# UNIT 7: Exploitation

#### Outline

#### Introduction

Balance and equilibrium Tendency to oscillate

#### A simple model

More detailed models Reciprocal control

#### Adding details

Dynamics

Equilibri

Who controls whom?

► Exploitation is when interactions between two species are good for one species and bad for the other

- ► Exploitation is when interactions between two species are good for one species and bad for the other
  - ► Typically, the "exploiter" is taking resources from the other species

- ► Exploitation is when interactions between two species are good for one species and bad for the other
  - Typically, the "exploiter" is taking resources from the other species
- ► Exploitation is widespread and highly diverse

- ► Exploitation is when interactions between two species are good for one species and bad for the other
  - Typically, the "exploiter" is taking resources from the other species
- Exploitation is widespread and highly diverse

► Antelopes graze on trees

- ► Antelopes graze on trees
- ► Lions eat antelopes

- ► Antelopes graze on trees
- ► Lions eat antelopes
- ► Ticks feed on lions

- ► Antelopes graze on trees
- ► Lions eat antelopes
- ► Ticks feed on lions
- ► Swallows eat ticks

- Antelopes graze on trees
- Lions eat antelopes
- ► Ticks feed on lions
- Swallows eat ticks
- ► Bacteria reproduce inside the swallow

- Antelopes graze on trees
- Lions eat antelopes
- ► Ticks feed on lions
- Swallows eat ticks
- ► Bacteria reproduce inside the swallow
- ► Viruses infect the bacteria ...

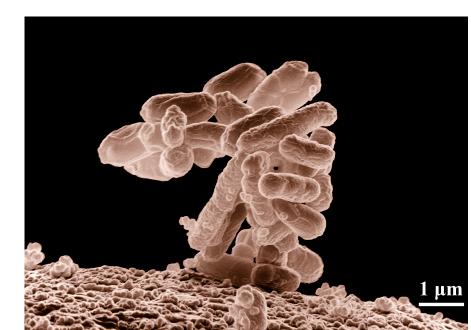
- Antelopes graze on trees
- Lions eat antelopes
- ► Ticks feed on lions
- Swallows eat ticks
- ► Bacteria reproduce inside the swallow
- Viruses infect the bacteria ...

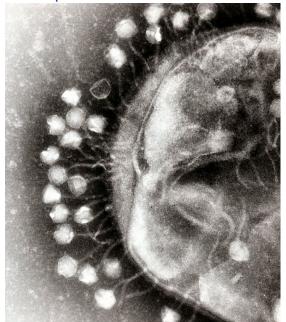












► These words are usually not used precisely, and I'm not going to test you on them

- ► These words are usually not used precisely, and I'm not going to test you on them
  - ► Predation: a predator kills and eats prey

- ► These words are usually not used precisely, and I'm not going to test you on them
  - Predation: a predator kills and eats prey
  - Parasitism: a parasite lives on or in a host and makes use of host resources

- These words are usually not used precisely, and I'm not going to test you on them
  - Predation: a predator kills and eats prey
  - Parasitism: a parasite lives on or in a host and makes use of host resources
    - Many parasites are pathogens, meaning that they cause disease

- ► These words are usually not used precisely, and I'm not going to test you on them
  - Predation: a predator kills and eats prey
  - Parasitism: a parasite lives on or in a host and makes use of host resources
    - Many parasites are pathogens, meaning that they cause disease
  - ► Parasitoidism: a parasitoid develops inside a host, but must kill the host to complete development

- ► These words are usually not used precisely, and I'm not going to test you on them
  - Predation: a predator kills and eats prey
  - Parasitism: a parasite lives on or in a host and makes use of host resources
    - Many parasites are pathogens, meaning that they cause disease
  - Parasitoidism: a parasitoid develops inside a host, but must kill the host to complete development
  - Grazing: a grazer takes food from another organism (typically a plant), and moves on

- These words are usually not used precisely, and I'm not going to test you on them
  - Predation: a predator kills and eats prey
  - Parasitism: a parasite lives on or in a host and makes use of host resources
    - Many parasites are pathogens, meaning that they cause disease
  - Parasitoidism: a parasitoid develops inside a host, but must kill the host to complete development
  - Grazing: a grazer takes food from another organism (typically a plant), and moves on

► The categories listed above are useful, but not precise – and not used precisely

- ► The categories listed above are useful, but not precise and not used precisely
  - ▶ Do rabbits predate small plants, or graze them?

- ► The categories listed above are useful, but not precise and not used precisely
  - ▶ Do rabbits predate small plants, or graze them?
  - ► Are small insects on large trees grazers, or parasites?

- ► The categories listed above are useful, but not precise and not used precisely
  - ▶ Do rabbits predate small plants, or graze them?
  - Are small insects on large trees grazers, or parasites?
  - ▶ Do intestinal worms in healthy people count as pathogens?

- The categories listed above are useful, but not precise and not used precisely
  - ▶ Do rabbits predate small plants, or graze them?
  - Are small insects on large trees grazers, or parasites?
  - Do intestinal worms in healthy people count as pathogens?
  - ► Anthrax is usually referred to as a parasite (or predator!), but should probably really be a parasitoid

- ► The categories listed above are useful, but not precise and not used precisely
  - ▶ Do rabbits predate small plants, or graze them?
  - Are small insects on large trees grazers, or parasites?
  - Do intestinal worms in healthy people count as pathogens?
  - Anthrax is usually referred to as a parasite (or predator!), but should probably really be a parasitoid

► Often interactions are grouped by the taxonomy of the species participating in the interaction

- ► Often interactions are grouped by the taxonomy of the species participating in the interaction
  - ► Herbivores eat plants

- ► Often interactions are grouped by the taxonomy of the species participating in the interaction
  - ► Herbivores eat plants
  - Carnivores eat animals

- ► Often interactions are grouped by the taxonomy of the species participating in the interaction
  - Herbivores eat plants
  - Carnivores eat animals
  - Micro-organisms are more likely than macro-organisms to be called parasites

# More vocabulary

- ► Often interactions are grouped by the taxonomy of the species participating in the interaction
  - Herbivores eat plants
  - Carnivores eat animals
  - Micro-organisms are more likely than macro-organisms to be called parasites
  - ► Insects living on animals are more likely to be called parasites than insects living on plants

# More vocabulary

- ► Often interactions are grouped by the taxonomy of the species participating in the interaction
  - Herbivores eat plants
  - Carnivores eat animals
  - Micro-organisms are more likely than macro-organisms to be called parasites
  - Insects living on animals are more likely to be called parasites than insects living on plants

When we talk about exploitation in general, we will refer generically to the species being exploited as the resource species

- When we talk about exploitation in general, we will refer generically to the species being exploited as the resource species
- ► There is a strong analogy between resource species, and **abiotic** resources like water, light and nitrogen

- When we talk about exploitation in general, we will refer generically to the species being exploited as the resource species
- ► There is a strong analogy between resource species, and **abiotic** resources like water, light and nitrogen
  - ▶ Both benefit the species that use them

- When we talk about exploitation in general, we will refer generically to the species being exploited as the resource species
- ► There is a strong analogy between resource species, and **abiotic** resources like water, light and nitrogen
  - ▶ Both benefit the species that use them
  - ► Both may, or may not, be depleted significantly by the activities of the species in question

- When we talk about exploitation in general, we will refer generically to the species being exploited as the resource species
- ► There is a strong analogy between resource species, and **abiotic** resources like water, light and nitrogen
  - ▶ Both benefit the species that use them
  - ▶ Both may, or may not, be depleted significantly by the activities of the species in question

#### Outline

#### Introduction

Balance and equilibrium

Tendency to oscillate

#### A simple model

More detailed models Reciprocal control

#### Adding details

Dynamics

Equilibria

Who controls whom?

► In an exploiter-resource system, each species has an indirect, negative effect on itself. Why?

► In an exploiter-resource system, each species has an indirect, negative effect on itself. Why?



- ► In an exploiter-resource system, each species has an indirect, negative effect on itself. Why?
  - ► \* As resource species population grows, the number of exploiters should increase, which is bad for the resource species

- ► In an exploiter-resource system, each species has an indirect, negative effect on itself. Why?
  - ► \* As resource species population grows, the number of exploiters should increase, which is bad for the resource species
    - \*

- ► In an exploiter-resource system, each species has an indirect, negative effect on itself. Why?
  - ► \* As resource species population grows, the number of exploiters should increase, which is bad for the resource species
  - \* As exploiter population grows, the population of the resource species should decrease, which is bad for the exploiter

- ► In an exploiter-resource system, each species has an indirect, negative effect on itself. Why?
  - ► \* As resource species population grows, the number of exploiters should increase, which is bad for the resource species
  - \* As exploiter population grows, the population of the resource species should decrease, which is bad for the exploiter
- ► Since each species has a negative effect on itself, these systems have a *tendency* to come to equilibrium

- ► In an exploiter-resource system, each species has an indirect, negative effect on itself. Why?
  - ► \* As resource species population grows, the number of exploiters should increase, which is bad for the resource species
  - \* As exploiter population grows, the population of the resource species should decrease, which is bad for the exploiter
- Since each species has a negative effect on itself, these systems have a tendency to come to equilibrium
  - ► Equilibrium may be reached, or we may cycle around it

- ► In an exploiter-resource system, each species has an indirect, negative effect on itself. Why?
  - ► \* As resource species population grows, the number of exploiters should increase, which is bad for the resource species
  - \* As exploiter population grows, the population of the resource species should decrease, which is bad for the exploiter
- Since each species has a negative effect on itself, these systems have a tendency to come to equilibrium
  - Equilibrium may be reached, or we may cycle around it

► What factors determine the equilibrium levels of a resource-exploiter system?

- What factors determine the equilibrium levels of a resource-exploiter system?
- ► What factors determine whether neither, one or both species survive?

- What factors determine the equilibrium levels of a resource-exploiter system?
- ► What factors determine whether neither, one or both species survive?
- ► What happens if people perturb the system (e.g., by eating a lot of one or the other species)?

- What factors determine the equilibrium levels of a resource-exploiter system?
- ► What factors determine whether neither, one or both species survive?
- ► What happens if people perturb the system (e.g., by eating a lot of one or the other species)?
- ▶ The equilibrium is of interest even if it is not reached:

- What factors determine the equilibrium levels of a resource-exploiter system?
- ► What factors determine whether neither, one or both species survive?
- ► What happens if people perturb the system (e.g., by eating a lot of one or the other species)?
- The equilibrium is of interest even if it is not reached:
  - if there are cycles, the equilibrium is what the system cycles around.

- What factors determine the equilibrium levels of a resource-exploiter system?
- ► What factors determine whether neither, one or both species survive?
- ► What happens if people perturb the system (e.g., by eating a lot of one or the other species)?
- ▶ The equilibrium is of interest even if it is not reached:
  - if there are cycles, the equilibrium is what the system cycles around.

