UNIT Extra notes

1 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.
  - **Answer:** Survival
  - **Answer:** Growth
  - **Answer:** Reproduction
  - **Answer:** 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

- 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.
  - **Answer:** Water, sunlight, nutrients
- Poll: What are some differences?
  - **Answer:** Oak trees are bigger
  - **Answer:** Oak trees wait longer to reproduce
  - **Answer:** Oak trees reproduce many times
  - **Answer:** Oak trees put much more energy into each seed
  - **Answer:** Dandelion seeds are dispersed by wind, acorns by animals

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

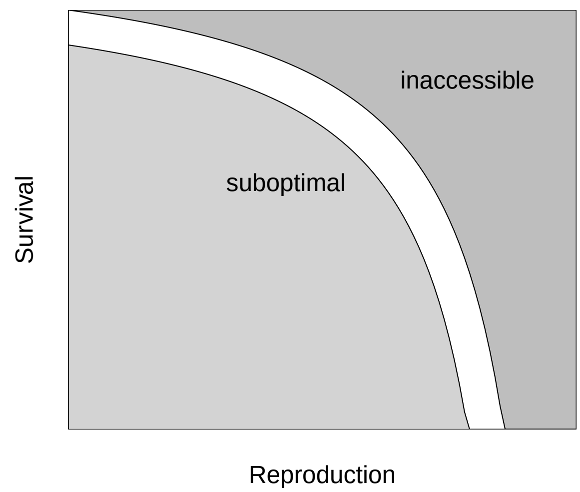
2 Tradeoffs

- 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

Optimization frontiers

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

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?
  - **Answer:** Natural selection is selecting random variants
  - **Answer:** 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

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

- 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?
  - **Answer:** "Closing the loop": f is not seeds per plant, it's plants per plant; not as high as you think
  - **Answer:** Population regulation: the long-term average value of λ is 1, so increasing f by 1 is a *lot*
  - **Answer:** Risky environments: long-lived organisms can deal better with variation in offspring 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?
  - **Answer:** Oaks vs. pines
  - **Answer:** Tsetses vs. mosquitoes
- Poll: What are potential advantages of producing fewer offspring with the same amount of energy?
  - **Answer:** Greater chance of survival (or reproductive success)
  - **Answer:** Dispersal
  - **Answer:** More energy left over?
    - **Answer:** No (see question)

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?
  - **Answer:** Parent-assisted dispersal is often their only chance to move.
- What are some example mechanisms?
  - **Answer:** Edible fruits
  - **Answer:** Helicopter attachments
  - **Answer:** Exploding seed pods

3 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.
  - **Answer:** r is the per-capita rate of growth, units ...
    - **Answer:** [1/t]
  - **Answer:** K is the stable, equilibrium level that we expect a population to reach, units ...
    - **Answer:** [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?
  - **Answer:** Because they are selected to maximize $r_{\max}$, the *rate* of exponential growth
  - **Answer:** 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

Measuring K

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

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**?
    * **Answer:** High $r_{\max}$ leads to faster exponential growth
  - In a crowded, stable old-growth forest?
    * **Answer:** 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.
    * **Answer:** 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

Changing conditions

- Recall, λ is usually between 1 and $\mathcal{R}$, gets closer to 1 when the life cycle is
  - **Answer:** slower
- When conditions are good ($\mathcal{R} > 1$), should organisms be fast or slow to maximize λ?
  - **Answer:** Fast
- Poll: When conditions are bad ($\mathcal{R} < 1$), should organisms be fast or slow to maximize λ?
  - **Answer:** Slow!
  - **Answer:** 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
  - **Answer:** Move slow when things are bad, and fast when things are good
- Poll: What are some examples?
  - **Answer:** Many animals reach sexual maturity faster under good conditions: horses, elephants
  - **Answer:** Trees may survive longer under bad conditions (by growing slowly and not allocating energy to reproduction)
  - **Answer:** 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?
  - **Answer:** 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?
  - **Answer:** grow faster
  - **Answer:** likely to respond well to disturbance
- Poll: What are some advantages of K strategists?
  - **Answer:** may be more sustainable to grow for a long time in a stable environment