# *Life history*

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## *Introduction*

### *Life history*

**Life history** refers to patterns of how organisms allocate resources to key components underlying fitness (reproductive success):

### *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
- But two organisms may be able to exploit the *same* resources using different life-history strategies

### *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.
- What is one difference in oak and dandelion life history?

### *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

*Tradeoffs*

- Some evolutionary changes simply help organisms function better
- 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

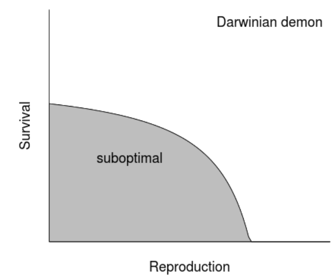



Figure 1: plot of chunk unnamed-chunk-1

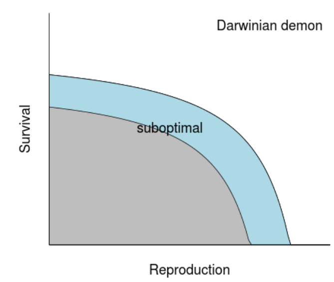
*Optimization frontiers*

*Evolution and optimization*

- We often think of organisms as making choices that maximize their evolutionary fitness.
- What process is really occurring to give the appearance of choice?

*Programmed optimization*

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

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*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

*Recall 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.
- Make sure you remember what $f$ and $p$ are!

*Responses to Cole*

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

*Tradeoff: 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 pair of ecologically similar organisms that produce wildly different numbers of offspring?

- What are potential advantages of producing fewer offspring with the same amount of energy?

*Tradeoff: direct investment vs. dispersal investment*

- Plants' investment in reproduction may not go directly to the offspring, but instead to mechanisms to help the offspring disperse

- This may be particularly important to plants because of the "eggs in one basket" problem

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

### *Connecting life history to regulation*

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

### *Reminder*

- Our mathematical model is: $\frac{dN}{dt} = (b(N) - d(N))N \equiv r(N)N$
- In the absence of Allee effects, the maximum per-capita growth rate is $r(0) = b(0) - d(0)$, achieved when the population is very small
- We call this value $r_0$.
- If $r_0 > 0$, and density dependence means that $r$ decreases as $N$ increases, we expect to find exactly one non-zero equilibrium, where $b(N) = d(N)$ – this is our regulated, stable equilibrium.
- We call this stable equilibrium value of $N$, $K$ – the **carrying capacity**

### *The logistic equation*

- The logistic equation is a common, simple way of making $r_0$ and $K$ concrete
- It is a special case of our model (above), and has the disadvantage of being less concrete – reliance on the logistic equation often means failing to disentangle birth rates and death rates
- $\frac{dN}{dt} = r_0(1 - N/K)N$
- This is the same as assuming that $r$ goes linearly from $r_0$ (at 0) to 0 (at $K$):
- $r(N) = r_0(1 - N/K)$

### *$r$ vs. $K$*

- Organisms can attempt to increase long-term fitness by increasing $r_0$, or by increasing $K$
- We call organisms that grow rapidly at low densities **"$r$-strategists"**

- They can rapidly take advantage of new opportunities
- We call organisms that compete well at high densities **“$K$-strategists”**
- If space is filling up, they maintain high growth rates up until a higher density

*Example: trees*

- Assuming there is a tradeoff between $r_0$ and $K$, would you expect individuals with high $r_0$, or high $K$, to do well:

- In an empty, suitable habitat after a fire, flood or other major **disturbance**?

- In a crowded, stable old-growth forest?

*$r$ vs. $K$ strategies*

- All species are selected for characteristics relating to both $r_0$ and $K$
- But it is often useful to compare species based on which they emphasize more heavily
- There will often be tradeoffs between $r_0$ 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
- Name another $r$-strategist organism

*Measuring $K$*

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

- Which has a higher value of $K$?

- How should we measure $K$?

*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 the presence of competition, these "quick" offspring may be out-competed by offspring with more resources
- Be more aggressive about dispersal

*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
- Some species mature slowly but reproduce only once (*semelparous*)
- Every species life history has specific, important *details*
- But general principles are very important to guide our understanding

*Changing conditions*

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

When conditions are bad ($R < 1$), what can organisms do to make $\lambda$ less extreme?

When conditions are good ($R > 1$), what can organisms do to make $\lambda$ more extreme?

