Bio 1M: Evolutionary processes (complete)

Evolution by natural selection

- What is the weak link in the story I told last chapter?
  - Heritable **variation** in traits
  - **Selection** (i.e., differential reproductive success) *based on* these traits
- **Answer:** Where does heritable variation in traits come from?

Some genetics

- Our basic traits are determined by **genes**
- A location where a gene can occur is called a **locus** (pl. **loci**)
- A particular version of a gene is called an **allele**
- Complex organisms usually have two alleles at each locus
  - These can be the same, or different

Loci

- Complex organisms usually have two alleles at each locus
  - These can be the same, or different
- An organism with different alleles at a particular locus is referred to as **heterozygous** (adj., n. form heterozygote)
- An organism with two copies of the same allele at a particular locus is referred to as **homozygous** (adj., n. form homozygote)

Two definitions of evolution

- *Lecture*: heritable changes in species traits over time
- *Book*: changes in allele frequencies
- These definitions are consistent; use the one which helps you think clearly

1 Analyzing genotype frequencies

Genotypes and phenotypes

- A **genotype** is the collection of an individual's genes
- A **phenotype** is the collection of an individual's physiological and physical traits
  - What we can observe about an individual
  - Phenotype is largely (but by no means entirely) determined by genotype

Example: peppered moths

- Kettlewell's experiment `https://en.wikipedia.org/wiki/Kettlewell%27s_experiment`
- Two different alleles possible at the wing color gene: A_1 and A_2.
  - Individuals with A_1A_1 *genotype* have light-winged *phenotype*
  - Individuals with A_2A_2 *genotype* have dark-winged *phenotype*.
  - Individuals with A_1A_2 *genotype* ???
- If individuals with genotype XY have the same phenotype (on average) as those with XX, we say that X is a **dominant** allele and Y is a **recessive** allele.
- If XY individuals have an intermediate phenotype (between XX and YY, we say X and Y are **incompletely dominant**.

Co-dominance

- Co-dominance means when both phenotypes are expressed. Whatever that would mean.
- Examples?
- a very particular term that should fall under incomplete dominance
- People shouldn't worry about this distinction, and you shouldn't worry about it for this course
  - Notice that it's not in bold
- *Comment:* Tell Dushoff to stop, if he's getting carried away

Analyzing genotype frequencies

- We analyze genotype frequencies as follows:
  - Make simple assumptions about how frequencies work
  - Calculate **expected frequencies** under our assumptions
  - Measure **observed frequencies** in the population
  - Look for evidence of systematic (not random) difference between expected and observed frequencies

Making simple assumptions

- Expected frequencies are usually calculated by assuming that alleles assort randomly and independently, like flipping two coins, or rolling two dice

Activity: Coin flipping

- I flip two fair coins (ie., each coin will land heads with probability 1/2).
- What is the probability of:
  - Two heads
  - Two tails?
  - One of each?
- **Answer:** 1/4, 1/4, 1/2.

Activity: Professional coin flipping

- A professional gambler can flip a coin so that it lands heads 70% of the time. She flips two coins.
- What is the probability of:
  - Two heads
  - Two tails?
  - One of each?
- **Answer:** 0.49, 0.09, 0.42

Hardy-Weinberg distribution

- The Hardy-Weinberg distribution is the distribution expected if alleles work like coins (random and independent).
- If p is frequency of allele A_1 and q is frequency of allele A_2, then:
  - Frequency of genotype A_1A_1 is p^2.
  - Frequency of genotype A_2A_2 is q^2.
  - Frequency of genotype A_1A_2 is $2pq$.
- Why the 2?
  - **Answer:** Because you could get A_1 from Mom and A_2 from Dad, or A_1 from Dad and A_2 from Mom ... two ways to do it

Example: calculating allele frequencies

- I collect 20 peppered moths from a particular place, and find that 4 have genotype A_1A_1, 8 have genotype A_1A_2, and 8 have genotype A_2A_2.
- What is the observed frequency of each allele?
- What is the expected frequency of each genotype under the Hardy-Weinberg assumptions?
- Is this population in Hardy-Weinberg equilibrium?
  - **Answer:** We see more homozygotes than expected
    - **Answer:** We can always summarize as more or less homozygotes
    - **Answer:** if allele frequency is right
  - **Answer:** But is this reliable evidence? That's a question for statistics.

