UNIT 5: Life history

Outline

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

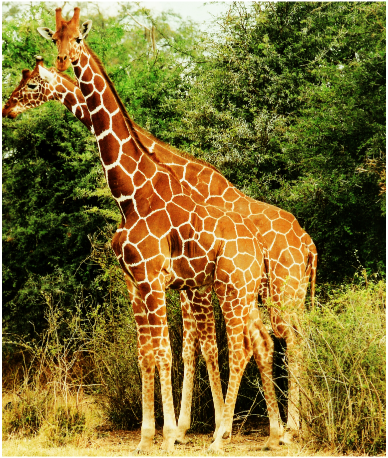
- Differing life-history **strategies** are part of the reason for the remarkable diversity of life
  - Organisms that are too similar are not expected to co-exist
    - One will out-compete the other
  - But two organisms may be able to exploit the same resources using different life-history strategies

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)

Outline

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

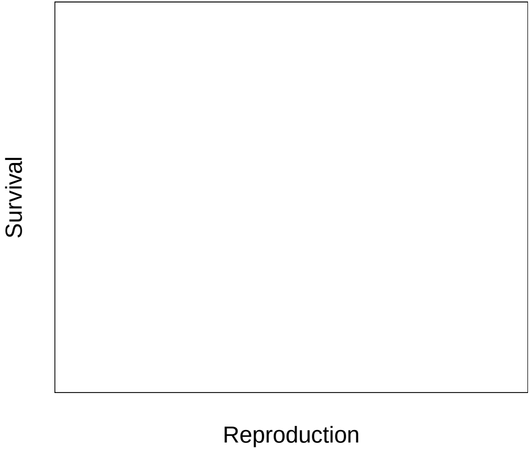
Tradeoffs (present)

Tradeoffs (present)

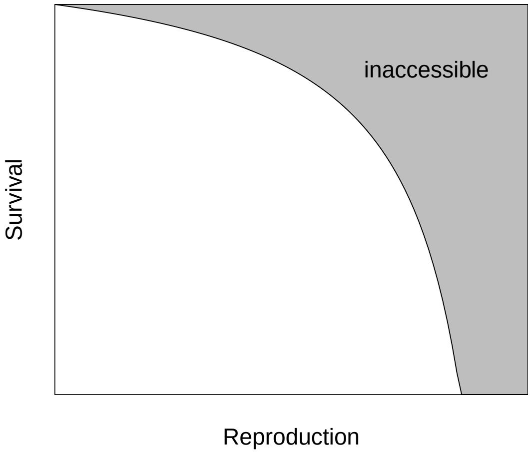
Optimization frontiers

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

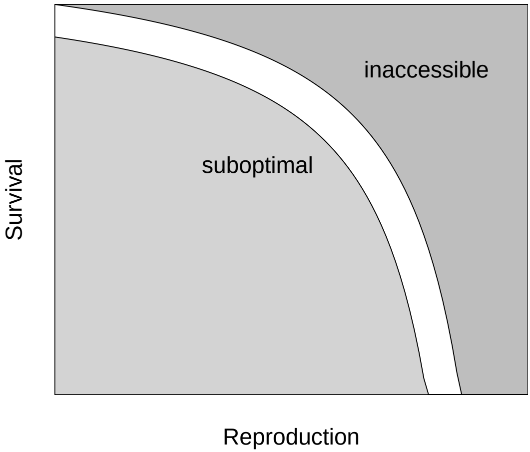
Optimization frontiers (present)



Optimization frontiers (present)

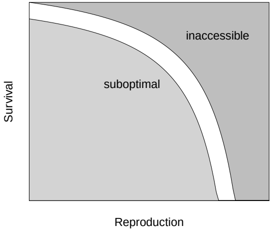


Optimization frontiers



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

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)

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)

Outline

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 $\mathcal{R}_{\text{max}}$, 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 r strategist: maple trees or marigolds?
  - * Marigolds: they are faster at invading new environments
  - * Maple trees do better at competing under stable conditions
- Which has a higher value of r_{max}?
  - * Marigolds
- Which has a higher value of K?
  - In [indiv/ha]?
  - 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
  - We think of maples as the K strategist here

