

Evolution lecture #12 -- **Selection** -- Dec. 3<sup>rd</sup>, 2008

479-486 (ch. 23) **in 8th ed.**

464-470 (ch. 23) **in 7th ed.**

### • **Summary of topics**

- Distinguish between **single** gene traits and **quantitative** traits
- Contrast the short and long term effects of **balancing** versus **directional** selection on the genetic structure of a population for Mendelian and quantitative traits
- Describe examples of **heterozygote advantage**, **disruptive selection**, etc.
- Relate observations on **artificial selection** to natural selection
- Contrast **Mullerian** and **Batesian** mimicry
- Understand the concept and describe examples of **sexual selection**
- Understand why sex exists!

### • **Introduction**

**Why are there so few good examples of selection?** selection has to be very strong to detect it via deviations from HW, or direct measurement of differential fitness or fertility. On the other hand, even relatively weak selection, e.g., 1%, can have a major effect on long term evolution.

**Malaria and selection:** one strong selective pressure, which has led to polymorphism of a number of genes in humans is malaria. Some examples related to *Plasmodium falciparum* are:

1. Variants at the hemoglobin  $\beta$  gene, notably Hb-S (homozygotes have sickle cell anemia, also see below), and also there is another variant Hb-C where homozygotes have a milder anemia, in both cases there is heterozygote advantage in malarial environments. Both alleles have relatively high frequencies in parts of Africa, the Mediterranean, the Middle East, and India (Fig. 23.17 (8th); Fig. 23.13 (7th)).
2. Both  $\alpha$  and  $\beta$  thalassemias are found where there is a reduced amount or no production of either the  $\alpha$  or  $\beta$  chains of hemoglobin (the hemoglobin molecule is a tetramer of 2  $\alpha$  and 2  $\beta$  chains). Again there is heterozygote advantage in malarial environments, affected individuals have mild to severe anemia, and these polymorphisms are relatively frequent in the Mediterranean and Asia.
3. An X-linked recessive trait, G6PD (glucose-6 phosphate-dehydrogenase) deficiency also provides protection against malaria; life threatening anemias can occur under certain conditions, e.g., eating fava beans or taking certain drugs. Different mutational origins led to the polymorphisms seen in the Mediterranean and Asia.

4. HLA associations: in the Gambia, the HLA alleles B53 and DR13 are relatively frequent and have been shown to provide protection from malaria.

**AIDS and selection:** two major examples of AIDS causing selection on common polymorphisms in humans are as follows (in these cases AIDS has not led to these polymorphisms, as in the malaria selection examples above, since it is much too recent a phenomenon):

1. Individuals homozygous for the CCR5  $\Delta 32$  mutation are protected from AIDS; this polymorphism is largely confined to individuals with European ancestry.

One possible explanation for its relatively high frequency is that it may have provided protection from smallpox; the *myxoma* virus, which is a member of the poxvirus family, also exploits CCR5 for infection.

**I. CCR5  $\Delta 32$  variant in a French population**

genotypes:	A/A	A/ $\Delta 32$	$\Delta 32/\Delta 32$	
observed numbers	795	190	15	Total: 1,000
expected HW	792.1	195.8	12.1	

**II. CCR5  $\Delta 32$  variant in a high risk HIV negative cohort in San Francisco**

genotypes:	A/A	A/ $\Delta 32$	$\Delta 32/\Delta 32$	
observed numbers	793	174	29	Total: 996
expected HW	777.5	205.0	13.5	

**III. CCR5  $\Delta 32$  variant in a HIV positive cohort in San Francisco**

genotypes:	A/A	A/ $\Delta 32$	$\Delta 32/\Delta 32$	
observed numbers	1,988	440	1	Total: 2,429
expected HW	2,007	401.9	20.1	

2. HLA: (a) specific HLA alleles provide protection, and (b) people heterozygous for a number of HLA genes (there are a total of 6 classical HLA genes) live longer after infection (presumably these individuals have a wider immune response).