What do we mean by expected?

- If we flip a fair coin 100 times, what is the expected number of heads?
  - What if we flip it 25 times?
- We don't expect to get exactly the expected value.
- The 'expected value' is an average of what is expected under our assumptions

How do you know a coin is perfectly fair?

- You can never be sure that a coin is perfectly fair, you can only evaluate your evidence that it's more or less close to fair.
- Similarly, we never have evidence that a population is exactly in Hardy-Weinberg equilibrium
- We can only evaluate our evidence that it is far from (or close to) equilibrium
- What's another way to think about the evidence?
  - **Answer:** How clear is it that we really have more (or less) homozygotes than expected?

Hardy-Weinberg equilibrium

- When do we expect genotype frequencies to behave like coins?
- Alleles selected at random from the previous generation:
  - **Answer:** Random mating within a closed population
  - **Answer:** No differences in fitness between genotypes
  - **Answer:** No mutation, no drift (see below)
- If these assumptions hold exactly, we expect **Hardy-Weinberg equilibrium**
  - Hardy-Weinberg distribution, with no change in allele frequencies from generation to generation.
- This never happens

Differences from equilibrium

- If we observe large differences from the Hardy-Weinberg equilibrium, this is usually a sign that mating is not random, or that natural selection is operating
- The analysis tells us that something is going on, but not what
- Hardy-Weinberg is a **null model**: it tells us what to expect if complicating effects are absent
- Without a null model, we couldn't start interpreting.

Example: Human blood groups

- MN blood groups in different human populations are very close to Hardy-Weinberg equilibrium
  - No evidence for non-random mating, or for fitness differences.
  - This *does not* mean it's not happening, but *probably* means that it's small

Activity: Human blood groups at the global level

- **Answer:** Observed 0.386; 0.361; 0.253
- **Answer:** Expected 0.321; 0.491; 0.188
- **Answer:** More homozygotes than expected
- **Answer:** They are not in equilibrium, because mating is not random across these groups
- **Answer:** These data are telling us different (reasonable) stories at different scales

Example: Human HLA genes

- HLA genes are used by the immune system to recognize disease-causing organisms
- Researchers hypothesized that heterozygous individuals may recognize more bacteria and viruses
- Data shows that more people are heterozygous for HLA genes than would be expected under the Hardy-Weinberg assumption

Heterozygous HLA genes

- Why might more people be heterozygous for HLA genes than predicted by Hardy-Weinberg?
  - **Answer:** Heterozygous people might be more likely to survive
  - **Answer:** Heterozygous people may have more offspring
    - **Answer:** Effects of this one are more complicated
    - **Answer:** Heterozygotes don't necessarily have heterozygous offspring
  - **Answer:** People might be more attracted to people with different HLA types
    - **Answer:** Maybe *evolved* this way because of reasons above

2 Types of natural selection

2.1 Directional selection

- **Directional selection** tends to move a population in a particular direction
  - Giraffe necks
  - Human brains

Multi-directional selection

- Directional selection can change through time with the environment
  - Swallows may get larger during extreme cold spells, smaller again during normal weather
    - But we need to know whether the changes we saw were heritable
  - Finch beaks get thicker when food is scarce, and smaller when food is abundant
- Why might small-beaked finches have advantages?
  - **Answer:** Can use the resources for something else
    - **Answer:** Faster growth, more fat storage

2.2 Stabilizing selection

- **Stabilizing selection** tends to keep the population where it is
  - Example: human birthweights

Connections between selection types

- What happens if the target of directional selection stays the same for a long time?
  - **Answer:** The population arrives at the target, and directional selection becomes stabilizing selection
- Examples?
  - **Answer:** Giraffe necks
  - **Answer:** Human brains
  - **Answer:** Almost everything we see
    - **Answer:** Things often develop by directional selection, but at any given time, most of what we see is under stabilizing selection

2.3 Disruptive selection

- Disruptive selection favors phenotypes *different* from the average value
  - Black-bellied seedcrackers
  - Animals that get eaten a lot may want to look different from their peers
- Disruptive selection may lead to **speciation** – the formation of new species.