► Imagine a pair of exploiter and resource species whose population densities are mostly regulated by each other

- Imagine a pair of exploiter and resource species whose population densities are mostly regulated by each other
  - ► The per capita growth rate of the exploiter population depends mostly on the density of the resource species

- Imagine a pair of exploiter and resource species whose population densities are mostly regulated by each other
  - ► The per capita growth rate of the exploiter population depends mostly on the density of the resource species
  - ► The per capita growth rate of the resource population depends mostly on the density of the exploiter species

- Imagine a pair of exploiter and resource species whose population densities are mostly regulated by each other
  - ► The per capita growth rate of the exploiter population depends mostly on the density of the resource species
  - ► The per capita growth rate of the resource population depends mostly on the density of the exploiter species
- ▶ Poll: What will determine equilibrium values?

- Imagine a pair of exploiter and resource species whose population densities are mostly regulated by each other
  - ► The per capita growth rate of the exploiter population depends mostly on the density of the resource species
  - ► The per capita growth rate of the resource population depends mostly on the density of the exploiter species
- ▶ Poll: What will determine equilibrium values?
  - \*

- Imagine a pair of exploiter and resource species whose population densities are mostly regulated by each other
  - ► The per capita growth rate of the exploiter population depends mostly on the density of the resource species
  - ► The per capita growth rate of the resource population depends mostly on the density of the exploiter species
- Poll: What will determine equilibrium values?
  - \* For equilibrium, each species must be at the density required to keep the *other* species balanced

- Imagine a pair of exploiter and resource species whose population densities are mostly regulated by each other
  - ► The per capita growth rate of the exploiter population depends mostly on the density of the resource species
  - ► The per capita growth rate of the resource population depends mostly on the density of the exploiter species
- Poll: What will determine equilibrium values?
  - \* For equilibrium, each species must be at the density required to keep the *other* species balanced
  - \*

- Imagine a pair of exploiter and resource species whose population densities are mostly regulated by each other
  - ► The per capita growth rate of the exploiter population depends mostly on the density of the resource species
  - ► The per capita growth rate of the resource population depends mostly on the density of the exploiter species
- Poll: What will determine equilibrium values?
  - ► \* For equilibrium, each species must be at the density required to keep the *other* species balanced
  - ▶ \* We should have about as many foxes as required to control the rabbit population, and about as many rabbits as required to keep the fox population about constant.

- Imagine a pair of exploiter and resource species whose population densities are mostly regulated by each other
  - ► The per capita growth rate of the exploiter population depends mostly on the density of the resource species
  - ► The per capita growth rate of the resource population depends mostly on the density of the exploiter species
- Poll: What will determine equilibrium values?
  - ► \* For equilibrium, each species must be at the density required to keep the *other* species balanced
  - ▶ \* We should have about as many foxes as required to control the rabbit population, and about as many rabbits as required to keep the fox population about constant.

#### Outline

#### Introduction

Balance and equilibrium Tendency to oscillate

#### A simple model

More detailed models Reciprocal control

#### Adding details

Dynamics Equilibria

Who controls whom?

► In an exploiter-resource system, each species has an indirect, negative effect on itself

- ► In an exploiter-resource system, each species has an indirect, negative effect on itself
- ► This effect is delayed in time: it takes time for each species to respond to the other

- ▶ In an exploiter-resource system, each species has an indirect, negative effect on itself
- ► This effect is delayed in time: it takes time for each species to respond to the other
- ▶ This means these systems have a tendency to oscillate

- ▶ In an exploiter-resource system, each species has an indirect, negative effect on itself
- ► This effect is delayed in time: it takes time for each species to respond to the other
- ▶ This means these systems have a tendency to oscillate
  - ► The same idea as from our population models, but with an explicit mechanism for delay

- ▶ In an exploiter-resource system, each species has an indirect, negative effect on itself
- ► This effect is delayed in time: it takes time for each species to respond to the other
- ▶ This means these systems have a tendency to oscillate
  - ► The same idea as from our population models, but with an explicit mechanism for delay
- ► There is a simple intuition for how these systems oscillate:

- ▶ In an exploiter-resource system, each species has an indirect, negative effect on itself
- ► This effect is delayed in time: it takes time for each species to respond to the other
- ▶ This means these systems have a tendency to oscillate
  - ► The same idea as from our population models, but with an explicit mechanism for delay
- ▶ There is a simple intuition for how these systems oscillate:
  - **>** \*

- ▶ In an exploiter-resource system, each species has an indirect, negative effect on itself
- ► This effect is delayed in time: it takes time for each species to respond to the other
- ▶ This means these systems have a tendency to oscillate
  - ► The same idea as from our population models, but with an explicit mechanism for delay
- ▶ There is a simple intuition for how these systems oscillate:
  - \* Exploiter goes up →Resource goes down →Exploiter goes down →Resource goes up →Exploiter goes up . . .

- ▶ In an exploiter-resource system, each species has an indirect, negative effect on itself
- ► This effect is delayed in time: it takes time for each species to respond to the other
- ▶ This means these systems have a tendency to oscillate
  - ► The same idea as from our population models, but with an explicit mechanism for delay
- ▶ There is a simple intuition for how these systems oscillate:
  - \* Exploiter goes up →Resource goes down →Exploiter goes down →Resource goes up →Exploiter goes up . . .

► Resource-exploiter systems have a *tendency* to oscillate

- ▶ Resource-exploiter systems have a *tendency* to oscillate
- ▶ In the simplest possible models, oscillations are **neutral**

- Resource-exploiter systems have a tendency to oscillate
- In the simplest possible models, oscillations are neutral
  - ► e.g., they don't get larger or smaller

- Resource-exploiter systems have a tendency to oscillate
- In the simplest possible models, oscillations are neutral
  - e.g., they don't get larger or smaller
- In more realistic models, large oscillations will tend to get smaller

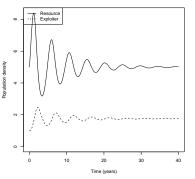
- Resource-exploiter systems have a tendency to oscillate
- In the simplest possible models, oscillations are neutral
  - e.g., they don't get larger or smaller
- In more realistic models, large oscillations will tend to get smaller
  - If small oscillations also tend to get smaller, we say that oscillations are damped

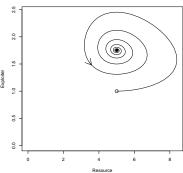
- Resource-exploiter systems have a tendency to oscillate
- In the simplest possible models, oscillations are neutral
  - e.g., they don't get larger or smaller
- In more realistic models, large oscillations will tend to get smaller
  - If small oscillations also tend to get smaller, we say that oscillations are damped
    - Oscillations which are not damped are persistent

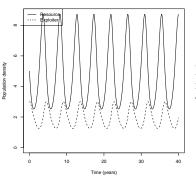
- Resource-exploiter systems have a tendency to oscillate
- In the simplest possible models, oscillations are neutral
  - e.g., they don't get larger or smaller
- In more realistic models, large oscillations will tend to get smaller
  - If small oscillations also tend to get smaller, we say that oscillations are damped
    - Oscillations which are not damped are persistent
  - ► If small oscillations tend to get larger, the system (usually) approaches a **limit cycle**

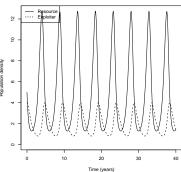
- Resource-exploiter systems have a tendency to oscillate
- In the simplest possible models, oscillations are neutral
  - e.g., they don't get larger or smaller
- In more realistic models, large oscillations will tend to get smaller
  - If small oscillations also tend to get smaller, we say that oscillations are damped
    - Oscillations which are not damped are persistent
  - If small oscillations tend to get larger, the system (usually) approaches a limit cycle

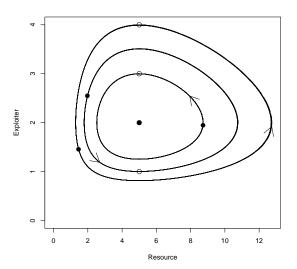
# Damped oscillations

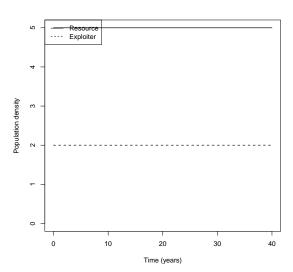


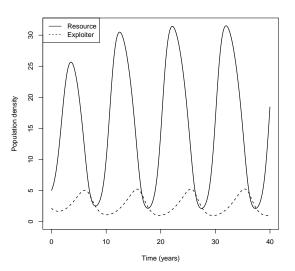


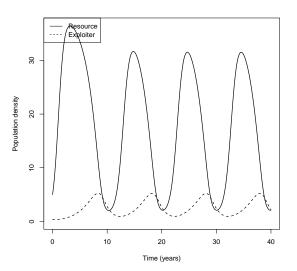


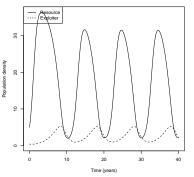


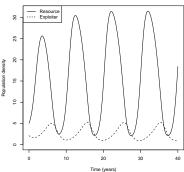


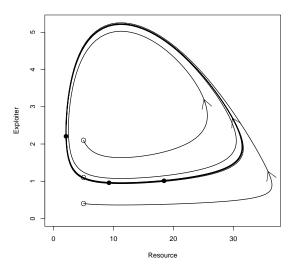












► Poll: What is the difference between neutral cycles and limit cycles?

▶ Poll: What is the difference between neutral cycles and limit cycles?



- ▶ Poll: What is the difference between neutral cycles and limit cycles?
  - ▶ \* Neutral cycles have no tendency to get larger or smaller

- ▶ Poll: What is the difference between neutral cycles and limit cycles?
  - ▶ \* Neutral cycles have no tendency to get larger or smaller

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

- ▶ Poll: What is the difference between neutral cycles and limit cycles?
  - ▶ \* Neutral cycles have no tendency to get larger or smaller
    - ▶ \* Large cycles stay large, small cycles stay small

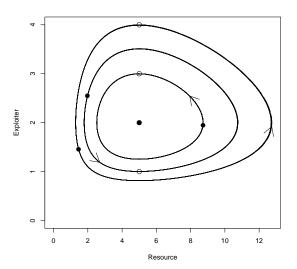
- ▶ Poll: What is the difference between neutral cycles and limit cycles?
  - ▶ \* Neutral cycles have no tendency to get larger or smaller
    - ▶ \* Large cycles stay large, small cycles stay small
  - \*

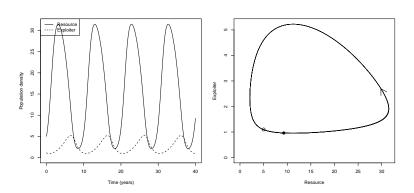
- ▶ Poll: What is the difference between neutral cycles and limit cycles?
  - ▶ \* Neutral cycles have no tendency to get larger or smaller
    - \* Large cycles stay large, small cycles stay small
  - ▶ \* Limit cycles converge to a limit

- ▶ Poll: What is the difference between neutral cycles and limit cycles?
  - ▶ \* Neutral cycles have no tendency to get larger or smaller
    - \* Large cycles stay large, small cycles stay small
  - ▶ \* Limit cycles converge to a limit
    - \*

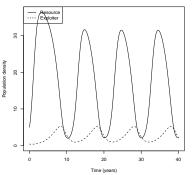
- ▶ Poll: What is the difference between neutral cycles and limit cycles?
  - ▶ \* Neutral cycles have no tendency to get larger or smaller
    - ▶ \* Large cycles stay large, small cycles stay small
  - \* Limit cycles converge to a limit
    - \* Large cycles get smaller, small cycles get larger

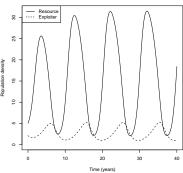
- ▶ Poll: What is the difference between neutral cycles and limit cycles?
  - ▶ \* Neutral cycles have no tendency to get larger or smaller
    - ▶ \* Large cycles stay large, small cycles stay small
  - \* Limit cycles converge to a limit
    - \* Large cycles get smaller, small cycles get larger

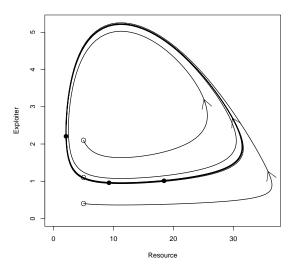




# Limit cycles (repeat)







#### Outline

#### Introduction

Balance and equilibriur Tendency to oscillate

# A simple model More detailed models Reciprocal control

Adding details

Dynamics

Equilibria

Who controls whom?

