

# UNIT 7: Predation

# Outline

## Introduction

- Balance and equilibrium

- Tendency to oscillate

## A simple model

- More detailed models

- Reciprocal control

## Adding details

- Dynamics

- Equilibria

## Who controls whom?

# Introduction

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

# Introduction

- ▶ 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

# Introduction

- ▶ 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

# Introduction

- ▶ 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

# Examples

- ▶ Antelopes graze on trees

# Examples

- ▶ Antelopes graze on trees
- ▶ Lions eat antelopes



# Examples

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

# Examples

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

# Examples

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

# Examples

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

# Examples

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

## Exploitation examples



## Exploitation examples



## Exploitation examples

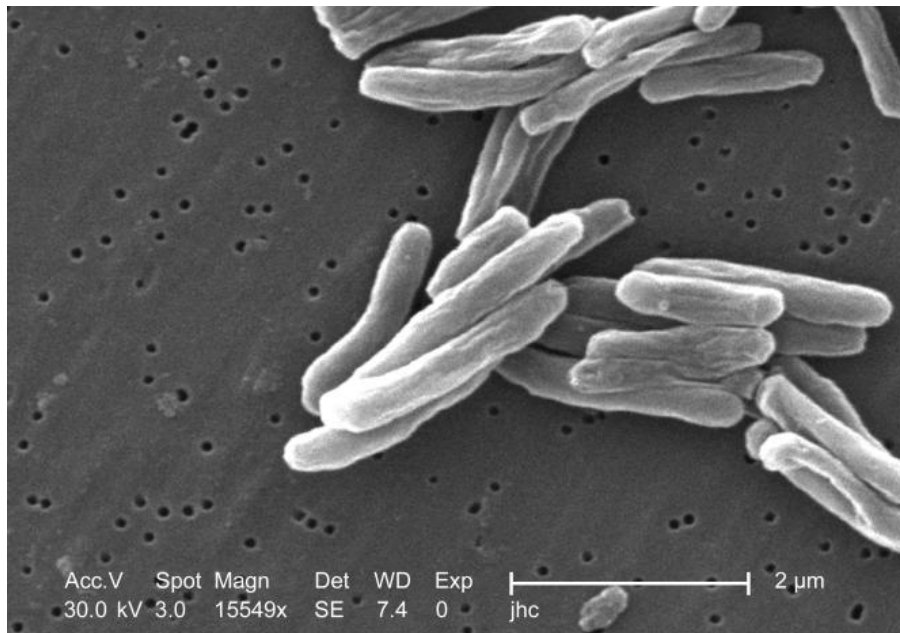




## Exploitation examples



## Exploitation examples



## Exploitation examples



# Types of exploitation

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

# Types of exploitation

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

# Types of exploitation

- ▶ 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

# Types of exploitation

- ▶ 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

# Types of exploitation

- ▶ 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



# Types of exploitation

- ▶ 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

# Types of exploitation

- ▶ 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

# Borderline cases

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

## Borderline cases

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

## Borderline cases

- ▶ 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?

## Borderline cases

- ▶ 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?

# Borderline cases

- ▶ 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

# Borderline cases

- ▶ 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



# Our course

- ▶ This unit will focus mostly on predation; also relevant for grazing

# Our course

- ▶ This unit will focus mostly on predation; also relevant for grazing
- ▶ The next unit (disease) will focus on micro-parasites: things that have populations inside individual hosts

# Our course

- ▶ This unit will focus mostly on predation; also relevant for grazing
- ▶ The next unit (disease) will focus on micro-parasites: things that have populations inside individual hosts

# Exploiters and resources

- ▶ In this unit, I will often refer to the species being exploited as the **resource species**

# Exploiters and resources

- ▶ In this unit, I will often refer 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

# Exploiters and resources

- ▶ In this unit, I will often refer 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

# Exploiters and resources

- ▶ In this unit, I will often refer 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

# Exploiters and resources

- ▶ In this unit, I will often refer 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?

# Balance and equilibrium

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

# Balance and equilibrium

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



# Balance and 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

# Balance and 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
  - ▶ \*

# Balance and 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

# Balance and 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

# Balance and 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



# Balance and 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

# Equilibrium questions

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

# Equilibrium questions

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

# Equilibrium questions

- ▶ 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)?

# Equilibrium questions

- ▶ 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:

# Equilibrium questions

- ▶ 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.

# Equilibrium questions

- ▶ 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.

# Reciprocal control

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



# Reciprocal control

- ▶ 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

# Reciprocal control

- ▶ 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

# Reciprocal control

- ▶ 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
- ▶ What will determine equilibrium values?

# Reciprocal control

- ▶ 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
- ▶ What will determine equilibrium values?
  - ▶ \*

# Reciprocal control

- ▶ 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
- ▶ What will determine equilibrium values?
  - ▶ \* For equilibrium, each species must be at the density required to keep the *other* species balanced

# Reciprocal control

- ▶ 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
- ▶ What will determine equilibrium values?
  - ▶ \* For equilibrium, each species must be at the density required to keep the *other* species balanced
  - ▶ \*

# Reciprocal control

- ▶ 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
- ▶ 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.

# Reciprocal control

- ▶ 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
- ▶ 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?

# Tendency to oscillate

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

# 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

# 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

# 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
  - ▶ \*

# 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
  - ▶ \* Exploiter goes up → Resource goes down → Exploiter goes down → Resource goes up → Exploiter goes up ...

# 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
  - ▶ \* Exploiter goes up → Resource goes down → Exploiter goes down → Resource goes up → Exploiter goes up . . .

## Persistence of oscillations

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



## Persistence of oscillations

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

## Persistence of oscillations

- ▶ 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

## Persistence of oscillations

- ▶ 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

## Persistence of oscillations

- ▶ 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**

## Persistence of oscillations

- ▶ 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**

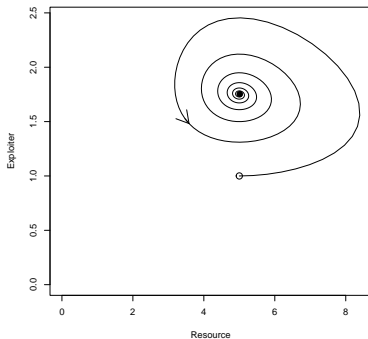
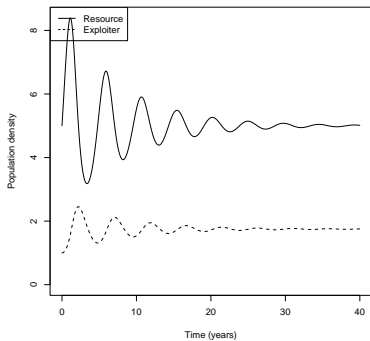
## Persistence of oscillations

- ▶ 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**

## Persistence of oscillations

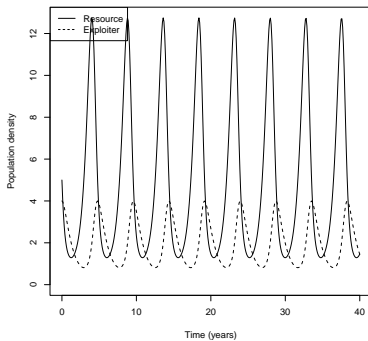
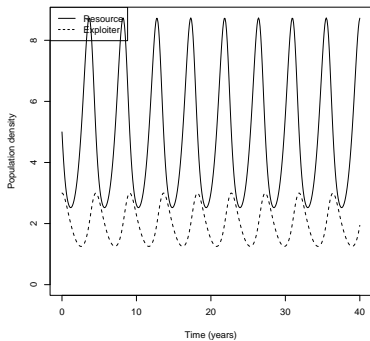
- ▶ Resource-exploiter systems have a *tendency* to oscillate
- ▶ In the simplest possible models, oscillations are **neutral**
  - ▶ e.g., they don't get larger or smaller
- ▶ In more realistic models, large oscillations will tend to get smaller
  - ▶ If small oscillations also tend to get smaller,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