*Changing life history*

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

*Applications*

- How would $r$ and $K$ strategists differ in their response to human activities/disturbance?
- Would $r$ or $K$ strategists be more useful for human production (eg. biofuels, agriculture, drug production etc..)?
- Name a possible advantage of $r$ specialists for human production

## *Bet hedging*

### *Bet hedging*

- In a risky world, you never want to put all your eggs in the same basket
- If all your offspring are in 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)
- All successful organisms have strategies for spreading risk

### *Averaging*

- Mathematically, we can think about bet-hedging strategies in terms of averages
- **Arithmetic** means are means with respect to addition:
- $x + y + z = m + m + m$ $(m = (x + y + z)/3)$
- Geometric means are means with respect to multiplication:
- $x \cdot y \cdot z = m \cdot m \cdot m$ $(m = (x \cdot y \cdot z)^{1/3})$
- We learned in the growth unit that the correct way of averaging $\lambda$ over time is . . .

### *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
- If the three kinds of year are equally likely, what is the long term average growth rate of the population?

### *Plant D*

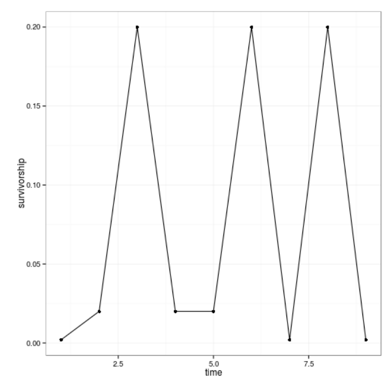
- Plant D is similar to plant Q, except that it produces seeds that disperse over great distances
- Because it has to invest in dispersal mechanisms, it only produces half as many seeds

- 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 the new variety?

*Averaging*

- Variation between organism generations is **multiplicative**; we understand its effect using the geometric mean
- Variation within a generation is **additive**; we understand its effect using the arithmetic mean
- The arithmetic mean is always $\geq$ than the geometric mean. When variation is high, it can be much greater
- What is the geometric mean of $\{0, 1000, 1000, 1000, 1000\}$ ?
- Therefore, organisms benefit from averaging within generations, rather than between generations

*Comparing averages: survivorship*

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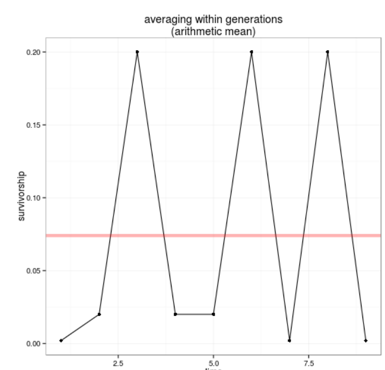


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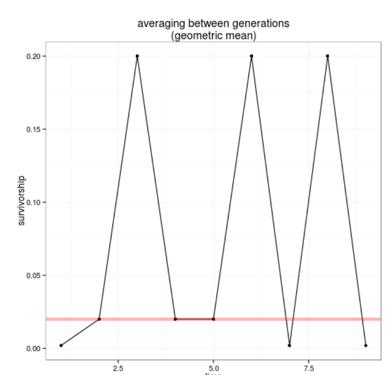


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## *Dispersal*

*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
- What is one advantage of dispersal?

*Spreading risk over time*

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

*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.

are "betting" all of your offspring on a single environment

## *Sex ratios*

*Sex ratios*

- Why might organisms allocate more resources to producing 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**
- Therefore, individuals should allocate resources equally to offspring of each type

*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 seals: details*

- Imagine a population where 90% of elephant seals born are males. A certain cohort 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?

### *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, females will have higher fitness, and I should make more females than males

### *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?

as high as female fitness

### *Example: Fig wasps*

- Many species of fig wasps have sex inside figs
- Most sex is between brothers and sisters
- How can the mother maximize fitness 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
- Would a mother benefit by producing more males than others do?

females as their siblings do

### *Female-biased sex ratios*

- Females *usually* contribute more resources per offspring than males
- Should invest more in females than in males whenever sex with kin is likely
- If males are more expensive, also expect more females
- Equal sex ratio is expected **at birth** (or end of parental investment): differential mortality can lead to biased *adult* sex ratios

*Variation in reproductive success*

- In many animals males have very large variation in reproductive success
- Elephant seal picture
- 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

*Equids*

- Horses and zebras produce offspring at similar rates through their adult lives
- The healthiest, middle-aged mares produce a greater fraction of males
- Presumably they are allocating more resources to these males (because they have more resources available)
- Not clear whether individuals' sex ratio balances out over their lifespan
- Or balances across the population
- These animals show skewed sex ratios of adults, probably for a related reason

*Parasites*

- female parasitoids lay more female eggs in large caterpillars) and more male eggs in smaller caterpillars
- parasitic nematodes have female-biased sex ratios, but not at "birth" (i.e. differential mortality is the cause)
- malaria gametocytes are female-biased, but become less female-biased when malaria is common (high prevalence)
- schistosomes are male-biased, at "birth": ????