## A simple model

► We can investigate exploiter-resource systems using simple models

- We can investigate exploiter-resource systems using simple models
- Resource-species growth rate may depend on density of exploiter, or resource species, or both:

- We can investigate exploiter-resource systems using simple models
- Resource-species growth rate may depend on density of exploiter, or resource species, or both:

- We can investigate exploiter-resource systems using simple models
- Resource-species growth rate may depend on density of exploiter, or resource species, or both:

Exploiter growth rate may depend on density of exploiter, or resource species, or both:

- We can investigate exploiter-resource systems using simple models
- Resource-species growth rate may depend on density of exploiter, or resource species, or both:

Exploiter growth rate may depend on density of exploiter, or resource species, or both:

$$\blacktriangleright \frac{dN_e}{dt} = r_e(N_e, N_f)N_e$$

- We can investigate exploiter-resource systems using simple models
- Resource-species growth rate may depend on density of exploiter, or resource species, or both:

- Exploiter growth rate may depend on density of exploiter, or resource species, or both:
- At equilibrium:

- We can investigate exploiter-resource systems using simple models
- Resource-species growth rate may depend on density of exploiter, or resource species, or both:

Exploiter growth rate may depend on density of exploiter, or resource species, or both:



- We can investigate exploiter-resource systems using simple models
- Resource-species growth rate may depend on density of exploiter, or resource species, or both:

Exploiter growth rate may depend on density of exploiter, or resource species, or both:

• \* 
$$r_e = r_f = 0$$

- We can investigate exploiter-resource systems using simple models
- Resource-species growth rate may depend on density of exploiter, or resource species, or both:

Exploiter growth rate may depend on density of exploiter, or resource species, or both:

At equilibrium:

• \* 
$$r_e = r_f = 0$$

**>** \*

- We can investigate exploiter-resource systems using simple models
- Resource-species growth rate may depend on density of exploiter, or resource species, or both:

Exploiter growth rate may depend on density of exploiter, or resource species, or both:

• \* 
$$r_e = r_f = 0$$

• \* 
$$r_f = N_e = 0$$

- We can investigate exploiter-resource systems using simple models
- Resource-species growth rate may depend on density of exploiter, or resource species, or both:

Exploiter growth rate may depend on density of exploiter, or resource species, or both:

• \* 
$$r_e = r_f = 0$$

• \* 
$$r_f = N_e = 0$$

- We can investigate exploiter-resource systems using simple models
- Resource-species growth rate may depend on density of exploiter, or resource species, or both:

Exploiter growth rate may depend on density of exploiter, or resource species, or both:

• \* 
$$r_e = r_f = 0$$

$$ightharpoonup * r_f = N_e = 0$$

• \* 
$$N_e = N_f = 0$$

- We can investigate exploiter-resource systems using simple models
- Resource-species growth rate may depend on density of exploiter, or resource species, or both:

Exploiter growth rate may depend on density of exploiter, or resource species, or both:

• \* 
$$r_e = r_f = 0$$

• \* 
$$r_f = N_e = 0$$

• \* 
$$N_e = N_f = 0$$



- We can investigate exploiter-resource systems using simple models
- Resource-species growth rate may depend on density of exploiter, or resource species, or both:

Exploiter growth rate may depend on density of exploiter, or resource species, or both:

• \* 
$$r_e = r_f = 0$$

• \* 
$$r_f = N_e = 0$$

• \* 
$$N_e = N_f = 0$$

▶ \* If 
$$N_f = 0$$
, what happens to  $r_e$ ?

- We can investigate exploiter-resource systems using simple models
- Resource-species growth rate may depend on density of exploiter, or resource species, or both:

Exploiter growth rate may depend on density of exploiter, or resource species, or both:

• \* 
$$r_e = r_f = 0$$

• \* 
$$r_f = N_e = 0$$

• \* 
$$N_e = N_f = 0$$

▶ \* If 
$$N_f = 0$$
, what happens to  $r_e$ ?

$$\blacktriangleright \ \frac{dN_e}{dt} = r_e(N_e, N_f)N_e$$

▶ What makes this a resource-exploiter system?

**,** 

What makes this a resource-exploiter system?

$$ightharpoonup rac{dN_e}{dt} = r_e(N_e, N_f)N_e$$

\* We expect the resource species to be good for the exploiter  $(r_e \text{ goes up as } N_f \text{ goes up})$ 

$$ightharpoonup$$
  $rac{dN_e}{dt} = r_e(N_e, N_f)N_e$ 

- \* We expect the resource species to be good for the exploiter  $(r_e \text{ goes up as } N_f \text{ goes up})$
- \*

- \* We expect the resource species to be good for the exploiter (r<sub>e</sub> goes up as N<sub>f</sub> goes up)
- ➤ \* We expect the exploiter to be bad for the resource species (r<sub>f</sub> goes down as N<sub>e</sub> goes up)

- \* We expect the resource species to be good for the exploiter (r<sub>e</sub> goes up as N<sub>f</sub> goes up)
- ➤ \* We expect the exploiter to be bad for the resource species (r<sub>f</sub> goes down as N<sub>e</sub> goes up)
- ► Mnemonic: *e* for exploiter, *f* for food.

- \* We expect the resource species to be good for the exploiter (r<sub>e</sub> goes up as N<sub>f</sub> goes up)
- ➤ \* We expect the exploiter to be bad for the resource species (r<sub>f</sub> goes down as N<sub>e</sub> goes up)
- ▶ Mnemonic: *e* for exploiter, *f* for food.

► The simplest model of resource-exploiter interaction is when their per-capita growth rates only respond to each other.

► The simplest model of resource-exploiter interaction is when their per-capita growth rates only respond to each other.

► The simplest model of resource-exploiter interaction is when their per-capita growth rates only respond to each other.

► The simplest model of resource-exploiter interaction is when their per-capita growth rates only respond to each other.

► This is a pure **reciprocal control** model: resource growth rate depends only on exploiter density, and vice verse

- ► The simplest model of resource-exploiter interaction is when their per-capita growth rates only respond to each other.
- ► This is a pure **reciprocal control** model: resource growth rate depends only on exploiter density, and vice verse

# Resource-exploiter interactions



# Resource-exploiter interactions



► This model assumes:

- ► This model assumes:
  - ► The rate at which individual fish get eaten depends on the total number of sharks

- ► This model assumes:
  - ► The rate at which individual fish get eaten depends on the total number of sharks
  - ► The rate at which individual sharks eat fish depend on the total number of fish

- This model assumes:
  - ► The rate at which individual fish get eaten depends on the total number of sharks
  - ► The rate at which individual sharks eat fish depend on the total number of fish
- The ratio of sharks to fish does not matter directly

- This model assumes:
  - The rate at which individual fish get eaten depends on the total number of sharks
  - ► The rate at which individual sharks eat fish depend on the total number of fish
- ▶ The ratio of sharks to fish does not matter directly
- ▶ Does this make sense? What happens in the model if there are too many sharks, for example?

- This model assumes:
  - The rate at which individual fish get eaten depends on the total number of sharks
  - ► The rate at which individual sharks eat fish depend on the total number of fish
- The ratio of sharks to fish does not matter directly
- ▶ Does this make sense? What happens in the model if there are too many sharks, for example?
  - **>** \*

- This model assumes:
  - ► The rate at which individual fish get eaten depends on the total number of sharks
  - ► The rate at which individual sharks eat fish depend on the total number of fish
- The ratio of sharks to fish does not matter directly
- ▶ Does this make sense? What happens in the model if there are too many sharks, for example?
  - ▶ \* The number of fish will go down

- This model assumes:
  - ► The rate at which individual fish get eaten depends on the total number of sharks
  - ► The rate at which individual sharks eat fish depend on the total number of fish
- ► The ratio of sharks to fish does not matter directly
- ▶ Does this make sense? What happens in the model if there are too many sharks, for example?
  - ► \* The number of fish will go down
  - \*

- This model assumes:
  - ► The rate at which individual fish get eaten depends on the total number of sharks
  - ► The rate at which individual sharks eat fish depend on the total number of fish
- ▶ The ratio of sharks to fish does not matter directly
- ▶ Does this make sense? What happens in the model if there are too many sharks, for example?
  - ► \* The number of fish will go down
  - ► \* Then the number of sharks will go down

- This model assumes:
  - The rate at which individual fish get eaten depends on the total number of sharks
  - ► The rate at which individual sharks eat fish depend on the total number of fish
- The ratio of sharks to fish does not matter directly
- ▶ Does this make sense? What happens in the model if there are too many sharks, for example?
  - ► \* The number of fish will go down
  - ▶ \* Then the number of sharks will go down
  - .

- This model assumes:
  - ► The rate at which individual fish get eaten depends on the total number of sharks
  - ► The rate at which individual sharks eat fish depend on the total number of fish
- ► The ratio of sharks to fish does not matter directly
- ▶ Does this make sense? What happens in the model if there are too many sharks, for example?
  - ► \* The number of fish will go down
  - ▶ \* Then the number of sharks will go down
  - ▶ \* Then the number of fish will go up ...

- This model assumes:
  - ► The rate at which individual fish get eaten depends on the total number of sharks
  - ► The rate at which individual sharks eat fish depend on the total number of fish
- ► The ratio of sharks to fish does not matter directly
- ▶ Does this make sense? What happens in the model if there are too many sharks, for example?
  - ► \* The number of fish will go down
  - ▶ \* Then the number of sharks will go down
  - ▶ \* Then the number of fish will go up ...

#### Outline

#### Introduction

Balance and equilibrium Tendency to oscillate

#### A simple model

More detailed models

Reciprocal control

#### Adding details

Dynamics

Equilibria

Who controls whom?

# How do populations affect their own growth rates?



► Poll: Why might we expect resource population to affect per-capita growth rate of the resource species?

▶ Poll: Why might we expect resource population to affect per-capita growth rate of the resource species?



