UNIT 3 Non-linear population models

Outline

Introduction Population Examples

Continuous-time regulation

A simple, continuous-time model Simulating model behaviour Equilibria and time scales

Discrete-time regulation

A simple, discrete-time model Simulating this system Interpreting complex behaviour

Delayed regulation

Small populations and stochasticity

Allee effects
Stochastic effects

► In **linear** population models, per capita rates are independent of population size

- ▶ In linear population models, per capita rates are independent of population size
- ► In non-linear models, not so much

- ▶ In linear population models, per capita rates are independent of population size
- In non-linear models, not so much
- ► Why might per capita birth and death rates change with population size?

- ▶ In linear population models, per capita rates are independent of population size
- In non-linear models, not so much
- ▶ Why might per capita birth and death rates change with population size?
- ► What does this imply about population dynamics

- ▶ In linear population models, per capita rates are independent of population size
- In non-linear models, not so much
- ▶ Why might per capita birth and death rates change with population size?
- What does this imply about population dynamics

► If individuals are behaving independently:

- ▶ If individuals are behaving independently:
 - ► the population-level rate of growth (or decline) is proportional to the population size

- If individuals are behaving independently:
 - ► the population-level rate of growth (or decline) is proportional to the population size
 - ▶ the population grows (or declines) exponentially

- If individuals are behaving independently:
 - ► the population-level rate of growth (or decline) is proportional to the population size
 - the population grows (or declines) exponentially

The second law of population dynamics

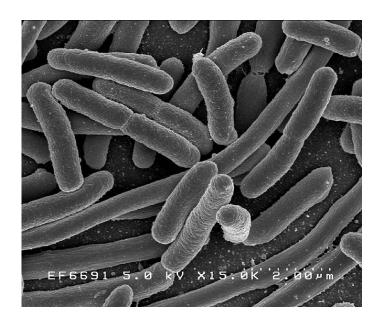
Exponential growth (or decline) cannot continue forever

The second law of population dynamics

- Exponential growth (or decline) cannot continue forever
- Something is changing the average rate at which populations we observe grow

The second law of population dynamics

- Exponential growth (or decline) cannot continue forever
- Something is changing the average rate at which populations we observe grow



 Exponential growth (or decline) cannot continue forever – even on average

- Exponential growth (or decline) cannot continue forever even on average
- ► Environmental variation cannot be the only thing that changes growth rates

- Exponential growth (or decline) cannot continue forever even on average
- Environmental variation cannot be the only thing that changes growth rates
- ► Populations are, directly or indirectly, limiting their own growth rates

- Exponential growth (or decline) cannot continue forever even on average
- Environmental variation cannot be the only thing that changes growth rates
- Populations are, directly or indirectly, limiting their own growth rates
- ► This is called **density dependence**

- Exponential growth (or decline) cannot continue forever even on average
- Environmental variation cannot be the only thing that changes growth rates
- Populations are, directly or indirectly, limiting their own growth rates
- ► This is called **density dependence**

Long-term growth rates

Populations maintain long-term growth rates very close to r = 0

Long-term growth rates

- Populations maintain long-term growth rates very close to r = 0
- ► This is almost certainly because factors affecting their growth rate change with the size of population.

Long-term growth rates

- Populations maintain long-term growth rates very close to r = 0
- ► This is almost certainly because factors affecting their growth rate change with the size of population.

► Poll: What is an example of a density-dependent mechanism that affects growth rate?

▶ Poll: What is an example of a density-dependent mechanism that affects growth rate?

,

- ▶ Poll: What is an example of a density-dependent mechanism that affects growth rate?
 - * Predators

- ▶ Poll: What is an example of a density-dependent mechanism that affects growth rate?
 - * Predators
 - **▶** *

- ▶ Poll: What is an example of a density-dependent mechanism that affects growth rate?
 - * Predators
 - * But! Unless the amount of predators increases as well, they might do worse at controlling the population

- ▶ Poll: What is an example of a density-dependent mechanism that affects growth rate?
 - * Predators
 - ► * But! Unless the amount of predators increases as well, they might do worse at controlling the population
 - **>** *

- ▶ Poll: What is an example of a density-dependent mechanism that affects growth rate?
 - * Predators
 - * But! Unless the amount of predators increases as well, they might do worse at controlling the population
 - * Diseases

- ▶ Poll: What is an example of a density-dependent mechanism that affects growth rate?
 - * Predators
 - * But! Unless the amount of predators increases as well, they might do worse at controlling the population
 - * Diseases
 - *

- ► Poll: What is an example of a density-dependent mechanism that affects growth rate?
 - * Predators
 - ► * But! Unless the amount of predators increases as well, they might do worse at controlling the population
 - * Diseases
 - * Also but. But diseases are very likely to increase in large populations.

- ▶ Poll: What is an example of a density-dependent mechanism that affects growth rate?
 - * Predators
 - * But! Unless the amount of predators increases as well, they might do worse at controlling the population
 - * Diseases
 - * Also but. But diseases are very likely to increase in large populations.
 - *

- ► Poll: What is an example of a density-dependent mechanism that affects growth rate?
 - * Predators
 - ► * But! Unless the amount of predators increases as well, they might do worse at controlling the population
 - * Diseases
 - * Also but. But diseases are very likely to increase in large populations.
 - * Insufficient resources

- ▶ Poll: What is an example of a density-dependent mechanism that affects growth rate?
 - * Predators
 - * But! Unless the amount of predators increases as well, they might do worse at controlling the population
 - * Diseases
 - * Also but. But diseases are very likely to increase in large populations.
 - * Insufficient resources
 - *

- ► Poll: What is an example of a density-dependent mechanism that affects growth rate?
 - * Predators
 - ► * But! Unless the amount of predators increases as well, they might do worse at controlling the population
 - * Diseases
 - * Also but. But diseases are very likely to increase in large populations.
 - * Insufficient resources
 - * Limitation: e.g., oak trees use all the available light

Changing growth rates

- ▶ Poll: What is an example of a density-dependent mechanism that affects growth rate?
 - * Predators
 - ► * But! Unless the amount of predators increases as well, they might do worse at controlling the population
 - * Diseases
 - * Also but. But diseases are very likely to increase in large populations.
 - * Insufficient resources
 - * Limitation: e.g., oak trees use all the available light
 - *

Changing growth rates

- ▶ Poll: What is an example of a density-dependent mechanism that affects growth rate?
 - * Predators
 - * But! Unless the amount of predators increases as well, they might do worse at controlling the population
 - * Diseases
 - * Also but. But diseases are very likely to increase in large populations.
 - * Insufficient resources
 - * Limitation: e.g., oak trees use all the available light
 - ► * Destruction: gypsy moths kill all the oak trees

Changing growth rates

- ▶ Poll: What is an example of a density-dependent mechanism that affects growth rate?
 - * Predators
 - * But! Unless the amount of predators increases as well, they might do worse at controlling the population
 - * Diseases
 - * Also but. But diseases are very likely to increase in large populations.
 - * Insufficient resources
 - * Limitation: e.g., oak trees use all the available light
 - ► * Destruction: gypsy moths kill all the oak trees

► All the populations we see are *regulated*

- ► All the populations we see are *regulated*
 - ► On average, population growth is higher when the population is lower

- ► All the populations we see are *regulated*
 - On average, population growth is higher when the population is lower
 - ► Maybe with a time delay

- All the populations we see are regulated
 - On average, population growth is higher when the population is lower
 - Maybe with a time delay
- ► Why is this interesting?

- All the populations we see are regulated
 - On average, population growth is higher when the population is lower
 - Maybe with a time delay
- Why is this interesting?
 - ► Lots of populations don't *look like* they are regulated

- All the populations we see are regulated
 - On average, population growth is higher when the population is lower
 - Maybe with a time delay
- ▶ Why is this interesting?
 - Lots of populations don't *look like* they are regulated

➤ Some species seem to fill a niche (mangroves)





- Some species seem to fill a niche (mangroves)
- or deplete their own food resources (gypsy moths)





- Some species seem to fill a niche (mangroves)
- or deplete their own food resources (gypsy moths)





 Other species seem like they could easily be more common (pine trees)



- Other species seem like they could easily be more common (pine trees)
 - ► May be controlled by cryptic (hard to see) natural enemies (like disease or parasites)



- Other species seem like they could easily be more common (pine trees)
 - May be controlled by cryptic (hard to see) natural enemies (like disease or parasites)
 - May be controlled by limitations that occur only at certain times (e.g., during regular droughts)



- Other species seem like they could easily be more common (pine trees)
 - May be controlled by cryptic (hard to see) natural enemies (like disease or parasites)
 - May be controlled by limitations that occur only at certain times (e.g., during regular droughts)



► Not every species is experiencing population regulation at every time

- Not every species is experiencing population regulation at every time
- ► A species that we see now may be expanding into a niche (e.g., because of climate change)

- Not every species is experiencing population regulation at every time
- ➤ A species that we see now may be expanding into a niche (e.g., because of climate change)
- ► Some species are controlled by big outbreaks of disease

- Not every species is experiencing population regulation at every time
- ➤ A species that we see now may be expanding into a niche (e.g., because of climate change)
- Some species are controlled by big outbreaks of disease
- Some species have big outbreaks into marginal habitat, and spend most of their time contracting back to their "core" habitat

- Not every species is experiencing population regulation at every time
- ➤ A species that we see now may be expanding into a niche (e.g., because of climate change)
- Some species are controlled by big outbreaks of disease
- Some species have big outbreaks into marginal habitat, and spend most of their time contracting back to their "core" habitat

► Poll: Why don't we believe that population growth is controlled by factors that don't depend on the population itself?

▶ Poll: Why don't we believe that population growth is controlled by factors that don't depend on the population itself?

*

- ▶ Poll: Why don't we believe that population growth is controlled by factors that don't depend on the population itself?
 - ▶ * Because the long-term average value of r has to be very close to 0

- ▶ Poll: Why don't we believe that population growth is controlled by factors that don't depend on the population itself?
 - ► * Because the long-term average value of r has to be very close to 0
 - *

- ▶ Poll: Why don't we believe that population growth is controlled by factors that don't depend on the population itself?
 - * Because the long-term average value of r has to be very close to 0
 - ► * This is true for *every* population

- ▶ Poll: Why don't we believe that population growth is controlled by factors that don't depend on the population itself?
 - ► * Because the long-term average value of r has to be very close to 0
 - ► * This is true for *every* population
 - *

- ▶ Poll: Why don't we believe that population growth is controlled by factors that don't depend on the population itself?
 - ▶ * Because the long-term average value of r has to be very close to 0
 - ► * This is true for *every* population
 - * This is unlikely to occur by chance

- ▶ Poll: Why don't we believe that population growth is controlled by factors that don't depend on the population itself?
 - ► * Because the long-term average value of r has to be very close to 0
 - ► * This is true for *every* population
 - ► * This is unlikely to occur by chance
 - *

- ▶ Poll: Why don't we believe that population growth is controlled by factors that don't depend on the population itself?
 - ► * Because the long-term average value of r has to be very close to 0
 - ► * This is true for *every* population
 - * This is unlikely to occur by chance
 - * Thus, it must be through direct or indirect responses to the population size

- ▶ Poll: Why don't we believe that population growth is controlled by factors that don't depend on the population itself?
 - ► * Because the long-term average value of r has to be very close to 0
 - ► * This is true for *every* population
 - * This is unlikely to occur by chance
 - * Thus, it must be through direct or indirect responses to the population size

Outline

Introduction Population Examples

Continuous-time regulation

A simple, continuous-time model Simulating model behaviour Equilibria and time scales

Discrete-time regulation

A simple, discrete-time model Simulating this system Interpreting complex behaviour

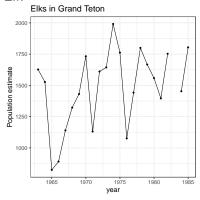
Delayed regulation

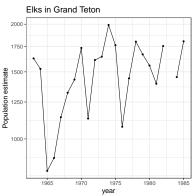
Small populations and stochasticity

Allee effects
Stochastic effects

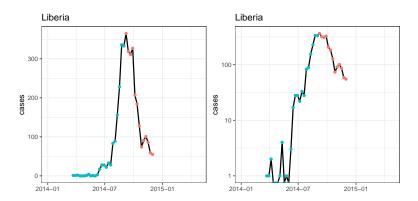
(preview)



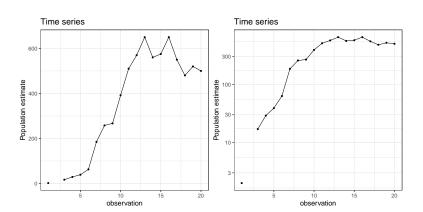




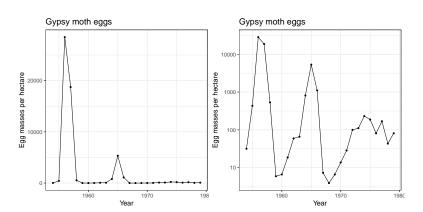
Ebola



Paramecia (preview)



Gypsy moths (preview)



► Poll: What are some factors that limit gypsy-moth populations?

- ▶ Poll: What are some factors that limit gypsy-moth populations?
- ► Which are likely to be affected by the moths?

- ▶ Poll: What are some factors that limit gypsy-moth populations?
- ▶ Which are likely to be affected by the moths?
 - ▶ Directly or indirectly, in the short or long term?

- ▶ Poll: What are some factors that limit gypsy-moth populations?
- ▶ Which are likely to be affected by the moths?
 - Directly or indirectly, in the short or long term?

Outline

Introduction

Population Examples

Continuous-time regulation

A simple, continuous-time model Simulating model behaviour Equilibria and time scales

Discrete-time regulation

A simple, discrete-time model Simulating this system Interpreting complex behaviour

Delayed regulation

Small populations and stochasticity

Allee effects
Stochastic effects

► Our linear population model is:

Our linear population model is:

Our linear population model is:

► Per-capita rates are constant

► Our linear population model is:

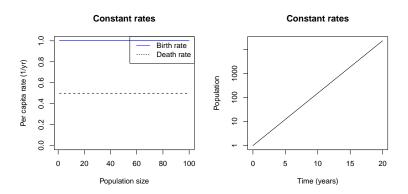
- Per-capita rates are constant
- ► Population-level rates are linear

Our linear population model is:

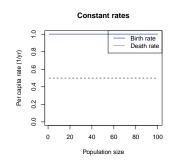
- Per-capita rates are constant
- Population-level rates are linear
- Behaviour is exponential

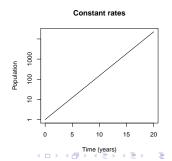
► Our linear population model is:

- Per-capita rates are constant
- Population-level rates are linear
- Behaviour is exponential

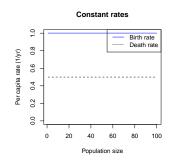


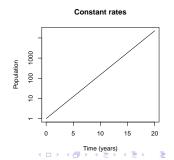
Per capita rate shows birth and death per individual



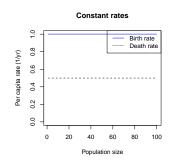


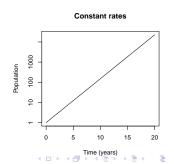
- Per capita rate shows birth and death per individual
- Corresponds to the time plot showing growth on a log scale



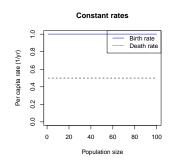


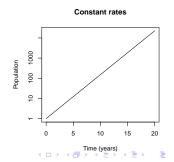
- Per capita rate shows birth and death per individual
- Corresponds to the time plot showing growth on a log scale
 - On the log scale we see multiplicative or proportional change

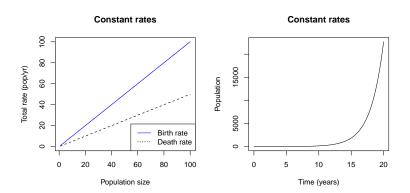




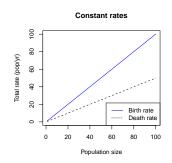
- Per capita rate shows birth and death per individual
- Corresponds to the time plot showing growth on a log scale
 - On the log scale we see multiplicative or proportional change

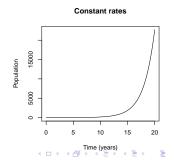




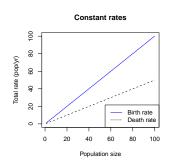


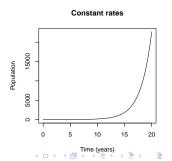
► Total rate shows birth and death for the whole population



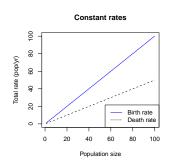


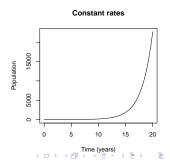
- ► Total rate shows birth and death for the whole population
- Corresponds to the time plot showing growth on a linear scale



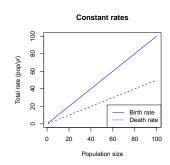


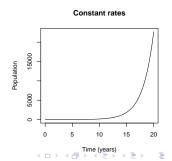
- ► Total rate shows birth and death for the whole population
- Corresponds to the time plot showing growth on a linear scale
 - ► On the linear scale we see additive or absolute change





- ► Total rate shows birth and death for the whole population
- Corresponds to the time plot showing growth on a linear scale
 - On the linear scale we see additive or absolute change





▶ Population has per capita birth rate b(N) and death rate d(N)

- Population has per capita birth rate b(N) and death rate d(N)
 - ▶ Per-capita rates change with the population size

- ▶ Population has per capita birth rate b(N) and death rate d(N)
 - ▶ Per-capita rates change with the population size
- ► Our non-linear model is: $\frac{dN}{dt} = (b(N) d(N))N \equiv r(N)N$

- ▶ Population has per capita birth rate b(N) and death rate d(N)
 - Per-capita rates change with the population size
- ▶ Our non-linear model is: $\frac{dN}{dt} = (b(N) d(N))N \equiv r(N)N$
 - ▶ Defines how fast the population is changing at any instant

- ▶ Population has per capita birth rate b(N) and death rate d(N)
 - Per-capita rates change with the population size
- ▶ Our non-linear model is: $\frac{dN}{dt} = (b(N) d(N))N \equiv r(N)N$
 - Defines how fast the population is changing at any instant

► **Recruitment** is when an organism moves from one life stage to another:

- ► **Recruitment** is when an organism moves from one life stage to another:
 - ► Seed \rightarrow seedling \rightarrow sapling \rightarrow tree

- ▶ **Recruitment** is when an organism moves from one life stage to another:
 - ► Seed →seedling →sapling →tree
 - ▶ Egg \rightarrow larva \rightarrow pupa \rightarrow moth

- ► **Recruitment** is when an organism moves from one life stage to another:
 - ▶ Seed \rightarrow seedling \rightarrow sapling \rightarrow tree
 - ► Egg \rightarrow larva \rightarrow pupa \rightarrow moth
- ► In simple continuous-time population models, recruitment is included in birth:

- ► **Recruitment** is when an organism moves from one life stage to another:
 - ▶ Seed \rightarrow seedling \rightarrow sapling \rightarrow tree
 - ► Egg \rightarrow larva \rightarrow pupa \rightarrow moth
- In simple continuous-time population models, recruitment is included in birth:
 - ▶ *b* is the rate at which adults produce new adults; or seeds produce new seeds we have to "close the loop"

- ► **Recruitment** is when an organism moves from one life stage to another:
 - ▶ Seed \rightarrow seedling \rightarrow sapling \rightarrow tree
 - ► Egg \rightarrow larva \rightarrow pupa \rightarrow moth
- In simple continuous-time population models, recruitment is included in birth:
 - ▶ b is the rate at which adults produce new adults; or seeds produce new seeds we have to "close the loop"

► When a population is crowded, the birth rate will usually go down



- When a population is crowded, the birth rate will usually go down
 - Resources are limited: space, food, light



- When a population is crowded, the birth rate will usually go down
 - Resources are limited: space, food, light
- ► But it may stay the same



- When a population is crowded, the birth rate will usually go down
 - Resources are limited: space, food, light
- But it may stay the same
- Or even go up



Birth rates

- When a population is crowded, the birth rate will usually go down
 - Resources are limited: space, food, light
- But it may stay the same
- Or even go up
 - If individuals shift their resources to reproduction instead of survival



Birth rates

- When a population is crowded, the birth rate will usually go down
 - Resources are limited: space, food, light
- But it may stay the same
- Or even go up
 - If individuals shift their resources to reproduction instead of survival



► When a population is crowded, the death rate will often go up



- ► When a population is crowded, the death rate will often go up
 - Individuals are starving, or conflict increases



- ► When a population is crowded, the death rate will often go up
 - Individuals are starving, or conflict increases
 - ► But it may stay the same



- When a population is crowded, the death rate will often go up
 - Individuals are starving, or conflict increases
 - But it may stay the same
 - if reproduction is limited by competition for breeding sites, or by recruitment of juveniles



- When a population is crowded, the death rate will often go up
 - Individuals are starving, or conflict increases
 - But it may stay the same
 - if reproduction is limited by competition for breeding sites, or by recruitment of juveniles
 - Or even go down



- When a population is crowded, the death rate will often go up
 - Individuals are starving, or conflict increases
 - But it may stay the same
 - if reproduction is limited by competition for breeding sites, or by recruitment of juveniles
 - Or even go down
 - if organisms go into some sort of "resting mode"



- When a population is crowded, the death rate will often go up
 - Individuals are starving, or conflict increases
 - But it may stay the same
 - if reproduction is limited by competition for breeding sites, or by recruitment of juveniles
 - Or even go down
 - if organisms go into some sort of "resting mode"



► Our model is:
$$\frac{dN}{dt} = (b(N) - d(N))N \equiv r(N)N$$

- Our model is: $\frac{dN}{dt} = (b(N) d(N))N \equiv r(N)N$
- ► Reproductive number now also changes with *N*:

• Our model is:
$$\frac{dN}{dt} = (b(N) - d(N))N \equiv r(N)N$$

 \triangleright Reproductive number now also changes with N:



- Our model is: $\frac{dN}{dt} = (b(N) d(N))N \equiv r(N)N$
- Reproductive number now also changes with N:

$$\blacktriangleright * \mathcal{R}(N) = b(N)/d(N)$$

- Our model is: $\frac{dN}{dt} = (b(N) d(N))N \equiv r(N)N$
- ▶ Reproductive number now also changes with *N*:
 - $\blacktriangleright * \mathcal{R}(N) = b(N)/d(N)$
- ► When the population is crowded, individuals are stressed and the reproductive number will typically go down.

- Our model is: $\frac{dN}{dt} = (b(N) d(N))N \equiv r(N)N$
- Reproductive number now also changes with N:

$$\blacktriangleright * \mathcal{R}(N) = b(N)/d(N)$$

▶ When the population is crowded, individuals are stressed and the reproductive number will typically go down.

▶ If a population has $\mathcal{R}(N) > 1$ when it's not crowded

- ▶ If a population has $\mathcal{R}(N) > 1$ when it's not crowded
- ► The population should increase

- ▶ If a population has $\mathcal{R}(N) > 1$ when it's not crowded
- ► The population should increase
- lacktriangle Eventually, ${\cal R}$ will decrease, and eventually cross ${\cal R}=1$

- ▶ If a population has $\mathcal{R}(N) > 1$ when it's not crowded
- ► The population should increase
- lacktriangle Eventually, ${\cal R}$ will decrease, and eventually cross ${\cal R}=1$
- ▶ We call the special value of N where $\mathcal{R}(N) = 1$, the **carrying** capacity, K

- ▶ If a population has $\mathcal{R}(N) > 1$ when it's not crowded
- ► The population should increase
- lacktriangle Eventually, ${\cal R}$ will decrease, and eventually cross ${\cal R}=1$
- We call the special value of N where $\mathcal{R}(N) = 1$, the **carrying** capacity, K
 - $ightharpoonup \mathcal{R}(K) \equiv 1$

- ▶ If a population has $\mathcal{R}(N) > 1$ when it's not crowded
- The population should increase
- lacktriangle Eventually, ${\cal R}$ will decrease, and eventually cross ${\cal R}=1$
- We call the special value of N where $\mathcal{R}(N) = 1$, the **carrying** capacity, K
 - $ightharpoonup \mathcal{R}(K) \equiv 1$
 - $b(K) \equiv d(K)$

- ▶ If a population has $\mathcal{R}(N) > 1$ when it's not crowded
- ► The population should increase
- lacktriangle Eventually, ${\cal R}$ will decrease, and eventually cross ${\cal R}=1$
- We call the special value of N where $\mathcal{R}(N) = 1$, the **carrying** capacity, K
 - $ightharpoonup \mathcal{R}(K) \equiv 1$
 - $b(K) \equiv d(K)$
- ▶ When N = K:

- ▶ If a population has $\mathcal{R}(N) > 1$ when it's not crowded
- ► The population should increase
- lacktriangle Eventually, ${\cal R}$ will decrease, and eventually cross ${\cal R}=1$
- We call the special value of N where $\mathcal{R}(N) = 1$, the **carrying** capacity, K
 - $ightharpoonup \mathcal{R}(K) \equiv 1$
 - $b(K) \equiv d(K)$
- ▶ When N = K:
 - •

- ▶ If a population has $\mathcal{R}(N) > 1$ when it's not crowded
- ► The population should increase
- lacktriangle Eventually, ${\cal R}$ will decrease, and eventually cross ${\cal R}=1$
- We call the special value of N where $\mathcal{R}(N) = 1$, the **carrying** capacity, K
 - $ightharpoonup \mathcal{R}(K) \equiv 1$
 - \blacktriangleright $b(K) \equiv d(K)$
- \blacktriangleright When N=K:
 - ▶ * Population stays the same, on average

- ▶ If a population has $\mathcal{R}(N) > 1$ when it's not crowded
- ► The population should increase
- lacktriangle Eventually, ${\cal R}$ will decrease, and eventually cross ${\cal R}=1$
- We call the special value of N where $\mathcal{R}(N) = 1$, the **carrying** capacity, K
 - $ightharpoonup \mathcal{R}(K) \equiv 1$
 - \blacktriangleright $b(K) \equiv d(K)$
- \blacktriangleright When N=K:
 - ▶ * Population stays the same, on average

► A popular model of density-dependent growth is the logistic model

- ► A popular model of density-dependent growth is the logistic model
- ightharpoonup Per capita instantaneous growth rate r is a function of N

- ► A popular model of density-dependent growth is the logistic model
- \triangleright Per capita instantaneous growth rate r is a function of N

$$r(N) = r_{\text{max}}(1 - N/K)$$

- A popular model of density-dependent growth is the logistic model
- \triangleright Per capita instantaneous growth rate r is a function of N
 - $ightharpoonup r(N) = r_{\text{max}}(1 N/K)$
 - ▶ Consistent with various assumptions about b(N) and d(N)

- A popular model of density-dependent growth is the logistic model
- Per capita instantaneous growth rate r is a function of N
 - $r(N) = r_{\mathsf{max}}(1 N/K)$
 - ightharpoonup Consistent with various assumptions about b(N) and d(N)
- Population increases to K and remans there

- A popular model of density-dependent growth is the logistic model
- Per capita instantaneous growth rate r is a function of N
 - $r(N) = r_{\mathsf{max}}(1 N/K)$
 - ▶ Consistent with various assumptions about b(N) and d(N)
- Population increases to K and remans there
 - ► Units of *N* must match units of *K*

- A popular model of density-dependent growth is the logistic model
- Per capita instantaneous growth rate r is a function of N
 - $r(N) = r_{\mathsf{max}}(1 N/K)$
 - ightharpoonup Consistent with various assumptions about b(N) and d(N)
- Population increases to K and remans there
 - Units of N must match units of K
- ► Not a linear model, because *population-level* rates are not linear

- A popular model of density-dependent growth is the logistic model
- Per capita instantaneous growth rate r is a function of N
 - $r(N) = r_{\mathsf{max}}(1 N/K)$
 - ▶ Consistent with various assumptions about b(N) and d(N)
- Population increases to K and remans there
 - Units of N must match units of K
- Not a linear model, because population-level rates are not linear

Exponential-rates model

▶ In this course, we'll mostly use another simple model:

Exponential-rates model

▶ In this course, we'll mostly use another simple model:

$$b(N) = b_0 \exp(-N/N_b)$$

Exponential-rates model

- ▶ In this course, we'll mostly use another simple model:
 - $b(N) = b_0 \exp(-N/N_b)$
 - $b d(N) = d_0 \exp(N/N_d)$

- ▶ In this course, we'll mostly use another simple model:
 - $b(N) = b_0 \exp(-N/N_b)$
 - $d(N) = d_0 \exp(N/N_d)$
- ► This is the simplest model that is smooth and keeps track of birth and death rates separately

- ▶ In this course, we'll mostly use another simple model:
 - $b(N) = b_0 \exp(-N/N_b)$
 - $d(N) = d_0 \exp(N/N_d)$
- This is the simplest model that is smooth and keeps track of birth and death rates separately
 - ightharpoonup Birth rate goes down with characteristic scale N_b

- ▶ In this course, we'll mostly use another simple model:
 - $b(N) = b_0 \exp(-N/N_b)$
 - $d(N) = d_0 \exp(N/N_d)$
- ▶ This is the simplest model that is smooth and keeps track of birth and death rates separately
 - ightharpoonup Birth rate goes down with characteristic scale N_b
 - ightharpoonup Death rate goes up with characteristic scale N_d

- ▶ In this course, we'll mostly use another simple model:
 - \blacktriangleright $b(N) = b_0 \exp(-N/N_b)$
 - $d(N) = d_0 \exp(N/N_d)$
- This is the simplest model that is smooth and keeps track of birth and death rates separately
 - \triangleright Birth rate goes down with characteristic scale N_b
 - ightharpoonup Death rate goes up with characteristic scale N_d

► The exponential-rates model is conceptually clearer

- ▶ The exponential-rates model is conceptually clearer
 - ► Birth and death rates are clearly defined

- The exponential-rates model is conceptually clearer
 - Birth and death rates are clearly defined
- ► Mathematically nicer

- The exponential-rates model is conceptually clearer
 - Birth and death rates are clearly defined
- ► Mathematically nicer
 - Rates always stay positive

- The exponential-rates model is conceptually clearer
 - Birth and death rates are clearly defined
- ► Mathematically nicer
 - Rates always stay positive
- ► The logistic *looks* less scary

- The exponential-rates model is conceptually clearer
 - Birth and death rates are clearly defined
- Mathematically nicer
 - Rates always stay positive
- ► The logistic *looks* less scary

Outline

Introduction

Population Examples

Continuous-time regulation

A simple, continuous-time model

Simulating model behaviour Equilibria and time scales

Discrete-time regulation

A simple, discrete-time model Simulating this system Interpreting complex behaviour

Delayed regulation

Small populations and stochasticity

Allee effects
Stochastic effects

► We model individual-level rates, but individuals are *not* independent: my rates depend on the number (or density) of individuals in the population

- We model individual-level rates, but individuals are not independent: my rates depend on the number (or density) of individuals in the population
- ► The population can be censused at any time

- ▶ We model individual-level rates, but individuals are not independent: my rates depend on the number (or density) of individuals in the population
- ▶ The population can be censused at any time
- ► Population size changes continuously

- We model individual-level rates, but individuals are not independent: my rates depend on the number (or density) of individuals in the population
- ▶ The population can be censused at any time
- Population size changes continuously
- ► All individuals are the same all the time

- We model individual-level rates, but individuals are not independent: my rates depend on the number (or density) of individuals in the population
- ▶ The population can be censused at any time
- Population size changes continuously
- ► All individuals are the same all the time
- ► Population changes deterministically

- We model individual-level rates, but individuals are not independent: my rates depend on the number (or density) of individuals in the population
- ▶ The population can be censused at any time
- Population size changes continuously
- ► All individuals are the same all the time
- ► Population changes deterministically

► If we have *N* individuals at time *t*, how does the population change?

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

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

- ▶ If we have *N* individuals at time *t*, how does the population change?
 - Individuals are giving birth at per-capita rate b(N)
 - Individuals are dying at per-capita rate d(N)
- ► Population dynamics follow:

- ▶ If we have *N* individuals at time *t*, how does the population change?
 - Individuals are giving birth at per-capita rate b(N)
 - Individuals are dying at per-capita rate d(N)
- ► Population dynamics follow:

- ▶ If we have *N* individuals at time *t*, how does the population change?
 - Individuals are giving birth at per-capita rate b(N)
 - ▶ Individuals are dying at per-capita rate d(N)
- ► Population dynamics follow:

▶ What variable or variables describe the state of this system?

▶ What variable or variables describe the state of this system?

*

- ▶ What variable or variables describe the state of this system?
 - ▶ * The same as before: population size (or density)

- ▶ What variable or variables describe the state of this system?
 - ► * The same as before: population size (or density)
 - *

- What variable or variables describe the state of this system?
 - ► * The same as before: population size (or density)
 - ▶ * We are still assuming that's all we need to know

- ▶ What variable or variables describe the state of this system?
 - ▶ * The same as before: population size (or density)
 - ▶ * We are still assuming that's all we need to know
 - *

- What variable or variables describe the state of this system?
 - ► * The same as before: population size (or density)
 - ▶ * We are still assuming that's all we need to know
 - * In other words, that all individuals are the same.

- What variable or variables describe the state of this system?
 - ► * The same as before: population size (or density)
 - ▶ * We are still assuming that's all we need to know
 - * In other words, that all individuals are the same.

▶ Poll: What quantities describe the rules for this system?

▶ Poll: What quantities describe the rules for this system?

*

- ▶ Poll: What quantities describe the rules for this system?
 - ▶ * *b*₀ [1/time]

- ▶ Poll: What quantities describe the rules for this system?
 - ▶ * *b*₀ [1/time]
 - >

- ▶ Poll: What quantities describe the rules for this system?
 - ▶ * *b*₀ [1/time]
 - ▶ * *d*₀ [1/time]

- ▶ Poll: What quantities describe the rules for this system?
 - ▶ * *b*₀ [1/time]
 - ▶ * *d*₀ [1/time]
 - >

- ▶ Poll: What quantities describe the rules for this system?
 - ▶ * *b*₀ [1/time]
 - ▶ * *d*₀ [1/time]
 - ► * N_b [indiv] (or [indiv/area])

- ▶ Poll: What quantities describe the rules for this system?
 - ▶ * *b*₀ [1/time]
 - ▶ * *d*₀ [1/time]
 - ► * N_b [indiv] (or [indiv/area])
 - **×**

- ▶ Poll: What quantities describe the rules for this system?
 - ▶ * *b*₀ [1/time]
 - ▶ * *d*₀ [1/time]
 - ► * N_b [indiv] (or [indiv/area])
 - ► * N_d [indiv] (or [indiv/area])

- ▶ Poll: What quantities describe the rules for this system?
 - ▶ * *b*₀ [1/time]
 - ▶ * *d*₀ [1/time]
 - ► * N_b [indiv] (or [indiv/area])
 - ► * N_d [indiv] (or [indiv/area])

► A characteristic scale for density dependence is analogous to a characteristic time

► A characteristic scale for density dependence is analogous to a characteristic time

► For example: $b(N) = b_0 \exp(-N/N_b)$

- ► A characteristic scale for density dependence is analogous to a characteristic time
- ▶ For example: $b(N) = b_0 \exp(-N/N_b)$
 - ► *N_b* is the characteristic scale of density-dependence in birth rate

- ► A characteristic scale for density dependence is analogous to a characteristic time
- ▶ For example: $b(N) = b_0 \exp(-N/N_b)$
 - N_b is the characteristic scale of density-dependence in birth rate
 - ▶ If $N \ll N_b$, density dependence is linear (and relatively small)

- A characteristic scale for density dependence is analogous to a characteristic time
- ▶ For example: $b(N) = b_0 \exp(-N/N_b)$
 - \triangleright N_b is the characteristic scale of density-dependence in birth rate
 - ▶ If $N \ll N_b$, density dependence is linear (and relatively small)
 - ► If $N \gg N_b$, density dependence is exponential, and very large (virtually no births)

- A characteristic scale for density dependence is analogous to a characteristic time
- ▶ For example: $b(N) = b_0 \exp(-N/N_b)$
 - N_b is the characteristic scale of density-dependence in birth rate
 - ▶ If $N \ll N_b$, density dependence is linear (and relatively small)
 - If $N \gg N_b$, density dependence is exponential, and very large (virtually no births)

► Dynamics:

Dynamics:

► Exact solution:

- Exact solution:
 - ► Insanely complicated

- Exact solution:
 - Insanely complicated
- Behaviour of the solution:

- Exact solution:
 - Insanely complicated
- Behaviour of the solution:
 - ► Pretty easy!