**• Selection on single gene (Mendelian) and quantitative traits**

**Relative fitness:** the average number of offspring produced by individuals with a certain genotype, relative to the number produced by individuals with other genotypes.

**Quantitative trait:** determined by a large number of genes each of small effect and environmental factors, e.g., height and weight.

## Types of selection:

**single gene traits:** 1. directional, 2. balancing (a. heterozygote advantage, b. frequency dependent), 3. heterozygote disadvantage (we will not consider this case)

**quantitative traits:** 1. directional, 2. stabilizing, 3. disruptive (diversifying)

## Single gene traits:

**1. directional selection:** leads to fixation of an allele. An example would be relative fitnesses:

genotype	AA	AB	BB
relative fitness	1.0	0.9	0.8

which would lead to fixation of the A allele.

**Industrial melanism:** is a term used to describe the evolutionary process by which initially light colored organisms become dark as a result of natural selection in an industrial environment. The process takes place because the dark organisms are better concealed from their predators in habitats that have been darkened by soot and other forms of industrial pollution.

**lead tolerance:** plants able to grow on lead-rich soil are found in association with mines less than a century old. Populations of the grass *Agrostis tenuis* are clearly able to evolve through changing their genotypic frequencies quickly when the environment demands it (Fig. 23.12 8th). Similar rapid changes have now been documented for other populations of organisms.

**2. balancing selection (balanced polymorphism):** 2 or more alleles are maintained in a population due to selection. Both heterozygote advantage and frequency dependent selection are examples of balancing selection, they both lead to a stable polymorphic equilibrium state.

**a. heterozygote advantage:** the heterozygote has a higher relative fitness than both homozygotes, this leads to a balanced polymorphism (see sickle cell anemia example below).

**sickle cell anemia:** Individuals with sickle cell trait (AS heterozygotes) are more resistant to malaria than individuals who are homozygous AA; SS individuals are also more resistant to malaria than AA individuals, but they have sickle cell anemia which drastically reduces their fitness. The relative fitness values in a malarial environment have been estimated as:

genotype	AA	AS	SS
relative fitness	0.88	1.0	0.14

The selection in this case is very strong and causes detectable deviations from HWP"

Genotypes	AA	AS	SS	
Observed no. among adults	9,365	2,993	29	Total: 12,387
Observed freq. among adults	0.756	0.242	0.002	
Expected no. among adults (HWP)	9,523	2,676	188	Total: 12,387
Expected freq. among adults (HWP)	0.769	0.216	0.015	

**other possible examples of heterozygote advantage:** there is some evidence with the following diseases of an advantage to heterozygotes (you do not need to memorize these examples):

(a) With phenylketonuria (PKU) excess of the amino acid phenylalanine in carriers (and those with the disease) inactivates ochratoxin A a fungal toxin that causes miscarriages. PKU carriers have a lower than average incidence of miscarriages. PKU is most frequent in Scotland and Ireland, and this may relate to times of famine when people were forced to eat moldy grains to survive.

(b) There is some evidence from World War II that healthy relatives of children who had Tay Sachs (hence the relatives are more likely to be carriers) did not contract tuberculosis as often as others in crowded ghetto conditions.

(c) In the case of cystic fibrosis, there may be protection from diarrheal diseases such as cholera and typhus; carriers have less chloride channels in intestinal cells, blocking cholera toxin entry, or *Salmonella typhi*, which uses the CFTR protein as a receptor.

**b. frequency dependent selection:** is another cause leading to balanced polymorphism (Fig. 23.18 (8th); Fig. 23.14 (7th)). The reproductive success of a phenotype depends on its frequency, with higher fitness associated with lower frequency of the phenotype in the population (advantage when rare).

An example is the balanced polymorphism for “right-mouthed” and “left-mouthed” cichlid fishes of a species that feeds on the scales of other fishes by approaching the prey from behind and using their mouths to snatch scales from the flanks of the prey.