- ▶ Poll: Why might we expect resource population to affect per-capita growth rate of the resource species?
  - \* Competition for resources, territory, mates (density dependence)

- ▶ Poll: Why might we expect resource population to affect per-capita growth rate of the resource species?
  - ► \* Competition for resources, territory, mates (density dependence)
  - \*

- ▶ Poll: Why might we expect resource population to affect per-capita growth rate of the resource species?
  - \* Competition for resources, territory, mates (density dependence)
  - \* Co-operation for protection, food-gathering (Allee effects)

- ▶ Poll: Why might we expect resource population to affect per-capita growth rate of the resource species?
  - \* Competition for resources, territory, mates (density dependence)
  - \* Co-operation for protection, food-gathering (Allee effects)
  - \*

- ▶ Poll: Why might we expect resource population to affect per-capita growth rate of the resource species?
  - \* Competition for resources, territory, mates (density dependence)
  - \* Co-operation for protection, food-gathering (Allee effects)
  - \* Protection by numbers (predator satiation)

- ▶ Poll: Why might we expect resource population to affect per-capita growth rate of the resource species?
  - \* Competition for resources, territory, mates (density dependence)
  - \* Co-operation for protection, food-gathering (Allee effects)
  - \* Protection by numbers (predator satiation)

► Why might we expect exploiter population to affect per-capita growth rate of the exploiter species?

► Why might we expect exploiter population to affect per-capita growth rate of the exploiter species?



- ▶ Why might we expect exploiter population to affect per-capita growth rate of the exploiter species?
  - \* Competition for resources, territory, mates (density dependence)

- ▶ Why might we expect exploiter population to affect per-capita growth rate of the exploiter species?
  - \* Competition for resources, territory, mates (density dependence)
  - > 1

- ▶ Why might we expect exploiter population to affect per-capita growth rate of the exploiter species?
  - \* Competition for resources, territory, mates (density dependence)
  - \* Co-operation for protection, food-gathering (Allee effects)

- ▶ Why might we expect exploiter population to affect per-capita growth rate of the exploiter species?
  - \* Competition for resources, territory, mates (density dependence)
  - \* Co-operation for protection, food-gathering (Allee effects)

► The simplest models of reciprocal control lead to neutral cycles

- ➤ The simplest models of reciprocal control lead to neutral cycles
  - Cycles starting from any starting point will go back through that starting point

- ➤ The simplest models of reciprocal control lead to neutral cycles
  - Cycles starting from any starting point will go back through that starting point
  - ► These seem unrealistic; why should there be no tendency to spiral out or in for any cycle?

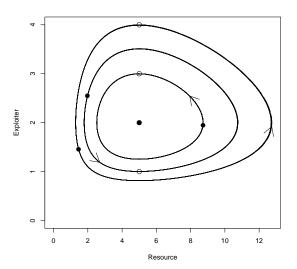
- ➤ The simplest models of reciprocal control lead to neutral cycles
  - Cycles starting from any starting point will go back through that starting point
  - ► These seem unrealistic; why should there be no tendency to spiral out or in for any cycle?
- ► To take the next step, we ask what factors will tend to:

- ► The simplest models of reciprocal control lead to neutral cycles
  - Cycles starting from any starting point will go back through that starting point
  - These seem unrealistic; why should there be no tendency to spiral out or in for any cycle?
- ▶ To take the next step, we ask what factors will tend to:
  - make cycles get smaller (approach equilibrium)?

- ► The simplest models of reciprocal control lead to neutral cycles
  - Cycles starting from any starting point will go back through that starting point
  - These seem unrealistic; why should there be no tendency to spiral out or in for any cycle?
- ▶ To take the next step, we ask what factors will tend to:
  - make cycles get smaller (approach equilibrium)?
  - make cycles get larger (move away from equilibrium)?

- ➤ The simplest models of reciprocal control lead to neutral cycles
  - Cycles starting from any starting point will go back through that starting point
  - These seem unrealistic; why should there be no tendency to spiral out or in for any cycle?
- ▶ To take the next step, we ask what factors will tend to:
  - make cycles get smaller (approach equilibrium)?
  - make cycles get larger (move away from equilibrium)?

# Neutral cycles



#### Outline

#### Introduction

Balance and equilibrium Tendency to oscillate

#### A simple model

More detailed models

Reciprocal control

#### Adding details

Dynamics

Equilibria

Who controls whom?

▶ In this model, what happens to the *equilibrium* of this system if we reduce  $r_f$ , without changing  $r_e$  (for example, we start catching a lot more cod)?

▶ In this model, what happens to the *equilibrium* of this system if we reduce  $r_f$ , without changing  $r_e$  (for example, we start catching a lot more cod)?

\*

- ▶ In this model, what happens to the *equilibrium* of this system if we reduce  $r_f$ , without changing  $r_e$  (for example, we start catching a lot more cod)?
  - ▶ \* The equation for change in  $N_e$  stays the same, so the equilibrium value of  $N_f$  must stay the same.

- ▶ In this model, what happens to the *equilibrium* of this system if we reduce  $r_f$ , without changing  $r_e$  (for example, we start catching a lot more cod)?
  - ▶ \* The equation for change in  $N_e$  stays the same, so the equilibrium value of  $N_f$  must stay the same.

- ▶ In this model, what happens to the *equilibrium* of this system if we reduce  $r_f$ , without changing  $r_e$  (for example, we start catching a lot more cod)?
  - ▶ \* The equation for change in  $N_e$  stays the same, so the equilibrium value of  $N_f$  must stay the same.
    - ► \* Unless N<sub>e</sub> goes to zero!

- ▶ In this model, what happens to the *equilibrium* of this system if we reduce  $r_f$ , without changing  $r_e$  (for example, we start catching a lot more cod)?
  - ▶ \* The equation for change in  $N_e$  stays the same, so the equilibrium value of  $N_f$  must stay the same.
    - ► \* Unless N<sub>e</sub> goes to zero!
  - \*

- ▶ In this model, what happens to the *equilibrium* of this system if we reduce  $r_f$ , without changing  $r_e$  (for example, we start catching a lot more cod)?
  - ▶ \* The equation for change in  $N_e$  stays the same, so the equilibrium value of  $N_f$  must stay the same.
    - ► \* Unless N<sub>e</sub> goes to zero!
  - $\blacktriangleright$  \* The value of  $r_f$  has gone down, so we must increase it

- ▶ In this model, what happens to the *equilibrium* of this system if we reduce  $r_f$ , without changing  $r_e$  (for example, we start catching a lot more cod)?
  - ▶ \* The equation for change in  $N_e$  stays the same, so the equilibrium value of  $N_f$  must stay the same.
    - ► \* Unless N<sub>e</sub> goes to zero!
  - $\blacktriangleright$  \* The value of  $r_f$  has gone down, so we must increase it
    - \*

- ▶ In this model, what happens to the *equilibrium* of this system if we reduce  $r_f$ , without changing  $r_e$  (for example, we start catching a lot more cod)?
  - ▶ \* The equation for change in  $N_e$  stays the same, so the equilibrium value of  $N_f$  must stay the same.
    - ► \* Unless N<sub>e</sub> goes to zero!
  - $\blacktriangleright$  \* The value of  $r_f$  has gone down, so we must increase it
    - \* by decreasing the number of exploiters

- ▶ In this model, what happens to the *equilibrium* of this system if we reduce  $r_f$ , without changing  $r_e$  (for example, we start catching a lot more cod)?
  - ▶ \* The equation for change in  $N_e$  stays the same, so the equilibrium value of  $N_f$  must stay the same.
    - ► \* Unless N<sub>e</sub> goes to zero!
  - $\blacktriangleright$  \* The value of  $r_f$  has gone down, so we must increase it
    - \* by decreasing the number of exploiters

▶ In this model, what happens to the *equilibrium* of this system if we are at equilibrium, and then we reduce  $r_e$  without changing  $r_f$  (for example, we start killing sharks):

In this model, what happens to the *equilibrium* of this system if we are at equilibrium, and then we reduce  $r_e$  without changing  $r_f$  (for example, we start killing sharks):

**>** \*

- In this model, what happens to the *equilibrium* of this system if we are at equilibrium, and then we reduce  $r_e$  without changing  $r_f$  (for example, we start killing sharks):
  - $ightharpoonup * r_f$  doesn't change, so  $N_e$  must stay the same

- In this model, what happens to the *equilibrium* of this system if we are at equilibrium, and then we reduce  $r_e$  without changing  $r_f$  (for example, we start killing sharks):
  - $ightharpoonup * r_f$  doesn't change, so  $N_e$  must stay the same
  - \*

- In this model, what happens to the *equilibrium* of this system if we are at equilibrium, and then we reduce  $r_e$  without changing  $r_f$  (for example, we start killing sharks):
  - $ightharpoonup * r_f$  doesn't change, so  $N_e$  must stay the same
  - ightharpoonup \*  $r_e$  of the old equilibrium goes down, so  $N_f$  must increase

- In this model, what happens to the *equilibrium* of this system if we are at equilibrium, and then we reduce  $r_e$  without changing  $r_f$  (for example, we start killing sharks):
  - $ightharpoonup * r_f$  doesn't change, so  $N_e$  must stay the same
  - $ightharpoonup * r_e$  of the old equilibrium goes down, so  $N_f$  must increase
  - \*

- In this model, what happens to the *equilibrium* of this system if we are at equilibrium, and then we reduce  $r_e$  without changing  $r_f$  (for example, we start killing sharks):
  - $ightharpoonup * r_f$  doesn't change, so  $N_e$  must stay the same
  - ightharpoonup \*  $r_e$  of the old equilibrium goes down, so  $N_f$  must increase
  - \* If we can't increase it enough, sharks go extinct, and fish increase to infinity.

- In this model, what happens to the *equilibrium* of this system if we are at equilibrium, and then we reduce  $r_e$  without changing  $r_f$  (for example, we start killing sharks):
  - $ightharpoonup * r_f$  doesn't change, so  $N_e$  must stay the same
  - ightharpoonup \*  $r_e$  of the old equilibrium goes down, so  $N_f$  must increase
  - \* If we can't increase it enough, sharks go extinct, and fish increase to infinity.

# People and the ocean



► Species under reciprocal control may respond to change in unexpected ways

- Species under reciprocal control may respond to change in unexpected ways
- ► Imagine a community of sharks and large fish whose densities are primarily controlled by their exploitative interactions (the sharks eat the fish)

- Species under reciprocal control may respond to change in unexpected ways
- Imagine a community of sharks and large fish whose densities are primarily controlled by their exploitative interactions (the sharks eat the fish)
- ▶ What will happen to these populations in the *short term* if people start fishing on a large scale (and catching large numbers of both sharks and fish)?

- Species under reciprocal control may respond to change in unexpected ways
- Imagine a community of sharks and large fish whose densities are primarily controlled by their exploitative interactions (the sharks eat the fish)
- What will happen to these populations in the short term if people start fishing on a large scale (and catching large numbers of both sharks and fish)?



- Species under reciprocal control may respond to change in unexpected ways
- Imagine a community of sharks and large fish whose densities are primarily controlled by their exploitative interactions (the sharks eat the fish)
- What will happen to these populations in the short term if people start fishing on a large scale (and catching large numbers of both sharks and fish)?
  - ▶ \* Populations will go down, because people are catching them

- Species under reciprocal control may respond to change in unexpected ways
- Imagine a community of sharks and large fish whose densities are primarily controlled by their exploitative interactions (the sharks eat the fish)
- What will happen to these populations in the short term if people start fishing on a large scale (and catching large numbers of both sharks and fish)?
  - ▶ \* Populations will go down, because people are catching them

► What will happen to happen to these reciprocally controlled populations of sharks and fish in the *long term* if people start fishing on a large scale?