- Exact solution:
 - Insanely complicated
- Behaviour of the solution:
 - Pretty easy!

What sort of dynamics do we expect from our conceptual model?

- ► What sort of **dynamics** do we expect from our conceptual model?
 - ► I.e., how will it change through time?

- What sort of dynamics do we expect from our conceptual model?
 - ► I.e., how will it change through time?
- ► What will the population do if it starts

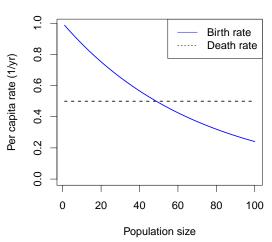
- What sort of dynamics do we expect from our conceptual model?
 - ► I.e., how will it change through time?
- ▶ What will the population do if it starts
 - ► near zero?

- What sort of dynamics do we expect from our conceptual model?
 - ► I.e., how will it change through time?
- ▶ What will the population do if it starts
 - near zero?
 - ► near the equilibrium?

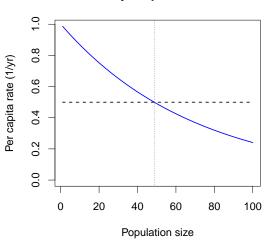
- What sort of dynamics do we expect from our conceptual model?
 - ► I.e., how will it change through time?
- ▶ What will the population do if it starts
 - near zero?
 - near the equilibrium?
 - ► at a high value?

- What sort of dynamics do we expect from our conceptual model?
 - ► I.e., how will it change through time?
- ▶ What will the population do if it starts
 - near zero?
 - near the equilibrium?
 - at a high value?

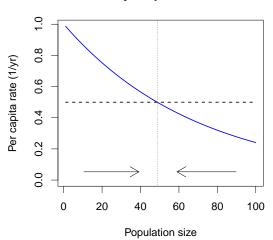
Density-dependent birth

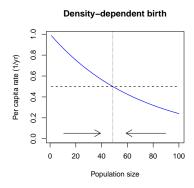


Density-dependent birth

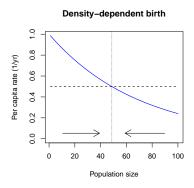


Density-dependent birth

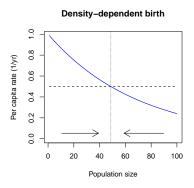




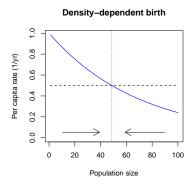
► Increase when population is below equilibrium



- Increase when population is below equilibrium
- ► Decrease when population is above equilibrium

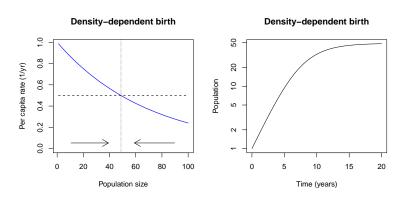


- Increase when population is below equilibrium
- ► Decrease when population is above equilibrium
- ► Converge

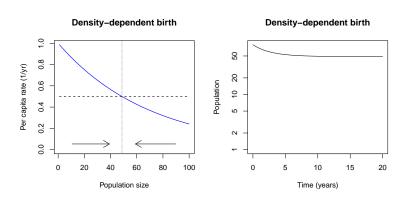


- ► Increase when population is below equilibrium
- Decrease when population is above equilibrium
- Converge

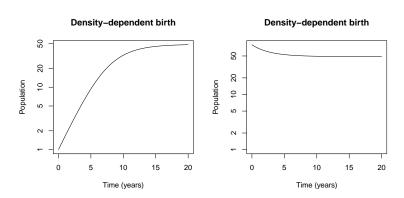
Low starting population example



High starting population example



Examples



Outline

Introduction

Population Examples

Continuous-time regulation

A simple, continuous-time model

Simulating model behaviour

Equilibria and time scales

Discrete-time regulation

A simple, discrete-time model Simulating this system Interpreting complex behaviour

Delayed regulation

Small populations and stochasticity

Allee effects

Stochastic effects

Simulations

► We will simulate the behaviour of populations in continuous time using the program R

Simulations

- ► We will simulate the behaviour of populations in continuous time using the program R
- ► This program generates the pictures in this section by implementing our model of how the population changes instantaneously

Simulations

- We will simulate the behaviour of populations in continuous time using the program R
- ► This program generates the pictures in this section by implementing our model of how the population changes instantaneously

 We can view graphs of our population assumptions on the individual scale

- We can view graphs of our population assumptions on the individual scale
 - per-capita birth and death rates

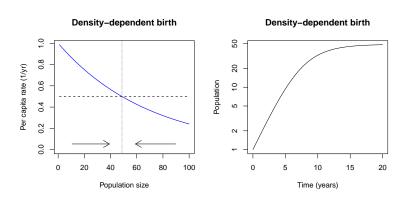
- We can view graphs of our population assumptions on the individual scale
 - per-capita birth and death rates
 - units [1/time]

- We can view graphs of our population assumptions on the individual scale
 - per-capita birth and death rates
 - units [1/time]
 - ▶ what is each individual doing (on average)?

- We can view graphs of our population assumptions on the individual scale
 - per-capita birth and death rates
 - units [1/time]
 - what is each individual doing (on average)?
 - corresponds to the dynamics we visualize on a log-scale graph of the population

- We can view graphs of our population assumptions on the individual scale
 - per-capita birth and death rates
 - units [1/time]
 - what is each individual doing (on average)?
 - corresponds to the dynamics we visualize on a log-scale graph of the population

What will this model do? (repeat)



► We can view graphs of our population assumptions on the population scale

- We can view graphs of our population assumptions on the population scale
 - total birth and death rates

- We can view graphs of our population assumptions on the population scale
 - total birth and death rates
 - units [indiv/time]

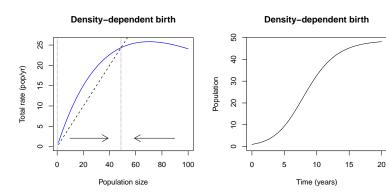
- We can view graphs of our population assumptions on the population scale
 - total birth and death rates
 - units [indiv/time]
 - ▶ or [density/time] = [(indiv/area)/time]

- We can view graphs of our population assumptions on the population scale
 - total birth and death rates
 - units [indiv/time]
 - or [density/time] = [(indiv/area)/time]
 - what is changing at the population level?

- We can view graphs of our population assumptions on the population scale
 - total birth and death rates
 - units [indiv/time]
 - or [density/time] = [(indiv/area)/time]
 - what is changing at the population level?
 - corresponds to the dynamics we visualize on a linear-scale graph of the population

- ► We can view graphs of our population assumptions on the population scale
 - total birth and death rates
 - units [indiv/time]
 - or [density/time] = [(indiv/area)/time]
 - what is changing at the population level?
 - corresponds to the dynamics we visualize on a linear-scale graph of the population

Population perspective picture



Decreasing birth rate

Decreasing birth rate (above) might be a good model for organisms that experience density dependence primarily in the recruitment stage



Decreasing birth rate

- Decreasing birth rate (above)
 might be a good model for
 organisms that experience density
 dependence primarily in the
 recruitment stage
- ► For example, we might count adult trees, and these might not die more at high density just fail to recruit younger ones



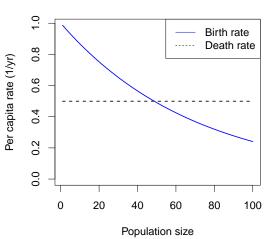
Decreasing birth rate

- Decreasing birth rate (above)
 might be a good model for
 organisms that experience density
 dependence primarily in the
 recruitment stage
- ► For example, we might count adult trees, and these might not die more at high density – just fail to recruit younger ones



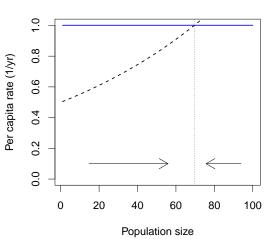
Decreasing birth rates (repeat)

Density-dependent birth



Increasing death rates

Density-dependent death



 Increasing death rate might be a good model for organisms that experience density dependence primarily as adults



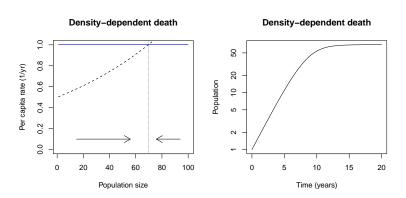
- Increasing death rate might be a good model for organisms that experience density dependence primarily as adults
- ► For example, in some environments, mussel density might be limited by adult crowding. Although juvenile mussels tend to have a hard time, this might not be density dependent



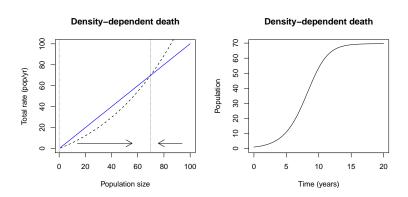
- Increasing death rate might be a good model for organisms that experience density dependence primarily as adults
- ➤ For example, in some environments, mussel density might be limited by adult crowding. Although juvenile mussels tend to have a hard time, this might not be density dependent



Individual perspective



Population perspective



Some organisms (such as many types of bacteria) slow down their metabolisms under density dependence, so that death rate decreases

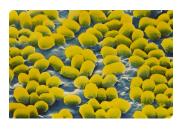


- Some organisms (such as many types of bacteria) slow down their metabolisms under density dependence, so that death rate decreases
- ► How is this consistent with density dependence?



- Some organisms (such as many types of bacteria) slow down their metabolisms under density dependence, so that death rate decreases
- How is this consistent with density dependence?





- Some organisms (such as many types of bacteria) slow down their metabolisms under density dependence, so that death rate decreases
- How is this consistent with density dependence?
 - * Birth rate must decrease even faster

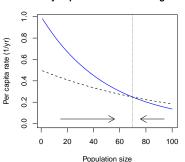


- Some organisms (such as many types of bacteria) slow down their metabolisms under density dependence, so that death rate decreases
- How is this consistent with density dependence?
 - * Birth rate must decrease even faster

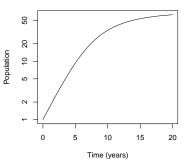


Individual perspective

Density dependence and slowing down



Density dependence and slowing down

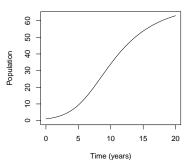


Population perspective

Density dependence and slowing down

0 20 40 60 80 100 Population size

Density dependence and slowing down



Other examples

► There are two other possible scenarios for density dependence

- ▶ There are two other possible scenarios for density dependence
 - ► For fun, you can try to think of what they are

- ▶ There are two other possible scenarios for density dependence
 - For fun, you can try to think of what they are
- ▶ But all of these examples have similar behaviour

- ▶ There are two other possible scenarios for density dependence
 - For fun, you can try to think of what they are
- But all of these examples have similar behaviour
 - ► Increase from low density

- ► There are two other possible scenarios for density dependence
 - For fun, you can try to think of what they are
- But all of these examples have similar behaviour
 - Increase from low density
 - Decrease from high density

- ► There are two other possible scenarios for density dependence
 - For fun, you can try to think of what they are
- But all of these examples have similar behaviour
 - Increase from low density
 - Decrease from high density
 - ► Approach carrying capacity

- ► There are two other possible scenarios for density dependence
 - For fun, you can try to think of what they are
- But all of these examples have similar behaviour
 - Increase from low density
 - Decrease from high density
 - Approach carrying capacity

▶ Poll: When does a population in this model have the fastest *per-capita* growth rate?

▶ Poll: When does a population in this model have the fastest *per-capita* growth rate?



▶ Poll: When does a population in this model have the fastest *per-capita* growth rate?

> *

▶ Poll: When does a population in this model have the fastest *per-capita* growth rate?

>

>

▶ Poll: When does a population in this model have the fastest *per-capita* growth rate?

>

*

▶ Poll: When does a population in this model have the fastest *per-capita* growth rate?

- k 🖊
- *
- ► Poll: When does a population in this model have the fastest *total* growth rate?

- ▶ Poll: When does a population in this model have the fastest *per-capita* growth rate?
 - **>** 4
 - *
- ▶ Poll: When does a population in this model have the fastest *total* growth rate?
 - *****

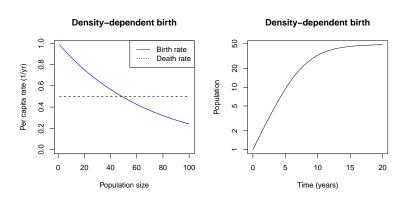
- ▶ Poll: When does a population in this model have the fastest *per-capita* growth rate?
 - **k**
 - *
- ▶ Poll: When does a population in this model have the fastest *total* growth rate?
 - *

- ▶ Poll: When does a population in this model have the fastest *per-capita* growth rate?
 - *
 - *
- ▶ Poll: When does a population in this model have the fastest *total* growth rate?
 - **▶** ≯
 - *

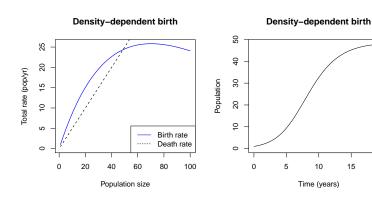
- ▶ Poll: When does a population in this model have the fastest *per-capita* growth rate?
 - *
 - *
- ▶ Poll: When does a population in this model have the fastest *total* growth rate?
 - >
 - *

- ▶ Poll: When does a population in this model have the fastest *per-capita* growth rate?
 - *
 - *
- ▶ Poll: When does a population in this model have the fastest *total* growth rate?
 - >
 - *

Individual perspective (repeat)



Population perspective (repeat)



20

► When does a population in this model have the fastest *per-capita* growth rate?

► When does a population in this model have the fastest *per-capita* growth rate?



- ▶ When does a population in this model have the fastest *per-capita* growth rate?
 - ▶ * When density is low.

- ▶ When does a population in this model have the fastest *per-capita* growth rate?
 - ► * When density is low.
 - >

- ▶ When does a population in this model have the fastest *per-capita* growth rate?
 - ► * When density is low.
 - ► * This is an assumption.

- ▶ When does a population in this model have the fastest per-capita growth rate?
 - * When density is low.
 - ▶ * This is an assumption.
- ► When does a population in this model have the fastest *total* growth rate?

- ▶ When does a population in this model have the fastest per-capita growth rate?
 - ► * When density is low.
 - * This is an assumption.
- ▶ When does a population in this model have the fastest *total* growth rate?
 - *

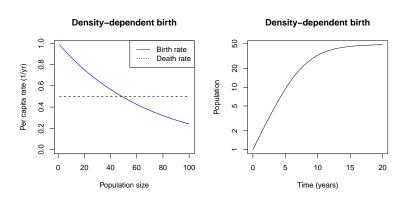
- ▶ When does a population in this model have the fastest per-capita growth rate?
 - ► * When density is low.
 - ► * This is an assumption.
- ▶ When does a population in this model have the fastest *total* growth rate?
 - ▶ * Intermediate between low density and the carrying capacity.

- ▶ When does a population in this model have the fastest per-capita growth rate?
 - ► * When density is low.
 - * This is an assumption.
- ▶ When does a population in this model have the fastest *total* growth rate?
 - * Intermediate between low density and the carrying capacity.
 - *

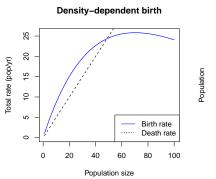
- ▶ When does a population in this model have the fastest per-capita growth rate?
 - ► * When density is low.
 - * This is an assumption.
- ▶ When does a population in this model have the fastest *total* growth rate?
 - * Intermediate between low density and the carrying capacity.
 - ▶ * This is a something we learn from the model

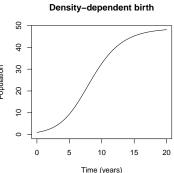
- ▶ When does a population in this model have the fastest per-capita growth rate?
 - ► * When density is low.
 - * This is an assumption.
- ▶ When does a population in this model have the fastest *total* growth rate?
 - * Intermediate between low density and the carrying capacity.
 - ▶ * This is a something we learn from the model

Individual perspective (repeat)



Population perspective (repeat)





Outline

Introduction

Population Examples

Continuous-time regulation

A simple, continuous-time model Simulating model behaviour Equilibria and time scales

Discrete-time regulation

A simple, discrete-time model Simulating this system Interpreting complex behaviour

Delayed regulation

Small populations and stochasticity

Allee effects
Stochastic effects

Equilibria and time scales

► We define **equilibrium** as when the population is not changing

Equilibria and time scales

- ▶ We define **equilibrium** as when the population is not changing
- ► Our simple model is $\frac{dN}{dt} = (b(N) d(N))N$

Equilibria and time scales

- ▶ We define **equilibrium** as when the population is not changing
- ► Our simple model is $\frac{dN}{dt} = (b(N) d(N))N$
- ▶ In this simple model, when does equilibrium occur?

- ▶ We define **equilibrium** as when the population is not changing
- ► Our simple model is $\frac{dN}{dt} = (b(N) d(N))N$
- In this simple model, when does equilibrium occur?



- ▶ We define **equilibrium** as when the population is not changing
- ► Our simple model is $\frac{dN}{dt} = (b(N) d(N))N$
- In this simple model, when does equilibrium occur?
 - ▶ * b(N) = d(N) (the carrying capacity)

- ▶ We define **equilibrium** as when the population is not changing
- ► Our simple model is $\frac{dN}{dt} = (b(N) d(N))N$
- In this simple model, when does equilibrium occur?
 - ▶ * b(N) = d(N) (the carrying capacity)
 - *

- ▶ We define **equilibrium** as when the population is not changing
- ► Our simple model is $\frac{dN}{dt} = (b(N) d(N))N$
- In this simple model, when does equilibrium occur?
 - ▶ * b(N) = d(N) (the carrying capacity)
 - * N = 0 (the population is absent)

- ▶ We define **equilibrium** as when the population is not changing
- ► Our simple model is $\frac{dN}{dt} = (b(N) d(N))N$
- In this simple model, when does equilibrium occur?
 - ▶ * b(N) = d(N) (the carrying capacity)
 - * N = 0 (the population is absent)

► Aren't equilibria always stable?

