wk} \cdot 0.02/\text{day}$?
 - ▶ * $1 \text{ wk} \cdot 0.02 \text{ day}$
 - ▶ * $1 \text{ wk} \cdot 0.02 \text{ day} \cdot \frac{7 \text{ day}}{\text{wk}}$
 - ▶ * 0.14



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 $1 \text{ wk} \cdot 0.02/\text{day}$?
 - ▶ * $1 \text{ wk} \cdot 0.02 \text{ day}$
 - ▶ * $1 \text{ wk} \cdot 0.02 \text{ day} \cdot \frac{7 \text{ day}}{\text{wk}}$
 - ▶ * 0.14



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 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 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

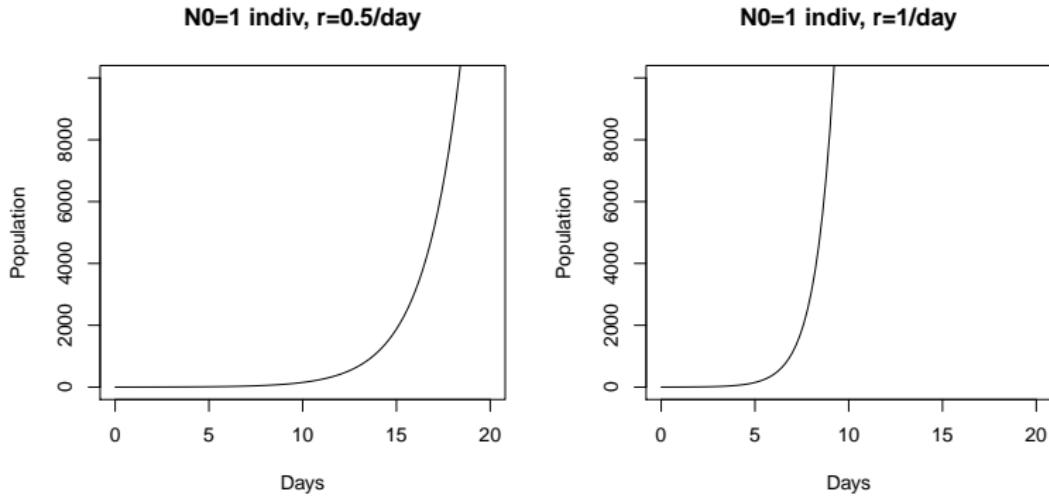
Scaling

- ▶ 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

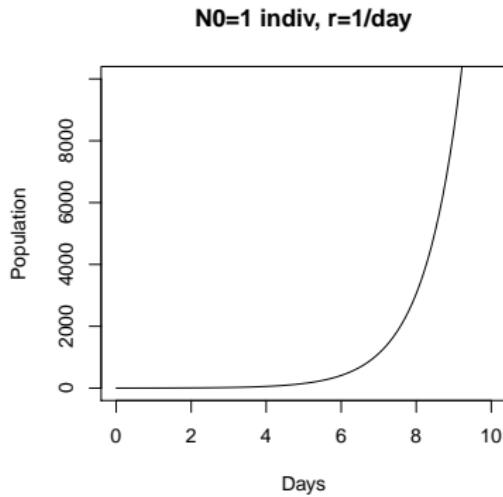
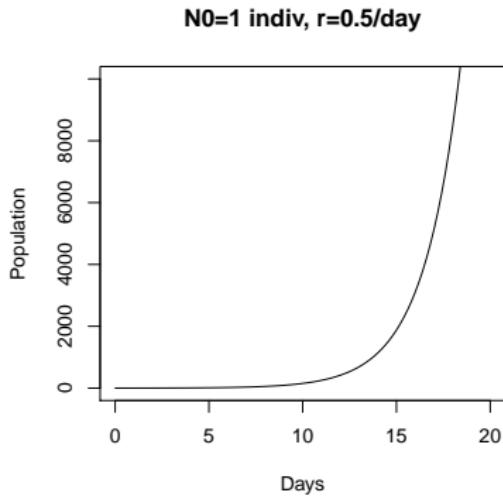
Scaling