▶ What will happen to happen to these reciprocally controlled populations of sharks and fish in the *long term* if people start fishing on a large scale?

> 3

- ▶ What will happen to happen to these reciprocally controlled populations of sharks and fish in the *long term* if people start fishing on a large scale?
  - ► \* Shark population will go down (less sharks are needed to keep the fish in balance)

- What will happen to happen to these reciprocally controlled populations of sharks and fish in the *long term* if people start fishing on a large scale?
  - \* Shark population will go down (less sharks are needed to keep the fish in balance)
  - **>** ×

- What will happen to happen to these reciprocally controlled populations of sharks and fish in the *long term* if people start fishing on a large scale?
  - \* Shark population will go down (less sharks are needed to keep the fish in balance)
  - ► \* Fish population will go up (more fish are needed to keep the sharks in balance)

- What will happen to happen to these reciprocally controlled populations of sharks and fish in the *long term* if people start fishing on a large scale?
  - \* Shark population will go down (less sharks are needed to keep the fish in balance)
  - ► \* Fish population will go up (more fish are needed to keep the sharks in balance)

► Until fairly recently, almost all species in the oceans were controlled primarily by interactions with other ocean species

- Until fairly recently, almost all species in the oceans were controlled primarily by interactions with other ocean species
  - ► Fishing food fish had little or no effect on the equilibrium number of fish at that **trophic level**

- Until fairly recently, almost all species in the oceans were controlled primarily by interactions with other ocean species
  - Fishing food fish had little or no effect on the equilibrium number of fish at that trophic level



- Until fairly recently, almost all species in the oceans were controlled primarily by interactions with other ocean species
  - Fishing food fish had little or no effect on the equilibrium number of fish at that trophic level
    - \* Decreased the number of sharks

- Until fairly recently, almost all species in the oceans were controlled primarily by interactions with other ocean species
  - Fishing food fish had little or no effect on the equilibrium number of fish at that trophic level
    - \* Decreased the number of sharks
  - Catching sharks directly had little or no effect on the number of sharks

- Until fairly recently, almost all species in the oceans were controlled primarily by interactions with other ocean species
  - Fishing food fish had little or no effect on the equilibrium number of fish at that trophic level
    - \* Decreased the number of sharks
  - Catching sharks directly had little or no effect on the number of sharks
    - \*

- Until fairly recently, almost all species in the oceans were controlled primarily by interactions with other ocean species
  - Fishing food fish had little or no effect on the equilibrium number of fish at that trophic level
    - \* Decreased the number of sharks
  - Catching sharks directly had little or no effect on the number of sharks
    - ▶ \* Increased the number of food fish

- Until fairly recently, almost all species in the oceans were controlled primarily by interactions with other ocean species
  - Fishing food fish had little or no effect on the equilibrium number of fish at that trophic level
    - \* Decreased the number of sharks
  - Catching sharks directly had little or no effect on the number of sharks
    - \* Increased the number of food fish
- ► As fishing increases, this link is eventually broken

- Until fairly recently, almost all species in the oceans were controlled primarily by interactions with other ocean species
  - Fishing food fish had little or no effect on the equilibrium number of fish at that trophic level
    - \* Decreased the number of sharks
  - Catching sharks directly had little or no effect on the number of sharks
    - \* Increased the number of food fish
- As fishing increases, this link is eventually broken
  - \*

- Until fairly recently, almost all species in the oceans were controlled primarily by interactions with other ocean species
  - Fishing food fish had little or no effect on the equilibrium number of fish at that trophic level
    - \* Decreased the number of sharks
  - Catching sharks directly had little or no effect on the number of sharks
    - \* Increased the number of food fish
- As fishing increases, this link is eventually broken
  - \* Fishing becomes an important regulator of ocean fish populations

## Real implications

- Until fairly recently, almost all species in the oceans were controlled primarily by interactions with other ocean species
  - Fishing food fish had little or no effect on the equilibrium number of fish at that trophic level
    - \* Decreased the number of sharks
  - Catching sharks directly had little or no effect on the number of sharks
    - \* Increased the number of food fish
- As fishing increases, this link is eventually broken
  - \* Fishing becomes an important regulator of ocean fish populations
    - \*

## Real implications

- Until fairly recently, almost all species in the oceans were controlled primarily by interactions with other ocean species
  - Fishing food fish had little or no effect on the equilibrium number of fish at that trophic level
    - \* Decreased the number of sharks
  - Catching sharks directly had little or no effect on the number of sharks
    - \* Increased the number of food fish
- As fishing increases, this link is eventually broken
  - ► \* Fishing becomes an important regulator of ocean fish populations
  - \* Further increases in fishing can cause rapid declines in fish populations

## Real implications

- Until fairly recently, almost all species in the oceans were controlled primarily by interactions with other ocean species
  - Fishing food fish had little or no effect on the equilibrium number of fish at that trophic level
    - \* Decreased the number of sharks
  - Catching sharks directly had little or no effect on the number of sharks
    - \* Increased the number of food fish
- As fishing increases, this link is eventually broken
  - ► \* Fishing becomes an important regulator of ocean fish populations
  - \* Further increases in fishing can cause rapid declines in fish populations

#### Outline

#### Introduction

Balance and equilibrium Tendency to oscillate

#### A simple model

More detailed models Reciprocal control

## Adding details

Dynamics

Equilibria

Who controls whom?

# How do populations affect their own growth rates?



▶ Poll: Why might we expect resource population to affect *per-capita* growth rate of the resource species?

▶ Poll: Why might we expect resource population to affect *per-capita* growth rate of the resource species?

**▶** \*

- ▶ Poll: Why might we expect resource population to affect *per-capita* growth rate of the resource species?
  - \* Competition for resources, territory, mates (density dependence)

- ▶ Poll: Why might we expect resource population to affect *per-capita* growth rate of the resource species?
  - \* Competition for resources, territory, mates (density dependence)
  - \*

- ▶ Poll: Why might we expect resource population to affect *per-capita* growth rate of the resource species?
  - ► \* Competition for resources, territory, mates (density dependence)
  - \* Co-operation for protection, food-gathering (Allee effects)

- ▶ Poll: Why might we expect resource population to affect *per-capita* growth rate of the resource species?
  - \* Competition for resources, territory, mates (density dependence)
  - \* Co-operation for protection, food-gathering (Allee effects)
  - \*

- ▶ Poll: Why might we expect resource population to affect *per-capita* growth rate of the resource species?
  - \* Competition for resources, territory, mates (density dependence)
  - \* Co-operation for protection, food-gathering (Allee effects)
  - \* Protection by numbers (predator satiation)

- ▶ Poll: Why might we expect resource population to affect *per-capita* growth rate of the resource species?
  - \* Competition for resources, territory, mates (density dependence)
  - \* Co-operation for protection, food-gathering (Allee effects)
  - \* Protection by numbers (predator satiation)

▶ Poll: Why might we expect exploiter population to affect *per-capita* growth rate of the exploiter species?

▶ Poll: Why might we expect exploiter population to affect *per-capita* growth rate of the exploiter species?

**>** \*

- ▶ Poll: Why might we expect exploiter population to affect *per-capita* growth rate of the exploiter species?
  - \* Competition for resources, territory, mates (density dependence)

- ▶ Poll: Why might we expect exploiter population to affect *per-capita* growth rate of the exploiter species?
  - \* Competition for resources, territory, mates (density dependence)
    - >

- ▶ Poll: Why might we expect exploiter population to affect *per-capita* growth rate of the exploiter species?
  - ► \* Competition for resources, territory, mates (density dependence)
  - ▶ \* Co-operation for protection, food-gathering (Allee effects)

- ▶ Poll: Why might we expect exploiter population to affect *per-capita* growth rate of the exploiter species?
  - ► \* Competition for resources, territory, mates (density dependence)
  - ▶ \* Co-operation for protection, food-gathering (Allee effects)

► The most unrealistic aspect of the current model is that, in the absence of the exploiter, the resource species increases without limit

- ► The most unrealistic aspect of the current model is that, in the absence of the exploiter, the resource species increases without limit
  - ▶ In reality, we would expect it, eventually, to be regulated.

- ► The most unrealistic aspect of the current model is that, in the absence of the exploiter, the resource species increases without limit
  - ▶ In reality, we would expect it, eventually, to be regulated.
- ► We can change our equations to allow the resource species to have a (negative) effect on itself:

- ► The most unrealistic aspect of the current model is that, in the absence of the exploiter, the resource species increases without limit
  - ▶ In reality, we would expect it, eventually, to be regulated.
- ► We can change our equations to allow the resource species to have a (negative) effect on itself:

$$\blacktriangleright \ \frac{dN_f}{dt} = r_f(N_e, N_f)N_f$$

- ► The most unrealistic aspect of the current model is that, in the absence of the exploiter, the resource species increases without limit
  - In reality, we would expect it, eventually, to be regulated.
- ► We can change our equations to allow the resource species to have a (negative) effect on itself:

$$\blacktriangleright \frac{dN_e}{dt} = r_e(N_f)N_e$$

- ► The most unrealistic aspect of the current model is that, in the absence of the exploiter, the resource species increases without limit
  - ▶ In reality, we would expect it, eventually, to be regulated.
- ► We can change our equations to allow the resource species to have a (negative) effect on itself:

► Another conceptual problem with the model is the idea that exploiter feeding is proportional to size of the resource population

- Another conceptual problem with the model is the idea that exploiter feeding is proportional to size of the resource population
- ► What is the effect on feeding rates if the density of the resource species increases?

- Another conceptual problem with the model is the idea that exploiter feeding is proportional to size of the resource population
- ▶ What is the effect on feeding rates if the density of the resource species increases?
  - From the point of view of the exploiter?

- Another conceptual problem with the model is the idea that exploiter feeding is proportional to size of the resource population
- ▶ What is the effect on feeding rates if the density of the resource species increases?
  - From the point of view of the exploiter?
    - ,

- Another conceptual problem with the model is the idea that exploiter feeding is proportional to size of the resource population
- ▶ What is the effect on feeding rates if the density of the resource species increases?
  - From the point of view of the exploiter?
    - \* Per-capita feeding goes up

- Another conceptual problem with the model is the idea that exploiter feeding is proportional to size of the resource population
- ▶ What is the effect on feeding rates if the density of the resource species increases?
  - From the point of view of the exploiter?
    - \* Per-capita feeding goes up
  - From the point of view of the resource species?