- Aren't equilibria always stable?
 - ▶ If we are at an equilibrium we expect to stay there

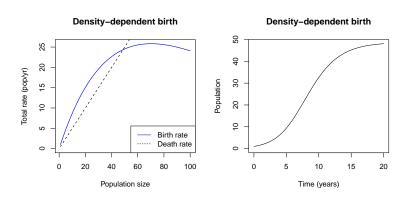
- Aren't equilibria always stable?
 - ▶ If we are at an equilibrium we expect to stay there
 - ► (in our simplified model, at least)

- ► Aren't equilibria always stable?
 - ▶ If we are at an equilibrium we expect to stay there
 - (in our simplified model, at least)
- ► An equilibrium is defined as stable if we expect to approach the equilibrium when we are near it.

- ► Aren't equilibria always stable?
 - ▶ If we are at an equilibrium we expect to stay there
 - (in our simplified model, at least)
- An equilibrium is defined as stable if we expect to approach the equilibrium when we are near it.
- ► An equilibrium is defined as unstable if we expect to move away from the equilibrium when we are near it.

- Aren't equilibria always stable?
 - ▶ If we are at an equilibrium we expect to stay there
 - (in our simplified model, at least)
- An equilibrium is defined as stable if we expect to approach the equilibrium when we are near it.
- An equilibrium is defined as unstable if we expect to move away from the equilibrium when we are near it.

Population perspective (repeat)



► How can we tell an equilibrium is stable?

- ▶ How can we tell an equilibrium is stable?
 - ► If population is just below the equilibrium:

- ► How can we tell an equilibrium is stable?
 - ▶ If population is just below the equilibrium:

- ► How can we tell an equilibrium is stable?
 - ▶ If population is just below the equilibrium:
 - ▶ * It should increase (b > d)

- ► How can we tell an equilibrium is stable?
 - ▶ If population is just below the equilibrium:
 - ▶ * It should increase (b > d)
 - ▶ If population is just above the equilibrium:

- How can we tell an equilibrium is stable?
 - ▶ If population is just below the equilibrium:
 - ▶ * It should increase (b > d)
 - ▶ If population is just above the equilibrium:
 - *

- How can we tell an equilibrium is stable?
 - ▶ If population is just below the equilibrium:
 - * It should increase (b > d)
 - ▶ If population is just above the equilibrium:
 - ► * It should decrease (d > b)

- How can we tell an equilibrium is stable?
 - ▶ If population is just below the equilibrium:
 - ▶ * It should increase (b > d)
 - ▶ If population is just above the equilibrium:
 - ► * It should decrease (d > b)

► The reproductive number of a population not affected by crowding is called the **basic reproductive number**

- ► The reproductive number of a population not affected by crowding is called the **basic reproductive number**
 - ▶ Written \mathcal{R}_0 or \mathcal{R}_{max} .

- ► The reproductive number of a population not affected by crowding is called the **basic reproductive number**
 - ▶ Written \mathcal{R}_0 or \mathcal{R}_{max} .
- ▶ In this model, when $\mathcal{R}_0 < 1$ the population:

- ► The reproductive number of a population not affected by crowding is called the **basic reproductive number**
 - ▶ Written \mathcal{R}_0 or \mathcal{R}_{max} .
- ▶ In this model, when $\mathcal{R}_0 < 1$ the population:
 - **▶** ≯

- ► The reproductive number of a population not affected by crowding is called the **basic reproductive number**
 - ▶ Written \mathcal{R}_0 or \mathcal{R}_{max} .
- ▶ In this model, when $\mathcal{R}_0 < 1$ the population:
 - * Always decreases

- ► The reproductive number of a population not affected by crowding is called the **basic reproductive number**
 - ▶ Written \mathcal{R}_0 or \mathcal{R}_{max} .
- ▶ In this model, when $\mathcal{R}_0 < 1$ the population:
 - * Always decreases
- ▶ When $\mathcal{R}_0 > 1$ the population:

- ► The reproductive number of a population not affected by crowding is called the **basic reproductive number**
 - ▶ Written \mathcal{R}_0 or \mathcal{R}_{max} .
- ▶ In this model, when $\mathcal{R}_0 < 1$ the population:
 - * Always decreases
- ▶ When $\mathcal{R}_0 > 1$ the population:
 - ,

- ► The reproductive number of a population not affected by crowding is called the **basic reproductive number**
 - Written \mathcal{R}_0 or $\mathcal{R}_{\mathsf{max}}$.
- ▶ In this model, when $\mathcal{R}_0 < 1$ the population:
 - * Always decreases
- When $\mathcal{R}_0 > 1$ the population:
 - * Increases when it is small

- ► The reproductive number of a population not affected by crowding is called the **basic reproductive number**
 - Written \mathcal{R}_0 or $\mathcal{R}_{\mathsf{max}}$.
- ▶ In this model, when $\mathcal{R}_0 < 1$ the population:
 - * Always decreases
- ▶ When $\mathcal{R}_0 > 1$ the population:
 - ▶ * Increases when it is small
 - *

- ► The reproductive number of a population not affected by crowding is called the **basic reproductive number**
 - Written \mathcal{R}_0 or \mathcal{R}_{max} .
- ▶ In this model, when $\mathcal{R}_0 < 1$ the population:
 - * Always decreases
- When $\mathcal{R}_0 > 1$ the population:
 - ▶ * Increases when it is small
 - ightharpoonup * Eventually $\mathcal R$ will decrease

- ► The reproductive number of a population not affected by crowding is called the **basic reproductive number**
 - Written \mathcal{R}_0 or \mathcal{R}_{max} .
- ▶ In this model, when $\mathcal{R}_0 < 1$ the population:
 - * Always decreases
- When $\mathcal{R}_0 > 1$ the population:
 - ▶ * Increases when it is small
 - ightharpoonup * Eventually $\mathcal R$ will decrease

▶ Poll: What is \mathcal{R}_0 in our current model?

▶ Poll: What is \mathcal{R}_0 in our current model?

*

- ▶ Poll: What is \mathcal{R}_0 in our current model?
 - * $\mathcal{R}_0 = b(0)/d(0)$

- ▶ Poll: What is \mathcal{R}_0 in our current model?
 - * $\mathcal{R}_0 = b(0)/d(0)$
- ▶ Does this make sene?

- ▶ Poll: What is \mathcal{R}_0 in our current model?
 - * $\mathcal{R}_0 = b(0)/d(0)$
- ► Does this make sene?
 - **>** *

- ▶ Poll: What is \mathcal{R}_0 in our current model?
 - * $\mathcal{R}_0 = b(0)/d(0)$
- Does this make sene?
 - ▶ * Not really; nothing actually grows or dies when N = 0

- ▶ Poll: What is \mathcal{R}_0 in our current model?
 - * $\mathcal{R}_0 = b(0)/d(0)$
- Does this make sene?
 - ▶ * Not really; nothing actually grows or dies when N = 0
 - **>** *

- ▶ Poll: What is \mathcal{R}_0 in our current model?
 - * $\mathcal{R}_0 = b(0)/d(0)$
- Does this make sene?
 - ▶ * Not really; nothing actually grows or dies when N = 0
 - * we resolve this by think of \mathcal{R}_0 , b(0), and d(0) as limits

- ▶ Poll: What is \mathcal{R}_0 in our current model?
 - * $\mathcal{R}_0 = b(0)/d(0)$
- ▶ Does this make sene?
 - ▶ * Not really; nothing actually grows or dies when N = 0
 - ▶ * we resolve this by think of \mathcal{R}_0 , b(0), and d(0) as limits



- ▶ Poll: What is \mathcal{R}_0 in our current model?
 - * $\mathcal{R}_0 = b(0)/d(0)$
- Does this make sene?
 - ▶ * Not really; nothing actually grows or dies when N = 0
 - * we resolve this by think of \mathcal{R}_0 , b(0), and d(0) as limits
 - * What are the values when density is very low?

- ▶ Poll: What is \mathcal{R}_0 in our current model?
 - * $\mathcal{R}_0 = b(0)/d(0)$
- Does this make sene?
 - ▶ * Not really; nothing actually grows or dies when N = 0
 - * we resolve this by think of \mathcal{R}_0 , b(0), and d(0) as limits
 - * What are the values when density is very low?

► We say a species can "invade" a system if its rate of change is positive when the population is small.

- ▶ We say a species can "invade" a system if its rate of change is positive when the population is small.
- ► In other words, population can invade if the extinction equilibrium is not stable

- ▶ We say a species can "invade" a system if its rate of change is positive when the population is small.
- ► In other words, population can invade if the extinction equilibrium is not stable
- ▶ In this conceptual model, this is the same as saying b(0) > d(0)

- ▶ We say a species can "invade" a system if its rate of change is positive when the population is small.
- ▶ In other words, population can invade if the extinction equilibrium is not stable
- In this conceptual model, this is the same as saying b(0) > d(0)
- ▶ Which is the same as saying $\mathcal{R}_0 > 1$

- We say a species can "invade" a system if its rate of change is positive when the population is small.
- ▶ In other words, population can invade if the extinction equilibrium is not stable
- In this conceptual model, this is the same as saying b(0) > d(0)
- ▶ Which is the same as saying $\mathcal{R}_0 > 1$

▶ Poll: What are some examples of biological invasions?

▶ Poll: What are some examples of biological invasions?

>

▶ Poll: What are some examples of biological invasions?

,

▶ Poll: What are some examples of biological invasions?

- •
- *****

- ▶ Poll: What are some examples of biological invasions?
 - **>** :
 - *

- ▶ Poll: What are some examples of biological invasions?
 - >
 - **>** *
 - *

- ▶ Poll: What are some examples of biological invasions?
 - **>** ×
 - *****
 - **k**

- ▶ Poll: What are some examples of biological invasions?
 - **>** ×
 - *
 - **k**
 - *

- ▶ Poll: What are some examples of biological invasions?
 - **>** *
 - *
 - *
 - *

- ▶ Poll: What are some examples of biological invasions?
 - **>** *
 - *
 - *
 - *

▶ When $\mathcal{R}_0 > 1$, the population invades

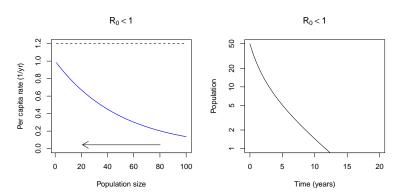
- ▶ When $\mathcal{R}_0 > 1$, the population invades
 - Zero equilibrium is unstable, carrying capacity equilibrium is stable

- ▶ When $\mathcal{R}_0 > 1$, the population invades
 - Zero equilibrium is unstable, carrying capacity equilibrium is stable
- ▶ When $\mathcal{R}_0 < 1$, the population fails to invade

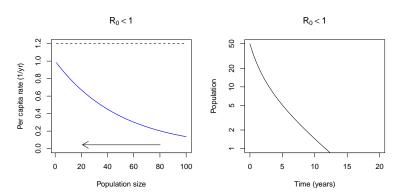
- ▶ When $\mathcal{R}_0 > 1$, the population invades
 - Zero equilibrium is unstable, carrying capacity equilibrium is stable
- ▶ When $\mathcal{R}_0 < 1$, the population fails to invade
 - Zero equilibrium is stable, carrying capacity equilibrium does not exist

- ▶ When $\mathcal{R}_0 > 1$, the population invades
 - Zero equilibrium is unstable, carrying capacity equilibrium is stable
- ▶ When $\mathcal{R}_0 < 1$, the population fails to invade
 - Zero equilibrium is stable, carrying capacity equilibrium does not exist

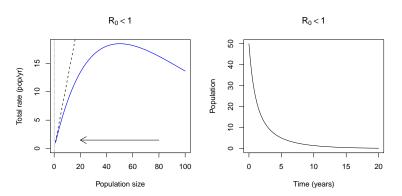
Individual perspective



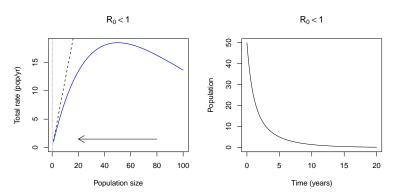
Individual perspective



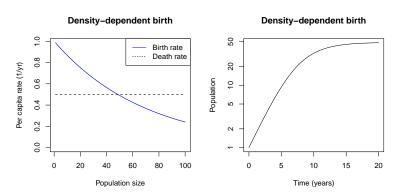
Population perspective



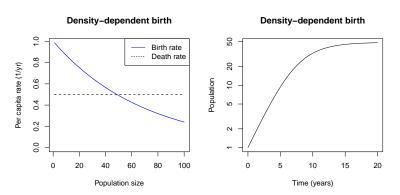
Population perspective



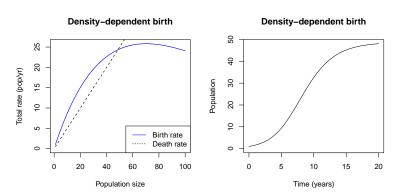
Individual perspective (repeat)



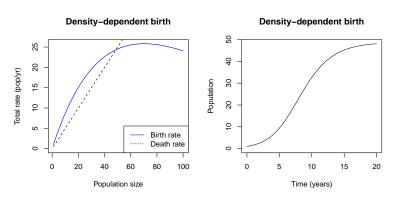
Individual perspective (repeat)



Population perspective (repeat)



Population perspective (repeat)



\mathcal{R}_0 and thresholds

ightharpoonup A population with $\mathcal{R}_0 < 1$ in general cannot survive in an area

\mathcal{R}_0 and thresholds

- lacktriangle A population with $\mathcal{R}_0 < 1$ in general cannot survive in an area
- ► As conditions get worse for a species in a particular area, or along a particular gradient:

- lacktriangle A population with $\mathcal{R}_0 < 1$ in general cannot survive in an area
- As conditions get worse for a species in a particular area, or along a particular gradient:
 - ► It will suddenly disappear at the population level

- lacktriangle A population with $\mathcal{R}_0 < 1$ in general cannot survive in an area
- As conditions get worse for a species in a particular area, or along a particular gradient:
 - ▶ It will suddenly disappear at the population level
 - Even while it can still survive and reproduce at an individual level

- lacktriangle A population with $\mathcal{R}_0 < 1$ in general cannot survive in an area
- As conditions get worse for a species in a particular area, or along a particular gradient:
 - It will suddenly disappear at the population level
 - Even while it can still survive and reproduce at an individual level
- ► This is why there are no white spruce trees in Cootes Paradise

- lacktriangle A population with $\mathcal{R}_0 < 1$ in general cannot survive in an area
- As conditions get worse for a species in a particular area, or along a particular gradient:
 - ▶ It will suddenly disappear at the population level
 - Even while it can still survive and reproduce at an individual level
- This is why there are no white spruce trees in Cootes Paradise
- ► And no malaria in the mainland United States

- lacktriangle A population with $\mathcal{R}_0 < 1$ in general cannot survive in an area
- As conditions get worse for a species in a particular area, or along a particular gradient:
 - ▶ It will suddenly disappear at the population level
 - Even while it can still survive and reproduce at an individual level
- This is why there are no white spruce trees in Cootes Paradise
- ► And no malaria in the mainland United States

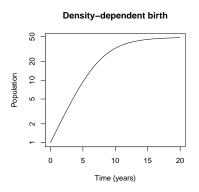
► Just like in the simple model, an equilibrium will have a characteristic time

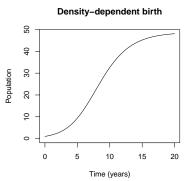
- ▶ Just like in the simple model, an equilibrium will have a characteristic time
- ▶ If I'm close to an equilibrium, how long would it take:

- Just like in the simple model, an equilibrium will have a characteristic time
- If I'm close to an equilibrium, how long would it take:
 - ▶ to go the distance to the equilibrium at my current "speed"

- Just like in the simple model, an equilibrium will have a characteristic time
- ▶ If I'm close to an equilibrium, how long would it take:
 - to go the distance to the equilibrium at my current "speed"
 - ▶ to actually get e times closer, or e times farther

- ▶ Just like in the simple model, an equilibrium will have a characteristic time
- If I'm close to an equilibrium, how long would it take:
 - to go the distance to the equilibrium at my current "speed"
 - to actually get e times closer, or e times farther





► Populations following this model change *smoothly*

- Populations following this model change smoothly
 - ► Equations tell how the population will change at each instant

- Populations following this model change smoothly
 - ▶ Equations tell how the population will change at each instant
- ► They have no memory

- Populations following this model change smoothly
 - ▶ Equations tell how the population will change at each instant
- ► They have no memory
 - Birth rate and death rate are determined by population size alone

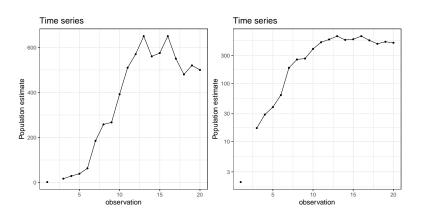
- Populations following this model change smoothly
 - ▶ Equations tell how the population will change at each instant
- ► They have no memory
 - Birth rate and death rate are determined by population size alone
- ► Cycling is impossible

- Populations following this model change smoothly
 - ▶ Equations tell how the population will change at each instant
- ► They have no memory
 - Birth rate and death rate are determined by population size alone
- Cycling is impossible
 - *

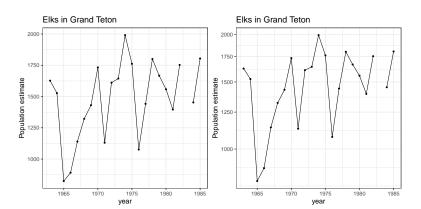
- Populations following this model change smoothly
 - ▶ Equations tell how the population will change at each instant
- ► They have no memory
 - Birth rate and death rate are determined by population size alone
- Cycling is impossible
 - * If I went from A to B, I can't go from B to A by following the same rules

- Populations following this model change smoothly
 - ▶ Equations tell how the population will change at each instant
- ► They have no memory
 - Birth rate and death rate are determined by population size alone
- Cycling is impossible
 - * If I went from A to B, I can't go from B to A by following the same rules

Paramecia



Elk



▶ Initial exponential growth and leveling off frequently observed

- Initial exponential growth and leveling off frequently observed
- Exponential approach to equilibrium hard to observe

- Initial exponential growth and leveling off frequently observed
- Exponential approach to equilibrium hard to observe
 - ► Real populations are subject to **stochastic** (random) effects

- Initial exponential growth and leveling off frequently observed
- Exponential approach to equilibrium hard to observe
 - Real populations are subject to stochastic (random) effects
 - ► Real populations are subject to changing conditions

