

# UNIT 5: Life history

# Outline

Introduction

Tradeoffs

The  $r$  vs.  $K$  metaphor

Bet hedging

Sex ratios

# Introduction

- ▶ **Life history** refers to patterns of how organisms allocate resources to key components underlying reproductive success:

# Introduction

- ▶ **Life history** refers to patterns of how organisms allocate resources to key components underlying reproductive success:
- ▶ Poll: Give a one-word example of a fundamental component of success

# Introduction

- ▶ **Life history** refers to patterns of how organisms allocate resources to key components underlying reproductive success:
- ▶ Poll: Give a one-word example of a fundamental component of success
  - ▶ \*

# Introduction

- ▶ **Life history** refers to patterns of how organisms allocate resources to key components underlying reproductive success:
- ▶ Poll: Give a one-word example of a fundamental component of success
  - ▶ \* Survival

# Introduction

- ▶ **Life history** refers to patterns of how organisms allocate resources to key components underlying reproductive success:
- ▶ Poll: Give a one-word example of a fundamental component of success
  - ▶ \* Survival
  - ▶ \*

# Introduction

- ▶ **Life history** refers to patterns of how organisms allocate resources to key components underlying reproductive success:
- ▶ Poll: Give a one-word example of a fundamental component of success
  - ▶ \* Survival
  - ▶ \* Growth

# Introduction

- ▶ **Life history** refers to patterns of how organisms allocate resources to key components underlying reproductive success:
- ▶ Poll: Give a one-word example of a fundamental component of success
  - ▶ \* Survival
  - ▶ \* Growth
  - ▶ \*

# Introduction

- ▶ **Life history** refers to patterns of how organisms allocate resources to key components underlying reproductive success:
- ▶ Poll: Give a one-word example of a fundamental component of success
  - ▶ \* Survival
  - ▶ \* Growth
  - ▶ \* Reproduction

# Introduction

- ▶ **Life history** refers to patterns of how organisms allocate resources to key components underlying reproductive success:
- ▶ Poll: Give a one-word example of a fundamental component of success
  - ▶ \* Survival
  - ▶ \* Growth
  - ▶ \* Reproduction
  - ▶ \*

# Introduction

- ▶ **Life history** refers to patterns of how organisms allocate resources to key components underlying reproductive success:
- ▶ Poll: Give a one-word example of a fundamental component of success
  - ▶ \* Survival
  - ▶ \* Growth
  - ▶ \* Reproduction
  - ▶ \* Dispersal

# Introduction

- ▶ **Life history** refers to patterns of how organisms allocate resources to key components underlying reproductive success:
- ▶ Poll: Give a one-word example of a fundamental component of success
  - ▶ \* Survival
  - ▶ \* Growth
  - ▶ \* Reproduction
  - ▶ \* Dispersal

# Diversity

- Differing life-history **strategies** are part of the reason for the remarkable diversity of life

# Diversity

- ▶ Differing life-history **strategies** are part of the reason for the remarkable diversity of life
  - ▶ Organisms that are too similar are not expected to co-exist

# Diversity

- ▶ Differing life-history **strategies** are part of the reason for the remarkable diversity of life
  - ▶ Organisms that are too similar are not expected to co-exist
    - ▶ One will out-compete the other

# Diversity

- ▶ Differing life-history **strategies** are part of the reason for the remarkable diversity of life
  - ▶ Organisms that are too similar are not expected to co-exist
    - ▶ One will out-compete the other
  - ▶ But two organisms may be able to exploit the same resources using different life-history strategies

# Diversity

- ▶ Differing life-history **strategies** are part of the reason for the remarkable diversity of life
  - ▶ Organisms that are too similar are not expected to co-exist
    - ▶ One will out-compete the other
  - ▶ But two organisms may be able to exploit the same resources using different life-history strategies

# Oaks and dandelions



# Oaks and dandelions

- We can think of acorns as machines for making more acorns, and dandelion seeds as machines for making more dandelion seeds

## Oaks and dandelions

- ▶ We can think of acorns as machines for making more acorns, and dandelion seeds as machines for making more dandelion seeds
- ▶ Both have access to very similar biochemical machinery. Both use the same resources.

## Oaks and dandelions

- ▶ We can think of acorns as machines for making more acorns, and dandelion seeds as machines for making more dandelion seeds
- ▶ Both have access to very similar biochemical machinery. Both use the same resources.
  - ▶ \*

## Oaks and dandelions

- ▶ We can think of acorns as machines for making more acorns, and dandelion seeds as machines for making more dandelion seeds
- ▶ Both have access to very similar biochemical machinery. Both use the same resources.
  - ▶ \* Water, sunlight, nutrients

## Oaks and dandelions

- ▶ We can think of acorns as machines for making more acorns, and dandelion seeds as machines for making more dandelion seeds
- ▶ Both have access to very similar biochemical machinery. Both use the same resources.
  - ▶ \* Water, sunlight, nutrients
- ▶ Poll: What are some differences?

## Oaks and dandelions

- ▶ We can think of acorns as machines for making more acorns, and dandelion seeds as machines for making more dandelion seeds
- ▶ Both have access to very similar biochemical machinery. Both use the same resources.
  - ▶ \* Water, sunlight, nutrients
- ▶ Poll: What are some differences?
  - ▶ \*

## Oaks and dandelions

- ▶ We can think of acorns as machines for making more acorns, and dandelion seeds as machines for making more dandelion seeds
- ▶ Both have access to very similar biochemical machinery. Both use the same resources.
  - ▶ \* Water, sunlight, nutrients
- ▶ Poll: What are some differences?
  - ▶ \* Oak trees are bigger

# Oaks and dandelions

- ▶ We can think of acorns as machines for making more acorns, and dandelion seeds as machines for making more dandelion seeds
- ▶ Both have access to very similar biochemical machinery. Both use the same resources.
  - ▶ \* Water, sunlight, nutrients
- ▶ Poll: What are some differences?
  - ▶ \* Oak trees are bigger
  - ▶ \*

# Oaks and dandelions

- ▶ We can think of acorns as machines for making more acorns, and dandelion seeds as machines for making more dandelion seeds
- ▶ Both have access to very similar biochemical machinery. Both use the same resources.
  - ▶ \* Water, sunlight, nutrients
- ▶ Poll: What are some differences?
  - ▶ \* Oak trees are bigger
  - ▶ \* Oak trees wait longer to reproduce

# Oaks and dandelions

- ▶ We can think of acorns as machines for making more acorns, and dandelion seeds as machines for making more dandelion seeds
- ▶ Both have access to very similar biochemical machinery. Both use the same resources.
  - ▶ \* Water, sunlight, nutrients
- ▶ Poll: What are some differences?
  - ▶ \* Oak trees are bigger
  - ▶ \* Oak trees wait longer to reproduce
  - ▶ \*

# Oaks and dandelions

- ▶ We can think of acorns as machines for making more acorns, and dandelion seeds as machines for making more dandelion seeds
- ▶ Both have access to very similar biochemical machinery. Both use the same resources.
  - ▶ \* Water, sunlight, nutrients
- ▶ Poll: What are some differences?
  - ▶ \* Oak trees are bigger
  - ▶ \* Oak trees wait longer to reproduce
  - ▶ \* Oak trees reproduce many times

# Oaks and dandelions

- ▶ We can think of acorns as machines for making more acorns, and dandelion seeds as machines for making more dandelion seeds
- ▶ Both have access to very similar biochemical machinery. Both use the same resources.
  - ▶ \* Water, sunlight, nutrients
- ▶ Poll: What are some differences?
  - ▶ \* Oak trees are bigger
  - ▶ \* Oak trees wait longer to reproduce
  - ▶ \* Oak trees reproduce many times
  - ▶ \*

# Oaks and dandelions

- ▶ We can think of acorns as machines for making more acorns, and dandelion seeds as machines for making more dandelion seeds
- ▶ Both have access to very similar biochemical machinery. Both use the same resources.
  - ▶ \* Water, sunlight, nutrients
- ▶ Poll: What are some differences?
  - ▶ \* Oak trees are bigger
  - ▶ \* Oak trees wait longer to reproduce
  - ▶ \* Oak trees reproduce many times
  - ▶ \* Oak trees put much more energy into each seed

# Oaks and dandelions

- ▶ We can think of acorns as machines for making more acorns, and dandelion seeds as machines for making more dandelion seeds
- ▶ Both have access to very similar biochemical machinery. Both use the same resources.
  - ▶ \* Water, sunlight, nutrients
- ▶ Poll: What are some differences?
  - ▶ \* Oak trees are bigger
  - ▶ \* Oak trees wait longer to reproduce
  - ▶ \* Oak trees reproduce many times
  - ▶ \* Oak trees put much more energy into each seed
  - ▶ \*

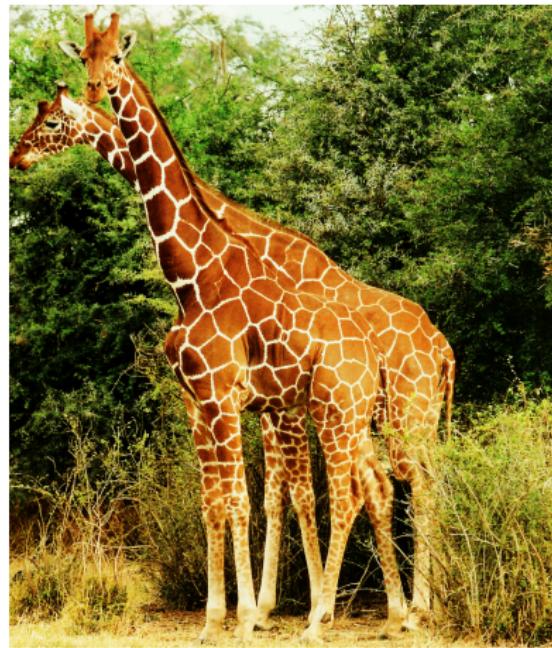
## Oaks and dandelions

- ▶ We can think of acorns as machines for making more acorns, and dandelion seeds as machines for making more dandelion seeds
- ▶ Both have access to very similar biochemical machinery. Both use the same resources.
  - ▶ \* Water, sunlight, nutrients
- ▶ Poll: What are some differences?
  - ▶ \* Oak trees are bigger
  - ▶ \* Oak trees wait longer to reproduce
  - ▶ \* Oak trees reproduce many times
  - ▶ \* Oak trees put much more energy into each seed
  - ▶ \* Dandelion seeds are dispersed by wind, acorns by animals

## Oaks and dandelions

- ▶ We can think of acorns as machines for making more acorns, and dandelion seeds as machines for making more dandelion seeds
- ▶ Both have access to very similar biochemical machinery. Both use the same resources.
  - ▶ \* Water, sunlight, nutrients
- ▶ Poll: What are some differences?
  - ▶ \* Oak trees are bigger
  - ▶ \* Oak trees wait longer to reproduce
  - ▶ \* Oak trees reproduce many times
  - ▶ \* Oak trees put much more energy into each seed
  - ▶ \* Dandelion seeds are dispersed by wind, acorns by animals

# Strategies



## Scales of competition

- ▶ Organisms compete with other individuals of the same species

## Scales of competition

- ▶ Organisms compete with other individuals of the same species
- ▶ They also compete with other species

## Scales of competition

- ▶ Organisms compete with other individuals of the same species
- ▶ They also compete with other species
- ▶ We think about life history on different scales

## Scales of competition

- ▶ Organisms compete with other individuals of the same species
- ▶ They also compete with other species
- ▶ We think about life history on different scales
  - ▶ Evolution within populations

## Scales of competition

- ▶ Organisms compete with other individuals of the same species
- ▶ They also compete with other species
- ▶ We think about life history on different scales
  - ▶ Evolution within populations
  - ▶ Competition between populations

## Scales of competition

- ▶ Organisms compete with other individuals of the same species
- ▶ They also compete with other species
- ▶ We think about life history on different scales
  - ▶ Evolution within populations
  - ▶ Competition between populations

## Within species



# Between populations



# Outline

Introduction

Tradeoffs

The  $r$  vs.  $K$  metaphor

Bet hedging

Sex ratios

# Tradeoffs

- ▶ Some evolutionary changes simply help organisms function better

# Tradeoffs

- ▶ Some evolutionary changes simply help organisms function better
  - ▶ Hemoglobin is highly evolved to bind and release oxygen

# Tradeoffs

- ▶ Some evolutionary changes simply help organisms function better
  - ▶ Hemoglobin is highly evolved to bind and release oxygen
- ▶ Most have advantages and disadvantages

# Tradeoffs

- ▶ Some evolutionary changes simply help organisms function better
  - ▶ Hemoglobin is highly evolved to bind and release oxygen
- ▶ Most have advantages and disadvantages
  - ▶ Building a strong immune system may reduce growth rates

# Tradeoffs

- ▶ Some evolutionary changes simply help organisms function better
  - ▶ Hemoglobin is highly evolved to bind and release oxygen
- ▶ Most have advantages and disadvantages
  - ▶ Building a strong immune system may reduce growth rates
  - ▶ A leaf that produces a lot of energy at high light may not be able to produce any at low light

# Tradeoffs

- ▶ Some evolutionary changes simply help organisms function better
  - ▶ Hemoglobin is highly evolved to bind and release oxygen
- ▶ Most have advantages and disadvantages
  - ▶ Building a strong immune system may reduce growth rates
  - ▶ A leaf that produces a lot of energy at high light may not be able to produce any at low light
- ▶ A **tradeoff** occurs when improvements in one area come at a cost of disadvantages in another area

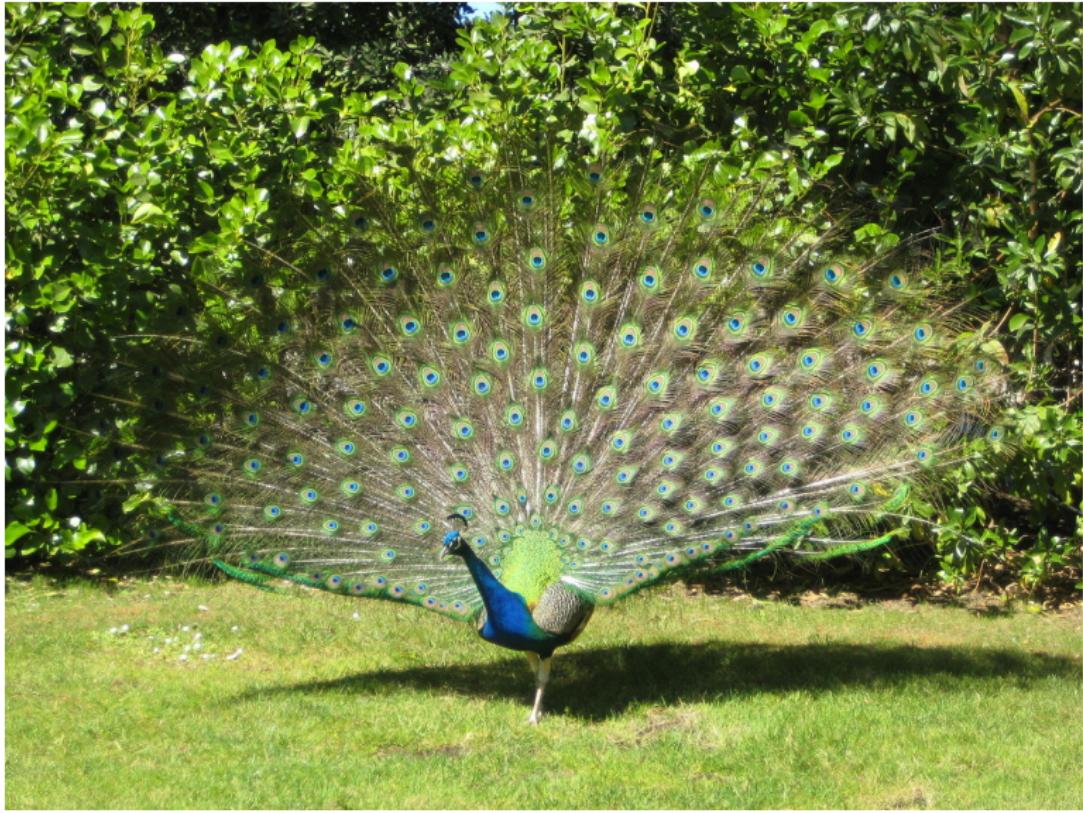
# Tradeoffs

- ▶ Some evolutionary changes simply help organisms function better
  - ▶ Hemoglobin is highly evolved to bind and release oxygen
- ▶ Most have advantages and disadvantages
  - ▶ Building a strong immune system may reduce growth rates
  - ▶ A leaf that produces a lot of energy at high light may not be able to produce any at low light
- ▶ A **tradeoff** occurs when improvements in one area come at a cost of disadvantages in another area

# Tradeoffs



# Tradeoffs



# Optimization frontiers

- We expect tradeoffs because:

# Optimization frontiers

- ▶ We expect tradeoffs because:
  - ▶ organisms have limited **resources**

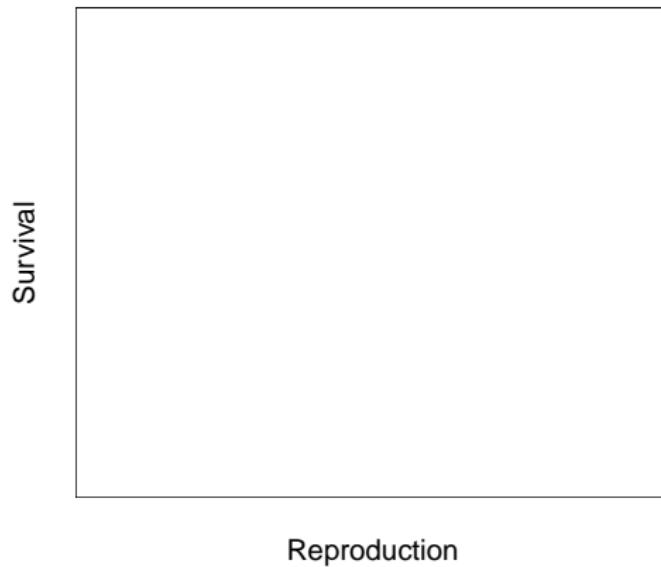
# Optimization frontiers

- ▶ We expect tradeoffs because:
  - ▶ organisms have limited **resources**
  - ▶ organisms are under natural selection in a complex world

