

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:
- ▶ 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
 - ▶ 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 (present)



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
- ▶ 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 (present)



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 (present)



Between populations (present)



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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 (present)



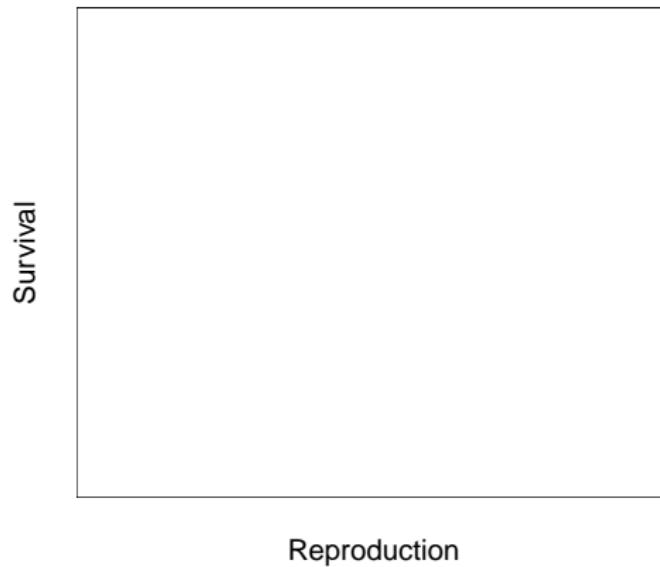
Tradeoffs (present)



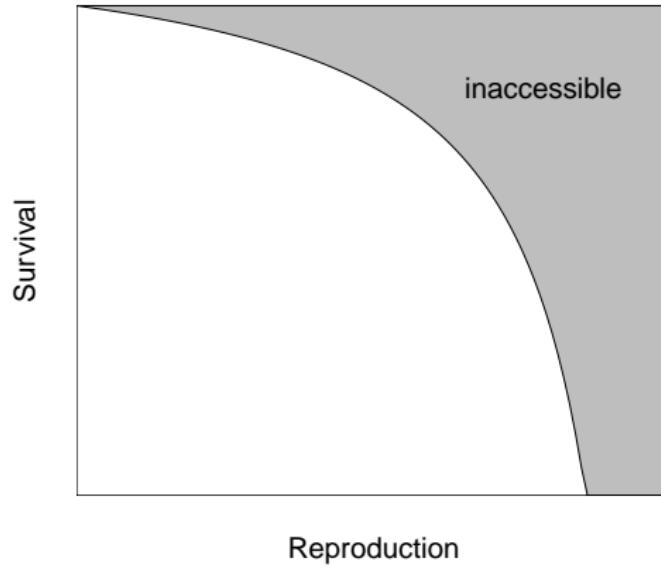
Optimization frontiers

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

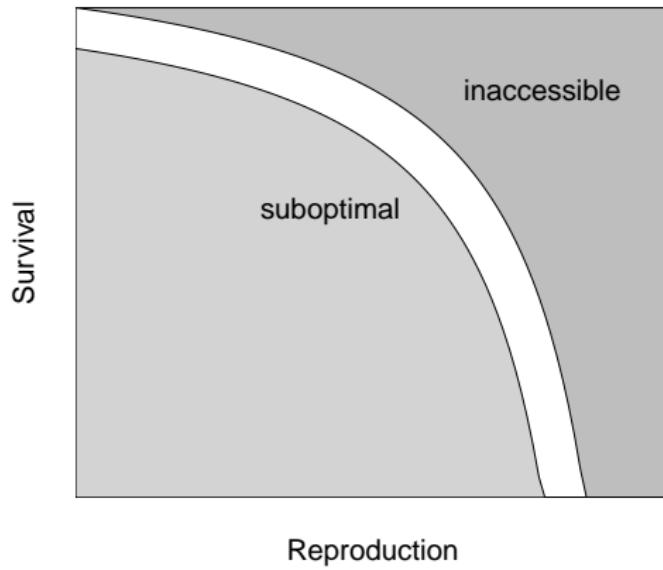
Optimization frontiers (present)



Optimization frontiers (present)

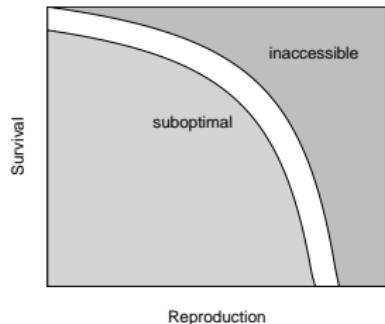


Optimization frontiers



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.
- ▶ 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
- ▶ But they don't know they're doing this
 - ▶ Plants sensing water environments
 - ▶ Moths circling light bulbs
 - ▶ People pursuing sexual opportunities