- Initial exponential growth and leveling off frequently observed
- Exponential approach to equilibrium hard to observe
 - Real populations are subject to stochastic (random) effects
 - Real populations are subject to changing conditions
- Some species seem to cycle predictably

- Initial exponential growth and leveling off frequently observed
- Exponential approach to equilibrium hard to observe
 - Real populations are subject to stochastic (random) effects
 - Real populations are subject to changing conditions
- Some species seem to cycle predictably

► Continuous-time regulation in simple models makes useful predictions:

- Continuous-time regulation in simple models makes useful predictions:
 - ► Threshold value for populations to survive

- Continuous-time regulation in simple models makes useful predictions:
 - ► Threshold value for populations to survive
 - ► Greatest population-level growth at intermediate density

- Continuous-time regulation in simple models makes useful predictions:
 - Threshold value for populations to survive
 - Greatest population-level growth at intermediate density
 - ► Greatest individual-level growth at low density

- Continuous-time regulation in simple models makes useful predictions:
 - Threshold value for populations to survive
 - Greatest population-level growth at intermediate density
 - Greatest individual-level growth at low density
- Cannot explain complicated dynamics

- Continuous-time regulation in simple models makes useful predictions:
 - ► Threshold value for populations to survive
 - Greatest population-level growth at intermediate density
 - Greatest individual-level growth at low density
- Cannot explain complicated dynamics
 - More mechanisms are needed

- Continuous-time regulation in simple models makes useful predictions:
 - ► Threshold value for populations to survive
 - Greatest population-level growth at intermediate density
 - Greatest individual-level growth at low density
- Cannot explain complicated dynamics
 - More mechanisms are needed

Outline

Introduction

Population Examples

Continuous-time regulation

A simple, continuous-time model Simulating model behaviour Equilibria and time scales

Discrete-time regulation

A simple, discrete-time model Simulating this system Interpreting complex behaviour

Delayed regulation

Small populations and stochasticity

Allee effects
Stochastic effects

Outline

Introduction

Population Examples

Continuous-time regulation

A simple, continuous-time model Simulating model behaviour Equilibria and time scales

Discrete-time regulation

A simple, discrete-time model

Simulating this system Interpreting complex behaviour

Delayed regulation

Small populations and stochasticity

Allee effects
Stochastic effects

▶ We extend our discrete-time model from the previous unit:

▶ We extend our discrete-time model from the previous unit:

$$N_{T+1} = (p+f)N_T \equiv \lambda N_T$$

- ▶ We extend our discrete-time model from the previous unit:
 - $ightharpoonup N_{T+1} = (p+f)N_T \equiv \lambda N_T$
 - ▶ $t_{T+1} = t_T + \Delta t$ (does not change)

- ▶ We extend our discrete-time model from the previous unit:
 - $ightharpoonup N_{T+1} = (p+f)N_T \equiv \lambda N_T$
- To:

- ▶ We extend our discrete-time model from the previous unit:
 - $ightharpoonup N_{T+1} = (p+f)N_T \equiv \lambda N_T$
 - $\qquad \qquad t_{T+1} = t_T + \Delta t \; \text{(does not change)}$
- To:

- ▶ We extend our discrete-time model from the previous unit:
 - $ightharpoonup N_{T+1} = (p+f)N_T \equiv \lambda N_T$
 - $\qquad \qquad t_{T+1} = t_T + \Delta t \; \text{(does not change)}$
- To:
 - $N_{T+1} = (p(N_T) + f(N_T))N_T \equiv \lambda(N_T)N_T$
- ► This means:

▶ We extend our discrete-time model from the previous unit:

$$N_{T+1} = (p+f)N_T \equiv \lambda N_T$$

$$\qquad \qquad t_{T+1} = t_T + \Delta t \; (\text{does not change})$$

► To:

$$N_{T+1} = (p(N_T) + f(N_T))N_T \equiv \lambda(N_T)N_T$$

► This means:



- ▶ We extend our discrete-time model from the previous unit:
 - $ightharpoonup N_{T+1} = (p+f)N_T \equiv \lambda N_T$
 - $\qquad \qquad t_{T+1} = t_T + \Delta t \; \text{(does not change)}$
- ► To:

$$N_{T+1} = (p(N_T) + f(N_T))N_T \equiv \lambda(N_T)N_T$$

- ▶ This means:
 - \triangleright * p and f can change when N changes

- ▶ We extend our discrete-time model from the previous unit:
 - $ightharpoonup N_{T+1} = (p+f)N_T \equiv \lambda N_T$
 - $\qquad \qquad t_{T+1} = t_T + \Delta t \; \text{(does not change)}$
- ► To:

$$N_{T+1} = (p(N_T) + f(N_T))N_T \equiv \lambda(N_T)N_T$$

- ▶ This means:
 - \triangleright * p and f can change when N changes

lacktriangle The population is censused at regular time intervals Δt

- lacktriangle The population is censused at regular time intervals Δt
- ► All individuals are the same at the time of census

- lacktriangle The population is censused at regular time intervals Δt
- ▶ All individuals are the same at the time of census
- ► Population changes deterministically

- lacktriangle The population is censused at regular time intervals Δt
- ▶ All individuals are the same at the time of census
- ▶ Population changes deterministically

For our examples, we will assume:

For our examples, we will assume:

$$f(N) = f_0 \exp(-N/N_f)$$

- For our examples, we will assume:
 - $f(N) = f_0 \exp(-N/N_f)$

- For our examples, we will assume:
 - $f(N) = f_0 \exp(-N/N_f)$
- ► This is the simplest model that is smooth and keeps track of birth and death rates separately

- For our examples, we will assume:
 - $f(N) = f_0 \exp(-N/N_f)$
 - $p(N) = p_0 \exp(-N/N_p)$
- ▶ This is the simplest model that is smooth and keeps track of birth and death rates separately
 - \triangleright Fecundity goes down with characteristic scale N_f

- For our examples, we will assume:
 - $f(N) = f_0 \exp(-N/N_f)$
- This is the simplest model that is smooth and keeps track of birth and death rates separately
 - ightharpoonup Fecundity goes down with characteristic scale N_f
 - ightharpoonup Survival goes down with characteristic scale N_p

- For our examples, we will assume:
 - $f(N) = f_0 \exp(-N/N_f)$
- This is the simplest model that is smooth and keeps track of birth and death rates separately
 - ightharpoonup Fecundity goes down with characteristic scale N_f
 - ightharpoonup Survival goes down with characteristic scale N_p

▶ What variable or variables describe the state of this system?

- What variable or variables describe the state of this system?
 - ► The same as before: population size (or density)

- What variable or variables describe the state of this system?
 - ► The same as before: population size (or density)
 - ► We are still assuming that's all we need to know

- What variable or variables describe the state of this system?
 - ► The same as before: population size (or density)
 - ► We are still assuming that's all we need to know

▶ What quantities describe the rules for this system?

▶ What quantities describe the rules for this system?

*

- ▶ What quantities describe the rules for this system?
 - * f_0 [1]

- ▶ What quantities describe the rules for this system?
 - ▶ * f₀ [1]
 - **>** ×

- ▶ What quantities describe the rules for this system?
 - ▶ * f₀ [1]
 - ▶ * p₀ [1]

- ▶ What quantities describe the rules for this system?
 - ▶ * f₀ [1]
 - ▶ * *p*₀ [1]
 - > 1

- ▶ What quantities describe the rules for this system?
 - ▶ * f₀ [1]
 - ▶ * *p*₀ [1]
 - ► * N_f [indiv] (or [indiv/area])

- ▶ What quantities describe the rules for this system?
 - ▶ * f₀ [1]
 - ▶ * p₀ [1]
 - ► * N_f [indiv] (or [indiv/area])
 - >

- ▶ What quantities describe the rules for this system?
 - ▶ * f₀ [1]
 - ▶ * p₀ [1]
 - ► * N_f [indiv] (or [indiv/area])
 - ► * N_p [indiv] (or [indiv/area])

- ▶ What quantities describe the rules for this system?
 - ▶ * f₀ [1]
 - ▶ * p₀ [1]
 - ► * N_f [indiv] (or [indiv/area])
 - ► * N_p [indiv] (or [indiv/area])

What is \mathcal{R}_0 ?

 $ightharpoonup \mathcal{R}$ is the fecundity multiplied by the lifespan

What is \mathcal{R}_0 ?

 $ightharpoonup \mathcal{R}$ is the fecundity multiplied by the lifespan

▶ *

• * Lifespan =
$$1/\mu = 1/(1-p)$$

• * Lifespan =
$$1/\mu = 1/(1-p)$$

• * Lifespan =
$$1/\mu = 1/(1-p)$$

$$\blacktriangleright * \mathcal{R} = f/(1-p)$$

 $ightharpoonup \mathcal{R}$ is the fecundity multiplied by the lifespan

• * Lifespan =
$$1/\mu = 1/(1-p)$$

$$\blacktriangleright * \mathcal{R} = f/(1-p)$$

 $ightharpoonup \mathcal{R}_0$ is \mathcal{R} in the limit where density is low

• * Lifespan =
$$1/\mu = 1/(1-p)$$

$$\blacktriangleright * \mathcal{R} = f/(1-p)$$

- $ightharpoonup \mathcal{R}_0$ is \mathcal{R} in the limit where density is low
 - *

 $ightharpoonup \mathcal{R}$ is the fecundity multiplied by the lifespan

• * Lifespan =
$$1/\mu = 1/(1-p)$$

$$\blacktriangleright * \mathcal{R} = f/(1-p)$$

 $ightharpoonup \mathcal{R}_0$ is \mathcal{R} in the limit where density is low

$$rac{1}{2} * f_0/(1-p_0)$$

 $ightharpoonup \mathcal{R}$ is the fecundity multiplied by the lifespan

• * Lifespan =
$$1/\mu = 1/(1-p)$$

$$\blacktriangleright * \mathcal{R} = f/(1-p)$$

 $ightharpoonup \mathcal{R}_0$ is \mathcal{R} in the limit where density is low

$$rac{1}{2} * f_0/(1-p_0)$$

▶ When $\mathcal{R}_0 < 1$ population always declines

- ▶ When $\mathcal{R}_0 < 1$ population always declines
- ▶ When $\mathcal{R}_0 > 1$, population can show:

- ▶ When $\mathcal{R}_0 < 1$ population always declines
- ▶ When $\mathcal{R}_0 > 1$, population can show:
 - ► Smooth behaviour (like the continuous-time model)

- ▶ When $\mathcal{R}_0 < 1$ population always declines
- ▶ When $\mathcal{R}_0 > 1$, population can show:
 - Smooth behaviour (like the continuous-time model)
 - ► Damped oscillations (like the delayed model)

- ▶ When $\mathcal{R}_0 < 1$ population always declines
- ▶ When $\mathcal{R}_0 > 1$, population can show:
 - Smooth behaviour (like the continuous-time model)
 - Damped oscillations (like the delayed model)
 - ► Two-year cycles (high \rightarrow low \rightarrow high \rightarrow low)

- ▶ When $\mathcal{R}_0 < 1$ population always declines
- ▶ When $\mathcal{R}_0 > 1$, population can show:
 - Smooth behaviour (like the continuous-time model)
 - Damped oscillations (like the delayed model)
 - ▶ Two-year cycles (high \rightarrow low \rightarrow high \rightarrow low)
 - ► All kinds of other stuff

- ▶ When $\mathcal{R}_0 < 1$ population always declines
- ▶ When $\mathcal{R}_0 > 1$, population can show:
 - Smooth behaviour (like the continuous-time model)
 - Damped oscillations (like the delayed model)
 - ▶ Two-year cycles (high \rightarrow low \rightarrow high \rightarrow low)
 - All kinds of other stuff

Outline

Introduction

Population Examples

Continuous-time regulation

A simple, continuous-time model Simulating model behaviour Equilibria and time scales

Discrete-time regulation

A simple, discrete-time model Simulating this system

Interpreting complex behaviour

Delayed regulation

Small populations and stochasticity

Allee effects
Stochastic effects

Simulating this system

► This system can be simulated very easily by following the rule for N_{T+1} as a function of N_T

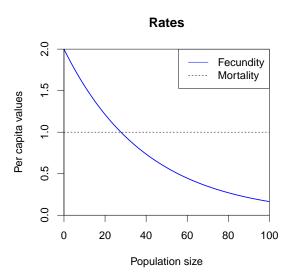
Simulating this system

- This system can be simulated very easily by following the rule for N_{T+1} as a function of N_T
- ► We can even do it in the spreadsheet if we have time

Simulating this system

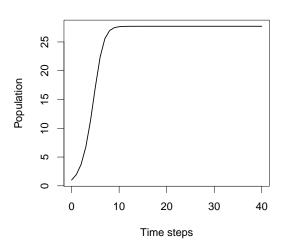
- ► This system can be simulated very easily by following the rule for N_{T+1} as a function of N_T
- ▶ We can even do it in the spreadsheet if we have time

What dynamics do we expect? (preview)

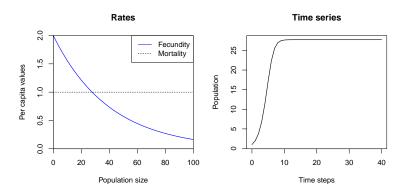


What dynamics do we expect? (preview)



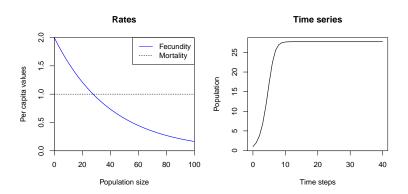


We expect simple dynamics

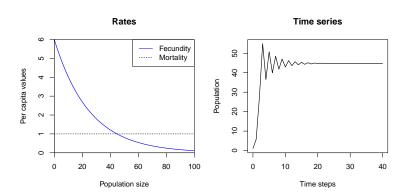


What dynamics do we get?

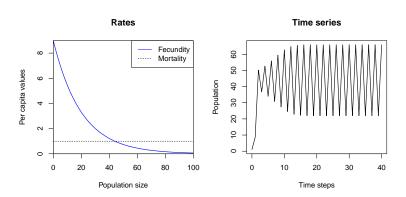
Simple dynamics (repeat)



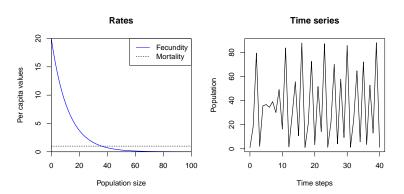
Damped oscillations



Persistent oscillations



Lots of other behaviours



Outline

Introduction

Population Examples

Continuous-time regulation

A simple, continuous-time model Simulating model behaviour Equilibria and time scales

Discrete-time regulation

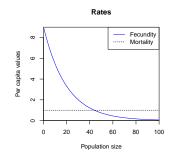
A simple, discrete-time model Simulating this system Interpreting complex behaviour

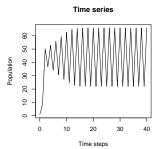
Delayed regulation

Small populations and stochasticity

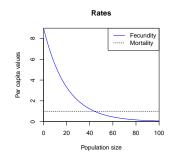
Stochastic effects

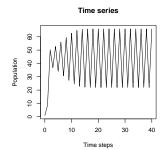
► In a simple cycle:





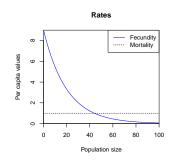
- ► In a simple cycle:
 - Low populations this year mean high populations next year

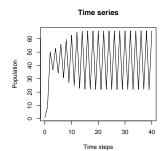






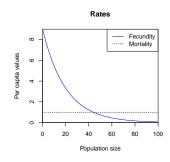
- ► In a simple cycle:
 - Low populations this year mean high populations next year
 - and vice versa

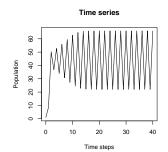






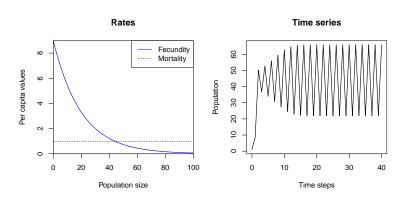
- ► In a simple cycle:
 - Low populations this year mean high populations next year
 - and vice versa







Interpreting complex behaviour (repeat)



▶ In our simple models, as N_T increases, what happens to λ ?

▶ In our simple models, as N_T increases, what happens to λ ?

- ▶ In our simple models, as N_T increases, what happens to λ ?
 - ► * We assume it goes down

- ▶ In our simple models, as N_T increases, what happens to λ ?
 - ▶ * We assume it goes down
- ▶ Poll: In our simple models, as N_T increases, what happens to next year's population?

- ▶ In our simple models, as N_T increases, what happens to λ ?
 - ► * We assume it goes down
- ▶ Poll: In our simple models, as N_T increases, what happens to next year's population?
 - *

- ▶ In our simple models, as N_T increases, what happens to λ ?
 - ▶ * We assume it goes down
- ▶ Poll: In our simple models, as N_T increases, what happens to next year's population?
 - \blacktriangleright * $N_{T+1} = \lambda(N)N_T$

- ▶ In our simple models, as N_T increases, what happens to λ ?
 - ► * We assume it goes down
- ▶ Poll: In our simple models, as N_T increases, what happens to next year's population?

$$\blacktriangleright$$
 * $N_{T+1} = \lambda(N)N_T$

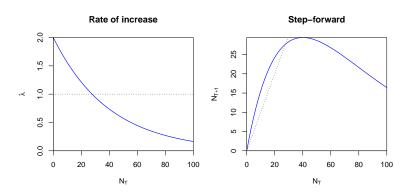
- ▶ In our simple models, as N_T increases, what happens to λ ?
 - ▶ * We assume it goes down
- ▶ Poll: In our simple models, as N_T increases, what happens to next year's population?
 - \blacktriangleright * $N_{T+1} = \lambda(N)N_T$
 - ▶ * It's not obvious! λ goes down, but N goes up.