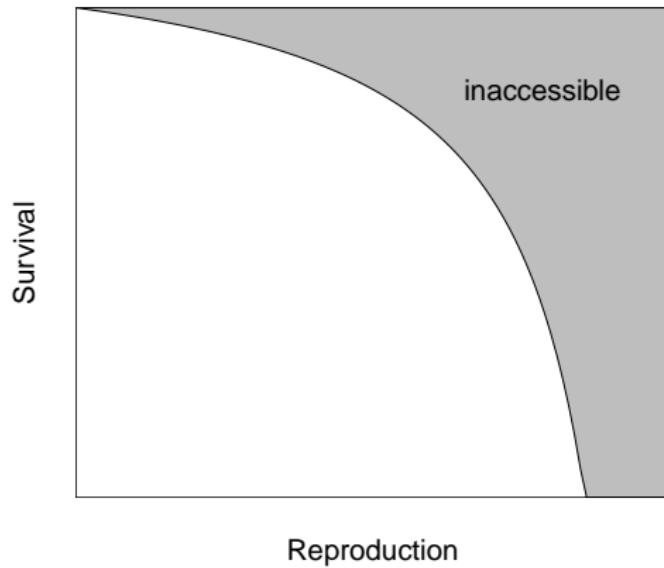
# Optimization frontiers

- ▶ We expect tradeoffs because:
  - ▶ organisms have limited **resources**
  - ▶ organisms are under natural selection in a complex world

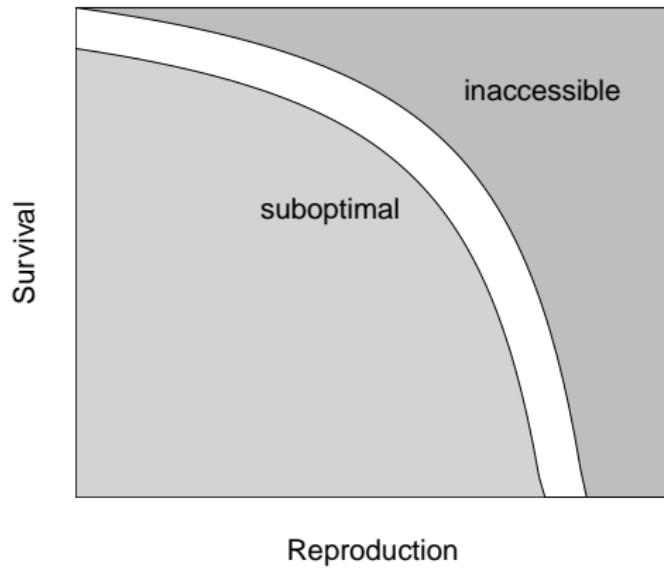
# Optimization frontiers



# Optimization frontiers

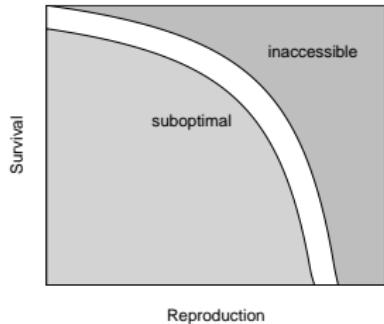


# Optimization frontiers



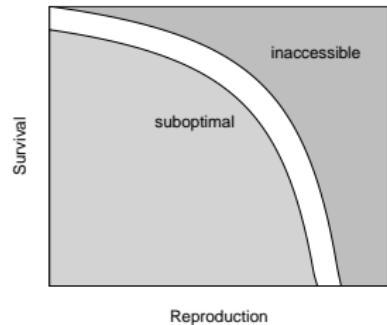
# Optimization frontiers

- ▶ Under natural selection, we expect organisms to be near the frontier of high fitness



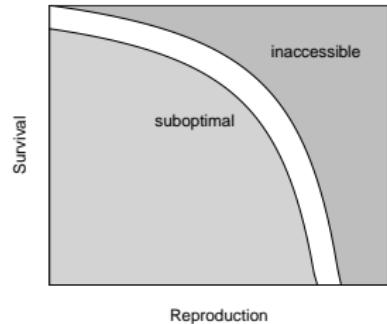
# Optimization frontiers

- ▶ Under natural selection, we expect organisms to be near the frontier of high fitness
- ▶ While they're near this frontier, it will be hard to improve one quality without a tradeoff that hurts another quality



# Optimization frontiers

- ▶ Under natural selection, we expect organisms to be near the frontier of high fitness
- ▶ While they're near this frontier, it will be hard to improve one quality without a tradeoff that hurts another quality



# Evolution and optimization

- We often think of organisms as making “choices” that maximize their evolutionary fitness.

## Evolution and optimization

- ▶ We often think of organisms as making “choices” that maximize their evolutionary fitness.
- ▶ Do oaks choose how big their acorns should be?

## Evolution and optimization

- ▶ We often think of organisms as making “choices” that maximize their evolutionary fitness.
- ▶ Do oaks choose how big their acorns should be?
- ▶ Then what's going on?

## Evolution and optimization

- ▶ We often think of organisms as making “choices” that maximize their evolutionary fitness.
- ▶ Do oaks choose how big their acorns should be?
- ▶ Then what's going on?
  - ▶ \*

## Evolution and optimization

- ▶ We often think of organisms as making “choices” that maximize their evolutionary fitness.
- ▶ Do oaks choose how big their acorns should be?
- ▶ Then what's going on?
  - ▶ \* Natural selection is selecting random variants

# Evolution and optimization

- ▶ We often think of organisms as making “choices” that maximize their evolutionary fitness.
- ▶ Do oaks choose how big their acorns should be?
- ▶ Then what's going on?
  - ▶ \* Natural selection is selecting random variants
  - ▶ \*

# Evolution and optimization

- ▶ We often think of organisms as making “choices” that maximize their evolutionary fitness.
- ▶ Do oaks choose how big their acorns should be?
- ▶ Then what's going on?
  - ▶ \* Natural selection is selecting random variants
  - ▶ \* On average, variants which survive are better at producing offspring over the long-term than those which don't survive

# Evolution and optimization

- ▶ We often think of organisms as making “choices” that maximize their evolutionary fitness.
- ▶ Do oaks choose how big their acorns should be?
- ▶ Then what's going on?
  - ▶ \* Natural selection is selecting random variants
  - ▶ \* On average, variants which survive are better at producing offspring over the long-term than those which don't survive

# Programmed optimization

- ▶ Organisms pursue very sophisticated strategies to optimize fitness

# Programmed optimization

- ▶ Organisms pursue very sophisticated strategies to optimize fitness
- ▶ But they don't know they're doing this

# Programmed optimization

- ▶ Organisms pursue very sophisticated strategies to optimize fitness
- ▶ But they don't know they're doing this
  - ▶ Plants sensing water environments

# Programmed optimization

- ▶ Organisms pursue very sophisticated strategies to optimize fitness
- ▶ But they don't know they're doing this
  - ▶ Plants sensing water environments
  - ▶ Moths circling light bulbs

# Programmed optimization

- ▶ Organisms pursue very sophisticated strategies to optimize fitness
- ▶ But they don't know they're doing this
  - ▶ Plants sensing water environments
  - ▶ Moths circling light bulbs
  - ▶ People pursuing sexual opportunities

# Programmed optimization

- ▶ Organisms pursue very sophisticated strategies to optimize fitness
- ▶ But they don't know they're doing this
  - ▶ Plants sensing water environments
  - ▶ Moths circling light bulbs
  - ▶ People pursuing sexual opportunities

# Programmed optimization



# Programmed optimization



## Tradeoff: Quick maturation vs. large final size

- ▶ A key component of a life history is how quickly an organism matures

## Tradeoff: Quick maturation vs. large final size

- ▶ A key component of a life history is how quickly an organism matures
- ▶ Organisms that mature quickly can reproduce quickly

## Tradeoff: Quick maturation vs. large final size

- ▶ A key component of a life history is how quickly an organism matures
- ▶ Organisms that mature quickly can reproduce quickly
- ▶ Organisms that mature slowly have more time to get large, or build lasting structures, before they reproduce

## Tradeoff: Quick maturation vs. large final size

- ▶ A key component of a life history is how quickly an organism matures
- ▶ Organisms that mature quickly can reproduce quickly
- ▶ Organisms that mature slowly have more time to get large, or build lasting structures, before they reproduce
  - ▶ they typically reproduce more (or for a longer time period) in the long run

## Tradeoff: Quick maturation vs. large final size

- ▶ A key component of a life history is how quickly an organism matures
- ▶ Organisms that mature quickly can reproduce quickly
- ▶ Organisms that mature slowly have more time to get large, or build lasting structures, before they reproduce
  - ▶ they typically reproduce more (or for a longer time period) in the long run
  - ▶ or allocate more energy to each offspring, giving the offspring a better chance to be successful

## Tradeoff: Quick maturation vs. large final size

- ▶ A key component of a life history is how quickly an organism matures
- ▶ Organisms that mature quickly can reproduce quickly
- ▶ Organisms that mature slowly have more time to get large, or build lasting structures, before they reproduce
  - ▶ they typically reproduce more (or for a longer time period) in the long run
  - ▶ or allocate more energy to each offspring, giving the offspring a better chance to be successful

## Tradeoff: large reproductive output vs. longevity

- Survival-reproduction balance: at a given time, organisms face a tradeoff between:

## Tradeoff: large reproductive output vs. longevity

- ▶ Survival-reproduction balance: at a given time, organisms face a tradeoff between:
  - ▶ energy spent on producing offspring

# Tradeoff: large reproductive output vs. longevity

- ▶ Survival-reproduction balance: at a given time, organisms face a tradeoff between:
  - ▶ energy spent on producing offspring
    - ▶ produce more offspring, or give more resources to helping each get started in life

## Tradeoff: large reproductive output vs. longevity

- ▶ Survival-reproduction balance: at a given time, organisms face a tradeoff between:
  - ▶ energy spent on producing offspring
    - ▶ produce more offspring, or give more resources to helping each get started in life
  - ▶ energy reserved for survival and future offspring

# Tradeoff: large reproductive output vs. longevity

- ▶ Survival-reproduction balance: at a given time, organisms face a tradeoff between:
  - ▶ energy spent on producing offspring
    - ▶ produce more offspring, or give more resources to helping each get started in life
  - ▶ energy reserved for survival and future offspring
    - ▶ **spend less energy reproducing this year, but live for longer**

## Tradeoff: large reproductive output vs. longevity

- ▶ Survival-reproduction balance: at a given time, organisms face a tradeoff between:
  - ▶ energy spent on producing offspring
    - ▶ produce more offspring, or give more resources to helping each get started in life
  - ▶ energy reserved for survival and future offspring
    - ▶ spend less energy reproducing this year, but live for longer

# Semelparity

- The extreme case of this balance is called **semelparity**: the life-history strategy of reproducing only once

# Semelparity

- ▶ The extreme case of this balance is called **semelparity**: the life-history strategy of reproducing only once
- ▶ Many organisms are semelparous

## Semelparity

- ▶ The extreme case of this balance is called **semelparity**: the life-history strategy of reproducing only once
- ▶ Many organisms are semelparous
  - ▶ We can imagine that converting all your resources to reproduction once you start could be very efficient

## Semelparity

- ▶ The extreme case of this balance is called **semelparity**: the life-history strategy of reproducing only once
- ▶ Many organisms are semelparous
  - ▶ We can imagine that converting all your resources to reproduction once you start could be very efficient
- ▶ Many organisms are **iteroparous**: they reproduce many times

# Semelparity

- ▶ The extreme case of this balance is called **semelparity**: the life-history strategy of reproducing only once
- ▶ Many organisms are semelparous
  - ▶ We can imagine that converting all your resources to reproduction once you start could be very efficient
- ▶ Many organisms are **iteroparous**: they reproduce many times

# Semele



## Cole's paradox



# Cole's paradox

- ▶ Why are many organisms iteroparous?



# Cole's paradox

- ▶ Why are many organisms iteroparous?
- ▶ If  $\lambda = f + p$ , surely it is easier to increase  $f$  by spending on reproduction, than to increase  $p$ , which can never be larger than 1.



# Cole's paradox

- ▶ Why are many organisms iteroparous?
- ▶ If  $\lambda = f + p$ , surely it is easier to increase  $f$  by spending on reproduction, than to increase  $p$ , which can never be larger than 1.
- ▶ Raising  $p$  from 0 to 1 becoming *immortal* instead of annual, is only as good as increasing  $f$  by 1



# Cole's paradox

- ▶ Why are many organisms iteroparous?
- ▶ If  $\lambda = f + p$ , surely it is easier to increase  $f$  by spending on reproduction, than to increase  $p$ , which can never be larger than 1.
- ▶ Raising  $p$  from 0 to 1 becoming *immortal* instead of annual, is only as good as increasing  $f$  by 1



## Responses to Cole

- ▶ What are some reasons why it makes evolutionary sense for organisms to be iteroparous, in light of Cole's arguments?

## Responses to Cole

- ▶ What are some reasons why it makes evolutionary sense for organisms to be iteroparous, in light of Cole's arguments?

▶ \*

## Responses to Cole

- ▶ What are some reasons why it makes evolutionary sense for organisms to be iteroparous, in light of Cole's arguments?
  - ▶ \* “Closing the loop”:  $f$  is not seeds per plant, it's plants per plant; not as high as you think

## Responses to Cole

- ▶ What are some reasons why it makes evolutionary sense for organisms to be iteroparous, in light of Cole's arguments?
  - ▶ \* “Closing the loop”:  $f$  is not seeds per plant, it's plants per plant; not as high as you think
  - ▶ \*

## Responses to Cole

- ▶ What are some reasons why it makes evolutionary sense for organisms to be iteroparous, in light of Cole's arguments?
  - ▶ \* “Closing the loop”:  $f$  is not seeds per plant, it’s plants per plant; not as high as you think
  - ▶ \* Population regulation: the long-term average value of  $\lambda$  is 1, so increasing  $f$  by 1 is a *lot*

## Responses to Cole

- ▶ What are some reasons why it makes evolutionary sense for organisms to be iteroparous, in light of Cole's arguments?
  - ▶ \* “Closing the loop”:  $f$  is not seeds per plant, it’s plants per plant; not as high as you think
  - ▶ \* Population regulation: the long-term average value of  $\lambda$  is 1, so increasing  $f$  by 1 is a *lot*
  - ▶ \*

## Responses to Cole

- ▶ What are some reasons why it makes evolutionary sense for organisms to be iteroparous, in light of Cole's arguments?
  - ▶ \* “Closing the loop”:  $f$  is not seeds per plant, it’s plants per plant; not as high as you think
  - ▶ \* Population regulation: the long-term average value of  $\lambda$  is 1, so increasing  $f$  by 1 is a *lot*
  - ▶ \* Risky environments: long-lived organisms can deal better with variation in offspring success.

## Responses to Cole

- ▶ What are some reasons why it makes evolutionary sense for organisms to be iteroparous, in light of Cole's arguments?
  - ▶ \* “Closing the loop”:  $f$  is not seeds per plant, it’s plants per plant; not as high as you think
  - ▶ \* Population regulation: the long-term average value of  $\lambda$  is 1, so increasing  $f$  by 1 is a *lot*
  - ▶ \* Risky environments: long-lived organisms can deal better with variation in offspring success.

# Responses to Cole



## Tradeoff example: many offspring vs. high-quality offspring

- Apart from how much energy to put into offspring now vs. later, organisms can make many or few offspring, using a given amount of energy

## Tradeoff example: many offspring vs. high-quality offspring

- ▶ Apart from how much energy to put into offspring now vs. later, organisms can make many or few offspring, using a given amount of energy
- ▶ What is a vivid example of ecologically similar organisms that produce wildly different numbers of offspring?

## Tradeoff example: many offspring vs. high-quality offspring

- ▶ Apart from how much energy to put into offspring now vs. later, organisms can make many or few offspring, using a given amount of energy
- ▶ What is a vivid example of ecologically similar organisms that produce wildly different numbers of offspring?
  - ▶ \*

## Tradeoff example: many offspring vs. high-quality offspring

- ▶ Apart from how much energy to put into offspring now vs. later, organisms can make many or few offspring, using a given amount of energy
- ▶ What is a vivid example of ecologically similar organisms that produce wildly different numbers of offspring?
  - ▶ \* Oaks vs. pines

## Tradeoff example: many offspring vs. high-quality offspring

- ▶ Apart from how much energy to put into offspring now vs. later, organisms can make many or few offspring, using a given amount of energy
- ▶ What is a vivid example of ecologically similar organisms that produce wildly different numbers of offspring?
  - ▶ \* Oaks vs. pines
  - ▶ \*

## Tradeoff example: many offspring vs. high-quality offspring

- ▶ Apart from how much energy to put into offspring now vs. later, organisms can make many or few offspring, using a given amount of energy
- ▶ What is a vivid example of ecologically similar organisms that produce wildly different numbers of offspring?
  - ▶ \* Oaks vs. pines
  - ▶ \* Tsetses vs. mosquitoes

## Tradeoff example: many offspring vs. high-quality offspring

- ▶ Apart from how much energy to put into offspring now vs. later, organisms can make many or few offspring, using a given amount of energy
- ▶ What is a vivid example of ecologically similar organisms that produce wildly different numbers of offspring?
  - ▶ \* Oaks vs. pines
  - ▶ \* Tsetses vs. mosquitoes
- ▶ Poll: What are potential advantages of producing fewer offspring with the same amount of energy?

## Tradeoff example: many offspring vs. high-quality offspring

- ▶ Apart from how much energy to put into offspring now vs. later, organisms can make many or few offspring, using a given amount of energy
- ▶ What is a vivid example of ecologically similar organisms that produce wildly different numbers of offspring?
  - ▶ \* Oaks vs. pines
  - ▶ \* Tsetses vs. mosquitoes
- ▶ Poll: What are potential advantages of producing fewer offspring with the same amount of energy?
  - ▶ \*

## Tradeoff example: many offspring vs. high-quality offspring

- ▶ Apart from how much energy to put into offspring now vs. later, organisms can make many or few offspring, using a given amount of energy
- ▶ What is a vivid example of ecologically similar organisms that produce wildly different numbers of offspring?
  - ▶ \* Oaks vs. pines
  - ▶ \* Tsetses vs. mosquitoes
- ▶ Poll: What are potential advantages of producing fewer offspring with the same amount of energy?
  - ▶ \* Greater chance of survival (or reproductive success)

## Tradeoff example: many offspring vs. high-quality offspring

- ▶ Apart from how much energy to put into offspring now vs. later, organisms can make many or few offspring, using a given amount of energy
- ▶ What is a vivid example of ecologically similar organisms that produce wildly different numbers of offspring?
  - ▶ \* Oaks vs. pines
  - ▶ \* Tsetses vs. mosquitoes
- ▶ Poll: What are potential advantages of producing fewer offspring with the same amount of energy?
  - ▶ \* Greater chance of survival (or reproductive success)
  - ▶ \*

## Tradeoff example: many offspring vs. high-quality offspring

- ▶ Apart from how much energy to put into offspring now vs. later, organisms can make many or few offspring, using a given amount of energy
- ▶ What is a vivid example of ecologically similar organisms that produce wildly different numbers of offspring?
  - ▶ \* Oaks vs. pines
  - ▶ \* Tsetses vs. mosquitoes
- ▶ Poll: What are potential advantages of producing fewer offspring with the same amount of energy?
  - ▶ \* Greater chance of survival (or reproductive success)
  - ▶ \* Dispersal

## Tradeoff example: many offspring vs. high-quality offspring

- ▶ Apart from how much energy to put into offspring now vs. later, organisms can make many or few offspring, using a given amount of energy
- ▶ What is a vivid example of ecologically similar organisms that produce wildly different numbers of offspring?
  - ▶ \* Oaks vs. pines
  - ▶ \* Tsetses vs. mosquitoes
- ▶ Poll: What are potential advantages of producing fewer offspring with the same amount of energy?
  - ▶ \* Greater chance of survival (or reproductive success)
  - ▶ \* Dispersal
  - ▶ \*

## Tradeoff example: many offspring vs. high-quality offspring

- ▶ Apart from how much energy to put into offspring now vs. later, organisms can make many or few offspring, using a given amount of energy
- ▶ What is a vivid example of ecologically similar organisms that produce wildly different numbers of offspring?
  - ▶ \* Oaks vs. pines
  - ▶ \* Tsetses vs. mosquitoes
- ▶ Poll: What are potential advantages of producing fewer offspring with the same amount of energy?
  - ▶ \* Greater chance of survival (or reproductive success)
  - ▶ \* Dispersal
  - ▶ \* More energy left over?