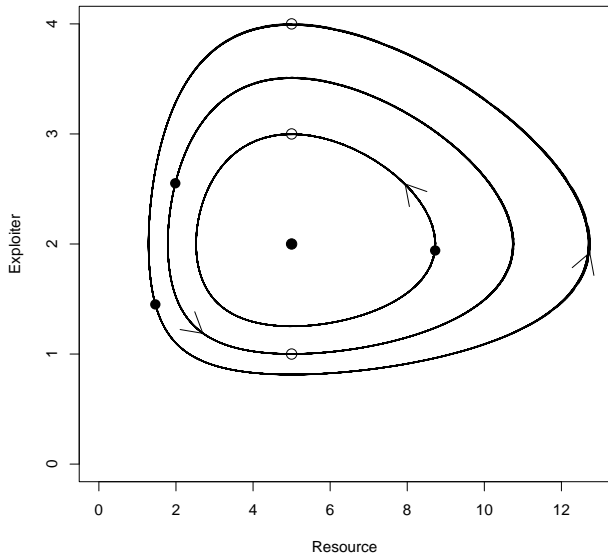




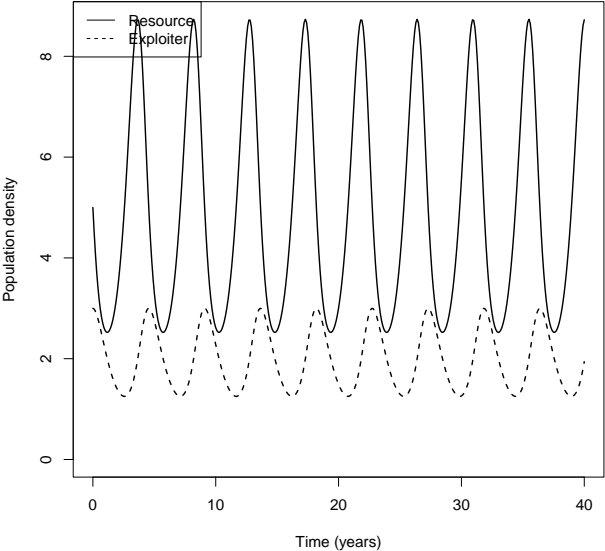
## Neutral cycles



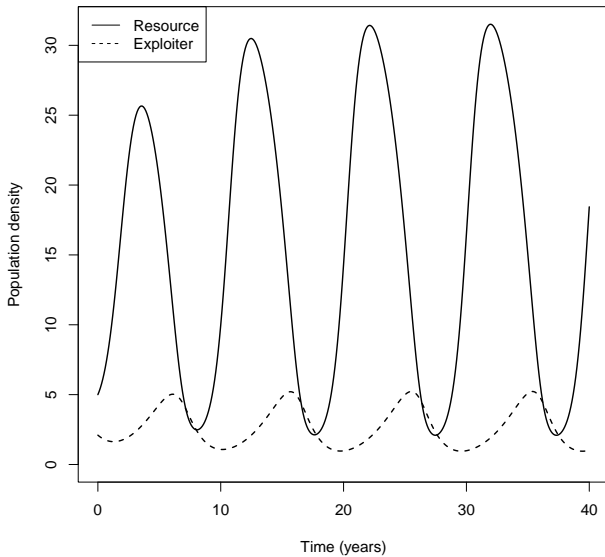
## Neutral cycles



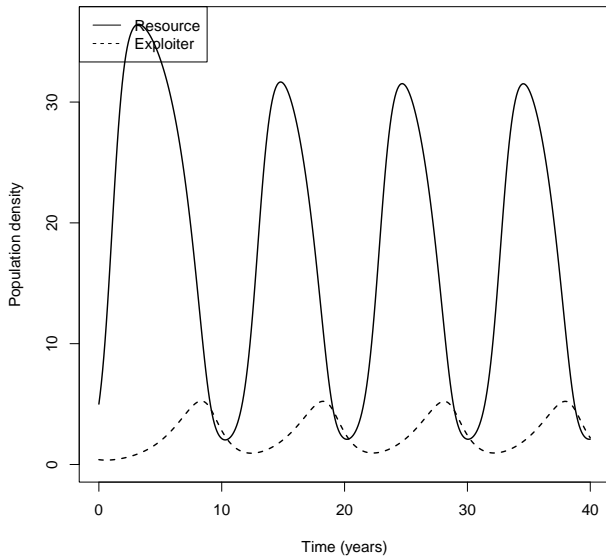
# Neutral cycles



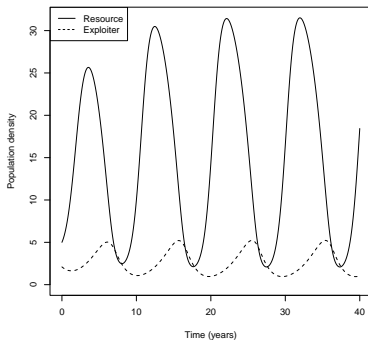
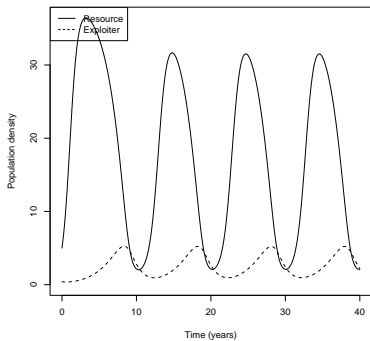
# Limit cycles



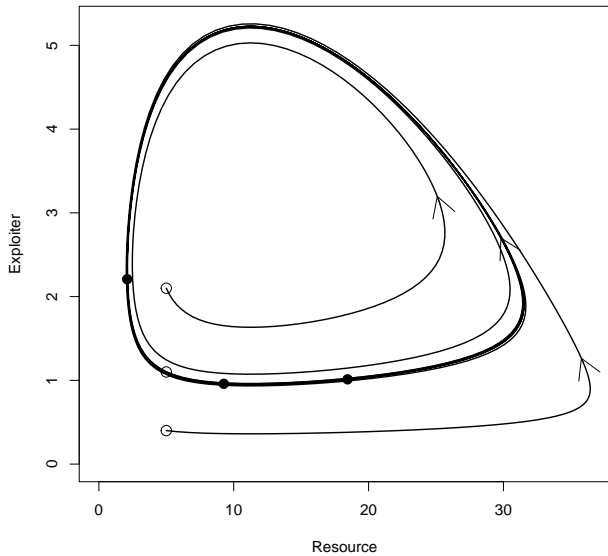
# Limit cycles



## Limit cycles



# Limit cycles



## Neutral vs. limit cycles

- ▶ What is the difference between neutral cycles and limit cycles?



## Neutral vs. limit cycles

- ▶ What is the difference between neutral cycles and limit cycles?



## Neutral vs. limit cycles

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

## Neutral vs. limit cycles

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

## Neutral vs. limit cycles

- ▶ 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

## Neutral vs. limit cycles

- ▶ 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
  - ▶ \*

## Neutral vs. limit cycles

- ▶ 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

## Neutral vs. limit cycles

- ▶ 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
    - ▶ \*

## Neutral vs. limit cycles

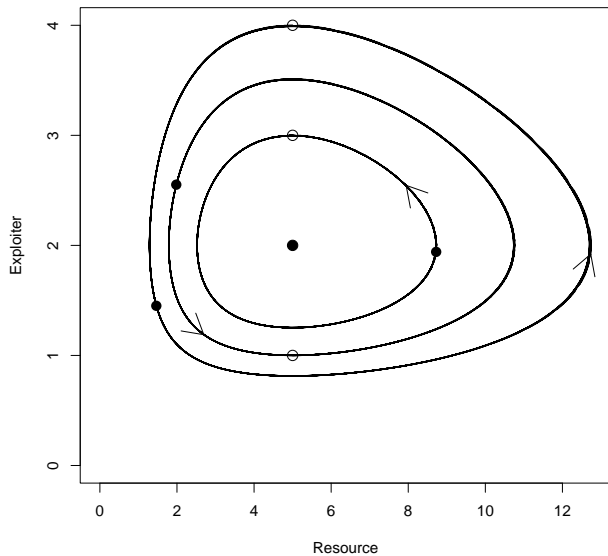
- ▶ What is the difference between neutral cycles and limit cycles?
  - ▶ \* Neutral cycles have no tendency to get larger or smaller
    - ▶ \* Large cycles stay large, small cycles stay small
  - ▶ \* Limit cycles converge to a limit
    - ▶ \* Large cycles get smaller, small cycles get larger



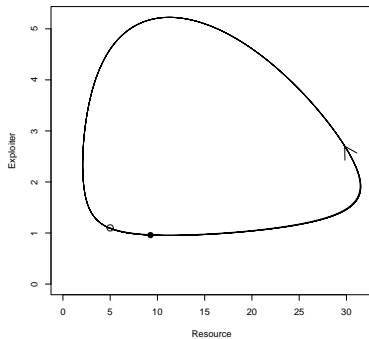
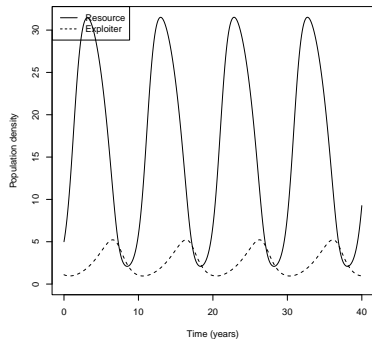
## Neutral vs. limit cycles

- ▶ 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

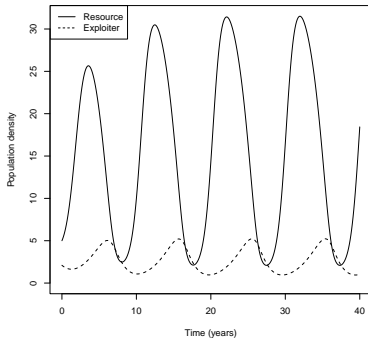
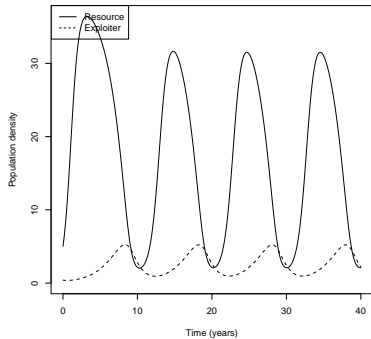
# Neutral cycles



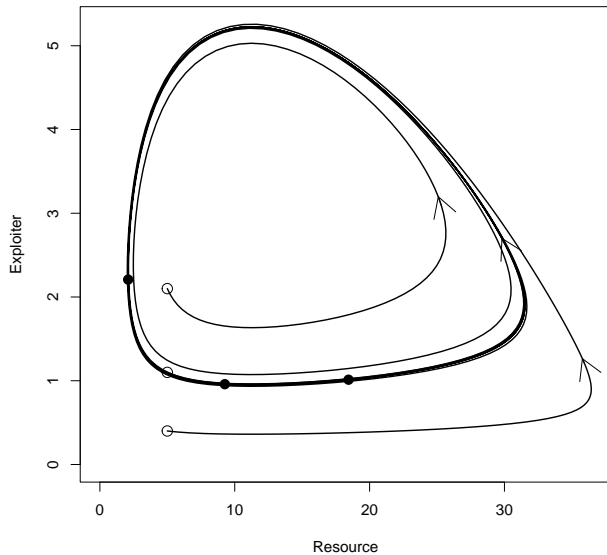
# Limit cycles



## Limit cycles (repeat)



# Limit cycles



# Outline

## Introduction

Balance and equilibrium

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

# A simple model

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



## A simple model

- ▶ We can investigate exploiter-resource systems using simple models
- ▶ Resource-species growth rate may depend on density of exploiter, or resource species, or both:
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$

