Sexual Selection

Evolutionary Mechanisms
- Genetic Drift
- Migration
- Mutations
- Natural Selection
  - Non-adaptive
  - Adaptive

Natural Selection

OUTLINE
1. Sexual Selection
2. Constraints on Natural Selection
   - Pleiotropy
   - Evolutionary Tradeoffs
   - Genetic Drift and Natural Selection

- There are species with 3 or more sexes (some ciliates have 32)... Too complex to discuss here
- Restrict my discussion here to 2 sexes

Male

Female
Male
Female

Red deer

Male
Female

HUH?

What about us???
(New World Monkeys)

Theory of Sexual Selection

- The sex bearing a higher cost to reproduction or has higher parental investment will generally be the chooser (has more to lose from bad choice)
- Whereas the sex bearing the lesser cost of reproduction or parental investment generally competes more heavily for mates (Bateman 1948)
Asymmetric Limits on Fitness

- The sex that has higher reproductive cost will be the choosers
  - If you’re allocating a lot of resources toward offspring and are limited in the number of offspring you can have, you won’t mate with just anyone
- The sex that is being selected (under sexual selection) will be competitive
  - Fight with each other, fight for resources, fight for access to or control of the other sex

Theory of Sexual Selection

- In sexual species, it is usually males who invest less in each offspring → it is typical for males to compete for access to females
- In 90% of mammal species, females provide substantial parental care, while males provide little or none (Woodroffe and Vincent 1994)
- And as a consequence, it is often males of many species that are typically larger and have brighter coloration than the females (Andersson 1996 - also book: Sexual Selection by Andersson)
- In many species of fish, it’s often the opposite, where the males provide all the paternal care (garibaldi, stickleback, some sunfish, sea horses, etc.)
- Sexual selection leads to sexual dimorphism

Sexual Dimorphism: differences in morphology between males and females

- Sexual dimorphism arises because of sexual selection
- When sexual selection goes down, the differences between the sexes go down
- In monogamous mating systems, sexual selection is much less intense, because most of the males get to mate and produce offspring (their alleles get passed on, so they are not selected out) → lowered variance in male reproductive success
- Sexual selection arises when only a few males (or females) mate and produce offspring, passing only their heritable traits (small % of population) to the next generation

Males have much higher variance in mating success and offspring number than females

Sexual dimorphism has been declining during the course of Hominid (great apes) evolution

- Changes in sexual mating system???
- Humans in the process of shifting from polygamy → monogamy? (reduction in sexual selection?)

Sexual dimorphism has been declining during the course of Hominin (great apes) evolution

- Changes in sexual mating system???
- in the process of polygamy → monogamy (due to more immature offspring?)

Sexual dimorphism: Male/female body size ratio

- Gorilla: 2.37
- Orangutan: 2.23
- Bonobos: 1.36
- Chimpanzee: 1.29
- Australopithecine: 1.20 (Reno & Lovejoy 2015)
- Homo sapiens: 1.15

Future?? What do you think?
Hypothesis

- Bipedalism → difficult childbirth (pelvis opening too small)
- → children born more immature
- → need father’s help to raise child → more monogamy
- → reduction in sexual selection → reduced variance in male reproductive success
- → less sexual dimorphism

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Example of Sexual Selection in Humans

- Over the last several million years, hominids have been getting taller (including Homo sapiens sapiens)

  There is evidence that sexual selection favors greater stature in human males (Pawlowski et al. 2000, Nature; Husain & Firdous 1990; Meuller & Mazer 2001)

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Example of Sexual Selection in Humans

- In humans, females prefer taller men (Husain & Firdous 1990)
- In humans, taller males have greater fitness (Pawlowski et al. 2000, Nature; Meuller & Mazer 2001)
- In a study by Pawlowski et al. 2000, based on 3,201 healthy men aged 25–60, childless men were significantly shorter than those who have at least one child

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Example of Sexual Selection in Humans

- BUT, there are often constraints on selection
- In the case of selection on human height, there might be tradeoffs between the sexes
- Some evidence that shorter females on average have greater life time reproduction (reach maturity sooner)
- Some evidence for costs of being taller in males (Body height affects the strength of immune response in young men, but not young women, https://www.nature.com/articles/srep06223)
- So there might be conflicting forces affecting the evolution of human height (Evolutionary Tradeoffs)