## Tradeoff example: many offspring vs. high-quality offspring

- ▶ Apart from how much energy to put into offspring now vs. later, organisms can make many or few offspring, using a given amount of energy
- ▶ What is a vivid example of ecologically similar organisms that produce wildly different numbers of offspring?
  - ▶ \* Oaks vs. pines
  - ▶ \* Tsetses vs. mosquitoes
- ▶ Poll: What are potential advantages of producing fewer offspring with the same amount of energy?
  - ▶ \* Greater chance of survival (or reproductive success)
  - ▶ \* Dispersal
  - ▶ \* More energy left over?
    - ▶ \*

## Tradeoff example: many offspring vs. high-quality offspring

- ▶ Apart from how much energy to put into offspring now vs. later, organisms can make many or few offspring, using a given amount of energy
- ▶ What is a vivid example of ecologically similar organisms that produce wildly different numbers of offspring?
  - ▶ \* Oaks vs. pines
  - ▶ \* Tsetses vs. mosquitoes
- ▶ Poll: What are potential advantages of producing fewer offspring with the same amount of energy?
  - ▶ \* Greater chance of survival (or reproductive success)
  - ▶ \* Dispersal
  - ▶ \* More energy left over?
  - ▶ \* No (see question)

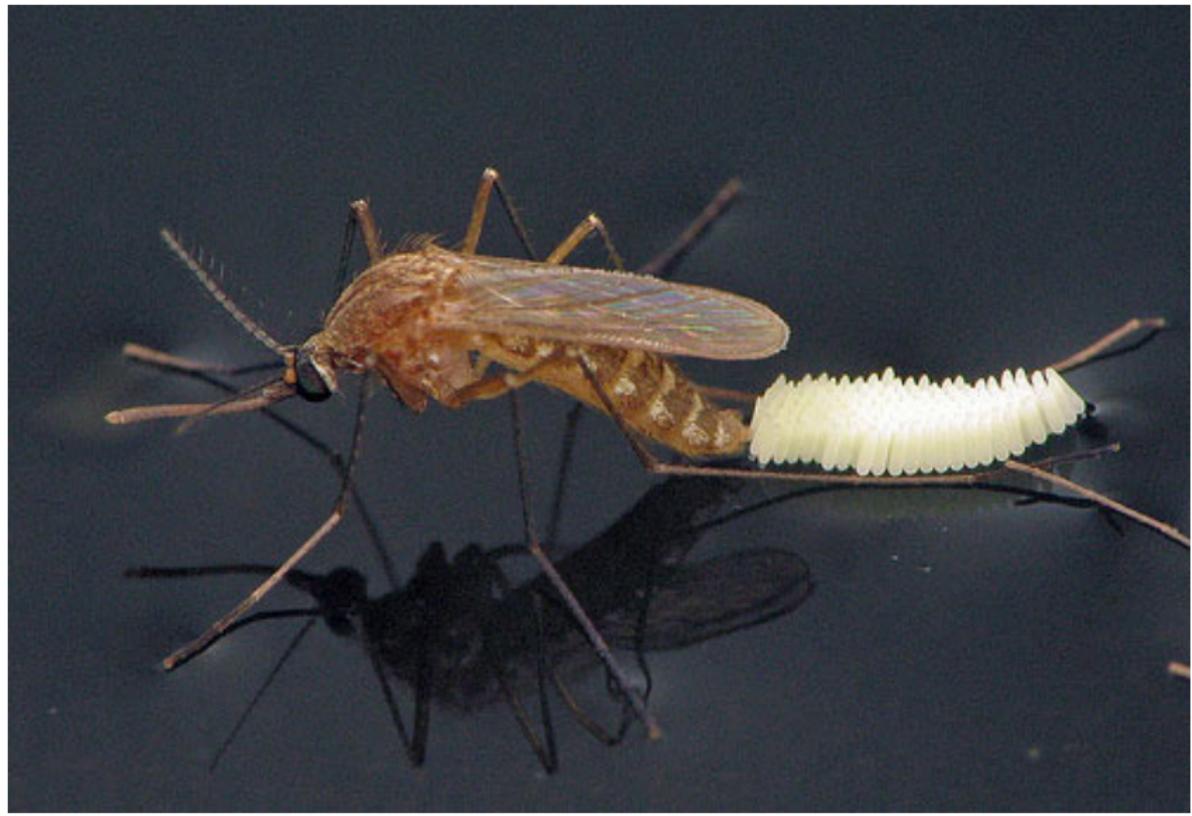
## Tradeoff example: many offspring vs. high-quality offspring

- ▶ Apart from how much energy to put into offspring now vs. later, organisms can make many or few offspring, using a given amount of energy
- ▶ What is a vivid example of ecologically similar organisms that produce wildly different numbers of offspring?
  - ▶ \* Oaks vs. pines
  - ▶ \* Tsetses vs. mosquitoes
- ▶ Poll: What are potential advantages of producing fewer offspring with the same amount of energy?
  - ▶ \* Greater chance of survival (or reproductive success)
  - ▶ \* Dispersal
  - ▶ \* More energy left over?
  - ▶ \* No (see question)

# How many offspring?



# How many offspring?



# How many offspring?



©Warren Photographic

## Tradeoff: direct investment vs. dispersal investment

- ▶ Investment in reproduction may not go directly to the offspring, but instead to mechanisms to help the offspring disperse.

## Tradeoff: direct investment vs. dispersal investment

- ▶ Investment in reproduction may not go directly to the offspring, but instead to mechanisms to help the offspring disperse.
- ▶ Why is this particularly important in plants?

## Tradeoff: direct investment vs. dispersal investment

- ▶ Investment in reproduction may not go directly to the offspring, but instead to mechanisms to help the offspring disperse.
- ▶ Why is this particularly important in plants?
  - ▶ \*

## Tradeoff: direct investment vs. dispersal investment

- ▶ Investment in reproduction may not go directly to the offspring, but instead to mechanisms to help the offspring disperse.
- ▶ Why is this particularly important in plants?
  - ▶ \* Parent-assisted dispersal is often their only chance to move.

## Tradeoff: direct investment vs. dispersal investment

- ▶ Investment in reproduction may not go directly to the offspring, but instead to mechanisms to help the offspring disperse.
- ▶ Why is this particularly important in plants?
  - ▶ \* Parent-assisted dispersal is often their only chance to move.
- ▶ What are some example mechanisms?

## Tradeoff: direct investment vs. dispersal investment

- ▶ Investment in reproduction may not go directly to the offspring, but instead to mechanisms to help the offspring disperse.
- ▶ Why is this particularly important in plants?
  - ▶ \* Parent-assisted dispersal is often their only chance to move.
- ▶ What are some example mechanisms?
  - ▶ \*

## Tradeoff: direct investment vs. dispersal investment

- ▶ Investment in reproduction may not go directly to the offspring, but instead to mechanisms to help the offspring disperse.
- ▶ Why is this particularly important in plants?
  - ▶ \* Parent-assisted dispersal is often their only chance to move.
- ▶ What are some example mechanisms?
  - ▶ \* Edible fruits

## Tradeoff: direct investment vs. dispersal investment

- ▶ Investment in reproduction may not go directly to the offspring, but instead to mechanisms to help the offspring disperse.
- ▶ Why is this particularly important in plants?
  - ▶ \* Parent-assisted dispersal is often their only chance to move.
- ▶ What are some example mechanisms?
  - ▶ \* Edible fruits
  - ▶ \*

## Tradeoff: direct investment vs. dispersal investment

- ▶ Investment in reproduction may not go directly to the offspring, but instead to mechanisms to help the offspring disperse.
- ▶ Why is this particularly important in plants?
  - ▶ \* Parent-assisted dispersal is often their only chance to move.
- ▶ What are some example mechanisms?
  - ▶ \* Edible fruits
  - ▶ \* Helicopter attachments

## Tradeoff: direct investment vs. dispersal investment

- ▶ Investment in reproduction may not go directly to the offspring, but instead to mechanisms to help the offspring disperse.
- ▶ Why is this particularly important in plants?
  - ▶ \* Parent-assisted dispersal is often their only chance to move.
- ▶ What are some example mechanisms?
  - ▶ \* Edible fruits
  - ▶ \* Helicopter attachments
  - ▶ \*

## Tradeoff: direct investment vs. dispersal investment

- ▶ Investment in reproduction may not go directly to the offspring, but instead to mechanisms to help the offspring disperse.
- ▶ Why is this particularly important in plants?
  - ▶ \* Parent-assisted dispersal is often their only chance to move.
- ▶ What are some example mechanisms?
  - ▶ \* Edible fruits
  - ▶ \* Helicopter attachments
  - ▶ \* Exploding seed pods

## Tradeoff: direct investment vs. dispersal investment

- ▶ Investment in reproduction may not go directly to the offspring, but instead to mechanisms to help the offspring disperse.
- ▶ Why is this particularly important in plants?
  - ▶ \* Parent-assisted dispersal is often their only chance to move.
- ▶ What are some example mechanisms?
  - ▶ \* Edible fruits
  - ▶ \* Helicopter attachments
  - ▶ \* Exploding seed pods

# Dispersal investment



# Dispersal investment



# Dispersal investment



# Outline

Introduction

Tradeoffs

The  $r$  vs.  $K$  metaphor

Bet hedging

Sex ratios

## The $r$ vs. $K$ metaphor

- Regulated growth provides a powerful metaphor for life-history tradeoffs involving growth vs. competitive ability

## The $r$ vs. $K$ metaphor

- ▶ Regulated growth provides a powerful metaphor for life-history tradeoffs involving growth vs. competitive ability
- ▶ Recall  $r$  and  $K$  from our regulated population models.

## The $r$ vs. $K$ metaphor

- ▶ Regulated growth provides a powerful metaphor for life-history tradeoffs involving growth vs. competitive ability
- ▶ Recall  $r$  and  $K$  from our regulated population models.
  - ▶ \*

## The $r$ vs. $K$ metaphor

- ▶ Regulated growth provides a powerful metaphor for life-history tradeoffs involving growth vs. competitive ability
- ▶ Recall  $r$  and  $K$  from our regulated population models.
  - ▶ \*  $r$  is the per-capita rate of growth, units ...

## The $r$ vs. $K$ metaphor

- ▶ Regulated growth provides a powerful metaphor for life-history tradeoffs involving growth vs. competitive ability
- ▶ Recall  $r$  and  $K$  from our regulated population models.
  - ▶ \*  $r$  is the per-capita rate of growth, units ...
  - ▶ \*

## The $r$ vs. $K$ metaphor

- ▶ Regulated growth provides a powerful metaphor for life-history tradeoffs involving growth vs. competitive ability
- ▶ Recall  $r$  and  $K$  from our regulated population models.
  - ▶ \*  $r$  is the per-capita rate of growth, units ...
  - ▶ \*  $[1/t]$

## The $r$ vs. $K$ metaphor

- ▶ Regulated growth provides a powerful metaphor for life-history tradeoffs involving growth vs. competitive ability
- ▶ Recall  $r$  and  $K$  from our regulated population models.
  - ▶ \*  $r$  is the per-capita rate of growth, units ...
    - ▶ \*  $[1/t]$
  - ▶ \*

## The $r$ vs. $K$ metaphor

- ▶ Regulated growth provides a powerful metaphor for life-history tradeoffs involving growth vs. competitive ability
- ▶ Recall  $r$  and  $K$  from our regulated population models.
  - ▶ \*  $r$  is the per-capita rate of growth, units ...
    - ▶ \* [1/t]
  - ▶ \*  $K$  is the stable, equilibrium level that we expect a population to reach, units ...

## The $r$ vs. $K$ metaphor

- ▶ Regulated growth provides a powerful metaphor for life-history tradeoffs involving growth vs. competitive ability
- ▶ Recall  $r$  and  $K$  from our regulated population models.
  - ▶ \*  $r$  is the per-capita rate of growth, units ...
    - ▶ \*  $[1/t]$
  - ▶ \*  $K$  is the stable, equilibrium level that we expect a population to reach, units ...
    - ▶ \*

## The $r$ vs. $K$ metaphor

- ▶ Regulated growth provides a powerful metaphor for life-history tradeoffs involving growth vs. competitive ability
- ▶ Recall  $r$  and  $K$  from our regulated population models.
  - ▶ \*  $r$  is the per-capita rate of growth, units ...
    - ▶ \*  $[1/t]$
  - ▶ \*  $K$  is the stable, equilibrium level that we expect a population to reach, units ...
    - ▶ \* [pop] or [pop density]

## The $r$ vs. $K$ metaphor

- ▶ Regulated growth provides a powerful metaphor for life-history tradeoffs involving growth vs. competitive ability
- ▶ Recall  $r$  and  $K$  from our regulated population models.
  - ▶ \*  $r$  is the per-capita rate of growth, units ...
    - ▶ \*  $[1/t]$
  - ▶ \*  $K$  is the stable, equilibrium level that we expect a population to reach, units ...
    - ▶ \* [pop] or [pop density]

## $r$ vs. $K$ strategies

- We call organisms that tend to out-perform other species at low densities “ $r$ -strategists”

## $r$ vs. $K$ strategies

- ▶ We call organisms that tend to out-perform other species at low densities “ $r$ -strategists”
  - ▶ They do well in recently disturbed, uncrowded environments

## *r* vs. *K* strategies

- ▶ We call organisms that tend to out-perform other species at low densities “*r*-strategists”
  - ▶ They do well in recently disturbed, uncrowded environments
- ▶ We call organisms that tend to out-perform other species at high densities “*K*-strategists”

## *r* vs. *K* strategies

- ▶ We call organisms that tend to out-perform other species at low densities “*r*-strategists”
  - ▶ They do well in recently disturbed, uncrowded environments
- ▶ We call organisms that tend to out-perform other species at high densities “*K*-strategists”
  - ▶ They do well in stable, crowded environments

## *r* vs. *K* strategies

- ▶ We call organisms that tend to out-perform other species at low densities “*r*-strategists”
  - ▶ They do well in recently disturbed, uncrowded environments
- ▶ We call organisms that tend to out-perform other species at high densities “*K*-strategists”
  - ▶ They do well in stable, crowded environments

## *r*-strategists

- All organisms tend to do well in uncrowded environments, but *r*-strategists are selected to do better than other species

## *r*-strategists

- ▶ All organisms tend to do well in uncrowded environments, but *r*-strategists are selected to do better than other species
- ▶ They are selected for a high rate of exponential growth during the relatively short time that the environment is uncrowded

## *r*-strategists

- ▶ All organisms tend to do well in uncrowded environments, but *r*-strategists are selected to do better than other species
- ▶ They are selected for a high rate of exponential growth during the relatively short time that the environment is uncrowded
- ▶ Why do we call them *r*-strategists, and not *R*-strategists?

## *r*-strategists

- ▶ All organisms tend to do well in uncrowded environments, but *r*-strategists are selected to do better than other species
- ▶ They are selected for a high rate of exponential growth during the relatively short time that the environment is uncrowded
- ▶ Why do we call them *r*-strategists, and not  $\mathcal{R}$ -strategists?
  - ▶ \*

## *r*-strategists

- ▶ All organisms tend to do well in uncrowded environments, but *r*-strategists are selected to do better than other species
- ▶ They are selected for a high rate of exponential growth during the relatively short time that the environment is uncrowded
- ▶ Why do we call them *r*-strategists, and not *R*-strategists?
  - ▶ \* Because they are selected to maximize  $r_{\max}$ , the *rate* of exponential growth

## *r*-strategists

- ▶ All organisms tend to do well in uncrowded environments, but *r*-strategists are selected to do better than other species
- ▶ They are selected for a high rate of exponential growth during the relatively short time that the environment is uncrowded
- ▶ Why do we call them *r*-strategists, and not *R*-strategists?
  - ▶ \* Because they are selected to maximize  $r_{\max}$ , the *rate* of exponential growth
  - ▶ \*

## *r*-strategists

- ▶ All organisms tend to do well in uncrowded environments, but *r*-strategists are selected to do better than other species
- ▶ They are selected for a high rate of exponential growth during the relatively short time that the environment is uncrowded
- ▶ Why do we call them *r*-strategists, and not  $\mathcal{R}$ -strategists?
  - ▶ \* Because they are selected to maximize  $r_{\max}$ , the *rate* of exponential growth
  - ▶ \* A species with a high value of  $\mathcal{R}_{\max}$ , but a slow life cycle, may not have enough time to capitalize on the opportunity

## *r*-strategists

- ▶ All organisms tend to do well in uncrowded environments, but *r*-strategists are selected to do better than other species
- ▶ They are selected for a high rate of exponential growth during the relatively short time that the environment is uncrowded
- ▶ Why do we call them *r*-strategists, and not  $\mathcal{R}$ -strategists?
  - ▶ \* Because they are selected to maximize  $r_{\max}$ , the *rate* of exponential growth
  - ▶ \* A species with a high value of  $\mathcal{R}_{\max}$ , but a slow life cycle, may not have enough time to capitalize on the opportunity

## *K*-strategists

- ▶ *K*-strategists are selected to do well in crowded environments

## *K*-strategists

- ▶ *K*-strategists are selected to do well in crowded environments
- ▶ *K* measures the maximum density at which a species can “make a living” – by keeping  $\mathcal{R} = 1$

## *K*-strategists

- ▶ *K*-strategists are selected to do well in crowded environments
- ▶  $K$  measures the maximum density at which a species can “make a living” – by keeping  $\mathcal{R} = 1$
- ▶ Comparing  $K$  between species can be tricky

## *K*-strategists

- ▶ *K*-strategists are selected to do well in crowded environments
- ▶ *K* measures the maximum density at which a species can “make a living” – by keeping  $\mathcal{R} = 1$
- ▶ Comparing *K* between species can be tricky

# Maples and marigolds



# Measuring $K$

- Which is the  $K$  strategist: maple trees or marigolds?