## A simple model

- ▶ We can investigate exploiter-resource systems using simple models
- ▶ Resource-species growth rate may depend on density of exploiter, or resource species, or both:
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
- ▶ Exploiter growth rate may depend on density of exploiter, or resource species, or both:

## A simple model

- ▶ We can investigate exploiter-resource systems using simple models
- ▶ Resource-species growth rate may depend on density of exploiter, or resource species, or both:
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
- ▶ Exploiter growth rate may depend on density of exploiter, or resource species, or both:
  - ▶  $\frac{dN_e}{dt} = r_e(N_e, N_f)N_e$

## A simple model

- ▶ We can investigate exploiter-resource systems using simple models
- ▶ Resource-species growth rate may depend on density of exploiter, or resource species, or both:
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
- ▶ Exploiter growth rate may depend on density of exploiter, or resource species, or both:
  - ▶  $\frac{dN_e}{dt} = r_e(N_e, N_f)N_e$
- ▶ At equilibrium:

## A simple model

- ▶ We can investigate exploiter-resource systems using simple models
- ▶ Resource-species growth rate may depend on density of exploiter, or resource species, or both:
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
- ▶ Exploiter growth rate may depend on density of exploiter, or resource species, or both:
  - ▶  $\frac{dN_e}{dt} = r_e(N_e, N_f)N_e$
- ▶ At equilibrium:
  - ▶ \*

## A simple model

- ▶ We can investigate exploiter-resource systems using simple models
- ▶ Resource-species growth rate may depend on density of exploiter, or resource species, or both:
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
- ▶ Exploiter growth rate may depend on density of exploiter, or resource species, or both:
  - ▶  $\frac{dN_e}{dt} = r_e(N_e, N_f)N_e$
- ▶ At equilibrium:
  - ▶ \*  $r_e = r_f = 0$

## A simple model

- ▶ We can investigate exploiter-resource systems using simple models
- ▶ Resource-species growth rate may depend on density of exploiter, or resource species, or both:
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
- ▶ Exploiter growth rate may depend on density of exploiter, or resource species, or both:
  - ▶  $\frac{dN_e}{dt} = r_e(N_e, N_f)N_e$
- ▶ At equilibrium:
  - ▶ \*  $r_e = r_f = 0$
  - ▶ \*

## A simple model

- ▶ We can investigate exploiter-resource systems using simple models
- ▶ Resource-species growth rate may depend on density of exploiter, or resource species, or both:
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
- ▶ Exploiter growth rate may depend on density of exploiter, or resource species, or both:
  - ▶  $\frac{dN_e}{dt} = r_e(N_e, N_f)N_e$
- ▶ At equilibrium:
  - ▶ \*  $r_e = r_f = 0$
  - ▶ \*  $r_f = N_e = 0$



## A simple model

- ▶ We can investigate exploiter-resource systems using simple models
- ▶ Resource-species growth rate may depend on density of exploiter, or resource species, or both:
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
- ▶ Exploiter growth rate may depend on density of exploiter, or resource species, or both:
  - ▶  $\frac{dN_e}{dt} = r_e(N_e, N_f)N_e$
- ▶ At equilibrium:
  - ▶ \*  $r_e = r_f = 0$
  - ▶ \*  $r_f = N_e = 0$
  - ▶ \*

## A simple model

- ▶ We can investigate exploiter-resource systems using simple models
- ▶ Resource-species growth rate may depend on density of exploiter, or resource species, or both:
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
- ▶ Exploiter growth rate may depend on density of exploiter, or resource species, or both:
  - ▶  $\frac{dN_e}{dt} = r_e(N_e, N_f)N_e$
- ▶ At equilibrium:
  - ▶ \*  $r_e = r_f = 0$
  - ▶ \*  $r_f = N_e = 0$
  - ▶ \*  $N_e = N_f = 0$

# A simple model

- ▶ We can investigate exploiter-resource systems using simple models
- ▶ Resource-species growth rate may depend on density of exploiter, or resource species, or both:
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
- ▶ Exploiter growth rate may depend on density of exploiter, or resource species, or both:
  - ▶  $\frac{dN_e}{dt} = r_e(N_e, N_f)N_e$
- ▶ At equilibrium:
  - ▶ \*  $r_e = r_f = 0$
  - ▶ \*  $r_f = N_e = 0$
  - ▶ \*  $N_e = N_f = 0$
  - ▶ \*

# A simple model

- ▶ We can investigate exploiter-resource systems using simple models
- ▶ Resource-species growth rate may depend on density of exploiter, or resource species, or both:
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
- ▶ Exploiter growth rate may depend on density of exploiter, or resource species, or both:
  - ▶  $\frac{dN_e}{dt} = r_e(N_e, N_f)N_e$
- ▶ At equilibrium:
  - ▶ \*  $r_e = r_f = 0$
  - ▶ \*  $r_f = N_e = 0$
  - ▶ \*  $N_e = N_f = 0$
  - ▶ \* If  $N_f = 0$ , what happens to  $r_e$ ?

# A simple model

- ▶ We can investigate exploiter-resource systems using simple models
- ▶ Resource-species growth rate may depend on density of exploiter, or resource species, or both:
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
- ▶ Exploiter growth rate may depend on density of exploiter, or resource species, or both:
  - ▶  $\frac{dN_e}{dt} = r_e(N_e, N_f)N_e$
- ▶ At equilibrium:
  - ▶ \*  $r_e = r_f = 0$
  - ▶ \*  $r_f = N_e = 0$
  - ▶ \*  $N_e = N_f = 0$
  - ▶ \* If  $N_f = 0$ , what happens to  $r_e$ ?

# Interactions

- ▶ What makes this a resource-exploiter system?

# Interactions

- ▶ What makes this a resource-exploiter system?

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

# Interactions

► What makes this a resource-exploiter system?

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

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



# Interactions

► What makes this a resource-exploiter system?

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

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



# Interactions

- ▶ What makes this a resource-exploiter system?
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_e, N_f)N_e$
- ▶ \* We expect the resource species to be good for the exploiter ( $r_e$  goes up as  $N_f$  goes up)

# Interactions

- ▶ What makes this a resource-exploiter system?
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_e, N_f)N_e$
- ▶ \* We expect the resource species to be good for the exploiter ( $r_e$  goes up as  $N_f$  goes up)
- ▶ \*

# Interactions

- ▶ What makes this a resource-exploiter system?
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_e, N_f)N_e$
- ▶ \* We expect the resource species to be good for the exploiter ( $r_e$  goes up as  $N_f$  goes up)
- ▶ \* We expect the exploiter to be bad for the resource species ( $r_f$  goes down as  $N_e$  goes up)

# Interactions

- ▶ What makes this a resource-exploiter system?
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_e, N_f)N_e$
- ▶ \* We expect the resource species to be good for the exploiter ( $r_e$  goes up as  $N_f$  goes up)
- ▶ \* We expect the exploiter to be bad for the resource species ( $r_f$  goes down as  $N_e$  goes up)
- ▶ Mnemonic:  $e$  for exploiter,  $f$  for food.

# Interactions

- ▶ What makes this a resource-exploiter system?
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_e, N_f)N_e$
- ▶ \* We expect the resource species to be good for the exploiter ( $r_e$  goes up as  $N_f$  goes up)
- ▶ \* We expect the exploiter to be bad for the resource species ( $r_f$  goes down as  $N_e$  goes up)
- ▶ Mnemonic:  $e$  for exploiter,  $f$  for food.

# Simplest model

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

# Simplest model

- ▶ The simplest model of resource-exploiter interaction is when their per-capita growth rates only respond to each other.
  - ▶  $\frac{dN_f}{dt} = r_f(N_e)N_f$



# Simplest model

- ▶ The simplest model of resource-exploiter interaction is when their per-capita growth rates only respond to each other.
  - ▶  $\frac{dN_f}{dt} = r_f(N_e)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$

# Simplest model

- ▶ The simplest model of resource-exploiter interaction is when their per-capita growth rates only respond to each other.
  - ▶  $\frac{dN_f}{dt} = r_f(N_e)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$
- ▶ This is a pure **reciprocal control** model: resource growth rate depends only on exploiter density, and vice versa

# Simplest model

- ▶ The simplest model of resource-exploiter interaction is when their per-capita growth rates only respond to each other.
  - ▶  $\frac{dN_f}{dt} = r_f(N_e)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$
- ▶ This is a pure **reciprocal control** model: resource growth rate depends only on exploiter density, and vice versa

# Resource-exploiter interactions



# Resource-exploiter interactions



# Ratios

- ▶ This model assumes:

# Ratios

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

# Ratios

- ▶ 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



# Ratios

- ▶ 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

# Ratios

- ▶ 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?

# Ratios

- ▶ 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?



# Ratios

- ▶ 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

# Ratios

- ▶ 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
  - ▶ \*

# Ratios

- ▶ 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

# Ratios

- ▶ 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
  - ▶ \*

# Ratios

- ▶ 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 ...



# Ratios

- ▶ 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?