- ▶ In our simple models, as N_T increases, what happens to λ ?
 - ► * We assume it goes down
- ▶ Poll: In our simple models, as N_T increases, what happens to next year's population?
 - \blacktriangleright * $N_{T+1} = \lambda(N)N_T$
 - ▶ * It's not obvious! λ goes down, but N goes up.
 - *

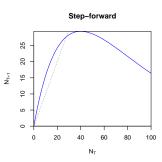
- ▶ In our simple models, as N_T increases, what happens to λ ?
 - ► * We assume it goes down
- ▶ Poll: In our simple models, as N_T increases, what happens to next year's population?
 - \blacktriangleright * $N_{T+1} = \lambda(N)N_T$
 - ▶ * It's not obvious! λ goes down, but N goes up.
 - ightharpoonup * In this model, N_{T+1} always goes down eventually, but other models may differ

- ▶ In our simple models, as N_T increases, what happens to λ ?
 - ► * We assume it goes down
- ▶ Poll: In our simple models, as N_T increases, what happens to next year's population?
 - \blacktriangleright * $N_{T+1} = \lambda(N)N_T$
 - ▶ * It's not obvious! λ goes down, but N goes up.
 - ightharpoonup * In this model, N_{T+1} always goes down eventually, but other models may differ

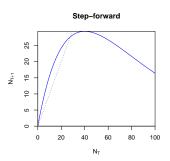
Response to population increase



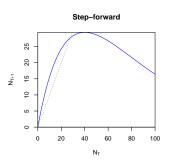
▶ When N_T is small, N_{T+1} increases with N.



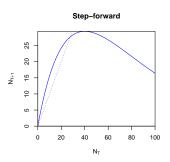
- ▶ When N_T is small, N_{T+1} increases with N.
- ► Complex behaviour arises when the relationship between N_T and N_{T+1} **turns over** below the equilibrium value



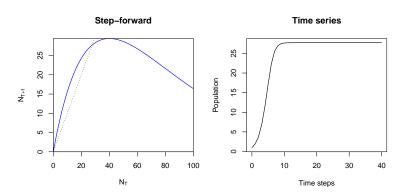
- ▶ When N_T is small, N_{T+1} increases with N.
- ► Complex behaviour arises when the relationship between *N_T* and *N_{T+1}* **turns over** below the equilibrium value
 - ► A small population this year leads to a large population next year



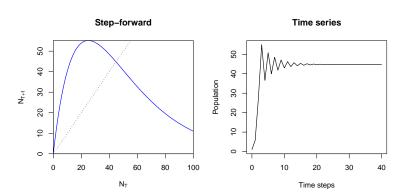
- ▶ When N_T is small, N_{T+1} increases with N.
- ► Complex behaviour arises when the relationship between *N_T* and *N_{T+1}* **turns over** below the equilibrium value
 - A small population this year leads to a large population next year



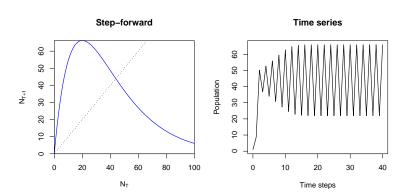
Simple dynamics



Damped oscillations



Persistent oscillations



▶ Biologically, when might we expect N_{T+1} to "turn over"?

▶ Biologically, when might we expect N_{T+1} to "turn over"?

- ▶ Biologically, when might we expect N_{T+1} to "turn over"?
 - ▶ * If resources are *depleted*

- ▶ Biologically, when might we expect N_{T+1} to "turn over"?
 - ▶ * If resources are *depleted*
 - **▶** ≯

- ▶ Biologically, when might we expect N_{T+1} to "turn over"?
 - ▶ * If resources are *depleted*
 - * If there is a *delayed* effect of individuals' not having enough resources

- ▶ Biologically, when might we expect N_{T+1} to "turn over"?
 - ▶ * If resources are *depleted*
 - * If there is a delayed effect of individuals' not having enough resources
- ► When should the mapping *not* turn over?

- ▶ Biologically, when might we expect N_{T+1} to "turn over"?
 - ▶ * If resources are *depleted*
 - * If there is a *delayed* effect of individuals' not having enough resources
- When should the mapping not turn over?
 - *

- ▶ Biologically, when might we expect N_{T+1} to "turn over"?
 - ► * If resources are *depleted*
 - * If there is a delayed effect of individuals' not having enough resources
- When should the mapping not turn over?
 - * When competition does not lead to depletion

- ▶ Biologically, when might we expect N_{T+1} to "turn over"?
 - ▶ * If resources are *depleted*
 - * If there is a *delayed* effect of individuals' not having enough resources
- When should the mapping not turn over?
 - * When competition does not lead to depletion
 - *

- ▶ Biologically, when might we expect N_{T+1} to "turn over"?
 - ▶ * If resources are *depleted*
 - * If there is a *delayed* effect of individuals' not having enough resources
- When should the mapping not turn over?
 - * When competition does not lead to depletion
 - * When effects of competition are immediate

- ▶ Biologically, when might we expect N_{T+1} to "turn over"?
 - ▶ * If resources are *depleted*
 - * If there is a delayed effect of individuals' not having enough resources
- When should the mapping not turn over?
 - * When competition does not lead to depletion
 - * When effects of competition are immediate
 - *

- ▶ Biologically, when might we expect N_{T+1} to "turn over"?
 - ▶ * If resources are *depleted*
 - * If there is a *delayed* effect of individuals' not having enough resources
- When should the mapping not turn over?
 - * When competition does not lead to depletion
 - * When effects of competition are immediate
 - * When dominant individuals are not affected by crowding

- ▶ Biologically, when might we expect N_{T+1} to "turn over"?
 - ▶ * If resources are *depleted*
 - * If there is a *delayed* effect of individuals' not having enough resources
- When should the mapping not turn over?
 - * When competition does not lead to depletion
 - * When effects of competition are immediate
 - * When dominant individuals are not affected by crowding

Scramble competition

► Scramble competition refers to the case where all individuals in a crowded population are gathering resources at similar rates: as the density goes up there is less resource for everyone, and everyone does less well

Scramble competition

- ➤ **Scramble** competition refers to the case where all individuals in a crowded population are gathering resources at similar rates: as the density goes up there is less resource for everyone, and everyone does less well
 - ► If there is any kind of delay, scramble competition can lead to turning over

Scramble competition

- ➤ **Scramble** competition refers to the case where all individuals in a crowded population are gathering resources at similar rates: as the density goes up there is less resource for everyone, and everyone does less well
 - ► If there is any kind of delay, scramble competition can lead to turning over

► Contest competition refers to a case where some individuals successfully control key resources and do well no matter how large the population is

- Contest competition refers to a case where some individuals successfully control key resources and do well no matter how large the population is
 - ► Contest competition doesn't usually lead to turning over, even with delay

- Contest competition refers to a case where some individuals successfully control key resources and do well no matter how large the population is
 - Contest competition doesn't usually lead to turning over, even with delay
- ► How does contest competition square with regulation?

- Contest competition refers to a case where some individuals successfully control key resources and do well no matter how large the population is
 - Contest competition doesn't usually lead to turning over, even with delay
- ▶ How does contest competition square with regulation?
 - **▶** ३

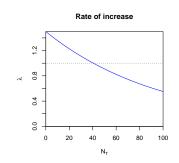
- Contest competition refers to a case where some individuals successfully control key resources and do well no matter how large the population is
 - Contest competition doesn't usually lead to turning over, even with delay
- ▶ How does contest competition square with regulation?
 - ***** Regulation means that λ has to go down with N_T ...

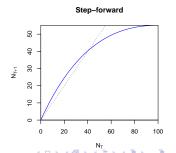
- Contest competition refers to a case where some individuals successfully control key resources and do well no matter how large the population is
 - Contest competition doesn't usually lead to turning over, even with delay
- ▶ How does contest competition square with regulation?
 - * Regulation means that λ has to go down with N_T ...
 - *

- Contest competition refers to a case where some individuals successfully control key resources and do well no matter how large the population is
 - Contest competition doesn't usually lead to turning over, even with delay
- ▶ How does contest competition square with regulation?
 - ***** Regulation means that λ has to go down with N_T ...
 - ▶ * *not* that N_{T+1} has to.

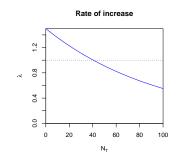
- Contest competition refers to a case where some individuals successfully control key resources and do well no matter how large the population is
 - Contest competition doesn't usually lead to turning over, even with delay
- ▶ How does contest competition square with regulation?
 - ***** Regulation means that λ has to go down with N_T ...
 - ▶ * *not* that N_{T+1} has to.

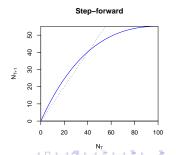
► How does contest competition square with regulation?



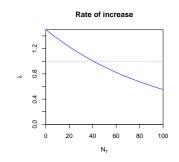


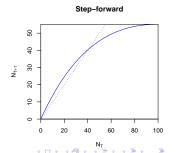
- ► How does contest competition square with regulation?
 - Regulation means that λ has to go down with N_T ...



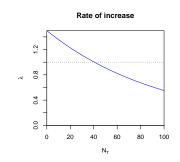


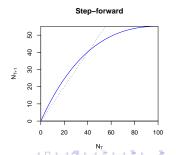
- ► How does contest competition square with regulation?
 - Regulation means that λ has to go down with N_T ...
 - ▶ not that N_{T+1} has to.



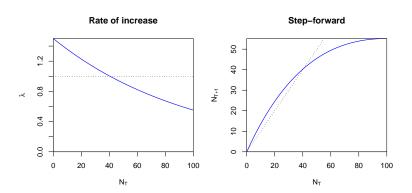


- ► How does contest competition square with regulation?
 - Regulation means that λ has to go down with N_T ...
 - ightharpoonup not that N_{T+1} has to.





Contest regulation



Some songbird populations are limited primarily by competition for breeding sites, whereas others are limited primarily by competition for insects to eat



Some songbird populations are limited primarily by competition for breeding sites, whereas others are limited primarily by competition for insects to eat



- Some songbird populations are limited primarily by competition for breeding sites, whereas others are limited primarily by competition for insects to eat
 - ▶ * Food can be depleted



- Some songbird populations are limited primarily by competition for breeding sites, whereas others are limited primarily by competition for insects to eat
 - * Food can be depleted





- Some songbird populations are limited primarily by competition for breeding sites, whereas others are limited primarily by competition for insects to eat
 - ► * Food can be depleted
 - * Making competition and turnover more likely



- Some songbird populations are limited primarily by competition for breeding sites, whereas others are limited primarily by competition for insects to eat
 - * Food can be depleted
 - * Making competition and turnover more likely





- Some songbird populations are limited primarily by competition for breeding sites, whereas others are limited primarily by competition for insects to eat
 - * Food can be depleted
 - * Making competition and turnover more likely
 - * Nest sites can be occupied, but they don't go away



- Some songbird populations are limited primarily by competition for breeding sites, whereas others are limited primarily by competition for insects to eat
 - * Food can be depleted
 - * Making competition and turnover more likely
 - * Nest sites can be occupied, but they don't go away



► Some plant populations are limited by water, and some by light



- Some plant populations are limited by water, and some by light
- ► Poll: Which is more likely to work out as a scramble?



- Some plant populations are limited by water, and some by light
- ► Poll: Which is more likely to work out as a scramble?

>



- Some plant populations are limited by water, and some by light
- Poll: Which is more likely to work out as a scramble?
 - * Light is very likely to work out as a "contest" – the taller individuals will win and do OK



- Some plant populations are limited by water, and some by light
- ▶ Poll: Which is more likely to work out as a scramble?
 - * Light is very likely to work out as a "contest" – the taller individuals will win and do OK

*



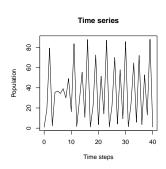
- Some plant populations are limited by water, and some by light
- Poll: Which is more likely to work out as a scramble?
 - * Light is very likely to work out as a "contest" – the taller individuals will win and do OK
 - * Water works as a scramble in some environments, and a contest in others



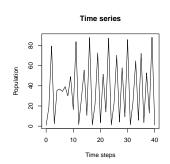
- Some plant populations are limited by water, and some by light
- Poll: Which is more likely to work out as a scramble?
 - * Light is very likely to work out as a "contest" – the taller individuals will win and do OK
 - * Water works as a scramble in some environments, and a contest in others



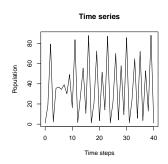
 It's interesting that we can get complicated behaviour from such a dead-simple model



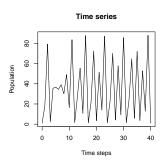
- It's interesting that we can get complicated behaviour from such a dead-simple model
- Complex dynamics may have simple causes



- It's interesting that we can get complicated behaviour from such a dead-simple model
- Complex dynamics may have simple causes
- People always tend to look for specific reasons, but sometimes the changes we observe are just natural dynamics



- It's interesting that we can get complicated behaviour from such a dead-simple model
- Complex dynamics may have simple causes
- People always tend to look for specific reasons, but sometimes the changes we observe are just natural dynamics



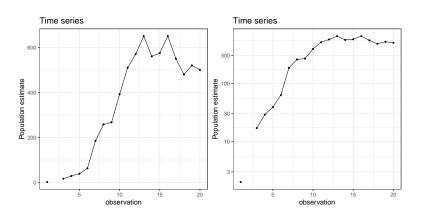
▶ We can plot λ and N_{T+1} vs. N for real population data

- We can plot λ and N_{T+1} vs. N for real population data
- ▶ We expect λ to decrease (on average)

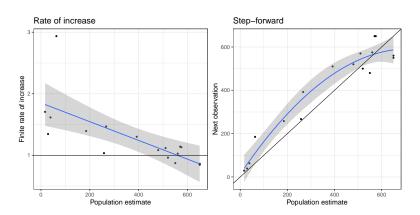
- We can plot λ and N_{T+1} vs. N for real population data
- We expect λ to decrease (on average)
- \blacktriangleright We're curious about N_{T+1} .

- We can plot λ and N_{T+1} vs. N for real population data
- We expect λ to decrease (on average)
- \triangleright We're curious about N_{T+1} .

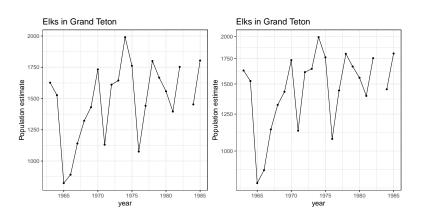
Paramecia (repeat)



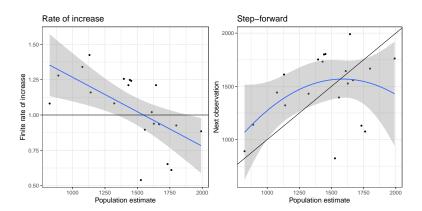
Paramecia



Elk (repeat)



Elk



Real populations

► It's hard to find examples of turnover from real population data.

- ► It's hard to find examples of turnover from real population data.
- ► So how do we explain real population cycles?

- ► It's hard to find examples of turnover from real population data.
- So how do we explain real population cycles?
 - ► Regulation may happen on a longer time scale

- ▶ It's hard to find examples of turnover from real population data.
- So how do we explain real population cycles?
 - Regulation may happen on a longer time scale
 - ► May be hard to see because of "noise" i.e., other sources of variation

- ▶ It's hard to find examples of turnover from real population data.
- So how do we explain real population cycles?
 - Regulation may happen on a longer time scale
 - May be hard to see because of "noise" i.e., other sources of variation
 - Cycles may be due to more complicated mechanisms

- ▶ It's hard to find examples of turnover from real population data.
- So how do we explain real population cycles?
 - Regulation may happen on a longer time scale
 - May be hard to see because of "noise" i.e., other sources of variation
 - Cycles may be due to more complicated mechanisms

Outline

Introduction

Population Examples

Continuous-time regulation

A simple, continuous-time model Simulating model behaviour Equilibria and time scales

Discrete-time regulation

A simple, discrete-time model Simulating this system Interpreting complex behaviour

Delayed regulation

Small populations and stochasticity

Allee effects
Stochastic effects

► One mechanism for population cycles might be if regulation is *delayed* in time

- ▶ One mechanism for population cycles might be if regulation is delayed in time
 - ▶ It takes time for individuals to complete their life cycle

- One mechanism for population cycles might be if regulation is delayed in time
 - ▶ It takes time for individuals to complete their life cycle
 - ► Recall that the life cycle is implicit in our simple models

- One mechanism for population cycles might be if regulation is delayed in time
 - It takes time for individuals to complete their life cycle
 - Recall that the life cycle is implicit in our simple models
 - ► It takes time for the population to damage its resources or build up natural enemies

- One mechanism for population cycles might be if regulation is delayed in time
 - ▶ It takes time for individuals to complete their life cycle
 - Recall that the life cycle is implicit in our simple models
 - It takes time for the population to damage its resources or build up natural enemies

► How would change a simple continuous-time model into a (relatively) simple time-delayed model?

How would change a simple continuous-time model into a (relatively) simple time-delayed model?

► Original model:
$$\frac{dN}{dt} = (b(N) - d(N))N$$

- How would change a simple continuous-time model into a (relatively) simple time-delayed model?
- ► Original model: $\frac{dN}{dt} = (b(N) d(N))N$
- ▶ Be explicit about time: $\frac{dN(t)}{dt} = (b(N(t)) d(N(t)))N(t)$

- How would change a simple continuous-time model into a (relatively) simple time-delayed model?
- ► Original model: $\frac{dN}{dt} = (b(N) d(N))N$
- ▶ Be explicit about time: $\frac{dN(t)}{dt} = (b(N(t)) d(N(t)))N(t)$

► Where should we add delays? Assume we leave the left-hand side alone (that's what we're trying to model).

▶ Where should we add delays? Assume we leave the left-hand side alone (that's what we're trying to model).