## Measuring $K$

- ▶ Which is the  $K$  strategist: maple trees or marigolds?
  - ▶ \*

# Measuring $K$

- ▶ Which is the  $K$  strategist: maple trees or marigolds?
  - ▶ \* Maple trees do better at competing under stable conditions

# Measuring $K$

- ▶ Which is the  $K$  strategist: maple trees or marigolds?
  - ▶ \* Maple trees do better at competing under stable conditions
  - ▶ \*

# Measuring $K$

- ▶ Which is the  $K$  strategist: maple trees or marigolds?
  - ▶ \* Maple trees do better at competing under stable conditions
  - ▶ \* Marigolds are faster at invading new environments

## Measuring $K$

- ▶ Which is the  $K$  strategist: maple trees or marigolds?
  - ▶ \* Maple trees do better at competing under stable conditions
  - ▶ \* Marigolds are faster at invading new environments
- ▶ Which has a higher value of  $r_{\max}$ ?

# Measuring $K$

- ▶ Which is the  $K$  strategist: maple trees or marigolds?
  - ▶ \* Maple trees do better at competing under stable conditions
  - ▶ \* Marigolds are faster at invading new environments
- ▶ Which has a higher value of  $r_{\max}$ ?
  - ▶ \*

# Measuring $K$

- ▶ Which is the  $K$  strategist: maple trees or marigolds?
  - ▶ \* Maple trees do better at competing under stable conditions
  - ▶ \* Marigolds are faster at invading new environments
  
- ▶ Which has a higher value of  $r_{\max}$ ?
  - ▶ \* Marigolds

# Measuring $K$

- ▶ Which is the  $K$  strategist: maple trees or marigolds?
  - ▶ \* Maple trees do better at competing under stable conditions
  - ▶ \* Marigolds are faster at invading new environments
- ▶ Which has a higher value of  $r_{\max}$ ?
  - ▶ \* Marigolds
- ▶ Which has a higher value of  $K$ ?

# Measuring $K$

- ▶ Which is the  $K$  strategist: maple trees or marigolds?
  - ▶ \* Maple trees do better at competing under stable conditions
  - ▶ \* Marigolds are faster at invading new environments
- ▶ Which has a higher value of  $r_{\max}$ ?
  - ▶ \* Marigolds
- ▶ Which has a higher value of  $K$ ?
  - ▶ Poll: In [indiv/ha]?

# Measuring $K$

- ▶ Which is the  $K$  strategist: maple trees or marigolds?
  - ▶ \* Maple trees do better at competing under stable conditions
  - ▶ \* Marigolds are faster at invading new environments
- ▶ Which has a higher value of  $r_{\max}$ ?
  - ▶ \* Marigolds
- ▶ Which has a higher value of  $K$ ?
  - ▶ Poll: In [indiv/ha]?
  - ▶ Poll: In [kg/ha]?

# Measuring $K$

- ▶ Which is the  $K$  strategist: maple trees or marigolds?
  - ▶ \* Maple trees do better at competing under stable conditions
  - ▶ \* Marigolds are faster at invading new environments
- ▶ Which has a higher value of  $r_{\max}$ ?
  - ▶ \* Marigolds
- ▶ Which has a higher value of  $K$ ?
  - ▶ Poll: In [indiv/ha]?
  - ▶ Poll: In [kg/ha]?
- ▶ To compare species, we attempt to measure  $K$  in units that reflect the effect of crowding on the competitive environment

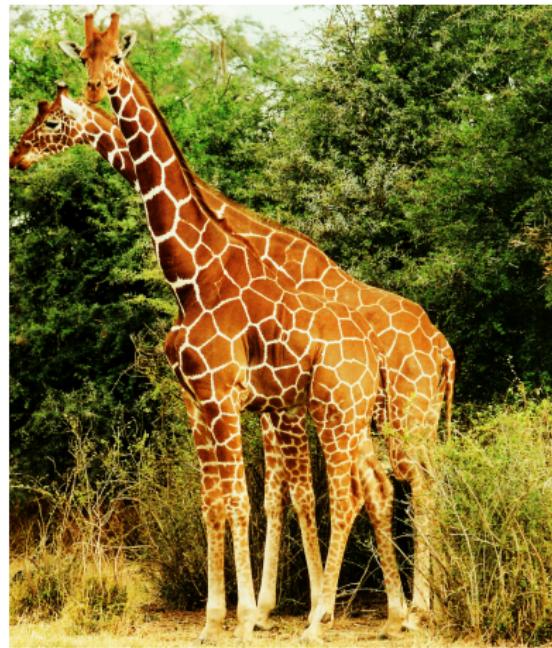
# Measuring $K$

- ▶ Which is the  $K$  strategist: maple trees or marigolds?
  - ▶ \* Maple trees do better at competing under stable conditions
  - ▶ \* Marigolds are faster at invading new environments
- ▶ Which has a higher value of  $r_{\max}$ ?
  - ▶ \* Marigolds
- ▶ Which has a higher value of  $K$ ?
  - ▶ Poll: In [indiv/ha]?
  - ▶ Poll: In [kg/ha]?
- ▶ To compare species, we attempt to measure  $K$  in units that reflect the effect of crowding on the competitive environment
  - ▶ biomass; area covered; resource consumed

## Measuring $K$

- ▶ Which is the  $K$  strategist: maple trees or marigolds?
  - ▶ \* Maple trees do better at competing under stable conditions
  - ▶ \* Marigolds are faster at invading new environments
- ▶ Which has a higher value of  $r_{\max}$ ?
  - ▶ \* Marigolds
- ▶ Which has a higher value of  $K$ ?
  - ▶ Poll: In [indiv/ha]?
  - ▶ Poll: In [kg/ha]?
- ▶ To compare species, we attempt to measure  $K$  in units that reflect the effect of crowding on the competitive environment
  - ▶ biomass; area covered; resource consumed

# Strategies



## Example: trees



# Open environment



# Stable environment



## Example: trees

- ▶ Assuming there is a tradeoff between  $r_{\max}$  and  $K$ , would you expect individuals with high  $r_{\max}$ , or high  $K$ , to do well:

## Example: trees

- ▶ Assuming there is a tradeoff between  $r_{\max}$  and  $K$ , would you expect individuals with high  $r_{\max}$ , or high  $K$ , to do well:
  - ▶ In an empty, suitable habitat after a fire, flood, clearcut or other major **disturbance**?

## Example: trees

- ▶ Assuming there is a tradeoff between  $r_{\max}$  and  $K$ , would you expect individuals with high  $r_{\max}$ , or high  $K$ , to do well:
  - ▶ In an empty, suitable habitat after a fire, flood, clearcut or other major **disturbance**?
    - ▶ \*

## Example: trees

- ▶ Assuming there is a tradeoff between  $r_{\max}$  and  $K$ , would you expect individuals with high  $r_{\max}$ , or high  $K$ , to do well:
  - ▶ In an empty, suitable habitat after a fire, flood, clearcut or other major **disturbance**?
    - ▶ \* High  $r_{\max}$  leads to faster exponential growth

## Example: trees

- ▶ Assuming there is a tradeoff between  $r_{\max}$  and  $K$ , would you expect individuals with high  $r_{\max}$ , or high  $K$ , to do well:
  - ▶ In an empty, suitable habitat after a fire, flood, clearcut or other major **disturbance**?
    - ▶ \* High  $r_{\max}$  leads to faster exponential growth
  - ▶ In a crowded, stable old-growth forest?

## Example: trees

- ▶ Assuming there is a tradeoff between  $r_{\max}$  and  $K$ , would you expect individuals with high  $r_{\max}$ , or high  $K$ , to do well:
  - ▶ In an empty, suitable habitat after a fire, flood, clearcut or other major **disturbance**?
    - ▶ \* High  $r_{\max}$  leads to faster exponential growth
  - ▶ In a crowded, stable old-growth forest?
    - ▶ \*

## Example: trees

- ▶ Assuming there is a tradeoff between  $r_{\max}$  and  $K$ , would you expect individuals with high  $r_{\max}$ , or high  $K$ , to do well:
  - ▶ In an empty, suitable habitat after a fire, flood, clearcut or other major **disturbance**?
    - ▶ \* High  $r_{\max}$  leads to faster exponential growth
  - ▶ In a crowded, stable old-growth forest?
    - ▶ \* High  $K$  means you can continue doing well when the forest is already too crowded for others

## Example: trees

- ▶ Assuming there is a tradeoff between  $r_{\max}$  and  $K$ , would you expect individuals with high  $r_{\max}$ , or high  $K$ , to do well:
  - ▶ In an empty, suitable habitat after a fire, flood, clearcut or other major **disturbance**?
    - ▶ \* High  $r_{\max}$  leads to faster exponential growth
  - ▶ In a crowded, stable old-growth forest?
    - ▶ \* High  $K$  means you can continue doing well when the forest is already too crowded for others

## $r$ vs. $K$ strategists

- All species are selected for characteristics relating to both  $r_{\max}$  and  $K$

## $r$ vs. $K$ strategists

- ▶ All species are selected for characteristics relating to both  $r_{\max}$  and  $K$
- ▶ But it is often useful to compare species based on which they emphasize more heavily

## $r$ vs. $K$ strategists

- ▶ All species are selected for characteristics relating to both  $r_{\max}$  and  $K$
- ▶ But it is often useful to compare species based on which they emphasize more heavily
  - ▶ There will often be tradeoffs between  $r_{\max}$  and  $K$

## $r$ vs. $K$ strategists

- ▶ All species are selected for characteristics relating to both  $r_{\max}$  and  $K$
- ▶ But it is often useful to compare species based on which they emphasize more heavily
  - ▶ There will often be tradeoffs between  $r_{\max}$  and  $K$
- ▶ Species that specialize in colonizing disturbed environments are thought of as  $r$  strategists

## $r$ vs. $K$ strategists

- ▶ All species are selected for characteristics relating to both  $r_{\max}$  and  $K$
- ▶ But it is often useful to compare species based on which they emphasize more heavily
  - ▶ There will often be tradeoffs between  $r_{\max}$  and  $K$
- ▶ Species that specialize in colonizing disturbed environments are thought of as  $r$  strategists
  - ▶ Apple trees are often the first to reproduce in abandoned fields

## $r$ vs. $K$ strategists

- ▶ All species are selected for characteristics relating to both  $r_{\max}$  and  $K$
- ▶ But it is often useful to compare species based on which they emphasize more heavily
  - ▶ There will often be tradeoffs between  $r_{\max}$  and  $K$
- ▶ Species that specialize in colonizing disturbed environments are thought of as  $r$  strategists
  - ▶ Apple trees are often the first to reproduce in abandoned fields
- ▶ Species that specialize in stable environments are thought of as  $K$  strategists

## $r$ vs. $K$ strategists

- ▶ All species are selected for characteristics relating to both  $r_{\max}$  and  $K$
- ▶ But it is often useful to compare species based on which they emphasize more heavily
  - ▶ There will often be tradeoffs between  $r_{\max}$  and  $K$
- ▶ Species that specialize in colonizing disturbed environments are thought of as  $r$  strategists
  - ▶ Apple trees are often the first to reproduce in abandoned fields
- ▶ Species that specialize in stable environments are thought of as  $K$  strategists
  - ▶ Hemlock trees do best in stable, closed forests

## *r* vs. *K* strategists

- ▶ All species are selected for characteristics relating to both  $r_{\max}$  and  $K$
- ▶ But it is often useful to compare species based on which they emphasize more heavily
  - ▶ There will often be tradeoffs between  $r_{\max}$  and  $K$
- ▶ Species that specialize in colonizing disturbed environments are thought of as *r* strategists
  - ▶ Apple trees are often the first to reproduce in abandoned fields
- ▶ Species that specialize in stable environments are thought of as *K* strategists
  - ▶ Hemlock trees do best in stable, closed forests

## Life-history characteristics

- Compared to  $K$  strategists,  $r$  strategists should:

## Life-history characteristics

- ▶ Compared to  $K$  strategists,  $r$  strategists should:
  - ▶ Have relatively fast life cycles

## Life-history characteristics

- ▶ Compared to  $K$  strategists,  $r$  strategists should:
  - ▶ Have relatively fast life cycles
    - ▶ Reach maturity earlier

## Life-history characteristics

- ▶ Compared to  $K$  strategists,  $r$  strategists should:
  - ▶ Have relatively fast life cycles
    - ▶ Reach maturity earlier
    - ▶ Allocate more resources to reproduction (and thus reproduce more and survive less)

## Life-history characteristics

- ▶ Compared to  $K$  strategists,  $r$  strategists should:
  - ▶ Have relatively fast life cycles
    - ▶ Reach maturity earlier
    - ▶ Allocate more resources to reproduction (and thus reproduce more and survive less)
  - ▶ Produce more offspring, with less resources for each

## Life-history characteristics

- ▶ Compared to  $K$  strategists,  $r$  strategists should:
  - ▶ Have relatively fast life cycles
    - ▶ Reach maturity earlier
    - ▶ Allocate more resources to reproduction (and thus reproduce more and survive less)
  - ▶ Produce more offspring, with less resources for each
    - ▶ This allows high growth rates in the absence of competition

## Life-history characteristics

- ▶ Compared to  $K$  strategists,  $r$  strategists should:
  - ▶ Have relatively fast life cycles
    - ▶ Reach maturity earlier
    - ▶ Allocate more resources to reproduction (and thus reproduce more and survive less)
  - ▶ Produce more offspring, with less resources for each
    - ▶ This allows high growth rates in the absence of competition
    - ▶ In crowded conditions, these “quick” offspring may be out-competed by offspring with more resources

# Life-history characteristics

- ▶ Compared to  $K$  strategists,  $r$  strategists should:
  - ▶ Have relatively fast life cycles
    - ▶ Reach maturity earlier
    - ▶ Allocate more resources to reproduction (and thus reproduce more and survive less)
  - ▶ Produce more offspring, with less resources for each
    - ▶ This allows high growth rates in the absence of competition
    - ▶ In crowded conditions, these “quick” offspring may be out-competed by offspring with more resources
  - ▶ Be more aggressive about dispersal.

## Life-history characteristics

- ▶ Compared to  $K$  strategists,  $r$  strategists should:
  - ▶ Have relatively fast life cycles
    - ▶ Reach maturity earlier
    - ▶ Allocate more resources to reproduction (and thus reproduce more and survive less)
  - ▶ Produce more offspring, with less resources for each
    - ▶ This allows high growth rates in the absence of competition
    - ▶ In crowded conditions, these “quick” offspring may be out-competed by offspring with more resources
  - ▶ Be more aggressive about dispersal.
    - ▶ \*

## Life-history characteristics

- ▶ Compared to  $K$  strategists,  $r$  strategists should:
  - ▶ Have relatively fast life cycles
    - ▶ Reach maturity earlier
    - ▶ Allocate more resources to reproduction (and thus reproduce more and survive less)
  - ▶ Produce more offspring, with less resources for each
    - ▶ This allows high growth rates in the absence of competition
    - ▶ In crowded conditions, these “quick” offspring may be out-competed by offspring with more resources
  - ▶ Be more aggressive about dispersal.
    - ▶ \* They need to find the next empty, suitable habitat before this one gets too crowded

## Life-history characteristics

- ▶ Compared to  $K$  strategists,  $r$  strategists should:
  - ▶ Have relatively fast life cycles
    - ▶ Reach maturity earlier
    - ▶ Allocate more resources to reproduction (and thus reproduce more and survive less)
  - ▶ Produce more offspring, with less resources for each
    - ▶ This allows high growth rates in the absence of competition
    - ▶ In crowded conditions, these “quick” offspring may be out-competed by offspring with more resources
  - ▶ Be more aggressive about dispersal.
    - ▶ \* They need to find the next empty, suitable habitat before this one gets too crowded

# Biology is complicated

- The  $r$ - $K$  dichotomy is useful for thinking about strategies, but organisms don't always fit it perfectly

# Biology is complicated

- ▶ The  $r$ - $K$  dichotomy is useful for thinking about strategies, but organisms don't always fit it perfectly
- ▶ Some species live long, but don't invest a lot in each offspring

# Biology is complicated

- ▶ The  $r$ - $K$  dichotomy is useful for thinking about strategies, but organisms don't always fit it perfectly
- ▶ Some species live long, but don't invest a lot in each offspring
  - ▶ Sea turtles, pine trees

# Biology is complicated

- ▶ The  $r$ - $K$  dichotomy is useful for thinking about strategies, but organisms don't always fit it perfectly
- ▶ Some species live long, but don't invest a lot in each offspring
  - ▶ Sea turtles, pine trees
- ▶ Some species mature slowly but reproduce only once

# Biology is complicated

- ▶ The  $r$ - $K$  dichotomy is useful for thinking about strategies, but organisms don't always fit it perfectly
- ▶ Some species live long, but don't invest a lot in each offspring
  - ▶ Sea turtles, pine trees
- ▶ Some species mature slowly but reproduce only once
  - ▶ 17-year cicadas, century plants

# Biology is complicated

- ▶ The  $r$ - $K$  dichotomy is useful for thinking about strategies, but organisms don't always fit it perfectly
- ▶ Some species live long, but don't invest a lot in each offspring
  - ▶ Sea turtles, pine trees
- ▶ Some species mature slowly but reproduce only once
  - ▶ 17-year cicadas, century plants
- ▶ Every species life history has specific, important *details*

# Biology is complicated

- ▶ The *r-K* dichotomy is useful for thinking about strategies, but organisms don't always fit it perfectly
- ▶ Some species live long, but don't invest a lot in each offspring
  - ▶ Sea turtles, pine trees
- ▶ Some species mature slowly but reproduce only once
  - ▶ 17-year cicadas, century plants
- ▶ Every species life history has specific, important *details*
  - ▶ But general principles are very important to guide our understanding

# Biology is complicated

- ▶ The  $r$ - $K$  dichotomy is useful for thinking about strategies, but organisms don't always fit it perfectly
- ▶ Some species live long, but don't invest a lot in each offspring
  - ▶ Sea turtles, pine trees
- ▶ Some species mature slowly but reproduce only once
  - ▶ 17-year cicadas, century plants
- ▶ Every species life history has specific, important *details*
  - ▶ But general principles are very important to guide our understanding

# Biology is complicated



## Changing conditions

- Recall,  $\lambda$  is usually between 1 and  $\mathcal{R}$ , gets closer to 1 when the life cycle is

## Changing conditions

- ▶ Recall,  $\lambda$  is usually between 1 and  $\mathcal{R}$ , gets closer to 1 when the life cycle is
  - ▶ \*

## Changing conditions

- ▶ Recall,  $\lambda$  is usually between 1 and  $\mathcal{R}$ , gets closer to 1 when the life cycle is
  - ▶ \* slower

# Changing conditions

- ▶ Recall,  $\lambda$  is usually between 1 and  $\mathcal{R}$ , gets closer to 1 when the life cycle is
  - ▶ \* slower
- ▶ When conditions are good ( $\mathcal{R} > 1$ ), should organisms be fast or slow to maximize  $\lambda$ ?