Programmed optimization (present)



Programmed optimization (present)



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:
 - ▶ 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
- ▶ 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

NULLSLIDE PSLIDE Semele



Cole's paradox (present)



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?
 - ▶ * “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 λ 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 (present)



Responses to Cole (present)



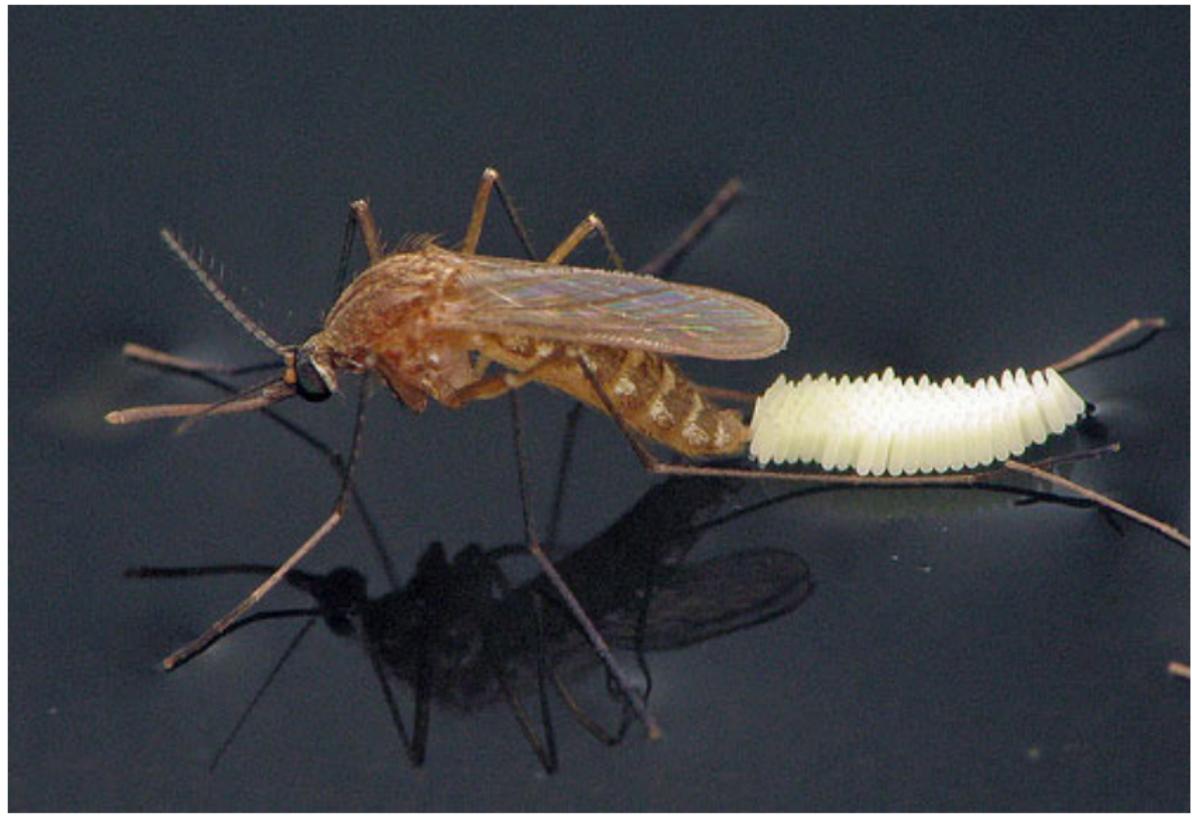
Tradeoff example: many offspring vs. high-quality offspring

- ▶ 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
- ▶ 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? (present)



How many offspring? (present)



How many offspring? (present)



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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 (present)



Dispersal investment (present)



Dispersal investment (present)



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The r vs. K metaphor

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Sex ratios

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”
 - ▶ 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
- ▶ 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* measures the maximum density at which a species can “make a living” – by keeping $\mathcal{R} = 1$
- ▶ Comparing *K* between species can be tricky