# Resource populations

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

# Resource populations

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

▶ \*

# Resource populations

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

# Resource populations

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

# Resource populations

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



# Resource populations

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

# Resource populations

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

# Resource populations

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

# Exploiter populations

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

# Exploiter populations

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



# Exploiter populations

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

# Exploiter populations

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

# Exploiter populations

- ▶ 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 food-gathering, competing with other exploiters (Allee effects)



# Exploiter populations

- ▶ 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 food-gathering, competing with other exploiters (Allee effects)

# Types of cycles

- ▶ The simplest models of reciprocal control lead to neutral cycles

# Types of cycles

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

# Types of cycles

- ▶ 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?

# Types of cycles

- ▶ 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:

# Types of cycles

- ▶ 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)?

# Types of cycles

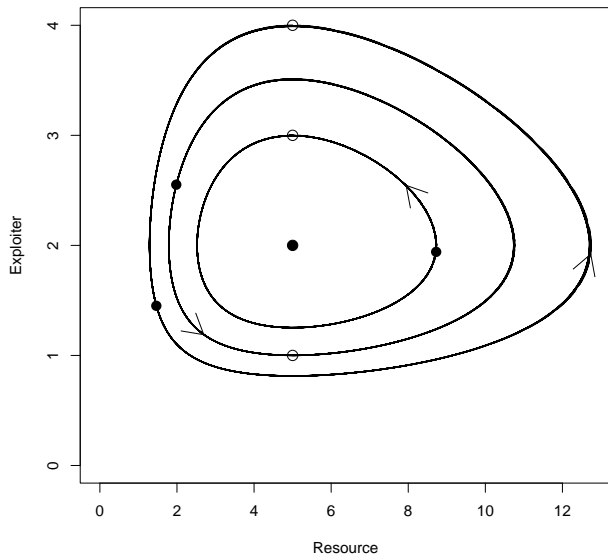
- ▶ The simplest models of reciprocal control lead to neutral cycles
  - ▶ Cycles starting from any starting point will go back through that starting point
  - ▶ These seem unrealistic; why should there be no tendency to spiral out or in for any cycle?
- ▶ To take the next step, we ask what factors will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

# Types of cycles

- ▶ 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?

# Reciprocal control

- ▶ 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)?

# Reciprocal control

- ▶ 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)?



# Reciprocal control

- ▶ 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.

# Reciprocal control

- ▶ 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.
  - ▶ \*

# Reciprocal control

- ▶ 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  $N_e$  goes to zero!

# Reciprocal control

- ▶ 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  $N_e$  goes to zero!
  - ▶ \*



# Reciprocal control

- ▶ 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  $N_e$  goes to zero!
  - ▶ \* The value of  $r_f$  has gone down, so we must increase it

# Reciprocal control

- ▶ 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  $N_e$  goes to zero!
  - ▶ \* The value of  $r_f$  has gone down, so we must increase it
    - ▶ \*

# Reciprocal control

- ▶ 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  $N_e$  goes to zero!
  - ▶ \* The value of  $r_f$  has gone down, so we must increase it
    - ▶ \* by decreasing the number of exploiters

# Reciprocal control

- ▶ 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  $N_e$  goes to zero!
  - ▶ \* The value of  $r_f$  has gone down, so we must increase it
    - ▶ \* by decreasing the number of exploiters

# Reciprocal control

- ▶ 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):

# Reciprocal control

- ▶ 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):



# Reciprocal control

- ▶ 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):
  - ▶ \*  $r_f$  doesn't change, so  $N_e$  must stay the same

# Reciprocal control

- ▶ 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):
  - ▶ \*  $r_f$  doesn't change, so  $N_e$  must stay the same
  - ▶ \*



# Reciprocal control

- ▶ 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):
  - ▶ \*  $r_f$  doesn't change, so  $N_e$  must stay the same
  - ▶ \*  $r_e$  of the old equilibrium goes down, so  $N_f$  must increase

# Reciprocal control

- ▶ 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):
  - ▶ \*  $r_f$  doesn't change, so  $N_e$  must stay the same
  - ▶ \*  $r_e$  of the old equilibrium goes down, so  $N_f$  must increase
  - ▶ \*

# Reciprocal control

- ▶ 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):
  - ▶ \*  $r_f$  doesn't change, so  $N_e$  must stay the same
  - ▶ \*  $r_e$  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.

# Reciprocal control

- ▶ 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):
  - ▶ \*  $r_f$  doesn't change, so  $N_e$  must stay the same
  - ▶ \*  $r_e$  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



# Harvesting response

- ▶ Species under reciprocal control may respond to change in unexpected ways

# Harvesting response

- ▶ 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)

# Harvesting response

- ▶ 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)?



# Harvesting response

- ▶ 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)?



# Harvesting response

- ▶ 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

# Harvesting response

- ▶ 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

# Harvesting equilibrium

- ▶ 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?

# Harvesting equilibrium

- ▶ 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?



# Harvesting equilibrium

- ▶ 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)

# Harvesting equilibrium

- ▶ What will 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)
  - ▶ \*

# Harvesting equilibrium

- ▶ What will 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)



# Harvesting equilibrium

- ▶ What will 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)

# Real implications

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

# 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**

# 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**
    - ▶ \*

# 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

# 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

# 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
    - ▶ \*

# 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*



# 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

# 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
  - ▶ \*

# 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
  - ▶ \*

# 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?





# Resource density-dependence

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

# Resource density-dependence

- ▶ 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.

# Resource density-dependence

- ▶ 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:

# Resource density-dependence

- ▶ 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:
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$

# Resource density-dependence

- ▶ 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:
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$

# Resource density-dependence

- ▶ 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:
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$

# Predator satiation

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

# Predator satiation

- ▶ 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?



# Predator satiation

- ▶ 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?

# Predator satiation

- ▶ 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?
    - ▶ \*

# Predator satiation

- ▶ 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

# Predator satiation

- ▶ 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?

# Predator satiation

- ▶ 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?
    - ▶ \*

# Predator satiation

- ▶ 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

- ▶ 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

# Predator satiation

- ▶ 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

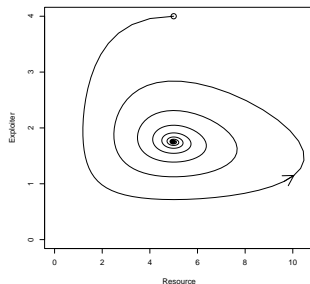
## Adding details

- Dynamics
- Equilibria

## Who controls whom?

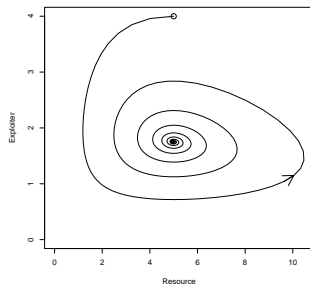
# Prey density dependence

- Reduces prey reproduction the most when prey numbers are highest



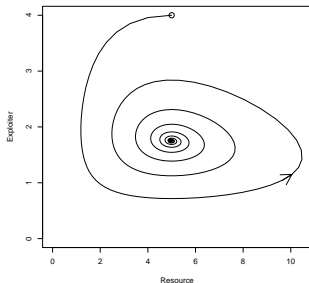
# Prey density dependence

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



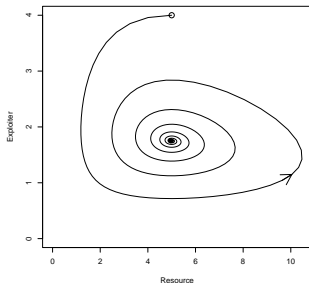
# Prey density dependence

- ▶ 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

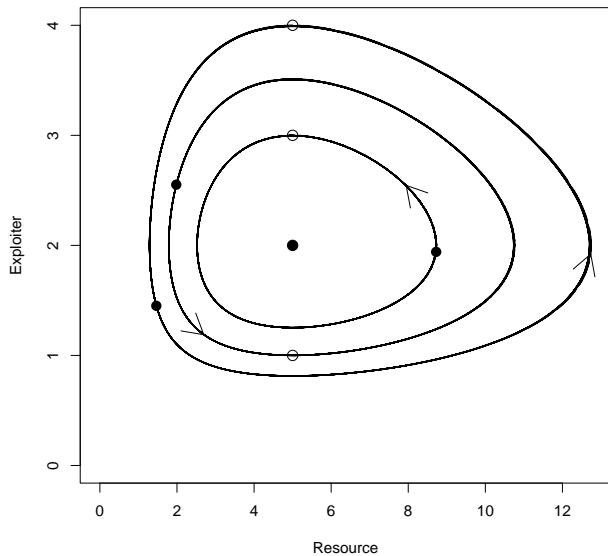


# Prey density dependence

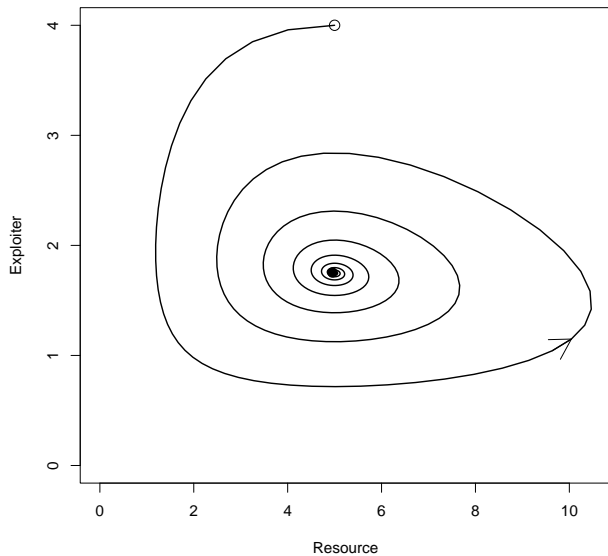
- ▶ Reduces prey reproduction the most when prey numbers are highest
- ▶ Tends to pull cycles towards the middle
- ▶ Makes cycles get smaller, leading to **damped** cycles