# Changing conditions

- ▶ Recall,  $\lambda$  is usually between 1 and  $\mathcal{R}$ , gets closer to 1 when the life cycle is
  - ▶ \* slower
- ▶ When conditions are good ( $\mathcal{R} > 1$ ), should organisms be fast or slow to maximize  $\lambda$ ?
  - ▶ \*

# Changing conditions

- ▶ Recall,  $\lambda$  is usually between 1 and  $\mathcal{R}$ , gets closer to 1 when the life cycle is
  - ▶ \* slower
- ▶ When conditions are good ( $\mathcal{R} > 1$ ), should organisms be fast or slow to maximize  $\lambda$ ?
  - ▶ \* Fast

## Changing conditions

- ▶ Recall,  $\lambda$  is usually between 1 and  $\mathcal{R}$ , gets closer to 1 when the life cycle is
  - ▶ \* slower
- ▶ When conditions are good ( $\mathcal{R} > 1$ ), should organisms be fast or slow to maximize  $\lambda$ ?
  - ▶ \* Fast
- ▶ Poll: When conditions are bad ( $\mathcal{R} < 1$ ), should organisms be fast or slow to maximize  $\lambda$ ?

## Changing conditions

- ▶ Recall,  $\lambda$  is usually between 1 and  $\mathcal{R}$ , gets closer to 1 when the life cycle is
  - ▶ \* slower
- ▶ When conditions are good ( $\mathcal{R} > 1$ ), should organisms be fast or slow to maximize  $\lambda$ ?
  - ▶ \* Fast
- ▶ Poll: When conditions are bad ( $\mathcal{R} < 1$ ), should organisms be fast or slow to maximize  $\lambda$ ?
  - ▶ \*

## Changing conditions

- ▶ Recall,  $\lambda$  is usually between 1 and  $\mathcal{R}$ , gets closer to 1 when the life cycle is
  - ▶ \* slower
- ▶ When conditions are good ( $\mathcal{R} > 1$ ), should organisms be fast or slow to maximize  $\lambda$ ?
  - ▶ \* Fast
- ▶ Poll: When conditions are bad ( $\mathcal{R} < 1$ ), should organisms be fast or slow to maximize  $\lambda$ ?
  - ▶ \* Slow!

# Changing conditions

- ▶ Recall,  $\lambda$  is usually between 1 and  $\mathcal{R}$ , gets closer to 1 when the life cycle is
  - ▶ \* slower
- ▶ When conditions are good ( $\mathcal{R} > 1$ ), should organisms be fast or slow to maximize  $\lambda$ ?
  - ▶ \* Fast
- ▶ Poll: When conditions are bad ( $\mathcal{R} < 1$ ), should organisms be fast or slow to maximize  $\lambda$ ?
  - ▶ \* Slow!
  - ▶ \*

## Changing conditions

- ▶ Recall,  $\lambda$  is usually between 1 and  $\mathcal{R}$ , gets closer to 1 when the life cycle is
  - ▶ \* slower
- ▶ When conditions are good ( $\mathcal{R} > 1$ ), should organisms be fast or slow to maximize  $\lambda$ ?
  - ▶ \* Fast
- ▶ Poll: When conditions are bad ( $\mathcal{R} < 1$ ), should organisms be fast or slow to maximize  $\lambda$ ?
  - ▶ \* Slow!
  - ▶ \* Decrease more slowly during the bad times

## Changing conditions

- ▶ Recall,  $\lambda$  is usually between 1 and  $\mathcal{R}$ , gets closer to 1 when the life cycle is
  - ▶ \* slower
- ▶ When conditions are good ( $\mathcal{R} > 1$ ), should organisms be fast or slow to maximize  $\lambda$ ?
  - ▶ \* Fast
- ▶ Poll: When conditions are bad ( $\mathcal{R} < 1$ ), should organisms be fast or slow to maximize  $\lambda$ ?
  - ▶ \* Slow!
  - ▶ \* Decrease more slowly during the bad times

# Changing life history

- Some organisms have evolved to change their life history patterns in response to good or bad conditions

# Changing life history

- ▶ Some organisms have evolved to change their life history patterns in response to good or bad conditions
  - ▶ \*

# Changing life history

- ▶ Some organisms have evolved to change their life history patterns in response to good or bad conditions
  - ▶ \* Move slow when things are bad, and fast when things are good

# Changing life history

- ▶ Some organisms have evolved to change their life history patterns in response to good or bad conditions
  - ▶ \* Move slow when things are bad, and fast when things are good
- ▶ Poll: What are some examples?

# Changing life history

- ▶ Some organisms have evolved to change their life history patterns in response to good or bad conditions
  - ▶ \* Move slow when things are bad, and fast when things are good
- ▶ Poll: What are some examples?
  - ▶ \*

# Changing life history

- ▶ Some organisms have evolved to change their life history patterns in response to good or bad conditions
  - ▶ \* Move slow when things are bad, and fast when things are good
- ▶ Poll: What are some examples?
  - ▶ \* Many animals reach sexual maturity faster under good conditions: horses, elephants

# Changing life history

- ▶ Some organisms have evolved to change their life history patterns in response to good or bad conditions
  - ▶ \* Move slow when things are bad, and fast when things are good
- ▶ Poll: What are some examples?
  - ▶ \* Many animals reach sexual maturity faster under good conditions: horses, elephants
  - ▶ \*

# Changing life history

- ▶ Some organisms have evolved to change their life history patterns in response to good or bad conditions
  - ▶ \* Move slow when things are bad, and fast when things are good
- ▶ Poll: What are some examples?
  - ▶ \* Many animals reach sexual maturity faster under good conditions: horses, elephants
  - ▶ \* Trees may survive longer under bad conditions (by growing slowly and not allocating energy to reproduction)

# Changing life history

- ▶ Some organisms have evolved to change their life history patterns in response to good or bad conditions
  - ▶ \* Move slow when things are bad, and fast when things are good
- ▶ Poll: What are some examples?
  - ▶ \* Many animals reach sexual maturity faster under good conditions: horses, elephants
  - ▶ \* Trees may survive longer under bad conditions (by growing slowly and not allocating energy to reproduction)
  - ▶ \*

# Changing life history

- ▶ Some organisms have evolved to change their life history patterns in response to good or bad conditions
  - ▶ \* Move slow when things are bad, and fast when things are good
- ▶ Poll: What are some examples?
  - ▶ \* Many animals reach sexual maturity faster under good conditions: horses, elephants
  - ▶ \* Trees may survive longer under bad conditions (by growing slowly and not allocating energy to reproduction)
  - ▶ \* Bacteria enter “stationary state” when conditions are bad – don’t reproduce or grow at all, but may survive for a long time

# Changing life history

- ▶ Some organisms have evolved to change their life history patterns in response to good or bad conditions
  - ▶ \* Move slow when things are bad, and fast when things are good
- ▶ Poll: What are some examples?
  - ▶ \* Many animals reach sexual maturity faster under good conditions: horses, elephants
  - ▶ \* Trees may survive longer under bad conditions (by growing slowly and not allocating energy to reproduction)
  - ▶ \* Bacteria enter “stationary state” when conditions are bad – don’t reproduce or grow at all, but may survive for a long time

# Applications

- ▶ How would  $r$  and  $K$  strategists differ in their response to human activities/disturbance?

# Applications

- ▶ How would  $r$  and  $K$  strategists differ in their response to human activities/disturbance?
  - ▶ \*

## Applications

- ▶ How would  $r$  and  $K$  strategists differ in their response to human activities/disturbance?
  - ▶ \*  $r$  strategists will generally deal with disturbance better

# Applications

- ▶ How would  $r$  and  $K$  strategists differ in their response to human activities/disturbance?
  - ▶ \*  $r$  strategists will generally deal with disturbance better
- ▶ What are advantages of  $r$  or  $K$  strategists for human production (eg. biofuels, agriculture, drug production etc..)?

# Applications

- ▶ How would  $r$  and  $K$  strategists differ in their response to human activities/disturbance?
  - ▶ \*  $r$  strategists will generally deal with disturbance better
- ▶ What are advantages of  $r$  or  $K$  strategists for human production (eg. biofuels, agriculture, drug production etc..)?
- ▶ Poll: What are some advantages of  $r$  strategists?

# Applications

- ▶ How would  $r$  and  $K$  strategists differ in their response to human activities/disturbance?
  - ▶ \*  $r$  strategists will generally deal with disturbance better
- ▶ What are advantages of  $r$  or  $K$  strategists for human production (eg. biofuels, agriculture, drug production etc..)?
- ▶ Poll: What are some advantages of  $r$  strategists?
  - ▶ \*

# Applications

- ▶ How would  $r$  and  $K$  strategists differ in their response to human activities/disturbance?
  - ▶ \*  $r$  strategists will generally deal with disturbance better
- ▶ What are advantages of  $r$  or  $K$  strategists for human production (eg. biofuels, agriculture, drug production etc..)?
- ▶ Poll: What are some advantages of  $r$  strategists?
  - ▶ \* grow faster

# Applications

- ▶ How would  $r$  and  $K$  strategists differ in their response to human activities/disturbance?
  - ▶ \*  $r$  strategists will generally deal with disturbance better
- ▶ What are advantages of  $r$  or  $K$  strategists for human production (eg. biofuels, agriculture, drug production etc..)?
- ▶ Poll: What are some advantages of  $r$  strategists?
  - ▶ \* grow faster
  - ▶ \*

## Applications

- ▶ How would  $r$  and  $K$  strategists differ in their response to human activities/disturbance?
  - ▶ \*  $r$  strategists will generally deal with disturbance better
- ▶ What are advantages of  $r$  or  $K$  strategists for human production (eg. biofuels, agriculture, drug production etc..)?
- ▶ Poll: What are some advantages of  $r$  strategists?
  - ▶ \* grow faster
  - ▶ \* likely to respond well to disturbance

# Applications

- ▶ How would  $r$  and  $K$  strategists differ in their response to human activities/disturbance?
  - ▶ \*  $r$  strategists will generally deal with disturbance better
- ▶ What are advantages of  $r$  or  $K$  strategists for human production (eg. biofuels, agriculture, drug production etc..)?
- ▶ Poll: What are some advantages of  $r$  strategists?
  - ▶ \* grow faster
  - ▶ \* likely to respond well to disturbance
- ▶ Poll: What are some advantages of  $K$  strategists?

## Applications

- ▶ How would  $r$  and  $K$  strategists differ in their response to human activities/disturbance?
  - ▶ \*  $r$  strategists will generally deal with disturbance better
- ▶ What are advantages of  $r$  or  $K$  strategists for human production (eg. biofuels, agriculture, drug production etc..)?
- ▶ Poll: What are some advantages of  $r$  strategists?
  - ▶ \* grow faster
  - ▶ \* likely to respond well to disturbance
- ▶ Poll: What are some advantages of  $K$  strategists?
  - ▶ \*

# Applications

- ▶ How would  $r$  and  $K$  strategists differ in their response to human activities/disturbance?
  - ▶ \*  $r$  strategists will generally deal with disturbance better
- ▶ What are advantages of  $r$  or  $K$  strategists for human production (eg. biofuels, agriculture, drug production etc..)?
- ▶ Poll: What are some advantages of  $r$  strategists?
  - ▶ \* grow faster
  - ▶ \* likely to respond well to disturbance
- ▶ Poll: What are some advantages of  $K$  strategists?
  - ▶ \* may be more sustainable to grow for a long time in a stable environment

# Applications

- ▶ How would  $r$  and  $K$  strategists differ in their response to human activities/disturbance?
  - ▶ \*  $r$  strategists will generally deal with disturbance better
- ▶ What are advantages of  $r$  or  $K$  strategists for human production (eg. biofuels, agriculture, drug production etc..)?
- ▶ Poll: What are some advantages of  $r$  strategists?
  - ▶ \* grow faster
  - ▶ \* likely to respond well to disturbance
- ▶ Poll: What are some advantages of  $K$  strategists?
  - ▶ \* may be more sustainable to grow for a long time in a stable environment

# Outline

Introduction

Tradeoffs

The  $r$  vs.  $K$  metaphor

Bet hedging

Sex ratios

# Bet hedging

- In a risky world, you never want to put all your eggs in the same basket

## Bet hedging

- ▶ In a risky world, you never want to put all your eggs in the same basket
  - ▶ If all your offspring are born into similar conditions, they can all do well together – or they can all die together

## Bet hedging

- ▶ In a risky world, you never want to put all your eggs in the same basket
  - ▶ If all your offspring are born into similar conditions, they can all do well together – or they can all die together
- ▶ Strategies that *usually* do well aren't good enough

## Bet hedging

- ▶ In a risky world, you never want to put all your eggs in the same basket
  - ▶ If all your offspring are born into similar conditions, they can all do well together – or they can all die together
- ▶ Strategies that *usually* do well aren't good enough
  - ▶ The species we see now have survived for billions of years (if we include ancestral species, who also had to survive)

# Bet hedging

- ▶ In a risky world, you never want to put all your eggs in the same basket
  - ▶ If all your offspring are born into similar conditions, they can all do well together – or they can all die together
- ▶ Strategies that *usually* do well aren't good enough
  - ▶ The species we see now have survived for billions of years (if we include ancestral species, who also had to survive)
    - ▶ Floods, fires, ice ages, disease outbreaks

# Bet hedging

- ▶ In a risky world, you never want to put all your eggs in the same basket
  - ▶ If all your offspring are born into similar conditions, they can all do well together – or they can all die together
- ▶ Strategies that *usually* do well aren't good enough
  - ▶ The species we see now have survived for billions of years (if we include ancestral species, who also had to survive)
    - ▶ Floods, fires, ice ages, disease outbreaks
- ▶ All “successful” organisms have strategies for spreading risk

# Bet hedging

- ▶ In a risky world, you never want to put all your eggs in the same basket
  - ▶ If all your offspring are born into similar conditions, they can all do well together – or they can all die together
- ▶ Strategies that *usually* do well aren't good enough
  - ▶ The species we see now have survived for billions of years (if we include ancestral species, who also had to survive)
    - ▶ Floods, fires, ice ages, disease outbreaks
- ▶ All “successful” organisms have strategies for spreading risk
  - ▶ \*

# Bet hedging

- ▶ In a risky world, you never want to put all your eggs in the same basket
  - ▶ If all your offspring are born into similar conditions, they can all do well together – or they can all die together
- ▶ Strategies that *usually* do well aren't good enough
  - ▶ The species we see now have survived for billions of years (if we include ancestral species, who also had to survive)
    - ▶ Floods, fires, ice ages, disease outbreaks
- ▶ All “successful” organisms have strategies for spreading risk
  - ▶ \* By successful organism, I mean surviving organism

# Bet hedging

- ▶ In a risky world, you never want to put all your eggs in the same basket
  - ▶ If all your offspring are born into similar conditions, they can all do well together – or they can all die together
- ▶ Strategies that *usually* do well aren't good enough
  - ▶ The species we see now have survived for billions of years (if we include ancestral species, who also had to survive)
    - ▶ Floods, fires, ice ages, disease outbreaks
- ▶ All “successful” organisms have strategies for spreading risk
  - ▶ \* By successful organism, I mean surviving organism

# Averaging

- Mathematically, we can think about bet-hedging strategies in terms of averages

# Averaging

- ▶ Mathematically, we can think about bet-hedging strategies in terms of averages
- ▶ Arithmetic means are means with respect to addition:

# Averaging

- ▶ Mathematically, we can think about bet-hedging strategies in terms of averages
- ▶ Arithmetic means are means with respect to addition:
  - ▶  $x + y + z = m + m + m$

# Averaging

- ▶ Mathematically, we can think about bet-hedging strategies in terms of averages
- ▶ Arithmetic means are means with respect to addition:
  - ▶  $x + y + z = m + m + m$
- ▶ Geometric means are means with respect to multiplication:

# Averaging

- ▶ Mathematically, we can think about bet-hedging strategies in terms of averages
- ▶ Arithmetic means are means with respect to addition:
  - ▶  $x + y + z = m + m + m$
- ▶ Geometric means are means with respect to multiplication:
  - ▶  $x * y * z = m * m * m$

## Averaging

- ▶ Mathematically, we can think about bet-hedging strategies in terms of averages
- ▶ Arithmetic means are means with respect to addition:
  - ▶  $x + y + z = m + m + m$
- ▶ Geometric means are means with respect to multiplication:
  - ▶  $x * y * z = m * m * m$

## Averaging

- A population has a different growth rate ( $\lambda$ ) each year. The long term growth rate would be the same if it grew by what constant amount each year?

## Averaging

- ▶ A population has a different growth rate ( $\lambda$ ) each year. The long term growth rate would be the same if it grew by what constant amount each year?
  - ▶ \*

## Averaging

- ▶ A population has a different growth rate ( $\lambda$ ) each year. The long term growth rate would be the same if it grew by what constant amount each year?
  - ▶ \* The geometric mean growth rate

## Averaging

- ▶ A population has a different growth rate ( $\lambda$ ) each year. The long term growth rate would be the same if it grew by what constant amount each year?
  - ▶ \* The geometric mean growth rate
- ▶ A farmer harvests dandelion seeds from 5 different fields. Each field produces a different number of seeds. The harvest would be the same if each field produced what constant amount?

## Averaging

- ▶ A population has a different growth rate ( $\lambda$ ) each year. The long term growth rate would be the same if it grew by what constant amount each year?
  - ▶ \* The geometric mean growth rate
- ▶ A farmer harvests dandelion seeds from 5 different fields. Each field produces a different number of seeds. The harvest would be the same if each field produced what constant amount?
  - ▶ \*

## Averaging

- ▶ A population has a different growth rate ( $\lambda$ ) each year. The long term growth rate would be the same if it grew by what constant amount each year?
  - ▶ \* The geometric mean growth rate
- ▶ A farmer harvests dandelion seeds from 5 different fields. Each field produces a different number of seeds. The harvest would be the same if each field produced what constant amount?
  - ▶ \* The arithmetic mean seed production

## Averaging

- ▶ A population has a different growth rate ( $\lambda$ ) each year. The long term growth rate would be the same if it grew by what constant amount each year?
  - ▶ \* The geometric mean growth rate
- ▶ A farmer harvests dandelion seeds from 5 different fields. Each field produces a different number of seeds. The harvest would be the same if each field produced what constant amount?
  - ▶ \* The arithmetic mean seed production

## Example: plant Q

- ▶ Plant Q is an annual plant.