- Another conceptual problem with the model is the idea that exploiter feeding is proportional to size of the resource population
- ▶ What is the effect on feeding rates if the density of the resource species increases?
  - From the point of view of the exploiter?
    - \* Per-capita feeding goes up
  - ► From the point of view of the resource species?
    - **>** \*

- Another conceptual problem with the model is the idea that exploiter feeding is proportional to size of the resource population
- ▶ What is the effect on feeding rates if the density of the resource species increases?
  - From the point of view of the exploiter?
    - \* Per-capita feeding goes up
  - From the point of view of the resource species?
    - \* Per-capita feeding goes down

- Another conceptual problem with the model is the idea that exploiter feeding is proportional to size of the resource population
- ▶ What is the effect on feeding rates if the density of the resource species increases?
  - From the point of view of the exploiter?
    - \* Per-capita feeding goes up
  - From the point of view of the resource species?
    - \* Per-capita feeding goes down
  - Predator satiation means the resource species density can sometimes have a positive effect on its growth in the short term

- Another conceptual problem with the model is the idea that exploiter feeding is proportional to size of the resource population
- ▶ What is the effect on feeding rates if the density of the resource species increases?
  - From the point of view of the exploiter?
    - \* Per-capita feeding goes up
  - From the point of view of the resource species?
    - \* Per-capita feeding goes down
  - Predator satiation means the resource species density can sometimes have a positive effect on its growth in the short term

#### Outline

#### Introduction

Balance and equilibrium Tendency to oscillate

#### A simple model

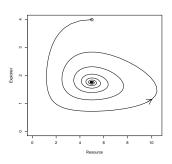
More detailed models Reciprocal control

# Adding details Dynamics

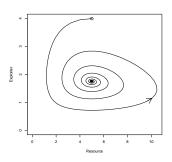
Equilibria

Who controls whom?

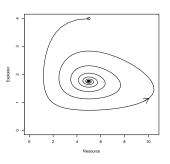
 Reduces prey reproduction the most when prey numbers are highest



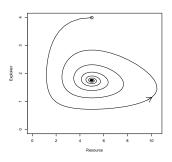
- Reduces prey reproduction the most when prey numbers are highest
- ► Tends to pull cycles towards the middle



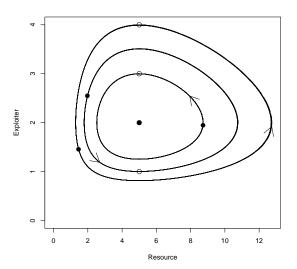
- Reduces prey reproduction the most when prey numbers are highest
- Tends to pull cycles towards the middle
- ► Makes cycles get smaller, leading to **damped** cycles

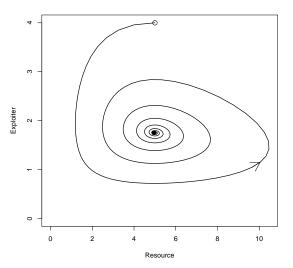


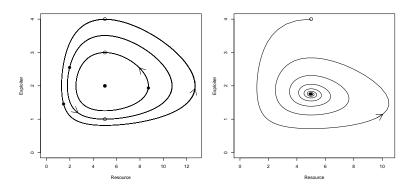
- Reduces prey reproduction the most when prey numbers are highest
- Tends to pull cycles towards the middle
- Makes cycles get smaller, leading to damped cycles



## Neutral cycles

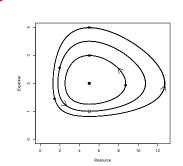




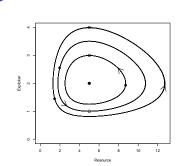


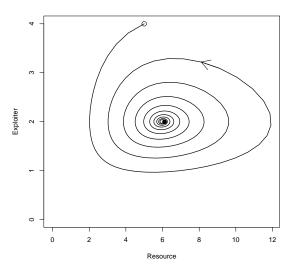
Poll: If we go back to neutral cycles, and add predator density dependence, do we expect cycles to spiral out, or spiral in?

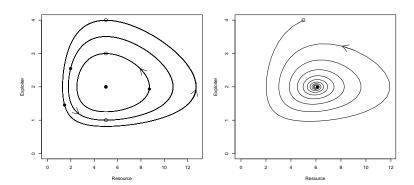
Poll: If we go back to neutral cycles, and add predator density dependence, do we expect cycles to spiral out, or spiral in?



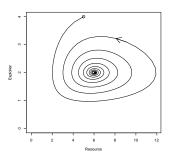
Poll: If we go back to neutral cycles, and add predator density dependence, do we expect cycles to spiral out, or spiral in?





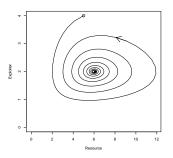


► Density dependence in the predator (exploiter species) has what effect on cycles?

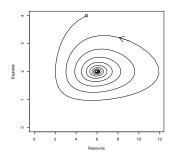


Density dependence in the predator (exploiter species) has what effect on cycles?

\*

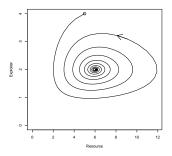


- Density dependence in the predator (exploiter species) has what effect on cycles?
  - \* Reduces predator reproduction when predators are the highest

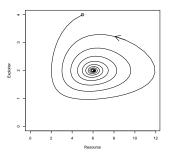


- Density dependence in the predator (exploiter species) has what effect on cycles?
  - \* Reduces predator reproduction when predators are the highest

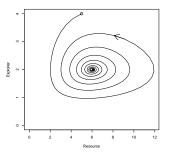
\*



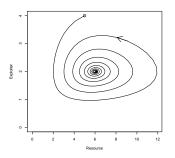
- Density dependence in the predator (exploiter species) has what effect on cycles?
  - \* Reduces predator reproduction when predators are the highest
  - \* This is not the same time as when prey are the highest, although we intuitively think that it is



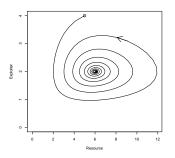
- Density dependence in the predator (exploiter species) has what effect on cycles?
  - \* Reduces predator reproduction when predators are the highest
  - \* This is not the same time as when prey are the highest, although we intuitively think that it is
  - \*



- Density dependence in the predator (exploiter species) has what effect on cycles?
  - \* Reduces predator reproduction when predators are the highest
  - \* This is not the same time as when prey are the highest, although we intuitively think that it is
  - \* Tends to cause damped cycles



- Density dependence in the predator (exploiter species) has what effect on cycles?
  - \* Reduces predator reproduction when predators are the highest
  - \* This is not the same time as when prey are the highest, although we intuitively think that it is
  - \* Tends to cause damped cycles



▶ Poll: The fact that predators can consume only limited amounts of prey has what effect on cycles?

▶ Poll: The fact that predators can consume only limited amounts of prey has what effect on cycles?

**>** \*

- ▶ Poll: The fact that predators can consume only limited amounts of prey has what effect on cycles?
  - \* Compared to neutral case, reduces predator reproduction when prey are the highest

- ▶ Poll: The fact that predators can consume only limited amounts of prey has what effect on cycles?
  - ► \* Compared to neutral case, reduces predator reproduction when prey are the highest
  - \*

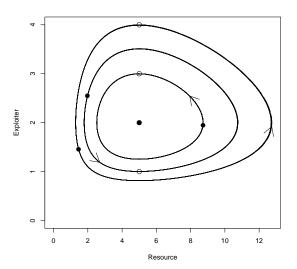
- ▶ Poll: The fact that predators can consume only limited amounts of prey has what effect on cycles?
  - ► \* Compared to neutral case, reduces predator reproduction when prey are the highest
  - ▶ \* Tends to make cycles get bigger

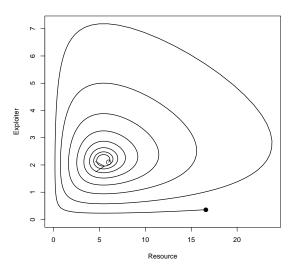
- ▶ Poll: The fact that predators can consume only limited amounts of prey has what effect on cycles?
  - ► \* Compared to neutral case, reduces predator reproduction when prey are the highest
  - ► \* Tends to make cycles get bigger
  - \*

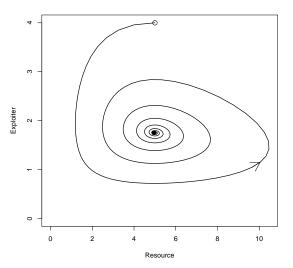
- ▶ Poll: The fact that predators can consume only limited amounts of prey has what effect on cycles?
  - \* Compared to neutral case, reduces predator reproduction when prey are the highest
  - \* Tends to make cycles get bigger
  - ightharpoonup \* Without density dependence, makes cycles get bigger forever (oscillations increase to  $\infty$ )

- ▶ Poll: The fact that predators can consume only limited amounts of prey has what effect on cycles?
  - \* Compared to neutral case, reduces predator reproduction when prey are the highest
  - \* Tends to make cycles get bigger
  - ightharpoonup \* Without density dependence, makes cycles get bigger forever (oscillations increase to  $\infty$ )

## Neutral cycles







▶ What sort of oscillations do we expect?

- ▶ What sort of oscillations do we expect?
  - ► If density dependence is relatively strong?

- ▶ What sort of oscillations do we expect?
  - ► If density dependence is relatively strong?
    - **>** \*

- ▶ What sort of oscillations do we expect?
  - ► If density dependence is relatively strong?
    - \* Damped oscillations

- What sort of oscillations do we expect?
  - ► If density dependence is relatively strong?
    - \* Damped oscillations
  - ► If density dependence is relatively weak?

- What sort of oscillations do we expect?
  - ► If density dependence is relatively strong?
    - \* Damped oscillations
  - ► If density dependence is relatively weak?
    - \*

- What sort of oscillations do we expect?
  - If density dependence is relatively strong?
    - \* Damped oscillations
  - If density dependence is relatively weak?
    - \* Close to equilibrium, we expect oscillations to increase

- ▶ What sort of oscillations do we expect?
  - If density dependence is relatively strong?
    - \* Damped oscillations
  - If density dependence is relatively weak?
    - \* Close to equilibrium, we expect oscillations to increase

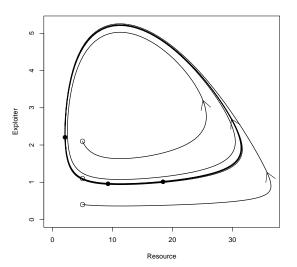
- ▶ What sort of oscillations do we expect?
  - If density dependence is relatively strong?
    - \* Damped oscillations
  - If density dependence is relatively weak?
    - \* Close to equilibrium, we expect oscillations to increase
    - \* Far from equilibrium, density dependence takes over (prey cannot increase beyond their predator-free equilibrium) and oscillations decrease

- ▶ What sort of oscillations do we expect?
  - If density dependence is relatively strong?
    - \* Damped oscillations
  - If density dependence is relatively weak?
    - \* Close to equilibrium, we expect oscillations to increase
    - \* Far from equilibrium, density dependence takes over (prey cannot increase beyond their predator-free equilibrium) and oscillations decrease
    - \*

- ▶ What sort of oscillations do we expect?
  - If density dependence is relatively strong?
    - \* Damped oscillations
  - If density dependence is relatively weak?
    - \* Close to equilibrium, we expect oscillations to increase
    - \* Far from equilibrium, density dependence takes over (prey cannot increase beyond their predator-free equilibrium) and oscillations decrease
    - ▶ \* We reach a "limit cycle" where the population oscillates

- ▶ What sort of oscillations do we expect?
  - If density dependence is relatively strong?
    - \* Damped oscillations
  - If density dependence is relatively weak?
    - \* Close to equilibrium, we expect oscillations to increase
    - \* Far from equilibrium, density dependence takes over (prey cannot increase beyond their predator-free equilibrium) and oscillations decrease
    - ▶ \* We reach a "limit cycle" where the population oscillates

# DD plus predator satiation



► Neutral cycles repeat from any starting point

- Neutral cycles repeat from any starting point
- ► *Damped* cycles spiral in to the equilibrium.