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

Outline

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: $\lambda = 0.6$
  - * Effective survival is the geometric mean of 0.2, 0.02 and 0.002

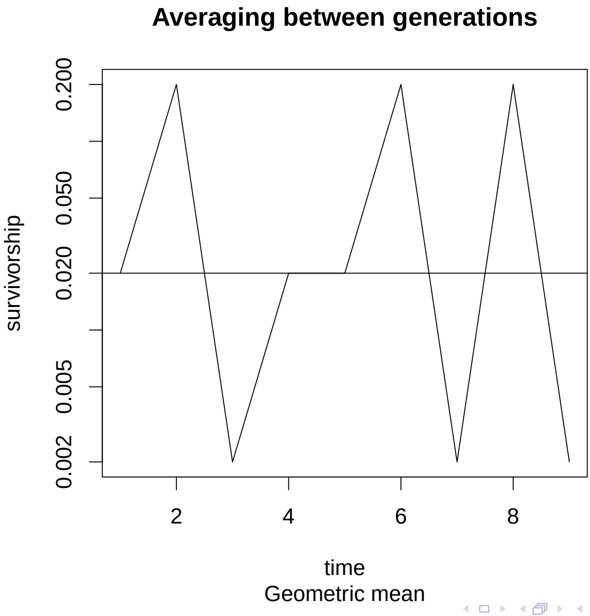
Plant D

- 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.
- 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: $\lambda = 1.11$

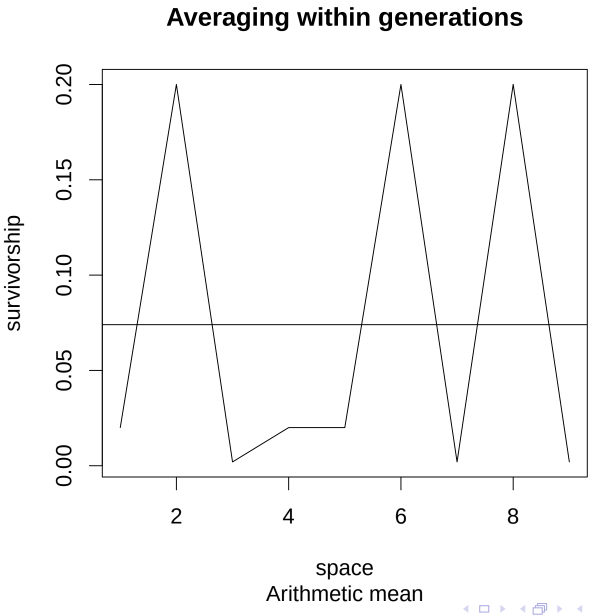
Averaging

- 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

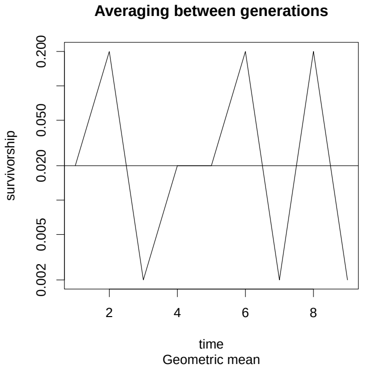
Comparing averages (present)

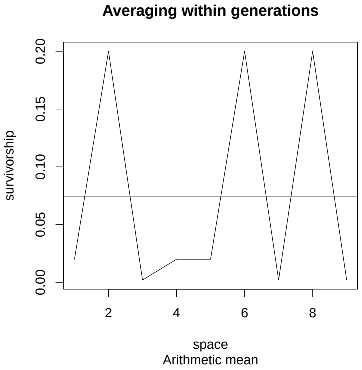


Comparing averages (present)



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?

- 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"

Outline

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

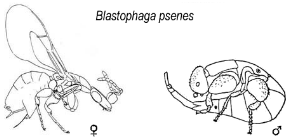


Fig wasp details

- 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