## Example: plant Q

- ▶ Plant Q is an annual plant.
- ▶ Each successful adult produces 30 offspring on average

## Example: plant Q

- ▶ Plant Q is an annual plant.
- ▶ Each successful adult produces 30 offspring on average
- ▶ In a good year, 20% of these offspring survive to reproduce; in a normal year 2% of the offspring survive to reproduce; in a bad year 0.2% of the offspring survive to reproduce

## Example: plant Q

- ▶ Plant Q is an annual plant.
- ▶ Each successful adult produces 30 offspring on average
- ▶ In a good year, 20% of these offspring survive to reproduce; in a normal year 2% of the offspring survive to reproduce; in a bad year 0.2% of the offspring survive to reproduce
- ▶ The three kinds of year are equally likely

## Example: plant Q

- ▶ Plant Q is an annual plant.
- ▶ Each successful adult produces 30 offspring on average
- ▶ In a good year, 20% of these offspring survive to reproduce; in a normal year 2% of the offspring survive to reproduce; in a bad year 0.2% of the offspring survive to reproduce
- ▶ The three kinds of year are equally likely
- ▶ Poll: What is the long term average growth rate of plant Q?

## Example: plant Q

- ▶ Plant Q is an annual plant.
- ▶ Each successful adult produces 30 offspring on average
- ▶ In a good year, 20% of these offspring survive to reproduce; in a normal year 2% of the offspring survive to reproduce; in a bad year 0.2% of the offspring survive to reproduce
- ▶ The three kinds of year are equally likely
- ▶ Poll: What is the long term average growth rate of plant Q?
  - ▶ \*

## Example: plant Q

- ▶ Plant Q is an annual plant.
- ▶ Each successful adult produces 30 offspring on average
- ▶ In a good year, 20% of these offspring survive to reproduce; in a normal year 2% of the offspring survive to reproduce; in a bad year 0.2% of the offspring survive to reproduce
- ▶ The three kinds of year are equally likely
- ▶ Poll: What is the long term average growth rate of plant Q?
  - ▶ \* The geometric mean of 6, 0.6 and 0.06:  $\lambda = 0.6$

## Example: plant Q

- ▶ Plant Q is an annual plant.
- ▶ Each successful adult produces 30 offspring on average
- ▶ In a good year, 20% of these offspring survive to reproduce; in a normal year 2% of the offspring survive to reproduce; in a bad year 0.2% of the offspring survive to reproduce
- ▶ The three kinds of year are equally likely
- ▶ Poll: What is the long term average growth rate of plant Q?
  - ▶ \* The geometric mean of 6, 0.6 and 0.06:  $\lambda = 0.6$

## Plant D

- ▶ Plant D is similar to plant Q, except that it produces seeds that disperse over great distances

## Plant D

- ▶ Plant D is similar to plant Q, except that it produces seeds that disperse over great distances
- ▶ Because it has to invest in dispersal mechanisms, it only produces half as many seeds.

## Plant D

- ▶ Plant D is similar to plant Q, except that it produces seeds that disperse over great distances
- ▶ Because it has to invest in dispersal mechanisms, it only produces half as many seeds.
- ▶ The seeds of the new variety do just as well as those of plant Q, but they disperse so far (in this hypothetical example) that 1/3 of them experience good, normal and bad conditions every year.

## Plant D

- ▶ Plant D is similar to plant Q, except that it produces seeds that disperse over great distances
- ▶ Because it has to invest in dispersal mechanisms, it only produces half as many seeds.
- ▶ The seeds of the new variety do just as well as those of plant Q, but they disperse so far (in this hypothetical example) that 1/3 of them experience good, normal and bad conditions every year.
- ▶ Poll: What is the average growth rate of plant D?

## Plant D

- ▶ Plant D is similar to plant Q, except that it produces seeds that disperse over great distances
- ▶ Because it has to invest in dispersal mechanisms, it only produces half as many seeds.
- ▶ The seeds of the new variety do just as well as those of plant Q, but they disperse so far (in this hypothetical example) that 1/3 of them experience good, normal and bad conditions every year.
- ▶ Poll: What is the average growth rate of plant D?
  - ▶ \*

## Plant D

- ▶ Plant D is similar to plant Q, except that it produces seeds that disperse over great distances
- ▶ Because it has to invest in dispersal mechanisms, it only produces half as many seeds.
- ▶ The seeds of the new variety do just as well as those of plant Q, but they disperse so far (in this hypothetical example) that 1/3 of them experience good, normal and bad conditions every year.
- ▶ Poll: What is the average growth rate of plant D?
  - ▶ \* Average survival is the mean of 0.2, 0.02, and 0.002

## Plant D

- ▶ Plant D is similar to plant Q, except that it produces seeds that disperse over great distances
- ▶ Because it has to invest in dispersal mechanisms, it only produces half as many seeds.
- ▶ The seeds of the new variety do just as well as those of plant Q, but they disperse so far (in this hypothetical example) that 1/3 of them experience good, normal and bad conditions every year.
- ▶ Poll: What is the average growth rate of plant D?
  - ▶ \* Average survival is the mean of 0.2, 0.02, and 0.002
  - ▶ \*

## Plant D

- ▶ Plant D is similar to plant Q, except that it produces seeds that disperse over great distances
- ▶ Because it has to invest in dispersal mechanisms, it only produces half as many seeds.
- ▶ The seeds of the new variety do just as well as those of plant Q, but they disperse so far (in this hypothetical example) that 1/3 of them experience good, normal and bad conditions every year.
- ▶ Poll: What is the average growth rate of plant D?
  - ▶ \* Average survival is the mean of 0.2, 0.02, and 0.002
  - ▶ \* Growth is the arithmetic mean of 3, 0.3 and 0.03:  $\lambda = 1.11$

## Plant D

- ▶ Plant D is similar to plant Q, except that it produces seeds that disperse over great distances
- ▶ Because it has to invest in dispersal mechanisms, it only produces half as many seeds.
- ▶ The seeds of the new variety do just as well as those of plant Q, but they disperse so far (in this hypothetical example) that 1/3 of them experience good, normal and bad conditions every year.
- ▶ Poll: What is the average growth rate of plant D?
  - ▶ \* Average survival is the mean of 0.2, 0.02, and 0.002
  - ▶ \* Growth is the arithmetic mean of 3, 0.3 and 0.03:  $\lambda = 1.11$

# Averaging

- Variation between organism generations is multiplicative; we understand its effect using the geometric mean

## Averaging

- ▶ Variation between organism generations is multiplicative; we understand its effect using the geometric mean

▶ \*

# Averaging

- ▶ Variation between organism generations is multiplicative; we understand its effect using the geometric mean
  - ▶ \* Because we multiply per-capita success in each generation to find out what happens to the population

# Averaging

- ▶ Variation between organism generations is multiplicative; we understand its effect using the geometric mean
  - ▶ \* Because we multiply per-capita success in each generation to find out what happens to the population
- ▶ Variation within a generation is additive; we understand its effect using the arithmetic mean

## Averaging

- ▶ Variation between organism generations is multiplicative; we understand its effect using the geometric mean
  - ▶ \* Because we multiply per-capita success in each generation to find out what happens to the population
- ▶ Variation within a generation is additive; we understand its effect using the arithmetic mean
  - ▶ \*

## Averaging

- ▶ Variation between organism generations is multiplicative; we understand its effect using the geometric mean
  - ▶ \* Because we multiply per-capita success in each generation to find out what happens to the population
- ▶ Variation within a generation is additive; we understand its effect using the arithmetic mean
  - ▶ \* Because lifetime reproductive success is calculated by adding components from different places or time periods

# Averaging

- ▶ Variation between organism generations is multiplicative; we understand its effect using the geometric mean
  - ▶ \* Because we multiply per-capita success in each generation to find out what happens to the population
- ▶ Variation within a generation is additive; we understand its effect using the arithmetic mean
  - ▶ \* Because lifetime reproductive success is calculated by adding components from different places or time periods
- ▶ The arithmetic mean is greater than the geometric mean. When variation is high, it can be much greater

# Averaging

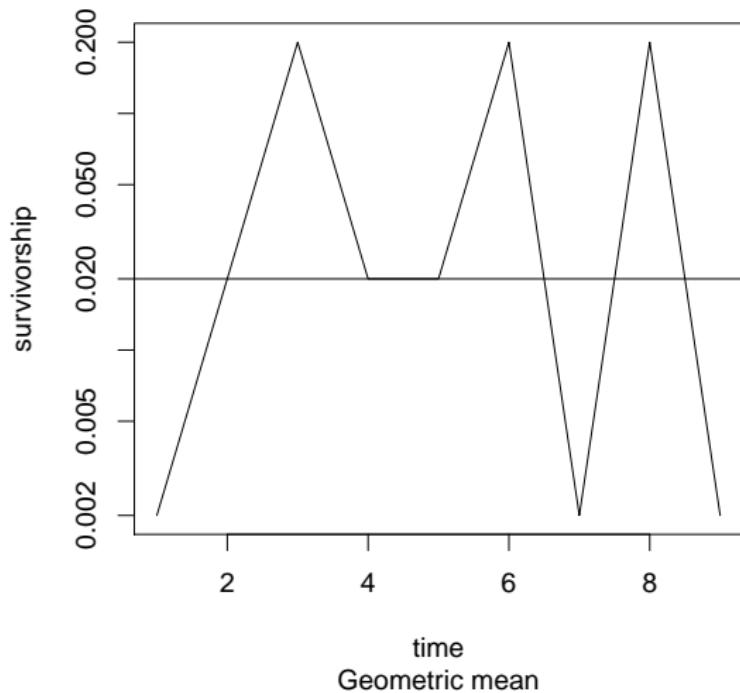
- ▶ Variation between organism generations is multiplicative; we understand its effect using the geometric mean
  - ▶ \* Because we multiply per-capita success in each generation to find out what happens to the population
- ▶ Variation within a generation is additive; we understand its effect using the arithmetic mean
  - ▶ \* Because lifetime reproductive success is calculated by adding components from different places or time periods
- ▶ The arithmetic mean is greater than the geometric mean. When variation is high, it can be much greater
  - ▶ Therefore, organisms benefit from averaging within generations, rather than between generations

# Averaging

- ▶ Variation between organism generations is multiplicative; we understand its effect using the geometric mean
  - ▶ \* Because we multiply per-capita success in each generation to find out what happens to the population
- ▶ Variation within a generation is additive; we understand its effect using the arithmetic mean
  - ▶ \* Because lifetime reproductive success is calculated by adding components from different places or time periods
- ▶ The arithmetic mean is greater than the geometric mean. When variation is high, it can be much greater
  - ▶ Therefore, organisms benefit from averaging within generations, rather than between generations

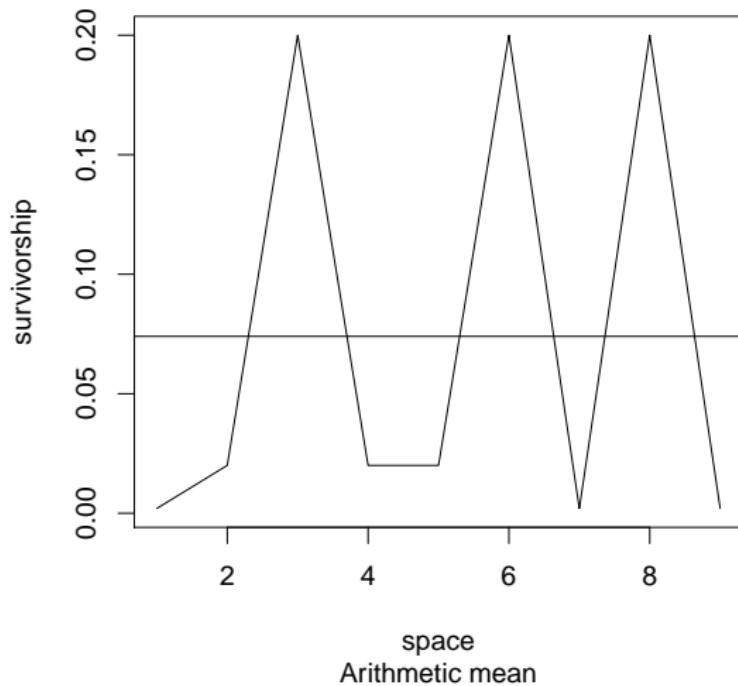
# Comparing averages

## Averaging between generations

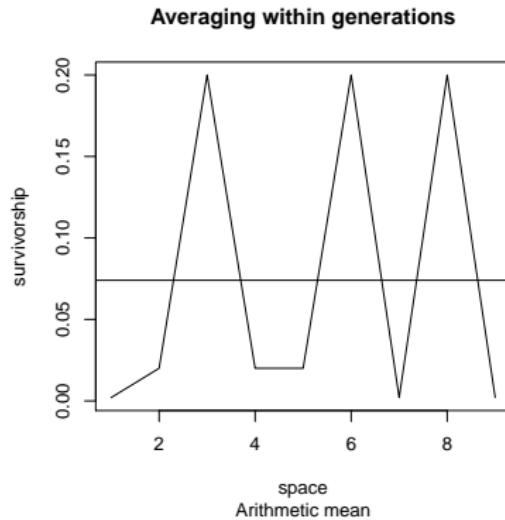
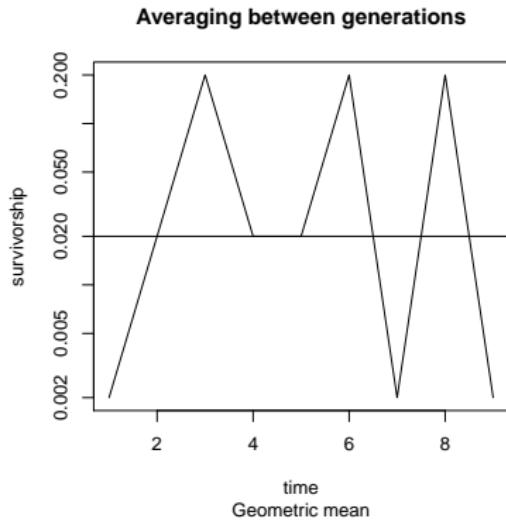


# Comparing averages

## Averaging within generations



# Comparing averages



# Dispersal, spreading risk over space

- As an organism, do I want my offspring to grow up where I grew up, or to disperse?

# Dispersal, spreading risk over space

- ▶ As an organism, do I want my offspring to grow up where I grew up, or to disperse?
- ▶ Advantages of staying home

## Dispersal, spreading risk over space

- ▶ As an organism, do I want my offspring to grow up where I grew up, or to disperse?
- ▶ Advantages of staying home
  - ▶ \*

# Dispersal, spreading risk over space

- ▶ As an organism, do I want my offspring to grow up where I grew up, or to disperse?
- ▶ Advantages of staying home
  - ▶ \* Dispersal is costly

# Dispersal, spreading risk over space

- ▶ As an organism, do I want my offspring to grow up where I grew up, or to disperse?
- ▶ Advantages of staying home
  - ▶ \* Dispersal is costly
  - ▶ \*

## Dispersal, spreading risk over space

- ▶ As an organism, do I want my offspring to grow up where I grew up, or to disperse?
- ▶ Advantages of staying home
  - ▶ \* Dispersal is costly
  - ▶ \* Home is apparently a good place to survive

# Dispersal, spreading risk over space

- ▶ As an organism, do I want my offspring to grow up where I grew up, or to disperse?
- ▶ Advantages of staying home
  - ▶ \* Dispersal is costly
  - ▶ \* Home is apparently a good place to survive
  - ▶ \*

# Dispersal, spreading risk over space

- ▶ As an organism, do I want my offspring to grow up where I grew up, or to disperse?
- ▶ Advantages of staying home
  - ▶ \* Dispersal is costly
  - ▶ \* Home is apparently a good place to survive
    - ▶ \* the parent survived and is reproducing

# Dispersal, spreading risk over space

- ▶ As an organism, do I want my offspring to grow up where I grew up, or to disperse?
- ▶ Advantages of staying home
  - ▶ \* Dispersal is costly
  - ▶ \* Home is apparently a good place to survive
    - ▶ \* the parent survived and is reproducing
  - ▶ \*

# Dispersal, spreading risk over space

- ▶ As an organism, do I want my offspring to grow up where I grew up, or to disperse?
- ▶ Advantages of staying home
  - ▶ \* Dispersal is costly
  - ▶ \* Home is apparently a good place to survive
    - ▶ \* the parent survived and is reproducing
  - ▶ \* Support from kin group

# Dispersal, spreading risk over space

- ▶ As an organism, do I want my offspring to grow up where I grew up, or to disperse?
- ▶ Advantages of staying home
  - ▶ \* Dispersal is costly
  - ▶ \* Home is apparently a good place to survive
    - ▶ \* the parent survived and is reproducing
  - ▶ \* Support from kin group
- ▶ Advantages of dispersal

# Dispersal, spreading risk over space

- ▶ As an organism, do I want my offspring to grow up where I grew up, or to disperse?
- ▶ Advantages of staying home
  - ▶ \* Dispersal is costly
  - ▶ \* Home is apparently a good place to survive
    - ▶ \* the parent survived and is reproducing
  - ▶ \* Support from kin group
- ▶ Advantages of dispersal
  - ▶ \*

# Dispersal, spreading risk over space

- ▶ As an organism, do I want my offspring to grow up where I grew up, or to disperse?
- ▶ Advantages of staying home
  - ▶ \* Dispersal is costly
  - ▶ \* Home is apparently a good place to survive
    - ▶ \* the parent survived and is reproducing
  - ▶ \* Support from kin group
- ▶ Advantages of dispersal
  - ▶ \* Reduce competition between offspring

# Dispersal, spreading risk over space

- ▶ As an organism, do I want my offspring to grow up where I grew up, or to disperse?
- ▶ Advantages of staying home
  - ▶ \* Dispersal is costly
  - ▶ \* Home is apparently a good place to survive
    - ▶ \* the parent survived and is reproducing
  - ▶ \* Support from kin group
- ▶ Advantages of dispersal
  - ▶ \* Reduce competition between offspring
  - ▶ \*