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Asymmetry of Sex

- Expensive egg, cheap sperm
- Females limited by cost of reproduction, little variation in mating success
- Males limited by ability to find mates, and have a greater variance in male reproduction
- Sexual selection tends to act more heavily on males, dictated by female choice
Most females mated two or three times, whereas majority of males never mated; a few males had 300 offspring or more. When sexual selection acts on males, males have much higher variance in mating success and offspring number than females. Most females mated two or three times, whereas majority of males never mated; a few males had 300 offspring or more.

Asymmetric Limits on Fitness

When Females are the sex with higher reproductive cost

- Male reproductive success is limited by access to mates (which is correlated with reproductive success)
- In contrast, female reproductive success is limited by the cost of making eggs or the cost of parental care

Asymmetry of Sex

- Higher mutation rate in male germ line
- In many species, greater sexual selection of males (driven by female choice)
- Is Male-driven Evolution common?

Most extreme genetically-documented case of skew in reproductive success in humans

- Genealogy based on Y-chromosome: paternally inherited, male line
- Survey of 16 populations throughout Asia found that 8% of men carry an unusual Y-chromosome that originated in Mongolia ~1000 years ago.
- The lineage is carried by likely male-line descendants of Genghis Khan


Typically sexual selection acts on males. However, when males provide greater allocation toward parental care than females, the pattern can be reversed.
In sharp contrast to the previous example, in the broad-nosed pipefish, the males provide all the parental care. In this case, females showed greater variance in reproductive success and were more limited by mating success.

In the broad-nosed pipefish, where males provide all the parental care, **FEMALE** reproductive success depends more heavily on their ability to mate than for males.

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**Hypotheses on causes of sexual selection**

- **What exactly is the choosier sex choosing?**
  - **Good genes** (certain traits, symmetry, developmental stability)
  - **Increased heterozygosity** (e.g., MHC loci)
  - **Access to resources** (a good nest, food, etc.)

These are not mutually exclusive (i.e., if a hypothesis is correct, it does not mean the others are invalid... Multiple forces could be acting simultaneously).

**Good Genes Hypothesis:**

A trait under selection that is correlated with fitness

A male gray tree frog (†*Hyla versicolor*)

**Females prefer male frogs that call longer, and such frogs produce offspring with higher fitness**

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<th>Fitness measure</th>
<th>High food</th>
<th>Low food</th>
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<th>Low food</th>
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<td>NSD</td>
<td>IC better</td>
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<td>Mass at metamorphosis</td>
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<tr>
<td>Postmetamorphic growth</td>
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**Sexual Selection for Heterozygosity**

(a type of Balancing Selection)

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doi/10.1093
Sexual Selection for Heterozygosity at MHC loci

What is Major Histocompatibility Complex (MHC)?

- MHC is a series of genes (a large gene family) in vertebrates that encode cell surface proteins which control the adaptive immune response.
- The function of these proteins is to present fragments of antigens (degradation products from within the cell) to T cells. The receptor of T cells can only recognize antigen fragments that are complexed with MHC proteins.
- Healthy cells will be ignored, while cells containing foreign proteins (and then displayed by MHC proteins) will be attacked by the immune system.

Why is it good to be heterozygous at MHC loci?

- The amount of genetic diversity within the MHC enables the immune system to recognize—and process—a broader range of foreign antigens and pathogens.
- The ability to process more antigens confers the ability to stimulate an immune response towards a wider range of antigens.
- More Heterozygous → Have more MHC alleles → recognize a greater diversity of pathogens.

The Sweaty T-shirt Experiment (Wedekind et al. 1995)

- Female and male students were genotyped for their MHC alleles (HLA-A, -B, and -DR).
- Each male student wore a T-shirt for two consecutive nights.
- Each female student was asked to rate the odors of six T-shirts.
- Results: Females scored male body odors as more pleasant when the men differed from them in their MHC alleles.

Sexual Selection for Heterozygosity at MHC loci

What is Major Histocompatibility Complex (MHC)?