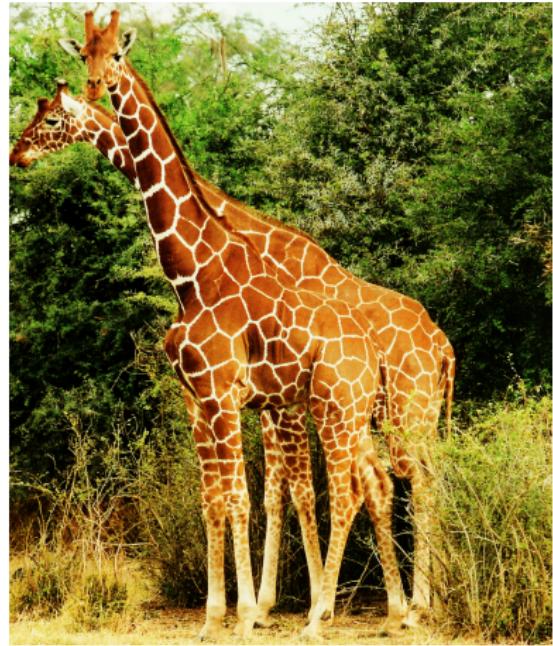
Maples and marigolds (present)



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 ?
 - ▶ $\ln [\text{indiv}/\text{ha}]?$
 - ▶ $\ln [\text{kg}/\text{ha}]?$
- ▶ 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 (present)



Example: trees (present)



Open environment (present)



Stable environment (present)



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
- ▶ 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:
 - ▶ 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
- ▶ 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 (present)



Changing conditions

- ▶ Recall, λ 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 λ ?
 - ▶ * Fast
- ▶ When conditions are bad ($\mathcal{R} < 1$), should organisms be fast or slow to maximize λ ?
 - ▶ * 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
 - ▶ * Move slow when things are bad, and fast when things are good
- ▶ 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?
 - ▶ * 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..)?
- ▶ What are some advantages of r strategists?
 - ▶ * grow faster
 - ▶ * likely to respond well to disturbance
- ▶ What are some advantages of K strategists?
 - ▶ * may be more sustainable to grow for a long time in a stable environment

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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
 - ▶ * *In fact, every organism must have successfully spread risk to survive to where you saw it*

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 (λ) 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.
- ▶ 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
- ▶ 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

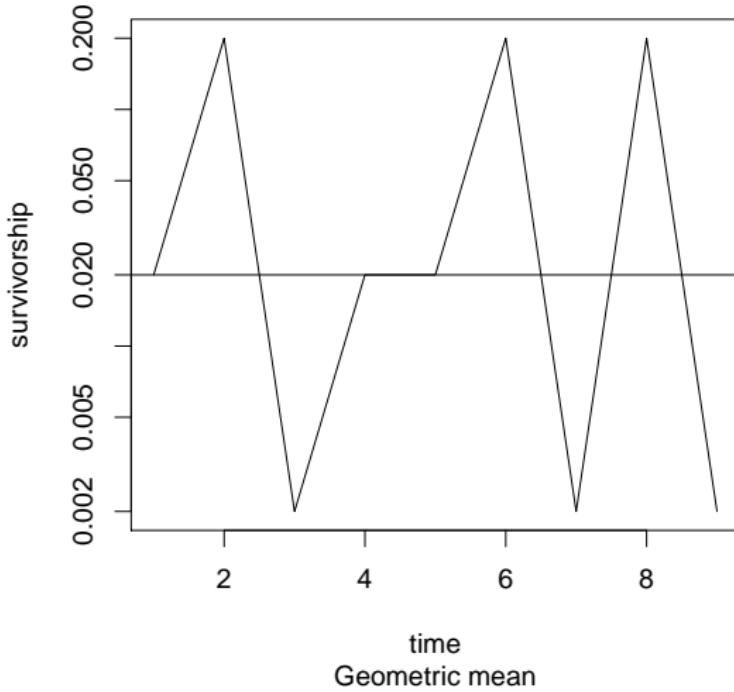
- ▶ Plant D is similar to plant Q, except that it produces seeds that disperse over great distances
- ▶ Because it has to invest in dispersal mechanisms, it only produces half as many seeds.
- ▶ The seeds of the new variety do just as well as those of plant Q, but they disperse so far (in this hypothetical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