- ▶ Where should we add delays? Assume we leave the left-hand side alone (that's what we're trying to model).
 - * rates at time t might depend on past conditions (population at time $t-\tau$)

- ▶ Where should we add delays? Assume we leave the left-hand side alone (that's what we're trying to model).
 - * rates at time t might depend on past conditions (population at time $t-\tau$)
 - ,

- ▶ Where should we add delays? Assume we leave the left-hand side alone (that's what we're trying to model).
 - * rates at time t might depend on past conditions (population at time $t \tau$)
 - * population at time t is just population at time t

- ▶ Where should we add delays? Assume we leave the left-hand side alone (that's what we're trying to model).
 - * rates at time t might depend on past conditions (population at time $t-\tau$)
 - * population at time t is just population at time t

4D > 4B > 4E > 4E > E 990

- ▶ Where should we add delays? Assume we leave the left-hand side alone (that's what we're trying to model).
 - * rates at time t might depend on past conditions (population at time $t-\tau$)
 - * population at time t is just population at time t
 - ▶ * that is the population that is experiencing births and deaths

- ▶ Where should we add delays? Assume we leave the left-hand side alone (that's what we're trying to model).
 - * rates at time t might depend on past conditions (population at time $t-\tau$)
 - * population at time t is just population at time t
 - * that is the population that is experiencing births and deaths
 - *

- ▶ Where should we add delays? Assume we leave the left-hand side alone (that's what we're trying to model).
 - * rates at time t might depend on past conditions (population at time $t-\tau$)
 - ightharpoonup * population at time t is just population at time t
 - * that is the population that is experiencing births and deaths

$$* \frac{dN(t)}{dt} = (b(N(t-\tau)) - d(N(t-\tau)))N(t)$$

- ▶ Where should we add delays? Assume we leave the left-hand side alone (that's what we're trying to model).
 - * rates at time t might depend on past conditions (population at time $t-\tau$)
 - ightharpoonup * population at time t is just population at time t
 - * that is the population that is experiencing births and deaths

$$* \frac{dN(t)}{dt} = (b(N(t-\tau)) - d(N(t-\tau)))N(t)$$

► For simplicity, we assume that both rates are delayed by the same amount of time

- ► For simplicity, we assume that both rates are delayed by the same amount of time
- ► More realistic models might have different delays

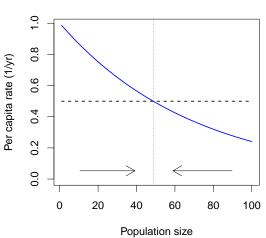
- ► For simplicity, we assume that both rates are delayed by the same amount of time
- More realistic models might have different delays
 - or delay in only one quantity

- ► For simplicity, we assume that both rates are delayed by the same amount of time
- More realistic models might have different delays
 - or delay in only one quantity
 - or distributed delays, so that the rate is some kind of average

- ► For simplicity, we assume that both rates are delayed by the same amount of time
- More realistic models might have different delays
 - or delay in only one quantity
 - or distributed delays, so that the rate is some kind of average

Arrows with time delay





► Poll: If a population is growing, what will happen as it approaches the equilibrium?

▶ Poll: If a population is growing, what will happen as it approaches the equilibrium?



- ▶ Poll: If a population is growing, what will happen as it approaches the equilibrium?
 - ► * It *keeps* growing

- ▶ Poll: If a population is growing, what will happen as it approaches the equilibrium?
 - ▶ * It *keeps* growing
 - *

Model dynamics

- ▶ Poll: If a population is growing, what will happen as it approaches the equilibrium?
 - ▶ * It *keeps* growing
 - * It needs to pass the equilibrium and look back in time before it will stop growing

Model dynamics

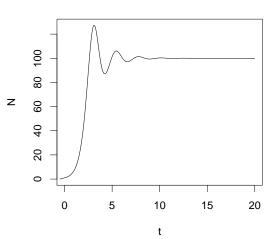
- Poll: If a population is growing, what will happen as it approaches the equilibrium?
 - ▶ * It *keeps* growing
 - * It needs to pass the equilibrium and look back in time before it will stop growing
- ► So what happens in the long term?

Model dynamics

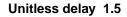
- ▶ Poll: If a population is growing, what will happen as it approaches the equilibrium?
 - ▶ * It keeps growing
 - * It needs to pass the equilibrium and look back in time before it will stop growing
- So what happens in the long term?

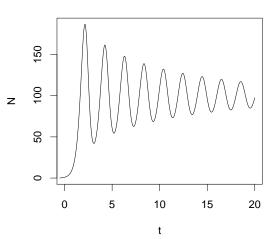
Time-delayed dynamics

Unitless delay 1

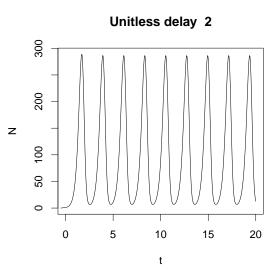


Time-delayed dynamics





Time-delayed dynamics



► Delayed population models show:

- ▶ Delayed population models show:
 - Damped oscillations (growing smaller and smaller) for shorter delays

- ▶ Delayed population models show:
 - Damped oscillations (growing smaller and smaller) for shorter delays
 - ► These could be so small that you wouldn't expect to notice them

- ▶ Delayed population models show:
 - Damped oscillations (growing smaller and smaller) for shorter delays
 - These could be so small that you wouldn't expect to notice them
 - ► Persistent oscillations for longer delays

- ▶ Delayed population models show:
 - Damped oscillations (growing smaller and smaller) for shorter delays
 - These could be so small that you wouldn't expect to notice them
 - Persistent oscillations for longer delays

► Oscillations will be bigger (and will switch from damped to persistent) if the time delay in the model is "long"

- Oscillations will be bigger (and will switch from damped to persistent) if the time delay in the model is "long"
- ► Long compared to what?

- Oscillations will be bigger (and will switch from damped to persistent) if the time delay in the model is "long"
- ► Long compared to what?
 - **▶** ≯

- Oscillations will be bigger (and will switch from damped to persistent) if the time delay in the model is "long"
- Long compared to what?
 - ▶ * It must be something else in the model with units of time

- Oscillations will be bigger (and will switch from damped to persistent) if the time delay in the model is "long"
- ► Long compared to what?
 - ▶ * It must be something else in the model with units of time
 - *

- Oscillations will be bigger (and will switch from damped to persistent) if the time delay in the model is "long"
- Long compared to what?
 - ▶ * It must be something else in the model with units of time
 - ► * It should have something to do with behaviour near the equilibrium

- Oscillations will be bigger (and will switch from damped to persistent) if the time delay in the model is "long"
- Long compared to what?
 - ▶ * It must be something else in the model with units of time
 - * It should have something to do with behaviour near the equilibrium
 - *

- Oscillations will be bigger (and will switch from damped to persistent) if the time delay in the model is "long"
- Long compared to what?
 - * It must be something else in the model with units of time
 - * It should have something to do with behaviour near the equilibrium
 - ► * In fact, we compare the time delay to the characteristic time of approach to the carrying capacity (calculated by ignoring the delays)

- Oscillations will be bigger (and will switch from damped to persistent) if the time delay in the model is "long"
- Long compared to what?
 - * It must be something else in the model with units of time
 - * It should have something to do with behaviour near the equilibrium
 - ► * In fact, we compare the time delay to the characteristic time of approach to the carrying capacity (calculated by ignoring the delays)

► The behaviour of any particular delay system is determined by one or more unitless quantities

- ► The behaviour of any particular delay system is determined by one or more unitless quantities
- ightharpoonup Our simple model is controlled by the ratio τ/t_c , where t_c is the characteristic time of approach to the carrying capacity in the absence of delay

- ► The behaviour of any particular delay system is determined by one or more unitless quantities
- Our simple model is controlled by the ratio τ/t_c , where t_c is the characteristic time of approach to the carrying capacity in the absence of delay
- ▶ In fact, cycles are persistent when $\tau/t_c > \pi/2!$

- ► The behaviour of any particular delay system is determined by one or more unitless quantities
- Our simple model is controlled by the ratio τ/t_c , where t_c is the characteristic time of approach to the carrying capacity in the absence of delay
- ▶ In fact, cycles are persistent when $\tau/t_c > \pi/2!$

► Time-delayed regulation produces simple cycles

- ► Time-delayed regulation produces simple cycles
 - ▶ Damped when delay is short ...

- ► Time-delayed regulation produces simple cycles
 - Damped when delay is short . . .
 - Persistent when delay is long . . .

- ► Time-delayed regulation produces simple cycles
 - Damped when delay is short . . .
 - Persistent when delay is long . . .
- ▶ ... compared to characteristic time of approach to equilibrium

- ► Time-delayed regulation produces simple cycles
 - Damped when delay is short . . .
 - Persistent when delay is long . . .
- ▶ ... compared to characteristic time of approach to equilibrium

Outline

Introduction

Population Examples

Continuous-time regulation

A simple, continuous-time model Simulating model behaviour Equilibria and time scales

Discrete-time regulation

A simple, discrete-time model Simulating this system Interpreting complex behaviour

Delayed regulation

Small populations and stochasticity
Allee effects
Stochastic effects

► Poll: What would happen if I released one butterfly into a new, highly suitable habitat?



► Poll: What would happen if I released one butterfly into a new, highly suitable habitat?





► Poll: What would happen if I released one butterfly into a new, highly suitable habitat?

*



► Poll: What would happen if I released one butterfly into a new, highly suitable habitat?

*

► What about two butterflies?



- ► Poll: What would happen if I released one butterfly into a new, highly suitable habitat?
 - *
- What about two butterflies?
 - **>** *



► Poll: What would happen if I released one butterfly into a new, highly suitable habitat?

*

What about two butterflies?

*



Example

► Poll: What would happen if I released one butterfly into a new, highly suitable habitat?

*

▶ What about two butterflies?

*



 Population success (reproductive number) may be lower for very small populations

- Population success (reproductive number) may be lower for very small populations
 - ► We've already assumed reproductive numbers are low for very large populations

- Population success (reproductive number) may be lower for very small populations
 - ► We've already assumed reproductive numbers are low for very large populations
- ► Small populations are likely to be harder to predict

- Population success (reproductive number) may be lower for very small populations
 - We've already assumed reproductive numbers are low for very large populations
- Small populations are likely to be harder to predict
 - More affected by stochasticity

- Population success (reproductive number) may be lower for very small populations
 - We've already assumed reproductive numbers are low for very large populations
- Small populations are likely to be harder to predict
 - More affected by stochasticity

Outline

Introduction

Population Examples

Continuous-time regulation

A simple, continuous-time model Simulating model behaviour Equilibria and time scales

Discrete-time regulation

A simple, discrete-time model Simulating this system Interpreting complex behaviour

Delayed regulation

Small populations and stochasticity Allee effects

Stochastic effects

Allee effects

► Effects which cause small populations to have low per-capita growth rates are called Allee effects

Allee effects

- ► Effects which cause small populations to have low per-capita growth rates are called Allee effects
 - ► Equivalent to saying that medium-sized populations have larger per-capita growth rates than small ones

Allee effects

- ► Effects which cause small populations to have low per-capita growth rates are called Allee effects
 - ► Equivalent to saying that medium-sized populations have larger per-capita growth rates than small ones

► Poll: Why might growth rates be low when populations are small?

► Poll: Why might growth rates be low when populations are small?



- ► Poll: Why might growth rates be low when populations are small?
 - * Individuals may have trouble finding mates

- ► Poll: Why might growth rates be low when populations are small?
 - * Individuals may have trouble finding mates
 - *

- ▶ Poll: Why might growth rates be low when populations are small?
 - * Individuals may have trouble finding mates
 - * Individuals in larger populations may protect each other from predators (birds) or from weather (plants)

- Poll: Why might growth rates be low when populations are small?
 - * Individuals may have trouble finding mates
 - * Individuals in larger populations may protect each other from predators (birds) or from weather (plants)

- ▶ Poll: Why might growth rates be low when populations are small?
 - * Individuals may have trouble finding mates
 - * Individuals in larger populations may protect each other from predators (birds) or from weather (plants)
 - ▶ * Individuals in larger populations may hunt co-operatively

- ▶ Poll: Why might growth rates be low when populations are small?
 - * Individuals may have trouble finding mates
 - * Individuals in larger populations may protect each other from predators (birds) or from weather (plants)
 - ▶ * Individuals in larger populations may hunt co-operatively
 - *

- ▶ Poll: Why might growth rates be low when populations are small?
 - * Individuals may have trouble finding mates
 - * Individuals in larger populations may protect each other from predators (birds) or from weather (plants)
 - ► * Individuals in larger populations may hunt co-operatively
 - * Genetic effects (inbreeding, loss of valuable variation)

- ▶ Poll: Why might growth rates be low when populations are small?
 - * Individuals may have trouble finding mates
 - * Individuals in larger populations may protect each other from predators (birds) or from weather (plants)
 - ▶ * Individuals in larger populations may hunt co-operatively
 - * Genetic effects (inbreeding, loss of valuable variation)

► Allee effects can affect the (per capita) birth rate

▶ Allee effects can affect the (per capita) birth rate

- ▶ Allee effects can affect the (per capita) birth rate
 - ▶ * if the rate is *smaller* when density is low

- ▶ Allee effects can affect the (per capita) birth rate
 - * if the rate is *smaller* when density is low
- ▶ ... or the (per capita) death rate

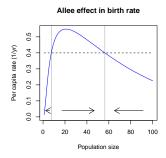
- ▶ Allee effects can affect the (per capita) birth rate
 - * if the rate is *smaller* when density is low
- ... or the (per capita) death rate
 - *

- ▶ Allee effects can affect the (per capita) birth rate
 - * if the rate is *smaller* when density is low
- ... or the (per capita) death rate
 - ▶ * if the rate is *larger* when density is low

- ▶ Allee effects can affect the (per capita) birth rate
 - * if the rate is *smaller* when density is low
- ... or the (per capita) death rate
 - ▶ * if the rate is *larger* when density is low

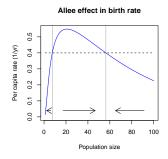
Allee effect models

► What will this model do, if the initial population is:



Allee effect models

- What will this model do, if the initial population is:
 - low, medium or high?

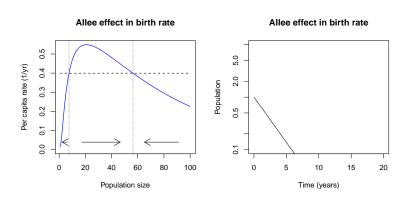


Allee effect models

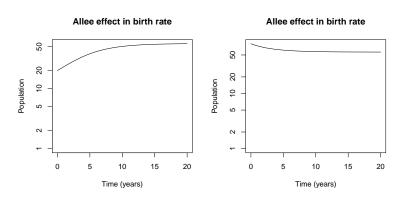
- What will this model do, if the initial population is:
 - low, medium or high?

Allee effect in birth rate

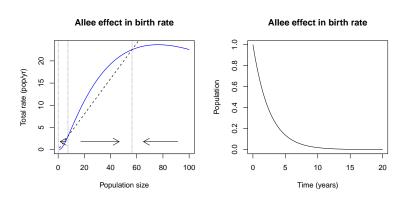
Individual perspective



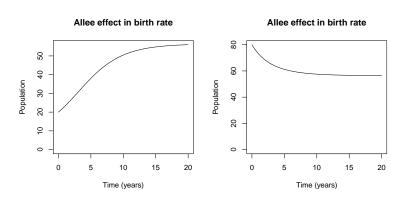
Individual perspective



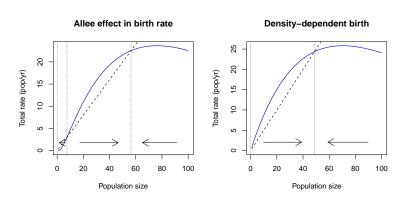
Population perspective



Population perspective

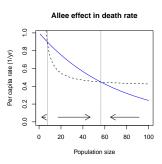


Population comparison (repeat)



Allee effect in death rate

► What is the difference between this example and the previous one?



Allee effect in death rate

- What is the difference between this example and the previous one?
- ► What will this model do, if the initial population is:

Allee effect in death rate

Allee effect in death rate

- ▶ What is the difference between this example and the previous one?
- What will this model do, if the initial population is:
 - low, medium or high?

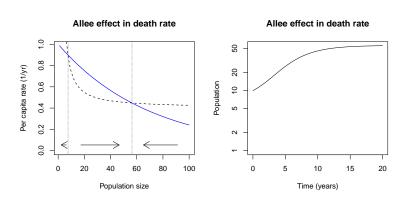
Allee effect in death rate

Allee effect in death rate

- What is the difference between this example and the previous one?
- What will this model do, if the initial population is:
 - low, medium or high?

Allee effect in death rate

Individual perspective



ightharpoonup The reproductive number $\mathcal R$ means the average lifetime number of offspring per individual

- The reproductive number \mathcal{R} means the average lifetime number of offspring per individual
 - ► Should be unitless, so we consider offspring at the same stage as the individual.