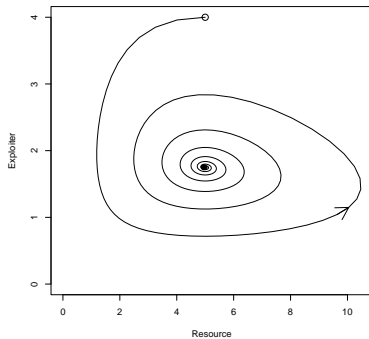
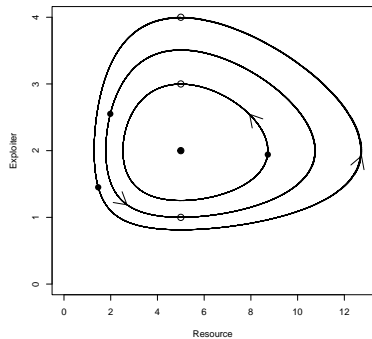
# Neutral cycles



# Prey density dependence



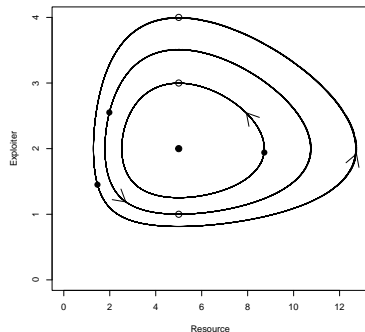
# Prey density dependence





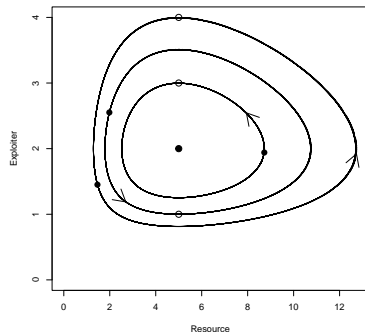
# Predator density dependence

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

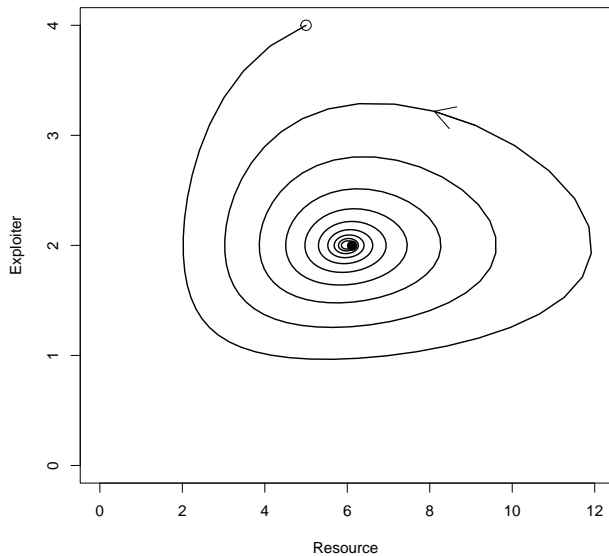


# Predator density dependence

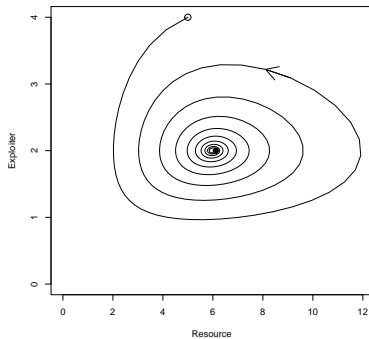
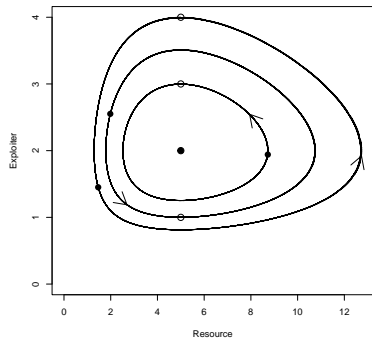
- If we go back to neutral cycles, and add predator density dependence, do we expect cycles to spiral out, or spiral in?



# Predator density dependence

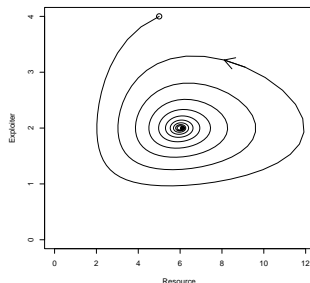


# Predator density dependence



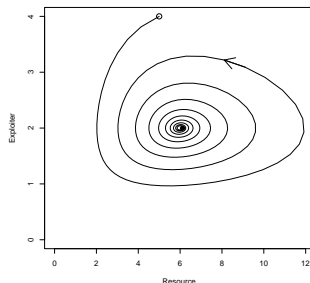
# Predator density dependence

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



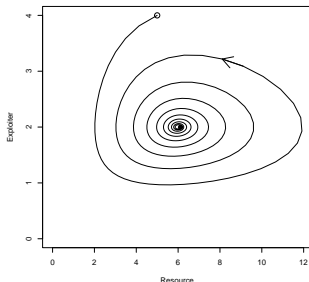
# Predator density dependence

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



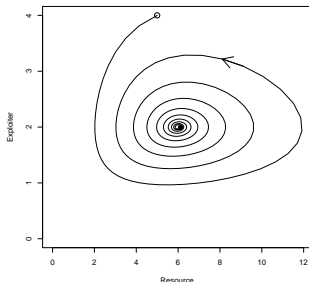
# Predator density dependence

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



# Predator density dependence

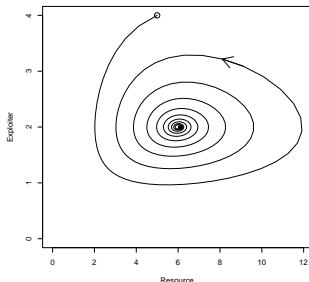
- ▶ Density dependence in the predator (exploiter species) has what effect on cycles?
  - ▶ \* Reduces predator reproduction when predators are the highest
  - ▶ \*





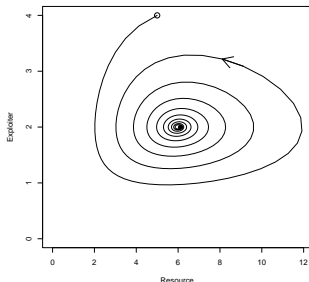
# Predator density dependence

- ▶ 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



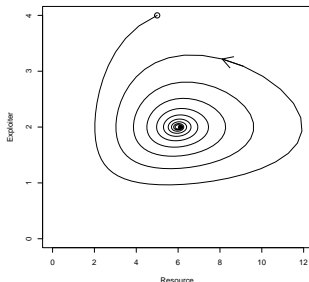
# Predator density dependence

- ▶ 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
  - ▶ \*



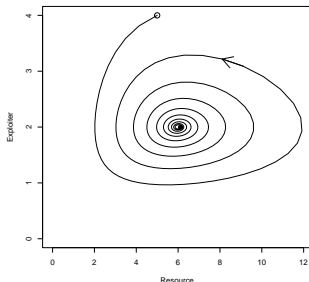
# Predator density dependence

- ▶ 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



# Predator density dependence

- ▶ 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



# Predator satiation

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

# Predator satiation

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



# Predator satiation

- ▶ 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

# Predator satiation

- ▶ 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
  - ▶ \*



# Predator satiation

- ▶ 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

# Predator satiation

- ▶ 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
  - ▶ \*

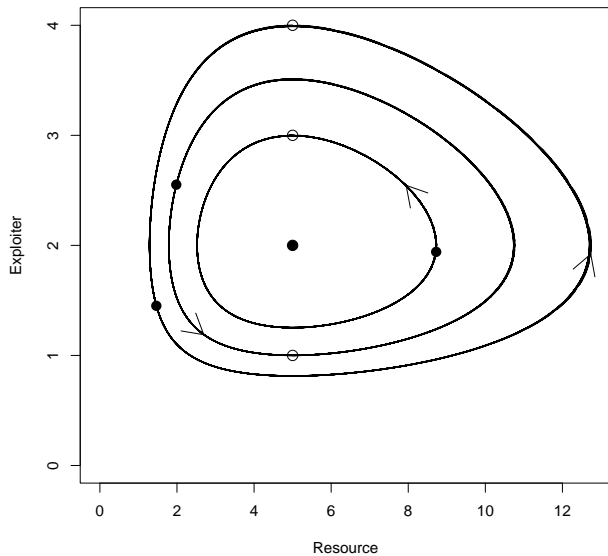
# Predator satiation

- ▶ 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
  - ▶ \* Without density dependence, makes cycles get bigger forever (oscillations increase to  $\infty$ )