# Dispersal, spreading risk over space

- ▶ As an organism, do I want my offspring to grow up where I grew up, or to disperse?
- ▶ Advantages of staying home
  - ▶ \* Dispersal is costly
  - ▶ \* Home is apparently a good place to survive
    - ▶ \* the parent survived and is reproducing
  - ▶ \* Support from kin group
- ▶ Advantages of dispersal
  - ▶ \* Reduce competition between offspring
  - ▶ \* Distribute risk – if you don't disperse, *all* of your offspring could die if there is a disturbance

# Dispersal, spreading risk over space

- ▶ As an organism, do I want my offspring to grow up where I grew up, or to disperse?
- ▶ Advantages of staying home
  - ▶ \* Dispersal is costly
  - ▶ \* Home is apparently a good place to survive
    - ▶ \* the parent survived and is reproducing
  - ▶ \* Support from kin group
- ▶ Advantages of dispersal
  - ▶ \* Reduce competition between offspring
  - ▶ \* Distribute risk – if you don't disperse, *all* of your offspring could die if there is a disturbance
  - ▶ \*

# Dispersal, spreading risk over space

- ▶ As an organism, do I want my offspring to grow up where I grew up, or to disperse?
- ▶ Advantages of staying home
  - ▶ \* Dispersal is costly
  - ▶ \* Home is apparently a good place to survive
    - ▶ \* the parent survived and is reproducing
  - ▶ \* Support from kin group
- ▶ Advantages of dispersal
  - ▶ \* Reduce competition between offspring
  - ▶ \* Distribute risk – if you don't disperse, *all* of your offspring could die if there is a disturbance
  - ▶ \* Reduce inbreeding

# Dispersal, spreading risk over space

- ▶ As an organism, do I want my offspring to grow up where I grew up, or to disperse?
- ▶ Advantages of staying home
  - ▶ \* Dispersal is costly
  - ▶ \* Home is apparently a good place to survive
    - ▶ \* the parent survived and is reproducing
  - ▶ \* Support from kin group
- ▶ Advantages of dispersal
  - ▶ \* Reduce competition between offspring
  - ▶ \* Distribute risk – if you don't disperse, *all* of your offspring could die if there is a disturbance
  - ▶ \* Reduce inbreeding
  - ▶ \*

# Dispersal, spreading risk over space

- ▶ As an organism, do I want my offspring to grow up where I grew up, or to disperse?
- ▶ Advantages of staying home
  - ▶ \* Dispersal is costly
  - ▶ \* Home is apparently a good place to survive
    - ▶ \* the parent survived and is reproducing
  - ▶ \* Support from kin group
- ▶ Advantages of dispersal
  - ▶ \* Reduce competition between offspring
  - ▶ \* Distribute risk – if you don't disperse, *all* of your offspring could die if there is a disturbance
  - ▶ \* Reduce inbreeding
  - ▶ \* May find a better place

# Dispersal, spreading risk over space

- ▶ As an organism, do I want my offspring to grow up where I grew up, or to disperse?
- ▶ Advantages of staying home
  - ▶ \* Dispersal is costly
  - ▶ \* Home is apparently a good place to survive
    - ▶ \* the parent survived and is reproducing
  - ▶ \* Support from kin group
- ▶ Advantages of dispersal
  - ▶ \* Reduce competition between offspring
  - ▶ \* Distribute risk – if you don't disperse, *all* of your offspring could die if there is a disturbance
  - ▶ \* Reduce inbreeding
  - ▶ \* May find a better place

# Spreading risk over time

- ▶ Organisms that disperse spread their risk across space

## Spreading risk over time

- ▶ Organisms that disperse spread their risk across space
- ▶ But some disturbances (bad weather, disease outbreaks) may cover very large areas

## Spreading risk over time

- ▶ Organisms that disperse spread their risk across space
- ▶ But some disturbances (bad weather, disease outbreaks) may cover very large areas
- ▶ Many organisms also have mechanisms for spreading risk over time

## Spreading risk over time

- ▶ Organisms that disperse spread their risk across space
- ▶ But some disturbances (bad weather, disease outbreaks) may cover very large areas
- ▶ Many organisms also have mechanisms for spreading risk over time
  - ▶ Iteroparity

# Spreading risk over time

- ▶ Organisms that disperse spread their risk across space
- ▶ But some disturbances (bad weather, disease outbreaks) may cover very large areas
- ▶ Many organisms also have mechanisms for spreading risk over time
  - ▶ Iteroparity
  - ▶ Delayed development: many semelparous organisms have mechanisms that allow a fraction of their offspring to remain **dormant** (ie., wait) before developing

## Spreading risk over time

- ▶ Organisms that disperse spread their risk across space
- ▶ But some disturbances (bad weather, disease outbreaks) may cover very large areas
- ▶ Many organisms also have mechanisms for spreading risk over time
  - ▶ Iteroparity
  - ▶ Delayed development: many semelparous organisms have mechanisms that allow a fraction of their offspring to remain **dormant** (ie., wait) before developing

# Why is it called bet hedging?

- ▶ Bet hedging means reducing your risk, or not betting everything you have on any one choice, even if it's a good choice.

## Why is it called bet hedging?

- ▶ Bet hedging means reducing your risk, or not betting everything you have on any one choice, even if it's a good choice.

▶ \*

# Why is it called bet hedging?

- ▶ Bet hedging means reducing your risk, or not betting everything you have on any one choice, even if it's a good choice.
  - ▶ \* If you don't disperse in space, or spread out risk in time, you are "betting" all of your offspring on a single environment

# Why is it called bet hedging?

- ▶ Bet hedging means reducing your risk, or not betting everything you have on any one choice, even if it's a good choice.
  - ▶ \* If you don't disperse in space, or spread out risk in time, you are "betting" all of your offspring on a single environment

# Outline

Introduction

Tradeoffs

The  $r$  vs.  $K$  metaphor

Bet hedging

Sex ratios

## Sex ratios

- ▶ Poll: To maximize fitness, should organisms allocate more resources to producing males or females?

## Sex ratios

- ▶ Poll: To maximize fitness, should organisms allocate more resources to producing males or females?
  - ▶ \*

## Sex ratios

- ▶ Poll: To maximize fitness, should organisms allocate more resources to producing males or females?
  - ▶ \* They should allocate more resources to females because it is females that limit the growth rate

## Sex ratios

- ▶ Poll: To maximize fitness, should organisms allocate more resources to producing males or females?
  - ▶ \* They should allocate more resources to females because it is females that limit the growth rate
  - ▶ \*

## Sex ratios

- ▶ Poll: To maximize fitness, should organisms allocate more resources to producing males or females?
  - ▶ \* They should allocate more resources to females because it is females that limit the growth rate
  - ▶ \* They should allocate the same amount of resources to males and females because males and females contribute the same amount of fitness to the next generation

## Sex ratios

- ▶ Poll: To maximize fitness, should organisms allocate more resources to producing males or females?
  - ▶ \* They should allocate more resources to females because it is females that limit the growth rate
  - ▶ \* They should allocate the same amount of resources to males and females because males and females contribute the same amount of fitness to the next generation
  - ▶ \*

## Sex ratios

- ▶ Poll: To maximize fitness, should organisms allocate more resources to producing males or females?
  - ▶ \* They should allocate more resources to females because it is females that limit the growth rate
  - ▶ \* They should allocate the same amount of resources to males and females because males and females contribute the same amount of fitness to the next generation
  - ▶ \* They should allocate more resources to males, because males have greater potential reproductive success

## Sex ratios

- ▶ Poll: To maximize fitness, should organisms allocate more resources to producing males or females?
  - ▶ \* They should allocate more resources to females because it is females that limit the growth rate
  - ▶ \* They should allocate the same amount of resources to males and females because males and females contribute the same amount of fitness to the next generation
  - ▶ \* They should allocate more resources to males, because males have greater potential reproductive success

## The balance argument

- ▶ In a sexual population, half of all the alleles in each generation come from males, and half from females

## The balance argument

- ▶ In a sexual population, half of all the alleles in each generation come from males, and half from females
- ▶ Therefore, the total fitness of males and the total fitness of females in the population is equal

## The balance argument

- ▶ In a sexual population, half of all the alleles in each generation come from males, and half from females
- ▶ Therefore, the total fitness of males and the total fitness of females in the population is equal
- ▶ Therefore, individuals should allocate resources equally to offspring of each type

## The balance argument

- ▶ In a sexual population, half of all the alleles in each generation come from males, and half from females
- ▶ Therefore, the total fitness of males and the total fitness of females in the population is equal
- ▶ Therefore, individuals should allocate resources equally to offspring of each type
  - ▶ \*

## The balance argument

- ▶ In a sexual population, half of all the alleles in each generation come from males, and half from females
- ▶ Therefore, the total fitness of males and the total fitness of females in the population is equal
- ▶ Therefore, individuals should allocate resources equally to offspring of each type
  - ▶ \* If the population on average is allocating more to one type, individuals who allocate more to the other type would do better than average

## The balance argument

- ▶ In a sexual population, half of all the alleles in each generation come from males, and half from females
- ▶ Therefore, the total fitness of males and the total fitness of females in the population is equal
- ▶ Therefore, individuals should allocate resources equally to offspring of each type
  - ▶ \* If the population on average is allocating more to one type, individuals who allocate more to the other type would do better than average

## Example: elephant seals

- ▶ Male elephant seals can control large territories and mate with very large numbers of females



## Example: elephant seals

- ▶ Male elephant seals can control large territories and mate with very large numbers of females
- ▶ Females produce at most 12 offspring over the course of their lives



## Example: elephant seals

- ▶ Male elephant seals can control large territories and mate with very large numbers of females
- ▶ Females produce at most 12 offspring over the course of their lives
  - ▶ And do all of the work of raising them



## Example: elephant seals

- ▶ Male elephant seals can control large territories and mate with very large numbers of females
- ▶ Females produce at most 12 offspring over the course of their lives
  - ▶ And do all of the work of raising them
- ▶ To maximize their fitness, should female elephant seals produce more male offspring, or more female offspring?



## Example: elephant seals

- ▶ Male elephant seals can control large territories and mate with very large numbers of females
- ▶ Females produce at most 12 offspring over the course of their lives
  - ▶ And do all of the work of raising them
- ▶ To maximize their fitness, should female elephant seals produce more male offspring, or more female offspring?



## Elephant seal details

- ▶ Imagine a population where 90% of elephant seals born are males. A certain “generation” of 400 elephant seals produces 600 successful offspring (counting in a reasonable, closed-loop way).

## Elephant seal details

- ▶ Imagine a population where 90% of elephant seals born are males. A certain “generation” of 400 elephant seals produces 600 successful offspring (counting in a reasonable, closed-loop way).
- ▶ What is the average fitness of the males and the females in this generation?

## Elephant seal details

- ▶ Imagine a population where 90% of elephant seals born are males. A certain “generation” of 400 elephant seals produces 600 successful offspring (counting in a reasonable, closed-loop way).
- ▶ What is the average fitness of the males and the females in this generation?
  - ▶ \*

## Elephant seal details

- ▶ Imagine a population where 90% of elephant seals born are males. A certain “generation” of 400 elephant seals produces 600 successful offspring (counting in a reasonable, closed-loop way).
- ▶ What is the average fitness of the males and the females in this generation?
  - ▶ \* Half of the genes, and half of the fitness comes from 360 males; half from 40 females

## Elephant seal details

- ▶ Imagine a population where 90% of elephant seals born are males. A certain “generation” of 400 elephant seals produces 600 successful offspring (counting in a reasonable, closed-loop way).
- ▶ What is the average fitness of the males and the females in this generation?
  - ▶ \* Half of the genes, and half of the fitness comes from 360 males; half from 40 females
  - ▶ \*

## Elephant seal details

- ▶ Imagine a population where 90% of elephant seals born are males. A certain “generation” of 400 elephant seals produces 600 successful offspring (counting in a reasonable, closed-loop way).
- ▶ What is the average fitness of the males and the females in this generation?
  - ▶ \* Half of the genes, and half of the fitness comes from 360 males; half from 40 females
  - ▶ \* Males' average fitness is  $300/360=0.83$ ; females' is  $300/40 = 7.5$

## Elephant seal details

- ▶ Imagine a population where 90% of elephant seals born are males. A certain “generation” of 400 elephant seals produces 600 successful offspring (counting in a reasonable, closed-loop way).
- ▶ What is the average fitness of the males and the females in this generation?
  - ▶ \* Half of the genes, and half of the fitness comes from 360 males; half from 40 females
  - ▶ \* Males' average fitness is  $300/360=0.83$ ; females' is  $300/40 = 7.5$

## Sex ratio and balance

- ▶ Imagine a population where organisms use the same amount of resources to produce male or female offspring

## Sex ratio and balance

- ▶ Imagine a population where organisms use the same amount of resources to produce male or female offspring
- ▶ Thus, the *number* of offspring I can make does not depend on sex

## Sex ratio and balance

- ▶ Imagine a population where organisms use the same amount of resources to produce male or female offspring
- ▶ Thus, the *number* of offspring I can make does not depend on sex
- ▶ Poll: If everyone else is making more males than females, what should I do?

## Sex ratio and balance

- ▶ Imagine a population where organisms use the same amount of resources to produce male or female offspring
- ▶ Thus, the *number* of offspring I can make does not depend on sex
- ▶ Poll: If everyone else is making more males than females, what should I do?
  - ▶ \*

## Sex ratio and balance

- ▶ Imagine a population where organisms use the same amount of resources to produce male or female offspring
- ▶ Thus, the *number* of offspring I can make does not depend on sex
- ▶ Poll: If everyone else is making more males than females, what should I do?
  - ▶ \* Make more females, because that will increase my average fitness

## Sex ratio and balance

- ▶ Imagine a population where organisms use the same amount of resources to produce male or female offspring
- ▶ Thus, the *number* of offspring I can make does not depend on sex
- ▶ Poll: If everyone else is making more males than females, what should I do?
  - ▶ \* Make more females, because that will increase my average fitness
- ▶ Poll: How will this population evolve in the long term?

## Sex ratio and balance

- ▶ Imagine a population where organisms use the same amount of resources to produce male or female offspring
- ▶ Thus, the *number* of offspring I can make does not depend on sex
- ▶ Poll: If everyone else is making more males than females, what should I do?
  - ▶ \* Make more females, because that will increase my average fitness
- ▶ Poll: How will this population evolve in the long term?
  - ▶ \*

## Sex ratio and balance

- ▶ Imagine a population where organisms use the same amount of resources to produce male or female offspring
- ▶ Thus, the *number* of offspring I can make does not depend on sex
- ▶ Poll: If everyone else is making more males than females, what should I do?
  - ▶ \* Make more females, because that will increase my average fitness
- ▶ Poll: How will this population evolve in the long term?
  - ▶ \* More and more females

## Sex ratio and balance

- ▶ Imagine a population where organisms use the same amount of resources to produce male or female offspring
- ▶ Thus, the *number* of offspring I can make does not depend on sex
- ▶ Poll: If everyone else is making more males than females, what should I do?
  - ▶ \* Make more females, because that will increase my average fitness
- ▶ Poll: How will this population evolve in the long term?
  - ▶ \* More and more females
  - ▶ \*

## Sex ratio and balance

- ▶ Imagine a population where organisms use the same amount of resources to produce male or female offspring
- ▶ Thus, the *number* of offspring I can make does not depend on sex
- ▶ Poll: If everyone else is making more males than females, what should I do?
  - ▶ \* Make more females, because that will increase my average fitness
- ▶ Poll: How will this population evolve in the long term?
  - ▶ \* More and more females
  - ▶ \* Eventually, a balanced sex ratio

## Sex ratio and balance

- ▶ Imagine a population where organisms use the same amount of resources to produce male or female offspring
- ▶ Thus, the *number* of offspring I can make does not depend on sex
- ▶ Poll: If everyone else is making more males than females, what should I do?
  - ▶ \* Make more females, because that will increase my average fitness
- ▶ Poll: How will this population evolve in the long term?
  - ▶ \* More and more females
  - ▶ \* Eventually, a balanced sex ratio

## Allocation and balance

- The balance argument is based on the idea that organisms have resources that they control and use for growth and reproduction

## Allocation and balance

- ▶ The balance argument is based on the idea that organisms have resources that they control and use for growth and reproduction
- ▶ What if organisms invest more resources in producing one sex than the other?

## Allocation and balance

- ▶ The balance argument is based on the idea that organisms have resources that they control and use for growth and reproduction
- ▶ What if organisms invest more resources in producing one sex than the other?
  - ▶ *What balances is the amount of resources spent on each sex*

## Allocation and balance

- ▶ The balance argument is based on the idea that organisms have resources that they control and use for growth and reproduction
- ▶ What if organisms invest more resources in producing one sex than the other?
  - ▶ What balances is the amount of *resources* spent on each sex
- ▶ Example: what if elephant seal mothers invest twice as much per males as per female, so their male offspring can compete?

## Allocation and balance

- ▶ The balance argument is based on the idea that organisms have resources that they control and use for growth and reproduction
- ▶ What if organisms invest more resources in producing one sex than the other?
  - ▶ What balances is the amount of *resources* spent on each sex
- ▶ Example: what if elephant seal mothers invest twice as much per males as per female, so their male offspring can compete?
  - ▶ \*

## Allocation and balance

- ▶ The balance argument is based on the idea that organisms have resources that they control and use for growth and reproduction
- ▶ What if organisms invest more resources in producing one sex than the other?
  - ▶ What balances is the amount of *resources* spent on each sex
- ▶ Example: what if elephant seal mothers invest twice as much per males as per female, so their male offspring can compete?
  - ▶ \* This means they can “choose” to produce one male, or two females

## Allocation and balance

- ▶ The balance argument is based on the idea that organisms have resources that they control and use for growth and reproduction
- ▶ What if organisms invest more resources in producing one sex than the other?
  - ▶ What balances is the amount of *resources* spent on each sex
- ▶ Example: what if elephant seal mothers invest twice as much per males as per female, so their male offspring can compete?
  - ▶ \* This means they can “choose” to produce one male, or two females
  - ▶ \*

## Allocation and balance

- ▶ The balance argument is based on the idea that organisms have resources that they control and use for growth and reproduction
- ▶ What if organisms invest more resources in producing one sex than the other?
  - ▶ What balances is the amount of *resources* spent on each sex
- ▶ Example: what if elephant seal mothers invest twice as much per males as per female, so their male offspring can compete?
  - ▶ \* This means they can “choose” to produce one male, or two females
  - ▶ \* Thus, the population will balance when male fitness is twice as high as female fitness

## Allocation and balance

- ▶ The balance argument is based on the idea that organisms have resources that they control and use for growth and reproduction
- ▶ What if organisms invest more resources in producing one sex than the other?
  - ▶ What balances is the amount of *resources* spent on each sex
- ▶ Example: what if elephant seal mothers invest twice as much per males as per female, so their male offspring can compete?
  - ▶ \* This means they can “choose” to produce one male, or two females
  - ▶ \* Thus, the population will balance when male fitness is twice as high as female fitness
  - ▶ \*

## Allocation and balance

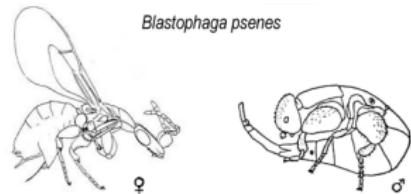
- ▶ The balance argument is based on the idea that organisms have resources that they control and use for growth and reproduction
- ▶ What if organisms invest more resources in producing one sex than the other?
  - ▶ What balances is the amount of *resources* spent on each sex
- ▶ Example: what if elephant seal mothers invest twice as much per males as per female, so their male offspring can compete?
  - ▶ \* This means they can “choose” to produce one male, or two females
  - ▶ \* Thus, the population will balance when male fitness is twice as high as female fitness
  - ▶ \* This happens when there are twice as many females as males – the *investment* in the two sexes is the same.