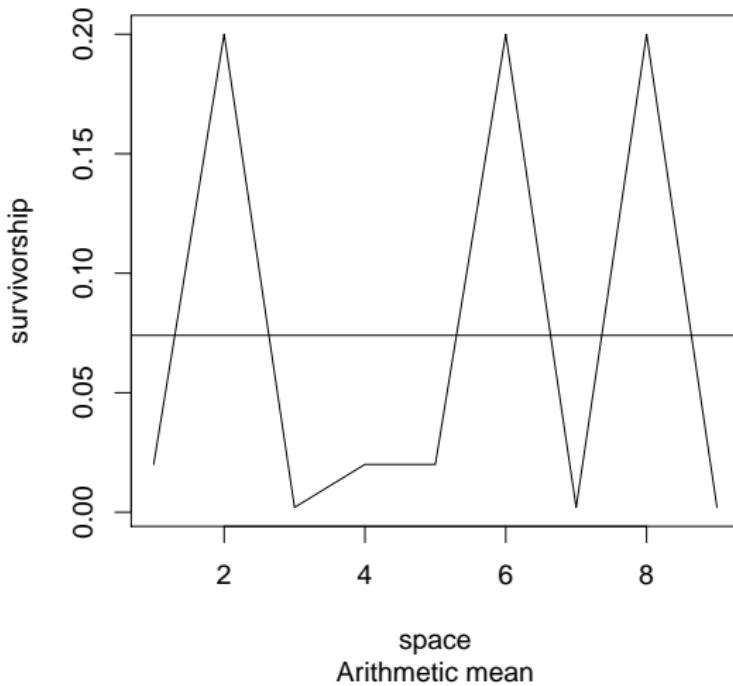
Comparing averages (present)

Averaging between generations



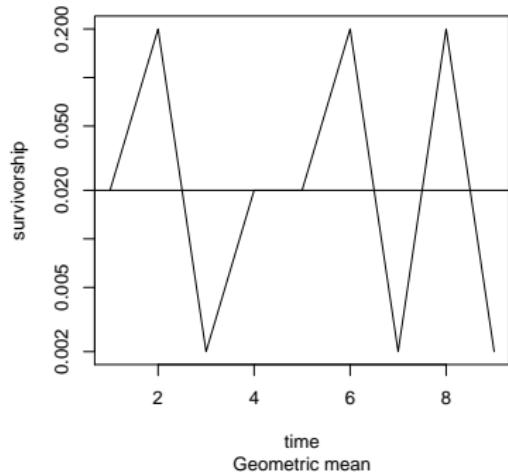
Comparing averages (present)

Averaging within generations

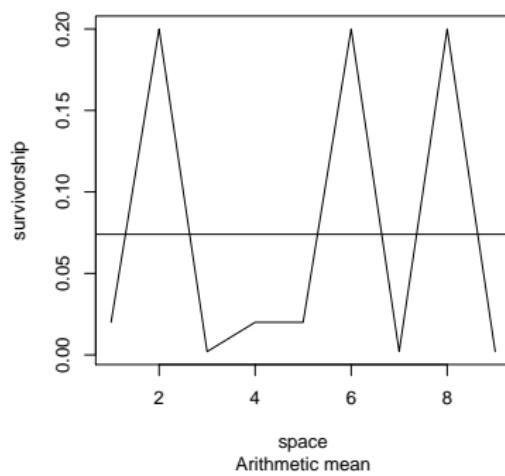


Comparing averages

Averaging between generations



Averaging within generations



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
- ▶ 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.
 - ▶ * If you don't disperse in space, or spread out risk in time, you are "betting" all of your offspring on a single environment
 - ▶ * If you bet on many different environments, you are reducing your risk, or "hedging"

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Sex ratios

- ▶ 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
- ▶ 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
- ▶ 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).
- ▶ 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
- ▶ Thus, the *number* of offspring I can make does not depend on sex
- ▶ If everyone else is making more males than females, what should I do?
 - ▶ * Make more females, because that will increase my average fitness
- ▶ 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
- ▶ 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
 - ▶ Most sex is between brothers and sisters
 - ▶ What offspring ratio would maximize the mother's fitness in this case?
 - ▶ * Have mostly female offspring

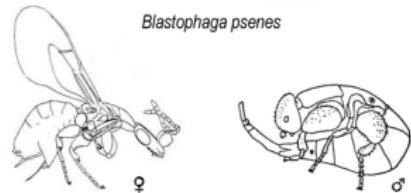


Fig wasp details

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

- ▶ What do you expect to happen in a population where males contribute 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 (present)



Midshipman nest (present)



Equids (present)



Equids (present)



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)
- ▶ 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 (present)



Kakapos

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