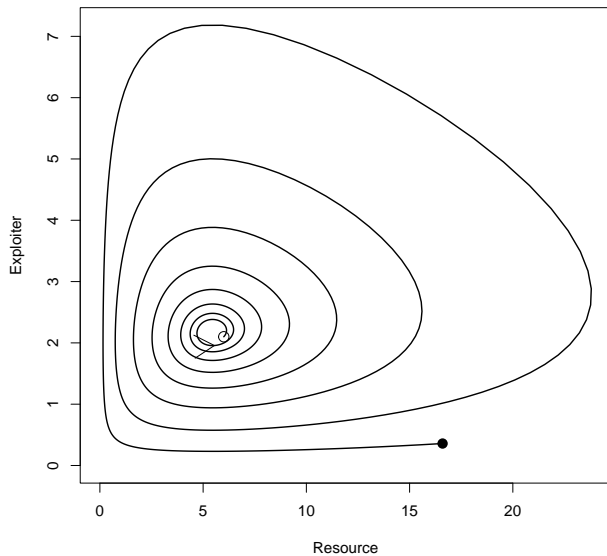
# Predator satiation

- ▶ 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
  - ▶ \* Without density dependence, makes cycles get bigger forever (oscillations increase to  $\infty$ )

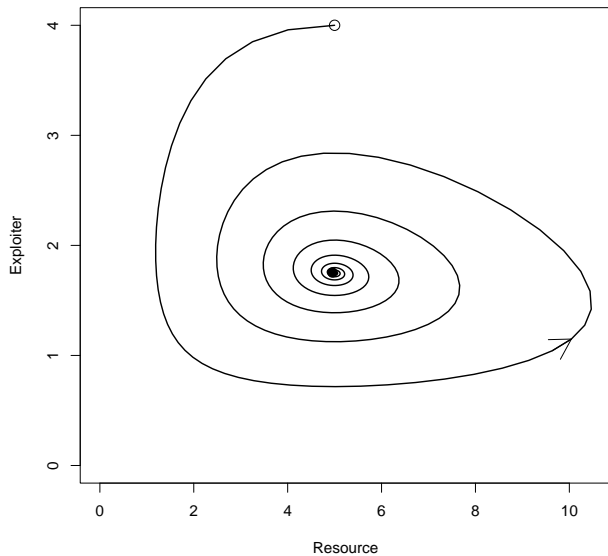
# Neutral cycles



# Predator satiation



# Prey density dependence



# Satiation with prey density dependence

- ▶ What sort of oscillations do we expect?



# Satiation with prey density dependence

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

# Satiation with prey density dependence

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

# Satiation with prey density dependence

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

# Satiation with prey density dependence

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

# Satiation with prey density dependence

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

# Satiation with prey density dependence

- ▶ 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

# Satiation with prey density dependence

- ▶ 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
    - ▶ \*

# Satiation with prey density dependence

- ▶ 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



# Satiation with prey density dependence

- ▶ 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
    - ▶ \*

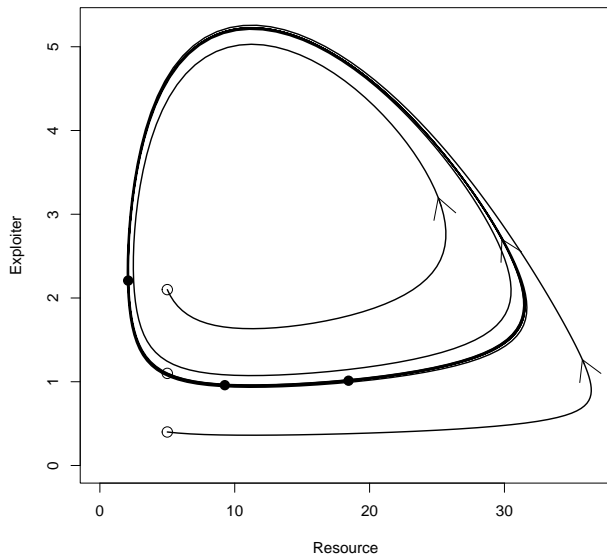
# Satiation with prey density dependence

- ▶ 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

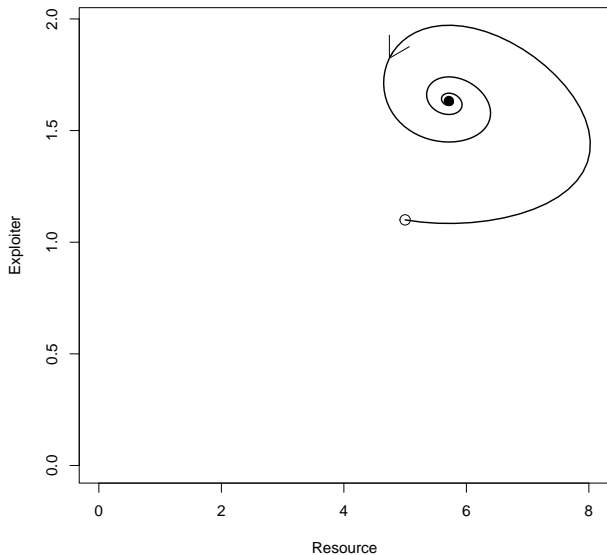
# Satiation with prey density dependence

- ▶ 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

# Density dependence plus predator satiation



# Density dependence plus weak predator satiation



# Oscillation summary

- ▶ *Neutral* cycles repeat from any starting point

# Oscillation summary

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

# Oscillation summary

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



# Oscillation summary

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

# Oscillation summary

- ▶ *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

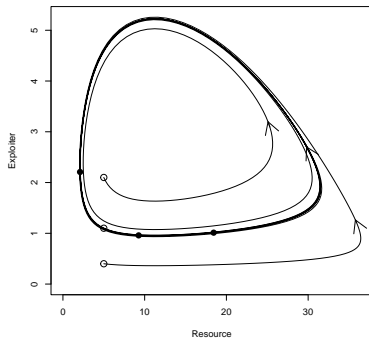
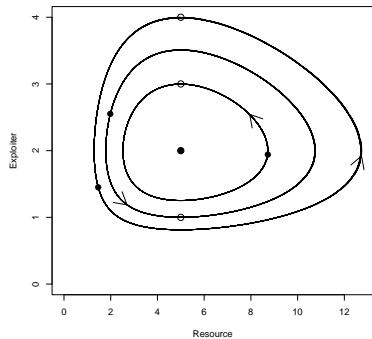
# Oscillation summary

- ▶ *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

# Oscillation summary

- ▶ *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 vs. limit cycles (repeat)



# Oscillations in a complex system

- ▶ All resource-exploiter systems have a tendency to oscillate

# Oscillations in a complex system

- ▶ 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

# Oscillations in a complex system

- ▶ 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



# Oscillations in a complex system

- ▶ 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

# Oscillations in a complex system

- ▶ 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

# Oscillations in a complex system

- ▶ 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

# Real-world implications

- ▶ 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)

# Real-world implications

- ▶ 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

# Real-world implications

- ▶ 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

# Real-world implications

- ▶ 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?



# Prey density dependence

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

# Prey density dependence

- ▶ Imagine that the resource species has a negative effect on its own growth rate

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

# Prey density dependence

- ▶ Imagine that the resource species has a negative effect on its own growth rate

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

- ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$

# Prey density dependence

- ▶ Imagine that the resource species has a negative effect on its own growth rate
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$
- ▶ What happens to the equilibrium if we start catching fish?

# Prey density dependence

- ▶ Imagine that the resource species has a negative effect on its own growth rate

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

- ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$

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



# Prey density dependence

- ▶ Imagine that the resource species has a negative effect on its own growth rate
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$
- ▶ What happens to the equilibrium if we start catching fish?
  - ▶ \*  $r_e$  doesn't change, so  $N_f$  can't change

# Prey density dependence

- ▶ Imagine that the resource species has a negative effect on its own growth rate
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$
- ▶ What happens to the equilibrium if we start catching fish?
  - ▶ \*  $r_e$  doesn't change, so  $N_f$  can't change
  - ▶ \*

# Prey density dependence

- ▶ Imagine that the resource species has a negative effect on its own growth rate
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$
- ▶ What happens to the equilibrium if we start catching fish?
  - ▶ \*  $r_e$  doesn't change, so  $N_f$  can't change
  - ▶ \*  $r_f$  goes down and must be balanced by less sharks



# Prey density dependence

- ▶ Imagine that the resource species has a negative effect on its own growth rate
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$
- ▶ What happens to the equilibrium if we start catching fish?
  - ▶ \*  $r_e$  doesn't change, so  $N_f$  can't change
  - ▶ \*  $r_f$  goes down and must be balanced by less sharks
- ▶ What if we start catching sharks?

# Prey density dependence

- ▶ Imagine that the resource species has a negative effect on its own growth rate
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$
- ▶ What happens to the equilibrium if we start catching fish?
  - ▶ \*  $r_e$  doesn't change, so  $N_f$  can't change
  - ▶ \*  $r_f$  goes down and must be balanced by less sharks
- ▶ What if we start catching sharks?
  - ▶ \*

# Prey density dependence

- ▶ Imagine that the resource species has a negative effect on its own growth rate
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$
- ▶ What happens to the equilibrium if we start catching fish?
  - ▶ \*  $r_e$  doesn't change, so  $N_f$  can't change
  - ▶ \*  $r_f$  goes down and must be balanced by less sharks
- ▶ What if we start catching sharks?
  - ▶ \*  $r_e$  goes down, so  $N_f$  must go up

# Prey density dependence

- ▶ Imagine that the resource species has a negative effect on its own growth rate
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$
- ▶ What happens to the equilibrium if we start catching fish?
  - ▶ \*  $r_e$  doesn't change, so  $N_f$  can't change
  - ▶ \*  $r_f$  goes down and must be balanced by less sharks
- ▶ What if we start catching sharks?
  - ▶ \*  $r_e$  goes down, so  $N_f$  must go up
  - ▶ \*

# Prey density dependence

- ▶ Imagine that the resource species has a negative effect on its own growth rate
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$
- ▶ What happens to the equilibrium if we start catching fish?
  - ▶ \*  $r_e$  doesn't change, so  $N_f$  can't change
  - ▶ \*  $r_f$  goes down and must be balanced by less sharks
- ▶ What if we start catching sharks?
  - ▶ \*  $r_e$  goes down, so  $N_f$  must go up
  - ▶ \* Increasing  $N_f$  decreases  $r_f$ , so  $N_e$  must go down

# Prey density dependence

- ▶ Imagine that the resource species has a negative effect on its own growth rate
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$
- ▶ What happens to the equilibrium if we start catching fish?
  - ▶ \*  $r_e$  doesn't change, so  $N_f$  can't change
  - ▶ \*  $r_f$  goes down and must be balanced by less sharks
- ▶ What if we start catching sharks?
  - ▶ \*  $r_e$  goes down, so  $N_f$  must go up
  - ▶ \* Increasing  $N_f$  decreases  $r_f$ , so  $N_e$  must go down

# Predator satiation

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

# Predator satiation

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

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



# Predator satiation

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

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

- ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$

# Predator satiation

- ▶ What if we also consider “satiation” – there is some limit to how much a predator can catch (or eat)
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$
- ▶ What happens to the equilibrium if we start catching fish?