## Allocation and balance

- ▶ The balance argument is based on the idea that organisms have resources that they control and use for growth and reproduction
- ▶ What if organisms invest more resources in producing one sex than the other?
  - ▶ What balances is the amount of *resources* spent on each sex
- ▶ Example: what if elephant seal mothers invest twice as much per males as per female, so their male offspring can compete?
  - ▶ \* This means they can “choose” to produce one male, or two females
  - ▶ \* Thus, the population will balance when male fitness is twice as high as female fitness
  - ▶ \* This happens when there are twice as many females as males – the *investment* in the two sexes is the same.

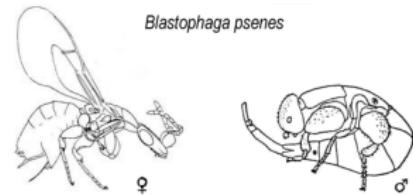
## Example: Fig wasps

- Many species of fig wasps have sex inside figs



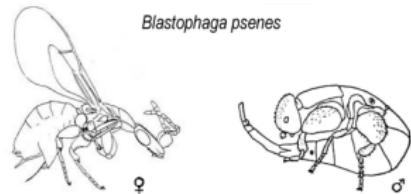
## Example: Fig wasps

- ▶ Many species of fig wasps have sex inside figs
  - ▶ Most sex is between brothers and sisters



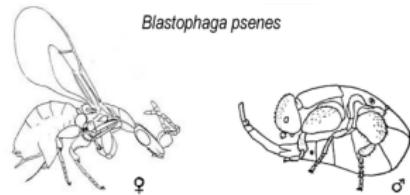
## Example: Fig wasps

- ▶ Many species of fig wasps have sex inside figs
  - ▶ Most sex is between brothers and sisters
  - ▶ Poll: What offspring ratio would maximize the mother's fitness in this case?



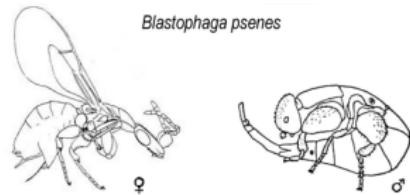
## Example: Fig wasps

- ▶ Many species of fig wasps have sex inside figs
  - ▶ Most sex is between brothers and sisters
  - ▶ Poll: What offspring ratio would maximize the mother's fitness in this case?
    - ▶ \*



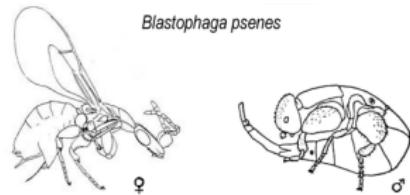
## Example: Fig wasps

- ▶ Many species of fig wasps have sex inside figs
  - ▶ Most sex is between brothers and sisters
  - ▶ Poll: What offspring ratio would maximize the mother's fitness in this case?
    - ▶ \* Have mostly female offspring



## Example: Fig wasps

- ▶ Many species of fig wasps have sex inside figs
  - ▶ Most sex is between brothers and sisters
  - ▶ Poll: What offspring ratio would maximize the mother's fitness in this case?
    - ▶ \* Have mostly female offspring



## Fig wasp details

- ▶ Why does the balance argument not work in this case?

## Fig wasp details

- ▶ Why does the balance argument not work in this case?
- ▶ Males have higher mean fitness than females in this population

## Fig wasp details

- ▶ Why does the balance argument not work in this case?
- ▶ Males have higher mean fitness than females in this population
- ▶ Would a mother benefit by producing more males than others do?

## Fig wasp details

- ▶ Why does the balance argument not work in this case?
- ▶ Males have higher mean fitness than females in this population
- ▶ Would a mother benefit by producing more males than others do?
  - ▶ \*

## Fig wasp details

- ▶ Why does the balance argument not work in this case?
- ▶ Males have higher mean fitness than females in this population
- ▶ Would a mother benefit by producing more males than others do?
  - ▶ \* No, because these males would not have access to the extra females produced by other mothers

## Fig wasp details

- ▶ Why does the balance argument not work in this case?
- ▶ Males have higher mean fitness than females in this population
- ▶ Would a mother benefit by producing more males than others do?
  - ▶ \* No, because these males would not have access to the extra females produced by other mothers
  - ▶ \*

## Fig wasp details

- ▶ Why does the balance argument not work in this case?
- ▶ Males have higher mean fitness than females in this population
- ▶ Would a mother benefit by producing more males than others do?
  - ▶ \* No, because these males would not have access to the extra females produced by other mothers
  - ▶ \* Producing males because average male fitness is higher works only if your males can *share* that average fitness

## Fig wasp details

- ▶ Why does the balance argument not work in this case?
- ▶ Males have higher mean fitness than females in this population
- ▶ Would a mother benefit by producing more males than others do?
  - ▶ \* No, because these males would not have access to the extra females produced by other mothers
  - ▶ \* Producing males because average male fitness is higher works only if your males can *share* that average fitness
  - ▶ \*

## Fig wasp details

- ▶ Why does the balance argument not work in this case?
- ▶ Males have higher mean fitness than females in this population
- ▶ Would a mother benefit by producing more males than others do?
  - ▶ \* No, because these males would not have access to the extra females produced by other mothers
  - ▶ \* Producing males because average male fitness is higher works only if your males can share that average fitness
  - ▶ \* In this case, if I produce more males, they would probably compete only with their brothers

## Fig wasp details

- ▶ Why does the balance argument not work in this case?
- ▶ Males have higher mean fitness than females in this population
- ▶ Would a mother benefit by producing more males than others do?
  - ▶ \* No, because these males would not have access to the extra females produced by other mothers
  - ▶ \* Producing males because average male fitness is higher works only if your males can share that average fitness
  - ▶ \* In this case, if I produce more males, they would probably compete only with their brothers

## Female-biased sex ratios

- In most organisms (not all) females contribute more direct resources to producing offspring than males

## Female-biased sex ratios

- ▶ In most organisms (not all) females contribute more direct resources to producing offspring than males
- ▶ Such organisms should invest more in females than in males whenever sex with kin is likely

## Female-biased sex ratios

- ▶ In most organisms (not all) females contribute more direct resources to producing offspring than males
- ▶ Such organisms should invest more in females than in males whenever sex with kin is likely
  - ▶ The kin group produces more offspring overall

## Female-biased sex ratios

- ▶ In most organisms (not all) females contribute more direct resources to producing offspring than males
- ▶ Such organisms should invest more in females than in males whenever sex with kin is likely
  - ▶ The kin group produces more offspring overall
- ▶ If organisms invest more per individual male, this could also bias the sex ratio in the same direction

## Female-biased sex ratios

- ▶ In most organisms (not all) females contribute more direct resources to producing offspring than males
- ▶ Such organisms should invest more in females than in males whenever sex with kin is likely
  - ▶ The kin group produces more offspring overall
- ▶ If organisms invest more per individual male, this could also bias the sex ratio in the same direction

## Variation in reproductive success

- You should recall that in many animals males have very large variation in reproductive success

## Variation in reproductive success

- ▶ You should recall that in many animals males have very large variation in reproductive success
- ▶ Variation in reproductive success does not affect the balance argument:

## Variation in reproductive success

- ▶ You should recall that in many animals males have very large variation in reproductive success
- ▶ Variation in reproductive success does not affect the balance argument:
  - ▶ We expect equal total resources to be used for females and males

## Variation in reproductive success

- ▶ You should recall that in many animals males have very large variation in reproductive success
- ▶ Variation in reproductive success does not affect the balance argument:
  - ▶ We expect equal total resources to be used for females and males
- ▶ Instead it affects allocation per individual

## Variation in reproductive success

- ▶ You should recall that in many animals males have very large variation in reproductive success
- ▶ Variation in reproductive success does not affect the balance argument:
  - ▶ We expect equal total resources to be used for females and males
- ▶ Instead it affects allocation per individual
  - ▶ \*

## Variation in reproductive success

- ▶ You should recall that in many animals males have very large variation in reproductive success
- ▶ Variation in reproductive success does not affect the balance argument:
  - ▶ We expect equal total resources to be used for females and males
- ▶ Instead it affects allocation per individual
  - ▶ \* Giving male offspring more resources has greater benefits than for female offspring

## Variation in reproductive success

- ▶ You should recall that in many animals males have very large variation in reproductive success
- ▶ Variation in reproductive success does not affect the balance argument:
  - ▶ We expect equal total resources to be used for females and males
- ▶ Instead it affects allocation per individual
  - ▶ \* Giving male offspring more resources has greater benefits than for female offspring
  - ▶ \*

## Variation in reproductive success

- ▶ You should recall that in many animals males have very large variation in reproductive success
- ▶ Variation in reproductive success does not affect the balance argument:
  - ▶ We expect equal total resources to be used for females and males
- ▶ Instead it affects allocation per individual
  - ▶ \* Giving male offspring more resources has greater benefits than for female offspring
  - ▶ \* Organisms should use more resources per male, and thus produce fewer male offspring

## Variation in reproductive success

- ▶ You should recall that in many animals males have very large variation in reproductive success
- ▶ Variation in reproductive success does not affect the balance argument:
  - ▶ We expect equal total resources to be used for females and males
- ▶ Instead it affects allocation per individual
  - ▶ \* Giving male offspring more resources has greater benefits than for female offspring
  - ▶ \* Organisms should use more resources per male, and thus produce fewer male offspring

## Sexual roles

- ▶ Poll: What do you expect to happen in a population where males contributing more to raising offspring than females do?

## Sexual roles

- ▶ Poll: What do you expect to happen in a population where males contributing more to raising offspring than females do?
  - ▶ \*

## Sexual roles

- ▶ Poll: What do you expect to happen in a population where males contributing more to raising offspring than females do?
  - ▶ \* All of these stories can be reversed

## Sexual roles

- ▶ Poll: What do you expect to happen in a population where males contributing more to raising offspring than females do?
  - ▶ \* All of these stories can be reversed
    - ▶ \*

## Sexual roles

- ▶ Poll: What do you expect to happen in a population where males contributing more to raising offspring than females do?
  - ▶ \* All of these stories can be reversed
  - ▶ \* Females compete for males

## Sexual roles

- ▶ Poll: What do you expect to happen in a population where males contributing more to raising offspring than females do?
  - ▶ \* All of these stories can be reversed
    - ▶ \* Females compete for males
    - ▶ \*

## Sexual roles

- ▶ Poll: What do you expect to happen in a population where males contributing more to raising offspring than females do?
  - ▶ \* All of these stories can be reversed
    - ▶ \* Females compete for males
    - ▶ \* Parents invest more in individual females

## Sexual roles

- ▶ Poll: What do you expect to happen in a population where males contributing more to raising offspring than females do?
  - ▶ \* All of these stories can be reversed
    - ▶ \* Females compete for males
    - ▶ \* Parents invest more in individual females
    - ▶ \*

# Sexual roles

- ▶ Poll: What do you expect to happen in a population where males contributing more to raising offspring than females do?
  - ▶ \* All of these stories can be reversed
    - ▶ \* Females compete for males
    - ▶ \* Parents invest more in individual females
    - ▶ \* Possible male-biased sex ratio

# Sexual roles

- ▶ Poll: What do you expect to happen in a population where males contributing more to raising offspring than females do?
  - ▶ \* All of these stories can be reversed
    - ▶ \* Females compete for males
    - ▶ \* Parents invest more in individual females
    - ▶ \* Possible male-biased sex ratio
- ▶ Can you think of any examples?

## Sexual roles

- ▶ Poll: What do you expect to happen in a population where males contributing more to raising offspring than females do?
  - ▶ \* All of these stories can be reversed
    - ▶ \* Females compete for males
    - ▶ \* Parents invest more in individual females
    - ▶ \* Possible male-biased sex ratio
- ▶ Can you think of any examples?
  - ▶ \*

## Sexual roles

- ▶ Poll: What do you expect to happen in a population where males contributing more to raising offspring than females do?
  - ▶ \* All of these stories can be reversed
    - ▶ \* Females compete for males
    - ▶ \* Parents invest more in individual females
    - ▶ \* Possible male-biased sex ratio
- ▶ Can you think of any examples?
  - ▶ \* Sea horses

# Sexual roles

- ▶ Poll: What do you expect to happen in a population where males contributing more to raising offspring than females do?
  - ▶ \* All of these stories can be reversed
    - ▶ \* Females compete for males
    - ▶ \* Parents invest more in individual females
    - ▶ \* Possible male-biased sex ratio
- ▶ Can you think of any examples?
  - ▶ \* Sea horses
  - ▶ \*

# Sexual roles

- ▶ Poll: What do you expect to happen in a population where males contributing more to raising offspring than females do?
  - ▶ \* All of these stories can be reversed
    - ▶ \* Females compete for males
    - ▶ \* Parents invest more in individual females
    - ▶ \* Possible male-biased sex ratio
- ▶ Can you think of any examples?
  - ▶ \* Sea horses
  - ▶ \* Nest-guarding fish

# Sexual roles

- ▶ Poll: What do you expect to happen in a population where males contributing more to raising offspring than females do?
  - ▶ \* All of these stories can be reversed
    - ▶ \* Females compete for males
    - ▶ \* Parents invest more in individual females
    - ▶ \* Possible male-biased sex ratio
- ▶ Can you think of any examples?
  - ▶ \* Sea horses
  - ▶ \* Nest-guarding fish

# Pregnant seahorse



# Midshipman nest



# Equids



# Equids



# Equids

- Horses and zebras have harem males who compete for access to females

# Equids

- ▶ Horses and zebras have harem males who compete for access to females
- ▶ Successful stallions can have very high fitness

# Equids

- ▶ Horses and zebras have harem males who compete for access to females
- ▶ Successful stallions can have very high fitness
- ▶ Females produce offspring at similar rates through their adult lives

# Equids

- ▶ Horses and zebras have harem males who compete for access to females
- ▶ Successful stallions can have very high fitness
- ▶ Females produce offspring at similar rates through their adult lives
- ▶ Healthy, middle-aged mares produce a greater fraction of males

# Equids

- ▶ Horses and zebras have harem males who compete for access to females
- ▶ Successful stallions can have very high fitness
- ▶ Females produce offspring at similar rates through their adult lives
- ▶ Healthy, middle-aged mares produce a greater fraction of males
  - ▶ Presumably they are allocating more resources to these males (because they have more resources available)

# Equids

- ▶ Horses and zebras have harem males who compete for access to females
- ▶ Successful stallions can have very high fitness
- ▶ Females produce offspring at similar rates through their adult lives
- ▶ Healthy, middle-aged mares produce a greater fraction of males
  - ▶ Presumably they are allocating more resources to these males (because they have more resources available)

## *Equids*

- It is not clear from studies whether they produce fewer males than females over their lifespan to compensate (balance would predict that they should)

# Equids

- ▶ It is not clear from studies whether they produce fewer males than females over their lifespan to compensate (balance would predict that they should)
- ▶ These animals *do* show female-biased sex ratios of adults

# Equids

- ▶ It is not clear from studies whether they produce fewer males than females over their lifespan to compensate (balance would predict that they should)
- ▶ These animals *do* show female-biased sex ratios of adults
- ▶ What is another possible, related reason?

## Equids

- ▶ It is not clear from studies whether they produce fewer males than females over their lifespan to compensate (balance would predict that they should)
- ▶ These animals *do* show female-biased sex ratios of adults
- ▶ What is another possible, related reason?
  - ▶ \*

# Equids

- ▶ It is not clear from studies whether they produce fewer males than females over their lifespan to compensate (balance would predict that they should)
- ▶ These animals *do* show female-biased sex ratios of adults
- ▶ What is another possible, related reason?
  - ▶ \* Males pursue high-risk development strategies, and therefore have lower survival

# Equids

- ▶ It is not clear from studies whether they produce fewer males than females over their lifespan to compensate (balance would predict that they should)
- ▶ These animals *do* show female-biased sex ratios of adults
- ▶ What is another possible, related reason?
  - ▶ \* Males pursue high-risk development strategies, and therefore have lower survival
  - ▶ \*

# Equids

- ▶ It is not clear from studies whether they produce fewer males than females over their lifespan to compensate (balance would predict that they should)
- ▶ These animals *do* show female-biased sex ratios of adults
- ▶ What is another possible, related reason?
  - ▶ \* Males pursue high-risk development strategies, and therefore have lower survival
  - ▶ \* High-risk, aggressive development increases the chance of being dominant and reproductively successful

# Equids

- ▶ It is not clear from studies whether they produce fewer males than females over their lifespan to compensate (balance would predict that they should)
- ▶ These animals *do* show female-biased sex ratios of adults
- ▶ What is another possible, related reason?
  - ▶ \* Males pursue high-risk development strategies, and therefore have lower survival
  - ▶ \* High-risk, aggressive development increases the chance of being dominant and reproductively successful

# Kakapos



# Kakapos

- Researchers tried to save the endangered kakapos by providing food to females.

# Kakapos

- ▶ Researchers tried to save the endangered kakapos by providing food to females.
- ▶ Females responded to these “good years” by producing too many males making population crisis worse

# Kakapos

- ▶ Researchers tried to save the endangered kakapos by providing food to females.
- ▶ Females responded to these “good years” by producing too many males making population crisis worse
- ▶ Consistent with adaptation for resource balance

# Kakapos

- ▶ Researchers tried to save the endangered kakapos by providing food to females.
- ▶ Females responded to these “good years” by producing too many males making population crisis worse
- ▶ Consistent with adaptation for resource balance



# Kakapos

- ▶ Researchers tried to save the endangered kakapos by providing food to females.
- ▶ Females responded to these “good years” by producing too many males making population crisis worse
- ▶ Consistent with adaptation for resource balance