- ▶ 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

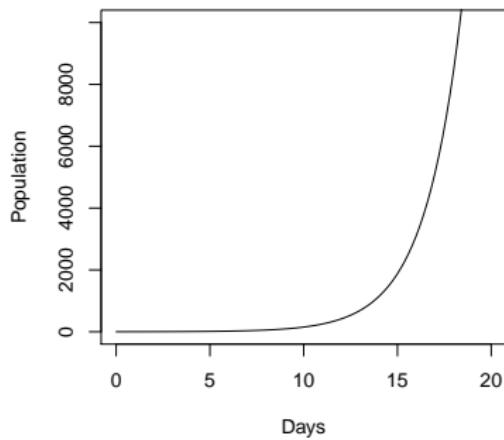


Scaling time in bacteria

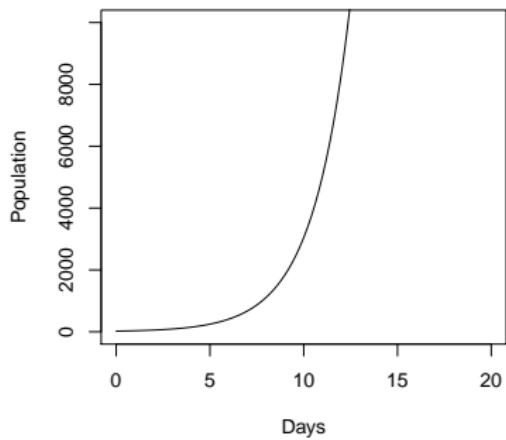


Scaling population

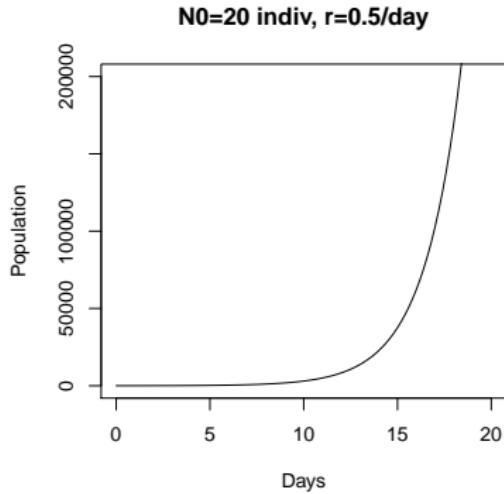
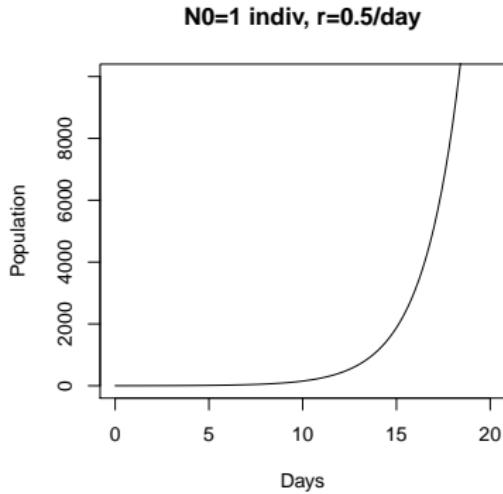
$N_0=1$ indiv, $r=0.5/\text{day}$



$N_0=20$ 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 day^2 – this *could* make sense, but it's 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 day^2 – this *could* make sense, but it's 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:
 - ▶ $0\text{km} = 0\text{cm}$
- ▶ Examples include λ and \mathcal{R} .

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:
 - ▶ $0\text{km} = 0\text{cm}$
- ▶ Examples include λ and \mathcal{R} .

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?
 - ▶ * $1.5 \text{ rA} / \text{rF}$
 - ▶ *

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?
 - ▶ * $1.5 \text{ rA} / \text{rF}$
 - ▶ * 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?
 - ▶ * $1.5 \text{ rA} / \text{rF}$
 - ▶ * Need to multiply by something with units rF/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 λ

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

Calculating λ

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

Calculating λ

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

Calculating λ

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

Calculating λ

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

Calculating λ

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

Calculating λ

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

Calculating λ

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

Calculating λ

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

Calculating λ

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

Finite rate of increase

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

Finite rate of increase

- ▶ Population increases when $\lambda > 1$
- ▶ So λ must be unitless
- ▶ But it is *associated with* the time step Δt
 - ▶ 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 λ must be unitless
- ▶ But it is *associated with* the time step Δt
 - ▶ 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 λ tell us about whether the population is increasing?

Is the population increasing?

- ▶ What does λ tell us about whether the population is increasing?
 - ▶ *

Is the population increasing?

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

Is the population increasing?

- ▶ What does λ 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 λ 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 λ 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 λ 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 λ 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 λ 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 λ 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 effectively 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 effectively 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 effectively 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 effectively 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]

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

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 λ) of:



Long-term growth rate (preview)

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



Long-term growth rate (preview)

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



Long-term growth rate (preview)

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



Long-term growth rate (preview)

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

Long-term growth rate

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

Long-term growth rate

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

Long-term growth rate

- ▶ What is the long-term average exponential growth rate (using either r or λ) 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 λ) 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 λ) 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 λ) 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 λ) 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 λ) 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 λ) 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 λ) 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 λ) 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 λ) 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 much smaller, it would disappear very fast*

Long-term growth rate

- ▶ What is the long-term average exponential growth rate (using either r or λ) 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 much smaller, it would disappear very fast*

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!