- The reproductive number \mathcal{R} means the average lifetime number of offspring per individual
 - ► Should be unitless, so we consider offspring at the same stage as the individual.
- ightharpoonup We can apply $\mathcal R$ in general for any set of conditions, or we can distinguish:

- ► The reproductive number \mathcal{R} means the average lifetime number of offspring per individual
 - Should be unitless, so we consider offspring at the same stage as the individual.
- We can apply \mathcal{R} in general for any set of conditions, or we can distinguish:
 - ▶ the **basic reproductive number** \mathcal{R}_0 : \mathcal{R} in the limit when the population is small, and

- ► The reproductive number \mathcal{R} means the average lifetime number of offspring per individual
 - Should be unitless, so we consider offspring at the same stage as the individual.
- We can apply \mathcal{R} in general for any set of conditions, or we can distinguish:
 - ▶ the **basic reproductive number** \mathcal{R}_0 : \mathcal{R} in the limit when the population is small, and
 - ▶ the maximal reproductive number \mathcal{R}_{max} : \mathcal{R} at whatever level is the peak

- ► The reproductive number \mathcal{R} means the average lifetime number of offspring per individual
 - Should be unitless, so we consider offspring at the same stage as the individual.
- We can apply \mathcal{R} in general for any set of conditions, or we can distinguish:
 - ▶ the **basic reproductive number** \mathcal{R}_0 : \mathcal{R} in the limit when the population is small, and
 - ▶ the maximal reproductive number \mathcal{R}_{max} : \mathcal{R} at whatever level is the peak

▶ We previously said that when $\mathcal{R}_0 < 1$, the population always went extinct

- \blacktriangleright We previously said that when $\mathcal{R}_0 < 1,$ the population always went extinct
 - ► A population that can't invade can never replace itself on average

- ▶ We previously said that when $\mathcal{R}_0 < 1$, the population always went extinct
 - ► A population that can't invade can never replace itself on average
- ▶ When Allee effects are present, it's no longer true that a species that can't invade can't persist

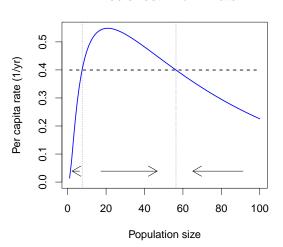
- ▶ We previously said that when $\mathcal{R}_0 < 1$, the population always went extinct
 - ► A population that can't invade can never replace itself on average
- When Allee effects are present, it's no longer true that a species that can't invade can't persist
 - **▶** ≯

- ▶ We previously said that when $\mathcal{R}_0 < 1$, the population always went extinct
 - ▶ A population that can't invade can never replace itself on average
- When Allee effects are present, it's no longer true that a species that can't invade can't persist
 - ▶ * If $\mathcal{R}_0 < 1$ population can't invade, but if $\mathcal{R}_{\text{max}} > 1$ it can still persist

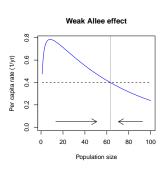
- We previously said that when $\mathcal{R}_0 < 1$, the population always went extinct
 - ▶ A population that can't invade can never replace itself on average
- When Allee effects are present, it's no longer true that a species that can't invade can't persist
 - ▶ * If $\mathcal{R}_0 < 1$ population can't invade, but if $\mathcal{R}_{\text{max}} > 1$ it can still persist

\mathcal{R}_0 and \mathcal{R}_{max} (repeat)

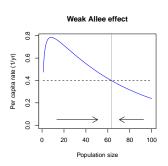
Allee effect in birth rate



► If birth rates go down or death rates go up at low density, we consider this an Allee effect

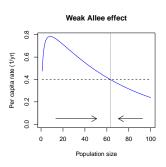


- ▶ If birth rates go down or death rates go up at low density, we consider this an Allee effect
- $\begin{tabular}{ll} \hline & If $\mathcal{R}_0 < 1$ we say it's a $strong$ \\ & Allee effect \\ \end{tabular}$

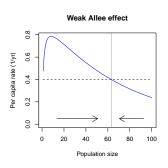


- ► If birth rates go down or death rates go up at low density, we consider this an Allee effect
- $\begin{tabular}{ll} \blacksquare & \begin{tabular}{ll} \blacksquare & \be$

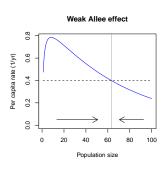
*



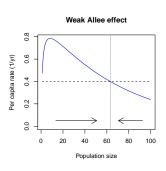
- If birth rates go down or death rates go up at low density, we consider this an Allee effect
- ▶ If $\mathcal{R}_0 < 1$ we say it's a *strong* Allee effect
 - * Population can't invade



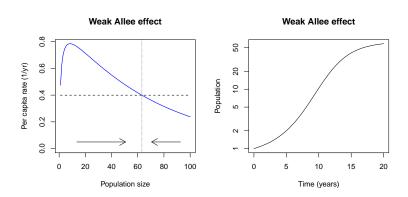
- ▶ If birth rates go down or death rates go up at low density, we consider this an Allee effect
- ▶ If $\mathcal{R}_0 < 1$ we say it's a *strong* Allee effect
 - * Population can't invade
- ▶ If $\mathcal{R}_0 > 1$ we say it's a *weak* Allee effect



- ▶ If birth rates go down or death rates go up at low density, we consider this an Allee effect
- ▶ If $\mathcal{R}_0 < 1$ we say it's a *strong* Allee effect
 - * Population can't invade
- ▶ If $\mathcal{R}_0 > 1$ we say it's a *weak* Allee effect



Individual perspective



▶ Population may go extinct if it drops below a certain threshold

- Population may go extinct if it drops below a certain threshold
- ▶ Poll: How come the population is there in the first place if there's an Allee effect?

- Population may go extinct if it drops below a certain threshold
- Poll: How come the population is there in the first place if there's an Allee effect?
 - **>** 3

- Population may go extinct if it drops below a certain threshold
- Poll: How come the population is there in the first place if there's an Allee effect?
 - * Maybe it's a weak effect

- Population may go extinct if it drops below a certain threshold
- Poll: How come the population is there in the first place if there's an Allee effect?
 - * Maybe it's a weak effect
 - *

- Population may go extinct if it drops below a certain threshold
- Poll: How come the population is there in the first place if there's an Allee effect?
 - * Maybe it's a weak effect
 - * Maybe conditions have changed (it used to be a weak effect, or no effect)

- Population may go extinct if it drops below a certain threshold
- Poll: How come the population is there in the first place if there's an Allee effect?
 - * Maybe it's a weak effect
 - * Maybe conditions have changed (it used to be a weak effect, or no effect)
 - *

- Population may go extinct if it drops below a certain threshold
- Poll: How come the population is there in the first place if there's an Allee effect?
 - * Maybe it's a weak effect
 - * Maybe conditions have changed (it used to be a weak effect, or no effect)
 - * Maybe a large initial group established by chance

- Population may go extinct if it drops below a certain threshold
- Poll: How come the population is there in the first place if there's an Allee effect?
 - * Maybe it's a weak effect
 - * Maybe conditions have changed (it used to be a weak effect, or no effect)
 - * Maybe a large initial group established by chance
 - *

- Population may go extinct if it drops below a certain threshold
- Poll: How come the population is there in the first place if there's an Allee effect?
 - * Maybe it's a weak effect
 - * Maybe conditions have changed (it used to be a weak effect, or no effect)
 - * Maybe a large initial group established by chance
 - * Maybe the population arrived recently (and won't necessarily stick around)

- Population may go extinct if it drops below a certain threshold
- Poll: How come the population is there in the first place if there's an Allee effect?
 - * Maybe it's a weak effect
 - * Maybe conditions have changed (it used to be a weak effect, or no effect)
 - * Maybe a large initial group established by chance
 - * Maybe the population arrived recently (and won't necessarily stick around)

Outline

Introduction

Population Examples

Continuous-time regulation

A simple, continuous-time model Simulating model behaviour Equilibria and time scales

Discrete-time regulation

A simple, discrete-time model Simulating this system Interpreting complex behaviour

Delayed regulation

Small populations and stochasticity

Allee effects

Stochastic effects

► The world is complicated and biological populations are not perfectly predictable

- ► The world is complicated and biological populations are not perfectly predictable
- ► Real populations don't go smoothly to equilibria, instead they bounce around (or sometimes do other wild stuff)

- ► The world is complicated and biological populations are not perfectly predictable
- Real populations don't go smoothly to equilibria, instead they bounce around (or sometimes do other wild stuff)
- ► We divide stochastic (or random) effects into demographic and environmental stochasticity

- ► The world is complicated and biological populations are not perfectly predictable
- Real populations don't go smoothly to equilibria, instead they bounce around (or sometimes do other wild stuff)
- ► We divide stochastic (or random) effects into demographic and environmental stochasticity

► Female butterflies of a certain species lay 200 eggs on average, of which:

- ► Female butterflies of a certain species lay 200 eggs on average, of which:
 - ► Half are female

- ► Female butterflies of a certain species lay 200 eggs on average, of which:
 - ► Half are female
 - ► 50% hatch successfully into larvae

- ► Female butterflies of a certain species lay 200 eggs on average, of which:
 - Half are female
 - ▶ 50% hatch successfully into larvae
 - ▶ 10% of larvae successfully pupate

- Female butterflies of a certain species lay 200 eggs on average, of which:
 - Half are female
 - ▶ 50% hatch successfully into larvae
 - ▶ 10% of larvae successfully pupate
 - ► 60% of pupae become adults

- Female butterflies of a certain species lay 200 eggs on average, of which:
 - Half are female
 - ▶ 50% hatch successfully into larvae
 - ▶ 10% of larvae successfully pupate
 - ▶ 60% of pupae become adults
 - ► Half of adult females successfully reproduce

- Female butterflies of a certain species lay 200 eggs on average, of which:
 - Half are female
 - ▶ 50% hatch successfully into larvae
 - ▶ 10% of larvae successfully pupate
 - ▶ 60% of pupae become adults
 - ► Half of adult females successfully reproduce
- ► A single gravid (pregnant) female butterfly is blown away by a freak storm, and lands by chance on a suitable island with no butterflies What do you expect to happen?

- Female butterflies of a certain species lay 200 eggs on average, of which:
 - ► Half are female
 - ▶ 50% hatch successfully into larvae
 - ▶ 10% of larvae successfully pupate
 - ▶ 60% of pupae become adults
 - ► Half of adult females successfully reproduce
- ➤ A single gravid (pregnant) female butterfly is blown away by a freak storm, and lands by chance on a suitable island with no butterflies What do you expect to happen?
 - *

- Female butterflies of a certain species lay 200 eggs on average, of which:
 - Half are female
 - ▶ 50% hatch successfully into larvae
 - ▶ 10% of larvae successfully pupate
 - ▶ 60% of pupae become adults
 - Half of adult females successfully reproduce
- ► A single gravid (pregnant) female butterfly is blown away by a freak storm, and lands by chance on a suitable island with no butterflies What do you expect to happen?
 - ightharpoonup * $\lambda=1.5$ (remember not to multiply by the sex ratio twice!)

- ► Female butterflies of a certain species lay 200 eggs on average, of which:
 - Half are female
 - ▶ 50% hatch successfully into larvae
 - ▶ 10% of larvae successfully pupate
 - ▶ 60% of pupae become adults
 - Half of adult females successfully reproduce
- ➤ A single gravid (pregnant) female butterfly is blown away by a freak storm, and lands by chance on a suitable island with no butterflies What do you expect to happen?
 - * $\lambda = 1.5$ (remember not to multiply by the sex ratio twice!)
 - *

- ► Female butterflies of a certain species lay 200 eggs on average, of which:
 - ► Half are female
 - ▶ 50% hatch successfully into larvae
 - ▶ 10% of larvae successfully pupate
 - ▶ 60% of pupae become adults
 - Half of adult females successfully reproduce
- ► A single gravid (pregnant) female butterfly is blown away by a freak storm, and lands by chance on a suitable island with no butterflies What do you expect to happen?
 - ightharpoonup * $\lambda=1.5$ (remember not to multiply by the sex ratio twice!)
 - * Almost anything can happen

- ► Female butterflies of a certain species lay 200 eggs on average, of which:
 - ► Half are female
 - ▶ 50% hatch successfully into larvae
 - ▶ 10% of larvae successfully pupate
 - ▶ 60% of pupae become adults
 - Half of adult females successfully reproduce
- ► A single gravid (pregnant) female butterfly is blown away by a freak storm, and lands by chance on a suitable island with no butterflies What do you expect to happen?
 - ightharpoonup * $\lambda=1.5$ (remember not to multiply by the sex ratio twice!)
 - * Almost anything can happen

► Depending on unknown conditions, especially in that first season, all of those probabilities could change dramatically

- ▶ Depending on unknown conditions, especially in that first season, all of those probabilities could change dramatically
- Even if we knew the probabilities, that would not guarantee an exact result

- ▶ Depending on unknown conditions, especially in that first season, all of those probabilities could change dramatically
- ► Even if we knew the *probabilities*, that would not guarantee an exact result
 - **k**

- ▶ Depending on unknown conditions, especially in that first season, all of those probabilities could change dramatically
- Even if we knew the probabilities, that would not guarantee an exact result
 - ► * Population could be lucky or unlucky

- Depending on unknown conditions, especially in that first season, all of those probabilities could change dramatically
- Even if we knew the probabilities, that would not guarantee an exact result
 - * Population could be lucky or unlucky
- ▶ What if λ < 1?

- Depending on unknown conditions, especially in that first season, all of those probabilities could change dramatically
- Even if we knew the probabilities, that would not guarantee an exact result
 - * Population could be lucky or unlucky
- ▶ What if λ < 1?
 - *****

- ▶ Depending on unknown conditions, especially in that first season, all of those probabilities could change dramatically
- Even if we knew the probabilities, that would not guarantee an exact result
 - * Population could be lucky or unlucky
- ▶ What if $\lambda < 1$?
 - ▶ * The population would go extinct eventually, even if it's lucky

- ▶ Depending on unknown conditions, especially in that first season, all of those probabilities could change dramatically
- Even if we knew the probabilities, that would not guarantee an exact result
 - * Population could be lucky or unlucky
- ▶ What if $\lambda < 1$?
 - ▶ * The population would go extinct eventually, even if it's lucky

▶ **Demographic** stochasticity is stochasticity that operates at the level of individuals

- ▶ Demographic stochasticity is stochasticity that operates at the level of individuals
 - ► Individuals don't increase gradually, they die or give birth

- Demographic stochasticity is stochasticity that operates at the level of individuals
 - Individuals don't increase gradually, they die or give birth
 - ► Individuals don't produce 1.2 offspring: they produce 0, 1, 2 or 3 ...

- Demographic stochasticity is stochasticity that operates at the level of individuals
 - Individuals don't increase gradually, they die or give birth
 - ► Individuals don't produce 1.2 offspring: they produce 0, 1, 2 or 3 . . .
- ► Even if we control conditions perfectly, we can't exactly predict the dynamics of small populations

- Demographic stochasticity is stochasticity that operates at the level of individuals
 - Individuals don't increase gradually, they die or give birth
 - ► Individuals don't produce 1.2 offspring: they produce 0, 1, 2 or 3 . . .
- Even if we control conditions perfectly, we can't exactly predict the dynamics of small populations
- Demographic stochasticity averages out in large populations

- Demographic stochasticity is stochasticity that operates at the level of individuals
 - Individuals don't increase gradually, they die or give birth
 - ► Individuals don't produce 1.2 offspring: they produce 0, 1, 2 or 3 . . .
- Even if we control conditions perfectly, we can't exactly predict the dynamics of small populations
- Demographic stochasticity averages out in large populations

► **Environmental** stochasticity is stochasticity that operates at the level of the population

- ► **Environmental** stochasticity is stochasticity that operates at the level of the population
 - ► E.g,. weather, pollution

- ► **Environmental** stochasticity is stochasticity that operates at the level of the population
 - ► E.g,. weather, pollution
- Environmental stochasticity can have large effects on any population

- ► **Environmental** stochasticity is stochasticity that operates at the level of the population
 - ► E.g,. weather, pollution
- Environmental stochasticity can have large effects on any population

- ► **Environmental** stochasticity is stochasticity that operates at the level of the population
 - ► E.g,. weather, pollution
- Environmental stochasticity can have large effects on any population
 - ► * A bad year is bad for everyone

- ► **Environmental** stochasticity is stochasticity that operates at the level of the population
 - ► E.g,. weather, pollution
- Environmental stochasticity can have large effects on any population
 - ► * A bad year is bad for everyone
- ▶ But small populations are the ones in danger of going extinct

- ► **Environmental** stochasticity is stochasticity that operates at the level of the population
 - ► E.g,. weather, pollution
- Environmental stochasticity can have large effects on any population
 - * A bad year is bad for everyone
- ▶ But small populations are the ones in danger of going extinct
 - **▶** ≯

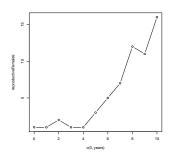
- ► **Environmental** stochasticity is stochasticity that operates at the level of the population
 - E.g,. weather, pollution
- Environmental stochasticity can have large effects on any population
 - * A bad year is bad for everyone
- But small populations are the ones in danger of going extinct
 - * Large populations can average out over time

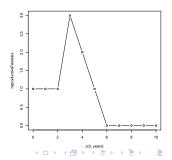
- ► **Environmental** stochasticity is stochasticity that operates at the level of the population
 - ► E.g,. weather, pollution
- Environmental stochasticity can have large effects on any population
 - * A bad year is bad for everyone
- ▶ But small populations are the ones in danger of going extinct
 - * Large populations can average out over time
 - *

- ► **Environmental** stochasticity is stochasticity that operates at the level of the population
 - ► E.g,. weather, pollution
- Environmental stochasticity can have large effects on any population
 - ► * A bad year is bad for everyone
- But small populations are the ones in danger of going extinct
 - * Large populations can average out over time
 - ▶ * If the "mean" value of R_0 is greater than 1, large population should survive the ups and downs

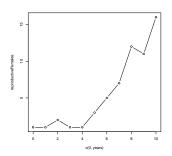
- ► **Environmental** stochasticity is stochasticity that operates at the level of the population
 - ► E.g,. weather, pollution
- Environmental stochasticity can have large effects on any population
 - ► * A bad year is bad for everyone
- But small populations are the ones in danger of going extinct
 - * Large populations can average out over time
 - ▶ * If the "mean" value of R_0 is greater than 1, large population should survive the ups and downs

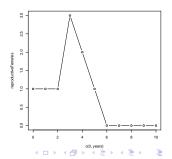
We can simulate stochastic systems very easily



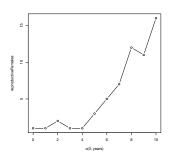


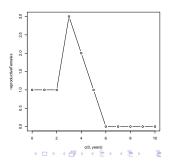
- We can simulate stochastic systems very easily
- ► But if we do the same simulation twice, we can get different answers



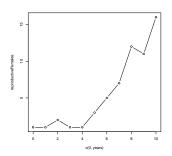


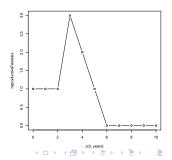
- We can simulate stochastic systems very easily
- ► But if we do the same simulation twice, we can get different answers
- ► Adds realism



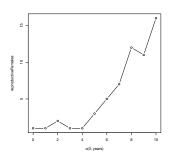


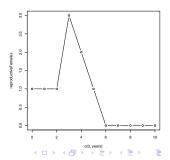
- We can simulate stochastic systems very easily
- ► But if we do the same simulation twice, we can get different answers
- Adds realism
 - ► But harder to interpret





- We can simulate stochastic systems very easily
- ► But if we do the same simulation twice, we can get different answers
- Adds realism
 - But harder to interpret





 Stochasticity is very important in real populations, but hard to study

- Stochasticity is very important in real populations, but hard to study
 - ► Mathematical analysis is very difficult

- Stochasticity is very important in real populations, but hard to study
 - ► Mathematical analysis is very difficult
 - Simulations are useful, but hard to interpret

- Stochasticity is very important in real populations, but hard to study
 - ► Mathematical analysis is very difficult
 - Simulations are useful, but hard to interpret
 - ► Each time you simulate, you get a different answer

- Stochasticity is very important in real populations, but hard to study
 - Mathematical analysis is very difficult
 - Simulations are useful, but hard to interpret
 - ► Each time you simulate, you get a different answer
- Ecologists need to learn to recognize and communicate our uncertainty about the future

- Stochasticity is very important in real populations, but hard to study
 - Mathematical analysis is very difficult
 - Simulations are useful, but hard to interpret
 - ▶ Each time you simulate, you get a different answer
- Ecologists need to learn to recognize and communicate our uncertainty about the future