- The MHC shows a high degree of polymorphism (100 times higher than the genome average).
- Rapid evolution of MHC is associated with rapid evolutionary response to diseases... MHC diversity → can present wider range of antigens on cell surface.
- MHC alleles determine organ donor compatibility. Defects in certain MHC genes lead to autoimmune disorders in which the body fails to recognize self-antigens. Examples include multiple sclerosis, some forms of arthritis and diabetes.

The Sweaty T-shirt Experiment (Wedekind et al. 1995)

- Females who were not taking oral contraceptives preferred odors of males that were dissimilar in MHC alleles.
- Females taking oral contraceptives preferred odors of MHC-similar males.
- Oral contraceptives mimic the physiological state of pregnancy and interfere with natural attraction.

Figure 1: Average score per male (taking study each odor as a standard only for females who were similar in their MHC; median and quartiles), (a) vs. (c). The odors were judged by females who did not take oral contraceptives (number of males = 30), and (c) vs. (d) judged for females who take the pill, number of males = 20. All p-values are two-sided (Wilcoxon signed-rank tests).
Selection for Heterozygosity at MHC

Additional studies:
- Couples who failed to achieve pregnancy after two or more attempts of *in vitro* fertilization (IVF) or tuba embryo transfer (TET) shared a significantly greater number of HLA antigens than did control couples who achieved viable pregnancy with their first IVF or TET (Weckstein et al. 1991)
- Couples who suffer from recurrent spontaneous abortions often share a higher proportion of their MHC than control couples (Beer et al. 1985; Bolis et al. 1985; Thomas et al. 1985; Karl et al. 1989; Ho et al. 1990; Koyama et al. 1991; Laitinen 1993)
- Genome scans showed that European American couples were significantly more MHC-dissimilar than random pairs of individuals, and that this pattern of dissimilarity was extreme when compared to the rest of the genome (Chaix et al. 2008)

Thus, attraction is in part encoded in your DNA

as stated in this popular song:
https://www.youtube.com/watch?v=MBdVXkSdh_wU (click on “cc” for subtitles, which states that attraction is not your choice, but encoded in your DNA)

Constraints on Natural Selection

- Genetic Variation: Selection can only act on existing genetic variation (we talked about this last lecture)
- Phylogenetic Inertia (Historical Constraints): can only build on what is there (hard to make wings without appendages)
- Pleiotropy: one gene might affect more than one trait. So if you alter a gene, it could have multiple effects. So you might not be able to alter that gene
- Evolutionary Trade-offs: there could be counteracting forces; A favorable trait could incur costs on a different trait (increase in fat to resist cold could lead to diabetes)
- Genetic Drift will interfere with the action of Natural Selection in small populations

Pleiotropy: when a gene affects many traits or functions

- Selection might not be able to act on trait if the gene that codes the trait is Pleiotropic, and also affects other traits. So, changing the gene could negatively affect the other traits
- Conversely, a seemingly unbeneficial trait might get selected for because the gene that codes for it also enhances fitness
- Pleiotropy could sometimes lead to evolutionary tradeoffs (you can have evolutionary tradeoffs that are not pleiotropic– between traits encoded by different genes)

Antagonistic Pleiotropy: when one gene controls for more than one trait where at least one of these traits is beneficial to the organism’s fitness and at least one is detrimental to the organism’s fitness.

Human Height is encoded by many genes but a set of them might be antagonistic pleiotropic for the tradeoff in Human Height.
Hard to select on a gene that affects multiple traits (pleiotropy)

Antagonist pleiotropy can lead to trade offs

- Water retention might be good for desiccation resistance, but also cause hypertension
- High estrogen could increase fertility, but also increases the chance of cancer (estrogen has many targets in the body, and many consequences)
- Some genes ("Thrifty genes") are helpful in famines but also lead to diabetes and obesity

http://genetics.cshlp.org/content/17/5/568.full.pdf+html

Other Examples of Evolutionary Trade-offs:

- Selection on HIV virulence in response to transmission rate - careful versus slow reverse transcription rate
- Sickle Cell Anemia - heterozygote resistance to malaria vs lethality of the recessive homozygote
- Degeneration during Aging - what might be beneficial early in life could be harmful later (ageing)
- What might be good in one environment could be bad in another:
  - Pale skin is helpful in Northern latitudes:
    - 6x rate of Vitamin D synthesis relative to darker skin
  - While, Pale skin is harmful in Southern latitudes:
    - 6x increase in skin cancer

Trade-offs during Aging

- Not all evolutionary tradeoffs are due to the same genes (like in the case of antagonistic pleiotropy)
- Tradeoff between cold and hot tolerance → hot and cold tolerance are encoded by different genes, but limited by the amount of energy available. Can’t be good at both

Natural Selection and Aging: Evolutionary Trade-off between early vs late life

- Selection might favor alleles that benefit early life stages even if they are deleterious later in life.
- Thus, deleterious traits accumulate after reproduction.
- Williams 1957: antagonistic pleiotropy theory of aging

Genetic Drift and Natural Selection

- Because of the randomness introduced by Genetic Drift, Natural Selection is less efficient when there is genetic drift
- Thus, Natural Selection is more efficient in larger populations, and less effective in smaller populations
Selection acts only on genes that are expressed

- Remember that selection acts on the phenotype... the traits that are expressed, given the genotype.

Concepts

- Natural Selection
- Sexual Selection
- Directional Selection
- Balancing Selection
- Evolutionary Tradeoffs
- Pleiotropy
- Antagonistic Pleiotropy

1. Which of the following is NOT an example of an Evolutionary Trade-off?
   (A) HIV, the virus that causes AIDS, normally has a reverse transcriptase that is prone to producing replication errors during rapid DNA synthesis, but undergoes selection for a reverse transcriptase that is less error prone, but slower, in the presence of AZT
   (B) Mutation rate increases exponentially in the male germ line, but the deleterious effects of such mutations are often hidden through dominance.
   (C) Lighter skin (lower melanin) allows greater synthesis of vitamin D, but has a higher incidence of skin cancer, while darker skin protects against UV radiation but has lower vitamin D synthesis.
   (D) Tahitians are islanders that traveled on long journeys on boats. They have high fat retention that is thought to enable survival on long trips. But in the modern day, they have high incidence of obesity and diabetes.

2. Which of the following cases is likely to lead to the LOWEST levels of sexual dimorphism?
   (a) Males and females invest equally in the care of offspring
   (b) Females lay one very large egg with lots of highly nutritious yolk, only once per year
   (c) Male fish spend lengthy periods of time brooding and caring for eggs until hatching, and competition for these males is fierce
   (d) Only one victorious male is able to mate after fighting among males, and the defeated males do not mate
   (e) Females of a species prefer larger males

3. During the course of Hominin evolution, sexual dimorphism (differences between sexes) has been declining. Which of the following would reduce sexual dimorphism in humans?
   (A) Males have an extremely high variance in reproductive success, where most males have no offspring
   (B) Monogamy, where most females and most males are able to mate and produce offspring
   (C) A few males sire most of the offspring in a population
   (D) Females that are choosy about mating partners
   (E) Females bear most of the cost of reproduction

4. Which of the following is NOT an example of an Evolutionary Tradeoff?
   (A) The heterozygote for the HbS gene encodes hemoglobin with reduced oxygen carrying capacity, but this hemoglobin also reduces infection in the presence of malaria.
   (B) In some species of mammals, large males are favored by sexual selection, but the large males also have reduced immune systems
   (C) HIV with high fidelity (careful) reverse transcriptase will make fewer errors during genome replication, but will have slower genome replication and will grow more slowly
   (D) Animals tend to favor MHC dissimilar mates so that they are heterozygous at MHC loci, so that they are resistant to a larger number of pathogens
5. In a species of birds, the males are brightly colored, whereas the females are brown and plain. Which scenario would most likely lead to such sexual dimorphism?

(A) Both males and females share the cost of caring for the offspring
(B) The males incubate the eggs and defend the nest
(C) The females bear most of the burden of reproductive cost
(D) The species is monogamous
(E) The males have a low variance in reproductive success (most males get to mate and produce offspring)

Answers:
1B
2A
3B
4D
5C