2.4 Balancing selection

- Balancing selection tends to maintain allele diversity
  - When there is no single best allele
- **Heterozygote advantage**: when heterozygotes have higher fitness
- **Frequency dependence**: when rare types have higher fitness

Example: The sickle cell phenotype

- Blood cells that can lose their shape and squash malaria parasites!
  - People heterozygous for this trait get less sick with malaria
  - People homozygous for this trait have too much instability and severe anemia
- This is an example of:
  - **Answer:** heterozygote advantage

Example: seedcrackers

- What would happen if almost all of the seedcrackers had large bills?
  - **<u>Answer</u>:** More small seeds available, small bills become an advantage, an example of . . .
    - **<u>Answer</u>:** frequency dependence
- What happens when large-billed and small-billed individuals breed?
  - **<u>Answer</u>:** They could have low-fitness offspring
  - **<u>Answer</u>:** Can lead to selection for less heritability
  - **<u>Answer</u>:** or selection on mate choice

3 Other evolutionary mechanisms

3.1 Genetic drift

- **Genetic drift** is change in allele frequencies due to random sampling:
  - Some individuals have more offspring than others due to chance events
  - Offspring receive certain parental alleles, and not others
- These factors will lead to an accumulation of random changes in allele frequencies

Thought experiment

- Imagine flipping a fair coin 100 times
  - Repeat
- Now imagine choosing 100 alleles at random (with replacement) from a population of 50 A and 50 B alleles
  - Repeat, using new population as a starting point

Small populations

- Drift is much stronger in small populations than in large ones (law of averages).
- Even if a population is big now, it may have been small in the past
  - **Founder effects** occur when a new population is started by a small number of individuals
  - **Bottlenecks** occur when a population becomes small, then large again
    - ... or, when a beneficial genetic mutation takes over a population
    - **<u>Answer</u>:** variation will be lost at that locus because the new gene is better
    - **<u>Answer</u>:** but it can also be lost at other loci at random, because the whole future population is descended from individuals with the new mutation

Fixation and loss

- An allele may drift to a frequency of 0 (it's **lost**) or of 1 (it's **fixed**)
- Advantageous alleles are often (not always) fixed
- Disadvantageous alleles are usually (not always) lost
- Alleles with **neutral** differences (no selective difference) will be fixed or lost at random
  - This is also true for alleles with small effects
- Drift tends to reduce genetic variation

3.2 Gene flow

- **Gene flow** is the movement of alleles from one population to another
  - This happens when individuals move from one population to another and breed
- How we think about gene flow depends on how we choose to define a 'population'
- Gene flow can be an obstacle to speciation; it helps keep populations similar

3.3 Mutation

- **Mutations** are heritable errors in copying DNA
- Mutations are rare; *by themselves* they don't cause much evolution
- Mutations are extremely important to evolution, however:
  - **Answer:** Mutations provide the variation on which natural selection acts
  - **Answer:** Mutation is the only source of new alleles

Types of mutations

- Mutations can occur at many scales:
  - a single DNA base might change
  - chunks of DNA can be added or subtracted
  - whole genes (or whole chromosomes) can be duplicated
- New genetic sequence can come from:
  - copying errors
  - other organisms! **lateral gene transfer**

Mutations are random

- Most mutations are **deleterious** – bad for fitness
- Very rarely mutations are **beneficial** – good for fitness
  - Such mutations are favored by natural selection

Complex organisms

- Can complex organisms arise through random mutations?
  - A central question of biology
  - Large-scale evolution takes a *long* time
  - Beneficial changes can accumulate gradually
  - Much evidence of intermediate forms
- Check out videos of "evolution of the eye"

What about sex?