# Predator satiation

- ▶ What if we also consider “satiation” – there is some limit to how much a predator can catch (or eat)
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$
- ▶ What happens to the equilibrium if we start catching fish?
  - ▶ \*

# Predator satiation

- ▶ What if we also consider “satiation” – there is some limit to how much a predator can catch (or eat)
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$
- ▶ What happens to the equilibrium if we start catching fish?
  - ▶ \*  $r_e$  doesn't change, so  $N_f$  can't change

# Predator satiation

- ▶ What if we also consider “satiation” – there is some limit to how much a predator can catch (or eat)
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$
- ▶ What happens to the equilibrium if we start catching fish?
  - ▶ \*  $r_e$  doesn't change, so  $N_f$  can't change
  - ▶ \*

# Predator satiation

- ▶ What if we also consider “satiation” – there is some limit to how much a predator can catch (or eat)
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$
- ▶ What happens to the equilibrium if we start catching fish?
  - ▶ \*  $r_e$  doesn't change, so  $N_f$  can't change
  - ▶ \*  $r_f$  goes down and must be balanced by less sharks

# Predator satiation

- ▶ What if we also consider “satiation” – there is some limit to how much a predator can catch (or eat)
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$
- ▶ What happens to the equilibrium if we start catching fish?
  - ▶ \*  $r_e$  doesn't change, so  $N_f$  can't change
  - ▶ \*  $r_f$  goes down and must be balanced by less sharks
- ▶ What if we start catching sharks?

# Predator satiation

- ▶ What if we also consider “satiation” – there is some limit to how much a predator can catch (or eat)
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$
- ▶ What happens to the equilibrium if we start catching fish?
  - ▶ \*  $r_e$  doesn't change, so  $N_f$  can't change
  - ▶ \*  $r_f$  goes down and must be balanced by less sharks
- ▶ What if we start catching sharks?
  - ▶ \*



# Predator satiation

- ▶ What if we also consider “satiation” – there is some limit to how much a predator can catch (or eat)
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$
- ▶ What happens to the equilibrium if we start catching fish?
  - ▶ \*  $r_e$  doesn't change, so  $N_f$  can't change
  - ▶ \*  $r_f$  goes down and must be balanced by less sharks
- ▶ What if we start catching sharks?
  - ▶ \*  $r_e$  goes down, so  $N_f$  must go up

# Predator satiation

- ▶ What if we also consider “satiation” – there is some limit to how much a predator can catch (or eat)
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$
- ▶ What happens to the equilibrium if we start catching fish?
  - ▶ \*  $r_e$  doesn't change, so  $N_f$  can't change
  - ▶ \*  $r_f$  goes down and must be balanced by less sharks
- ▶ What if we start catching sharks?
  - ▶ \*  $r_e$  goes down, so  $N_f$  must go up
  - ▶ \*

# Predator satiation

- ▶ What if we also consider “satiation” – there is some limit to how much a predator can catch (or eat)
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$
- ▶ What happens to the equilibrium if we start catching fish?
  - ▶ \*  $r_e$  doesn't change, so  $N_f$  can't change
  - ▶ \*  $r_f$  goes down and must be balanced by less sharks
- ▶ What if we start catching sharks?
  - ▶ \*  $r_e$  goes down, so  $N_f$  must go up
  - ▶ \* Satiation: More fish means higher  $r_f$  means more sharks at equilibrium!

# Predator satiation

- ▶ What if we also consider “satiation” – there is some limit to how much a predator can catch (or eat)
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$
- ▶ What happens to the equilibrium if we start catching fish?
  - ▶ \*  $r_e$  doesn't change, so  $N_f$  can't change
  - ▶ \*  $r_f$  goes down and must be balanced by less sharks
- ▶ What if we start catching sharks?
  - ▶ \*  $r_e$  goes down, so  $N_f$  must go up
  - ▶ \* Satiation: More fish means higher  $r_f$  means more sharks at equilibrium!
  - ▶ \*

# Predator satiation

- ▶ What if we also consider “satiation” – there is some limit to how much a predator can catch (or eat)
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$
- ▶ What happens to the equilibrium if we start catching fish?
  - ▶ \*  $r_e$  doesn't change, so  $N_f$  can't change
  - ▶ \*  $r_f$  goes down and must be balanced by less sharks
- ▶ What if we start catching sharks?
  - ▶ \*  $r_e$  goes down, so  $N_f$  must go up
  - ▶ \* Satiation: More fish means higher  $r_f$  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.

# Predator satiation

- ▶ What if we also consider “satiation” – there is some limit to how much a predator can catch (or eat)
  - ▶  $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - ▶  $\frac{dN_e}{dt} = r_e(N_f)N_e$
- ▶ What happens to the equilibrium if we start catching fish?
  - ▶ \*  $r_e$  doesn't change, so  $N_f$  can't change
  - ▶ \*  $r_f$  goes down and must be balanced by less sharks
- ▶ What if we start catching sharks?
  - ▶ \*  $r_e$  goes down, so  $N_f$  must go up
  - ▶ \* Satiation: More fish means higher  $r_f$  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.

# Examples

- ▶ Is reciprocal control realistic?

# Examples

- ▶ 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?



# Examples

- ▶ 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?
- ▶ What happens *first* in this model if I start feeding grouse?

# Examples

- ▶ 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?
- ▶ What happens *first* in this model if I start feeding grouse?
  - ▶ \*

# Examples

- ▶ 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?
- ▶ What happens *first* in this model if I start feeding grouse?
  - ▶ \* First we get more grouse ...

# Examples

- ▶ 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?
- ▶ What happens *first* in this model if I start feeding grouse?
  - ▶ \* First we get more grouse ...
  - ▶ \*

# Examples

- ▶ 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?
- ▶ 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, ...

# Examples

- ▶ 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?
- ▶ 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, ...
- ▶ What happens *eventually* in this model if I start feeding grouse?

# Examples

- ▶ 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?
- ▶ 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, ...
- ▶ What happens *eventually* in this model if I start feeding grouse?
  - ▶ \*

# Examples

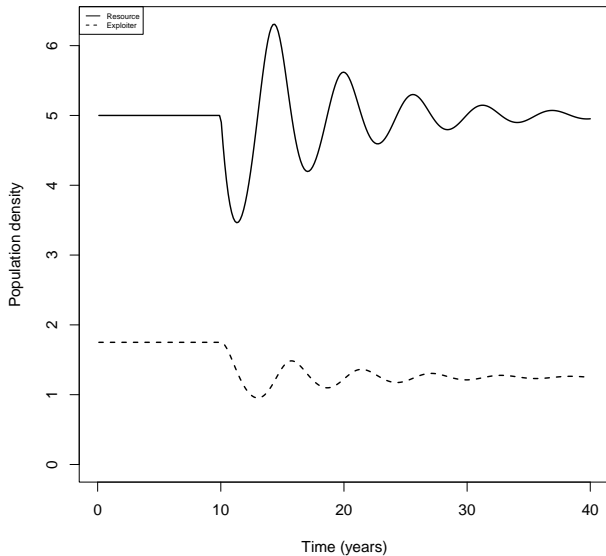
- ▶ Is reciprocal control realistic?
  - ▶ In the long term, catching fish isn't bad for fish populations?  
Feeding grouse doesn't improve long-term grouse populations?
- ▶ What happens *first* in this model if I start feeding grouse?
  - ▶ \* First we get more grouse ...
  - ▶ \* then we get more foxes,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



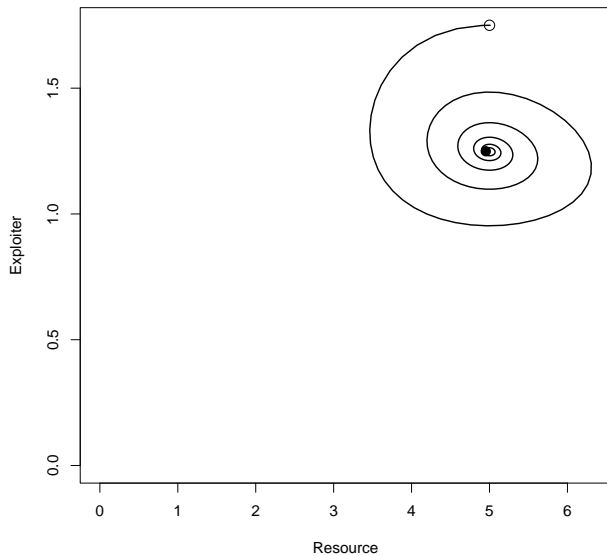
# Examples

- ▶ 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?
- ▶ 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, ...
- ▶ 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