- Neutral cycles repeat from any starting point
- Damped cycles spiral in to the equilibrium.
- Unstable cycles spiral out forever

- Neutral cycles repeat from any starting point
- Damped cycles spiral in to the equilibrium.
- Unstable cycles spiral out forever
  - ► Biologically unrealistic

- Neutral cycles repeat from any starting point
- ▶ *Damped* cycles spiral in to the equilibrium.
- Unstable cycles spiral out forever
  - Biologically unrealistic
- ► A *limit cycle* is approached by spiralling out from near the equilibrium, and by spiralling in from far away

- Neutral cycles repeat from any starting point
- Damped cycles spiral in to the equilibrium.
- Unstable cycles spiral out forever
  - Biologically unrealistic
- ► A *limit cycle* is approached by spiralling out from near the equilibrium, and by spiralling in from far away
- Any oscillations that are not damped are called persistent they don't go away

- Neutral cycles repeat from any starting point
- Damped cycles spiral in to the equilibrium.
- Unstable cycles spiral out forever
  - Biologically unrealistic
- ► A *limit cycle* is approached by spiralling out from near the equilibrium, and by spiralling in from far away
- Any oscillations that are not damped are called persistent they don't go away

► All resource-exploiter systems have a tendency to oscillate

- ► All resource-exploiter systems have a tendency to oscillate
- ► It often takes a long time for damped oscillations to die out, or for stable oscillations to converge

- ► All resource-exploiter systems have a tendency to oscillate
- ▶ It often takes a long time for damped oscillations to die out, or for stable oscillations to converge
- ► Other stuff is going on at the same time

- ► All resource-exploiter systems have a tendency to oscillate
- ▶ It often takes a long time for damped oscillations to die out, or for stable oscillations to converge
- ▶ Other stuff is going on at the same time
  - Other interactions

- ▶ All resource-exploiter systems have a tendency to oscillate
- It often takes a long time for damped oscillations to die out, or for stable oscillations to converge
- ▶ Other stuff is going on at the same time
  - Other interactions
  - ► Environmental perturbations weather, fire, people

- ▶ All resource-exploiter systems have a tendency to oscillate
- It often takes a long time for damped oscillations to die out, or for stable oscillations to converge
- Other stuff is going on at the same time
  - Other interactions
  - Environmental perturbations weather, fire, people

► If a resource-exploiter system is tightly linked, we expect to see some sort of noisy oscillations, with exploiter following resource (i.e., resource species goes up or down first)

- ▶ If a resource-exploiter system is tightly linked, we expect to see some sort of noisy oscillations, with exploiter following resource (i.e., resource species goes up or down first)
- ► If the basic interaction leads to damped oscillations, we expect to see relatively small oscillations in reality

- ▶ If a resource-exploiter system is tightly linked, we expect to see some sort of noisy oscillations, with exploiter following resource (i.e., resource species goes up or down first)
- ► If the basic interaction leads to damped oscillations, we expect to see relatively small oscillations in reality
- ► If the basic interaction leads to stable oscillations, we expect to see relatively large oscillations in reality

- ▶ If a resource-exploiter system is tightly linked, we expect to see some sort of noisy oscillations, with exploiter following resource (i.e., resource species goes up or down first)
- ► If the basic interaction leads to damped oscillations, we expect to see relatively small oscillations in reality
- ► If the basic interaction leads to stable oscillations, we expect to see relatively large oscillations in reality

#### Outline

#### Introduction

Balance and equilibrium Tendency to oscillate

#### A simple model

More detailed models Reciprocal control

#### Adding details

Dynamics

Equilibria

Who controls whom?

► Imagine that the resource species has a negative effect on its own growht rate

What happens to the equilibrium if we start catching fish?

- What happens to the equilibrium if we start catching fish?
  - **▶** ३

- What happens to the equilibrium if we start catching fish?
  - ightharpoonup \*  $r_e$  doesn't change, so  $N_f$  can't change

► Imagine that the resource species has a negative effect on its own growht rate

What happens to the equilibrium if we start catching fish?

- ightharpoonup \*  $r_e$  doesn't change, so  $N_f$  can't change
- \*

- What happens to the equilibrium if we start catching fish?
  - $ightharpoonup * r_e$  doesn't change, so  $N_f$  can't change
  - $ightharpoonup * r_f$  goes down and must be balanced by less sharks

- What happens to the equilibrium if we start catching fish?
  - ightharpoonup \*  $r_e$  doesn't change, so  $N_f$  can't change
  - $ightharpoonup * r_f$  goes down and must be balanced by less sharks
- ► What if we start catching sharks?

Imagine that the resource species has a negative effect on its own growht rate

What happens to the equilibrium if we start catching fish?

 $ightharpoonup * r_e$  doesn't change, so  $N_f$  can't change

ightharpoonup \*  $r_f$  goes down and must be balanced by less sharks

What if we start catching sharks?



Imagine that the resource species has a negative effect on its own growht rate

- What happens to the equilibrium if we start catching fish?
  - ightharpoonup \*  $r_{\rm e}$  doesn't change, so  $N_f$  can't change
  - ightharpoonup \*  $r_f$  goes down and must be balanced by less sharks
- What if we start catching sharks?
  - $\blacktriangleright$  \*  $r_e$  goes down, so  $N_f$  must go up

Imagine that the resource species has a negative effect on its own growht rate

What happens to the equilibrium if we start catching fish?

ightharpoonup \*  $r_{\rm e}$  doesn't change, so  $N_f$  can't change

ightharpoonup \*  $r_f$  goes down and must be balanced by less sharks

What if we start catching sharks?

ightharpoonup \*  $r_e$  goes down, so  $N_f$  must go up

\*

Imagine that the resource species has a negative effect on its own growht rate

- What happens to the equilibrium if we start catching fish?
  - ightharpoonup \*  $r_{\rm e}$  doesn't change, so  $N_f$  can't change
  - ightharpoonup \*  $r_f$  goes down and must be balanced by less sharks
- ▶ What if we start catching sharks?
  - $\blacktriangleright$  \*  $r_e$  goes down, so  $N_f$  must go up
  - ▶ \* Increasing  $N_f$  decreases  $r_f$ , so  $N_e$  must go down

Imagine that the resource species has a negative effect on its own growht rate

- What happens to the equilibrium if we start catching fish?
  - ightharpoonup \*  $r_{\rm e}$  doesn't change, so  $N_f$  can't change
  - ightharpoonup \*  $r_f$  goes down and must be balanced by less sharks
- ▶ What if we start catching sharks?
  - $\blacktriangleright$  \*  $r_e$  goes down, so  $N_f$  must go up
  - ▶ \* Increasing  $N_f$  decreases  $r_f$ , so  $N_e$  must go down

$$\blacktriangleright \ \frac{dN_f}{dt} = r_f(N_e, N_f)N_f$$

► What if we also consider "satiation" – there is some limit to how much a predator can catch (or eat)

$$ightharpoonup rac{dN_e}{dt} = r_e(N_f)N_e$$

► What happens to the equilibrium if we start catching fish?

► What if we also consider "satiation" – there is some limit to how much a predator can catch (or eat)

$$ightharpoonup rac{dN_e}{dt} = r_e(N_f)N_e$$

What happens to the equilibrium if we start catching fish?



- ▶ What if we also consider "satiation" there is some limit to how much a predator can catch (or eat)

  - $ightharpoonup rac{dN_e}{dt} = r_e(N_f)N_e$
- What happens to the equilibrium if we start catching fish?
  - ightharpoonup \*  $r_e$  doesn't change, so  $N_f$  can't change

$$ightharpoonup rac{dN_e}{dt} = r_e(N_f)N_e$$

- What happens to the equilibrium if we start catching fish?
  - ightharpoonup \*  $r_e$  doesn't change, so  $N_f$  can't change
  - \*

- ► What if we also consider "satiation" there is some limit to how much a predator can catch (or eat)
- ▶ What happens to the equilibrium if we start catching fish?
  - $ightharpoonup * r_e$  doesn't change, so  $N_f$  can't change
  - ightharpoonup \*  $r_f$  goes down and must be balanced by less sharks

- ▶ What if we also consider "satiation" there is some limit to how much a predator can catch (or eat)
- What happens to the equilibrium if we start catching fish?
  - $ightharpoonup * r_e$  doesn't change, so  $N_f$  can't change
  - ightharpoonup \*  $r_f$  goes down and must be balanced by less sharks
- ► What if we start catching sharks?

$$ightharpoonup rac{dN_e}{dt} = r_e(N_f)N_e$$

- What happens to the equilibrium if we start catching fish?
  - $ightharpoonup * r_e$  doesn't change, so  $N_f$  can't change
  - ightharpoonup \*  $r_f$  goes down and must be balanced by less sharks
- ▶ What if we start catching sharks?
  - \*

- What happens to the equilibrium if we start catching fish?
  - $ightharpoonup * r_e$  doesn't change, so  $N_f$  can't change
  - ightharpoonup \*  $r_f$  goes down and must be balanced by less sharks
- ▶ What if we start catching sharks?
  - ightharpoonup \*  $r_e$  goes down, so  $N_f$  must go up

▶ What if we also consider "satiation" – there is some limit to how much a predator can catch (or eat)

$$ightharpoonup rac{dN_e}{dt} = r_e(N_f)N_e$$

What happens to the equilibrium if we start catching fish?

- $ightharpoonup * r_e$  doesn't change, so  $N_f$  can't change
- ightharpoonup \*  $r_f$  goes down and must be balanced by less sharks
- ▶ What if we start catching sharks?
  - ightharpoonup \*  $r_e$  goes down, so  $N_f$  must go up
  - \*

- ▶ What if we also consider "satiation" there is some limit to how much a predator can catch (or eat)

  - $ightharpoonup rac{dN_e}{dt} = r_e(N_f)N_e$
- What happens to the equilibrium if we start catching fish?
  - $ightharpoonup * r_e$  doesn't change, so  $N_f$  can't change
  - ightharpoonup \*  $r_f$  goes down and must be balanced by less sharks
- ▶ What if we start catching sharks?
  - ightharpoonup \*  $r_e$  goes down, so  $N_f$  must go up
  - \* Satiation: More fish means higher r<sub>f</sub> means more sharks at equilibrium!

$$ightharpoonup rac{dN_e}{dt} = r_e(N_f)N_e$$

- What happens to the equilibrium if we start catching fish?
  - $ightharpoonup * r_e$  doesn't change, so  $N_f$  can't change
  - ightharpoonup \*  $r_f$  goes down and must be balanced by less sharks
- ▶ What if we start catching sharks?
  - ightharpoonup \*  $r_e$  goes down, so  $N_f$  must go up
  - \* Satiation: More fish means higher r<sub>f</sub> means more sharks at equilibrium!
    - \*

- What happens to the equilibrium if we start catching fish?
  - $ightharpoonup * r_e$  doesn't change, so  $N_f$  can't change
  - ightharpoonup \*  $r_f$  goes down and must be balanced by less sharks
- ▶ What if we start catching sharks?
  - $\blacktriangleright$  \*  $r_e$  goes down, so  $N_f$  must go up
  - ► \* Satiation: More fish means higher *r<sub>f</sub>* means more sharks at equilibrium!
  - ▶ \* This is the opposite of what we see for density dependence, so we would have to ask which is the stronger effect in particular circumstances.