- Sex does not *directly* change allele frequencies
  - Your book may say this means it's not an "evolutionary process" – don't worry about that
- It does act to bring alleles together (and to split them apart)
- Sex is not a source of new alleles
  - But it is a source of new combinations
- There is still active debate on the advantages and disadvantages of sex in evolution

4 Mating patterns

4.1 Inbreeding

- **Inbreeding** refers to mating between close relatives
- Since relatives will tend to share similar alleles, inbred populations will tend to differ from Hardy-Weinberg equilibrium in what way?
  - **Answer:** More homozygous loci

Inbreeding depression

- In many populations, it is observed that inbred individuals have lower fitness:
  - They are more likely to be homozygous for rare genetic defects
  - They are less likely to be heterozygous for immune-system genes
- Inbreeding depression is a serious concern for conservation
  - As populations get smaller, inbreeding becomes more common
- Wildlife studies show that panthers with both parents from Florida (small population) do not survive well
- Human demographic studies show strikingly lower survival for children of first cousins

4.2 Sexual selection

- **Sexual selection** is a form of natural selection
- Occurs when there is heritable variation in traits related to success in obtaining mates

Example: zebra finches

- Males but not females have colorful orange beaks
- Hypothesis: these beaks make males more attractive to females

Activity: Zebra finch experiments

- How would you test this hypothesis?
  - **Answer:** Make some males' beaks more orange. How?
  - **Answer:** Test whether they are preferred by females

Results: Zebra finch experiments

- **Answer:** Treatment males were fed enriched diets
  - **Answer:** Their beaks became more orange
  - **Answer:** They were preferred by females
- Why not simply find and use birds whose beaks are naturally more or less orange?
  - **Answer:** Orange-beaked birds may differ in other ways (bigger, healthier, etc.)
- What is a possible problem with the conclusion that females prefer birds with orange beaks?
  - **Answer:** The diet enrichment may have other effects

Why the males?

- Males often have striking traits that females lack, used in courtship, or in battles for mates
  - Sexual **dimorphism** refers to trait differences between males and females
- Why do males more often have these traits than females?
  - Investment in reproduction
  - Variation in reproductive success

Investment in reproduction

- In many species, females invest much more in each offspring than males do
  - Eggs are expensive, sperm are cheap
  - Females are often more involved in caring for offspring
- If females invest a lot in each offspring, they can maximize fitness by *being choosy about mates*
- If males invest little in each offspring, they can maximize fitness by *mating as much as possible*

Testing the theory

- How might we test the theory that males compete more sexually because females invest more in offspring?
  - **Answer:** Are there any species where these roles seem to be reversed?
    - **Answer:** Yes, in some species of pipefish (related to seahorses) the males spend more time and energy caring for young them females
  - **Answer:** In these species, do females compete for males?
    - **Answer:** Yes, females are larger than males, and develop bright colors at courtship time

Variation in reproductive success

- Males often have greater variation in reproductive success than females do
- This is a side-effect of the fact that females usually invest a lot in each offspring
  - Reduces potential total number of offspring
  - Makes females desirable to males
- Greater variation in reproductive success means that winning contests is more important to male than female fitness

Example: elephant seals

- Male elephant seals compete for control of breeding beaches
- Huge variation in reproductive success
- Huge size difference between males and females (strong sexual dimorphism)

What about people?

- Men and women have pretty clear size differences
- How unequal is child-rearing in people?
  - **Answer:** It's not so clear; need to think about evolutionarily relevant context
  - **Answer:** Caring fathers are not always biological fathers
    * **Answer:** Could increase advantages of larger males
- To what extent do these principles even apply to people?
  - **Answer:** To *some* extent
  - **Answer:** We have complicated brains, and complicated cultures
  - **Answer:** Under what conditions did our current traits evolve?

Conclusions

- **Mutation** (mistakes!) is the source of new variation
- **Natural selection** drives adaptation: selects variation that allows organisms to thrive in diverse settings
- **Sex** facilitates new combinations, but **sexual selection** can work against adaptation to the environment
- **Genetic drift** and **gene flow** are also non-adaptive drivers of evolution
- The adaptation we see is the result of all of these processes:
  - adaptive, non-adaptive, previously adaptive