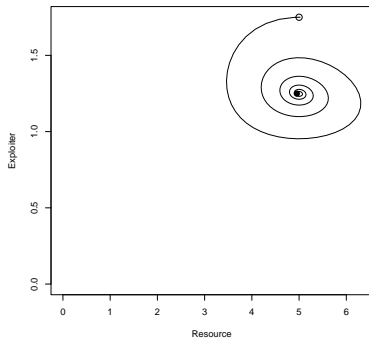
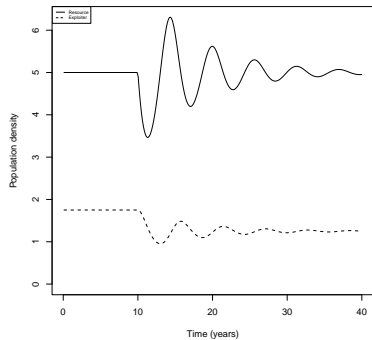
# Harvesting dynamics



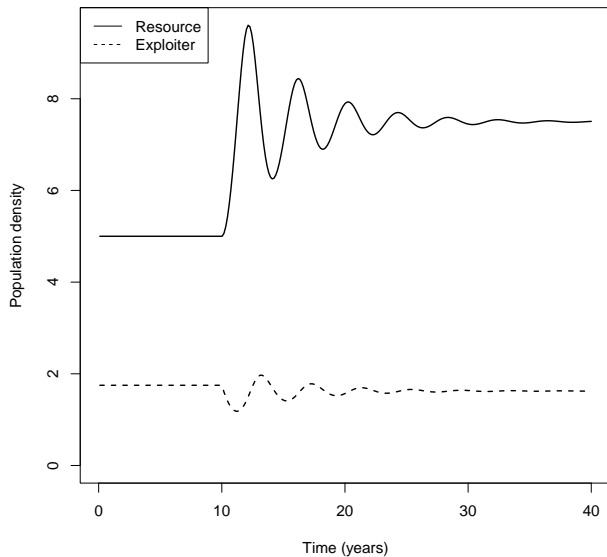
# Harvesting dynamics



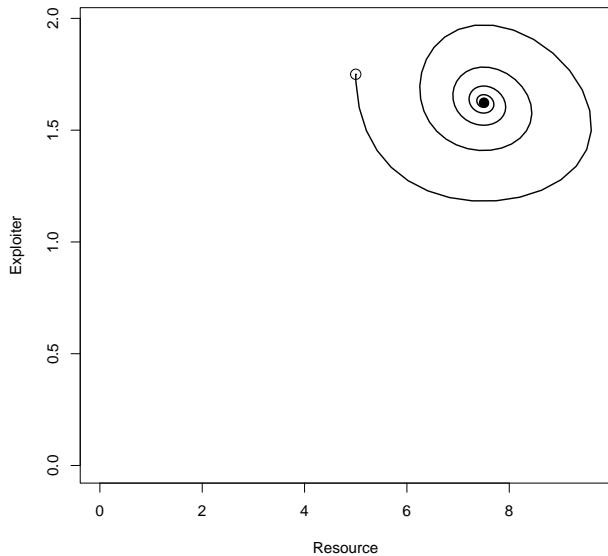
# Harvesting dynamics



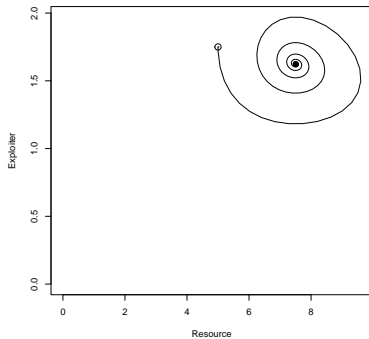
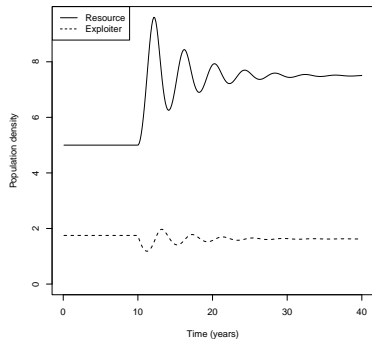
# Harvesting dynamics



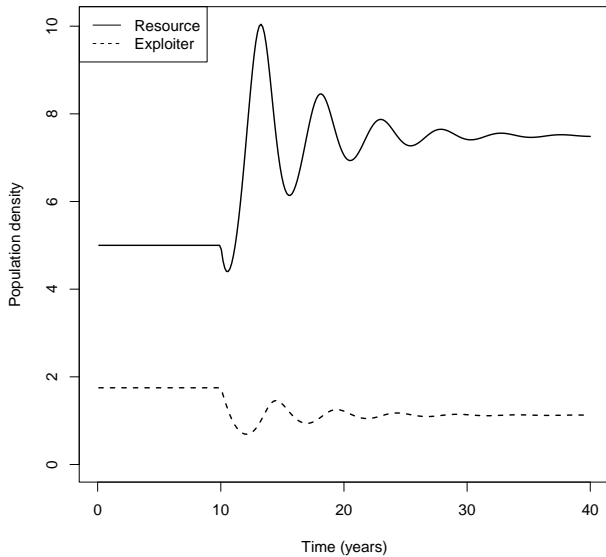
# Harvesting dynamics



# Harvesting dynamics

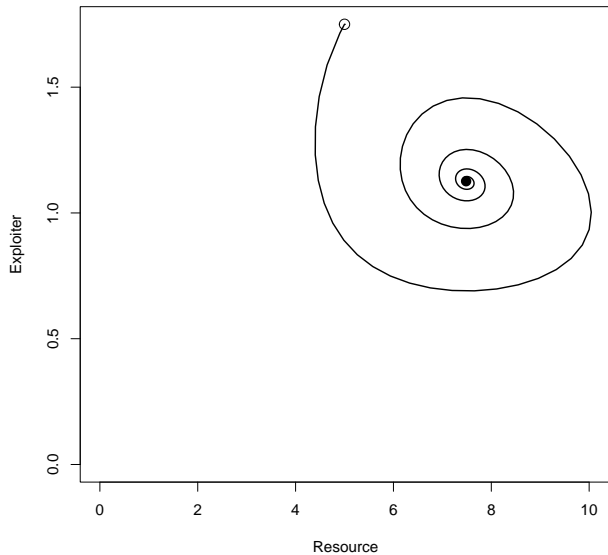


# Harvesting dynamics

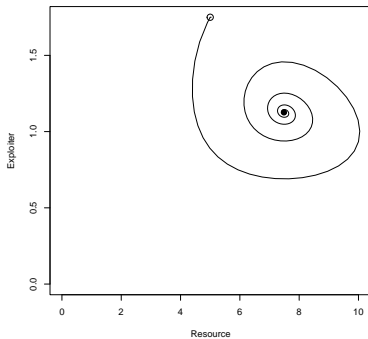
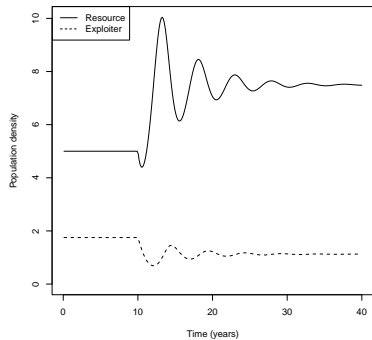




# Harvesting dynamics



# Harvesting dynamics



# Outline

## Introduction

- Balance and equilibrium
- Tendency to oscillate

## A simple model

- More detailed models
- Reciprocal control

## Adding details

- Dynamics
- Equilibria

## Who controls whom?

# Who controls whom?

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

# Who controls whom?

- ▶ 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?

# Who controls whom?

- ▶ 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?

# Who controls whom?

- ▶ 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

# Who controls whom?

- ▶ 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



# Who controls whom?

- ▶ 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?

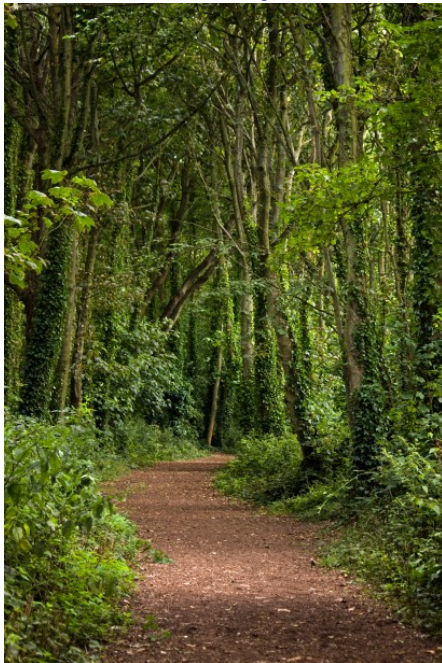
# Who controls whom?

- ▶ 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

# Who controls whom?

- ▶ 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

# What controls ecosystem-level balance?



# What controls ecosystem-level balance?

- ▶ Why is the earth green and the ocean blue?

# What controls ecosystem-level balance?

- ▶ Why is the earth green and the ocean blue?



# What controls ecosystem-level balance?

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

# What controls ecosystem-level balance?

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



# What controls ecosystem-level balance?

- ▶ 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?

# What controls ecosystem-level balance?

- ▶ 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?

# What controls ecosystem-level balance?

- ▶ 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

# What controls ecosystem-level balance?

- ▶ 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

# What controls ecosystem-level balance?

- ▶ 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

# What controls ecosystem-level balance?

- ▶ 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

# What controls ecosystem-level balance?