- What happens to the equilibrium if we start catching fish?
  - $ightharpoonup * r_e$  doesn't change, so  $N_f$  can't change
  - ightharpoonup \*  $r_f$  goes down and must be balanced by less sharks
- ▶ What if we start catching sharks?
  - $\blacktriangleright$  \*  $r_e$  goes down, so  $N_f$  must go up
  - ► \* Satiation: More fish means higher *r<sub>f</sub>* means more sharks at equilibrium!
  - ▶ \* This is the opposite of what we see for density dependence, so we would have to ask which is the stronger effect in particular circumstances.

► Is reciprocal control realistic?

- ► Is reciprocal control realistic?
  - ► In the long term, catching fish isn't bad for fish populations? Feeding grouse doesn't improve long-term grouse populations?

- Is reciprocal control realistic?
  - ▶ In the long term, catching fish isn't bad for fish populations? Feeding grouse doesn't improve long-term grouse populations?
- ► Poll: What happens *first* in this model if I start feeding grouse?

- ► Is reciprocal control realistic?
  - ► In the long term, catching fish isn't bad for fish populations? Feeding grouse doesn't improve long-term grouse populations?
- ▶ Poll: What happens *first* in this model if I start feeding grouse?
  - \*

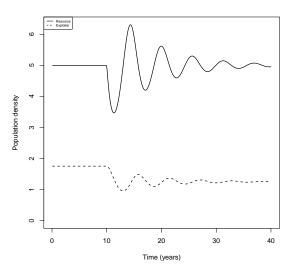
- Is reciprocal control realistic?
  - ▶ In the long term, catching fish isn't bad for fish populations? Feeding grouse doesn't improve long-term grouse populations?
- ▶ Poll: What happens *first* in this model if I start feeding grouse?
  - ► \* First we get more grouse, then we get more foxes, then we get less grouse, ...

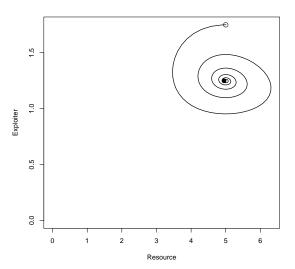
- Is reciprocal control realistic?
  - ▶ In the long term, catching fish isn't bad for fish populations? Feeding grouse doesn't improve long-term grouse populations?
- Poll: What happens first in this model if I start feeding grouse?
  - ► \* First we get more grouse, then we get more foxes, then we get less grouse, ...
- ► Poll: What happens *eventually* in this model if I start feeding grouse?

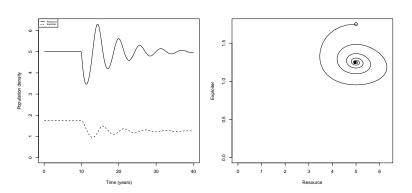
- Is reciprocal control realistic?
  - ▶ In the long term, catching fish isn't bad for fish populations? Feeding grouse doesn't improve long-term grouse populations?
- Poll: What happens first in this model if I start feeding grouse?
  - ► \* First we get more grouse, then we get more foxes, then we get less grouse, ...
- ▶ Poll: What happens *eventually* in this model if I start feeding grouse?
  - \*

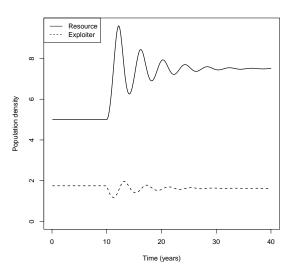
- Is reciprocal control realistic?
  - ▶ In the long term, catching fish isn't bad for fish populations? Feeding grouse doesn't improve long-term grouse populations?
- Poll: What happens first in this model if I start feeding grouse?
  - ► \* First we get more grouse, then we get more foxes, then we get less grouse, ...
- Poll: What happens eventually in this model if I start feeding grouse?
  - ► \* Population eventually approaches (or orbits around) a new equilibrium, with more foxes, and the same amount of grouse as before

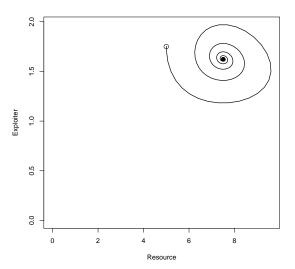
- Is reciprocal control realistic?
  - ▶ In the long term, catching fish isn't bad for fish populations? Feeding grouse doesn't improve long-term grouse populations?
- Poll: What happens first in this model if I start feeding grouse?
  - ► \* First we get more grouse, then we get more foxes, then we get less grouse, ...
- Poll: What happens eventually in this model if I start feeding grouse?
  - ► \* Population eventually approaches (or orbits around) a new equilibrium, with more foxes, and the same amount of grouse as before

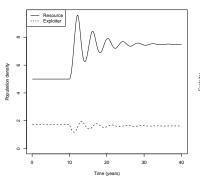


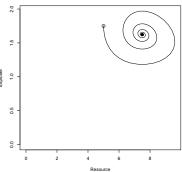


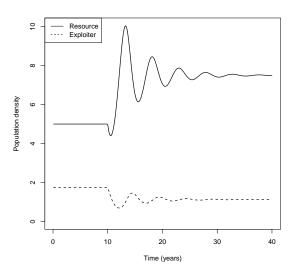




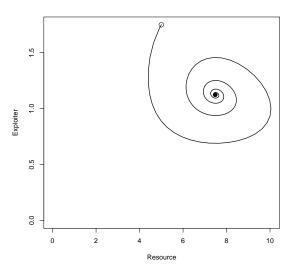




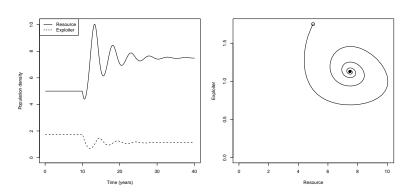




## Harvesting dynamics



# Harvesting dynamics



### Outline

#### Introduction

Balance and equilibrium Tendency to oscillate

### A simple model

More detailed models Reciprocal control

### Adding details

Dynamics Equilibria

► These results tell us that how ecosystems respond to perturbation depends not only on the perturbation, but on how the ecosystems are regulated

- These results tell us that how ecosystems respond to perturbation depends not only on the perturbation, but on how the ecosystems are regulated
- ▶ What controls populations of large fish in the ocean?

- These results tell us that how ecosystems respond to perturbation depends not only on the perturbation, but on how the ecosystems are regulated
- What controls populations of large fish in the ocean?
  - ► Sharks that eat them? Small fish that they eat?

- These results tell us that how ecosystems respond to perturbation depends not only on the perturbation, but on how the ecosystems are regulated
- What controls populations of large fish in the ocean?
  - Sharks that eat them? Small fish that they eat?
- Studies of snowshoe hares

- These results tell us that how ecosystems respond to perturbation depends not only on the perturbation, but on how the ecosystems are regulated
- What controls populations of large fish in the ocean?
  - Sharks that eat them? Small fish that they eat?
- Studies of snowshoe hares
  - Very simple ecology: a few food species, one major predator

- These results tell us that how ecosystems respond to perturbation depends not only on the perturbation, but on how the ecosystems are regulated
- What controls populations of large fish in the ocean?
  - Sharks that eat them? Small fish that they eat?
- Studies of snowshoe hares
  - Very simple ecology: a few food species, one major predator
  - ► Food availability? Food edibility? Predators? Diseases?

- These results tell us that how ecosystems respond to perturbation depends not only on the perturbation, but on how the ecosystems are regulated
- What controls populations of large fish in the ocean?
  - Sharks that eat them? Small fish that they eat?
- Studies of snowshoe hares
  - Very simple ecology: a few food species, one major predator
  - ► Food availability? Food edibility? Predators? Diseases?
- ► It's never a simple question

- These results tell us that how ecosystems respond to perturbation depends not only on the perturbation, but on how the ecosystems are regulated
- What controls populations of large fish in the ocean?
  - Sharks that eat them? Small fish that they eat?
- Studies of snowshoe hares
  - Very simple ecology: a few food species, one major predator
  - Food availability? Food edibility? Predators? Diseases?
- It's never a simple question





▶ Poll: Why is the earth green and the ocean blue?

▶ Poll: Why is the earth green and the ocean blue?

\*

- ▶ Poll: Why is the earth green and the ocean blue?
  - ▶ \* The ocean could be green, and the earth could be brown

- ▶ Poll: Why is the earth green and the ocean blue?
  - ▶ \* The ocean could be green, and the earth could be brown
  - **▶** \*

- Poll: Why is the earth green and the ocean blue?
  - ▶ \* The ocean could be green, and the earth could be brown
  - \* Why does the earth seem to be covered by plants, and the ocean doesn't?

- Poll: Why is the earth green and the ocean blue?
  - ▶ \* The ocean could be green, and the earth could be brown
  - \* Why does the earth seem to be covered by plants, and the ocean doesn't?
- ► The question is: what trophic levels provide the primary control for which other trophic levels?

- Poll: Why is the earth green and the ocean blue?
  - ▶ \* The ocean could be green, and the earth could be brown
  - \* Why does the earth seem to be covered by plants, and the ocean doesn't?
- ► The question is: what trophic levels provide the primary control for which other trophic levels?
  - ► Top-down control theory: on land, herbivores are mostly controlled by carnivores, rather than by food

- Poll: Why is the earth green and the ocean blue?
  - ▶ \* The ocean could be green, and the earth could be brown
  - \* Why does the earth seem to be covered by plants, and the ocean doesn't?
- ► The question is: what trophic levels provide the primary control for which other trophic levels?
  - Top-down control theory: on land, herbivores are mostly controlled by carnivores, rather than by food
  - ► Plants fight back theory: plants invest enough in "defense" to escape herbivore control and compete with each other

- ▶ Poll: Why is the earth green and the ocean blue?
  - ▶ \* The ocean could be green, and the earth could be brown
  - \* Why does the earth seem to be covered by plants, and the ocean doesn't?
- ► The question is: what trophic levels provide the primary control for which other trophic levels?
  - Top-down control theory: on land, herbivores are mostly controlled by carnivores, rather than by food
  - ▶ Plants fight back theory: plants invest enough in "defense" to escape herbivore control and compete with each other
- ► For each case, we can ask why the ocean is different

- ▶ Poll: Why is the earth green and the ocean blue?
  - ▶ \* The ocean could be green, and the earth could be brown
  - \* Why does the earth seem to be covered by plants, and the ocean doesn't?
- ► The question is: what trophic levels provide the primary control for which other trophic levels?
  - Top-down control theory: on land, herbivores are mostly controlled by carnivores, rather than by food
  - ▶ Plants fight back theory: plants invest enough in "defense" to escape herbivore control and compete with each other
- For each case, we can ask why the ocean is different