In frequency-dependent selection, the fitness of any morph declines if it becomes too common in the population

### **Quantitative traits (Fig 23.13 (8th); Fig 23.12 (7th))**

**1. directional selection:** selection acts to eliminate one extreme from an array of phenotypes.

**2. stabilizing selection:** selection acts to eliminate both extremes from an array of phenotypes (this is the quantitative equivalent of balancing selection for a single gene trait). Birth weight in humans demonstrates stabilizing selection.; there is selection against very small and very large birth weights.

**3. disruptive selection:** (also called diversifying selection) selection acts to eliminate the intermediate type, favoring both extremes (this is the quantitative equivalent of heterozygote disadvantage for a single gene trait).

**Factors maintaining variability:**

Diploidy

Balanced polymorphisms

- Heterozygote advantage
- Frequency dependent selection

Environmental heterogeneity

- space
- time

• **Artificial selection:** selective breeding, carried out by humans, to alter a population.

Artificial selection in domesticated animals and plants demonstrates the ability to change the gene pool in a small amount of time if the selection is strong. Some examples are:

(1) Selection of cattle for meat quantity and quality.

(2) Selection of cows for milk yield.

(3) selection of sheep for meat or for specific types of fleece to make into wool.

(4) Selection of horses for speed, strength, or racing ability.

(5) Selection of specific features of plants. For example broccoli, cauliflower, cabbages, kale, and brussel sprouts all have a common ancestor in one species of wild mustard. By selecting different parts of the plant to accentuate, breeders have obtained these divergent results.

(6) Selection for increased yield and conformity of size and shape for mechanical harvesting and durability for travel to market, e.g., tomato.

(7) Selection of all the different breeds of dogs has taken place over approximately 5,000 years with specializations for different features such as hunting ability, etc.

• **Mimicry**

**Batesian mimicry:** a **palatable** species **masquerades** as an **unpalatable** one.

**Mullerian mimicry:** several unpalatable species **converge** in appearance, each species gaining protection from its similarity to the other one.

• **Sexual selection:**

Differential reproduction owing to variation in the **ability to obtain mates**, i.e., selection on mating behavior, either through:

(1) choice by members of one sex (usually females) of certain members of the other sex, e.g., the showy plumage of many male birds (intersexual selection) or  
(2) through competition among members of one sex (usually males) for access to members of the other sex, e.g., male competition can take the form of direct fighting (intrasexual selection)

Darwin first developed this body of theory, when he recognized that many features of plants and animals could not be explained by natural selection because they did not seem to make species better adapted to their environments. Instead, characters, such as the peacock's tail, the antlers of a deer, or the horn of a stag beetle, seemed to impede survival.

Darwin recognized that the struggle for existence was both between members of different species for limiting resources and between members of the same species for the opportunity to reproduce.

Darwin's theory of sexual selection explains the existence of sexual dimorphism including anisogamy (i.e., having gametes of different size in two sexes).

If reproduction is limited by the production of eggs or ovules and not sperm or pollen, then males are competing for females, who become a limiting resource.

Darwin recognized that any characteristic that would increase an individual's chance of finding a mate and having offspring would be favored by natural selection, even if it resulted in a decreased rate of survival. He called this kind of natural selection, sexual selection.

## • Why is there sex?

Sexual modes of reproduction persist despite the two-fold cost of sex.

Females that reproduce asexually and produce all daughters should be able to produce twice as many daughters as those who reproduce sexually and produce equal numbers of sons and daughters. This is the two-fold cost.

Asexual reproduction is not hypothetical. Many species of plants and animals can do it by a variety of means, budding, clonal growth, and parthenogenesis. But some of these species have not lost the ability to reproduce sexually. Usually sexual reproduction is induced by environmental stress, as in aphids or mushrooms.

The reason that sexual reproduction persists is that natural selection favors the production of genetically diverse offspring. There are several reasons for thinking this. One is that sexual reproduction is often associated with stress or environmental change, which is when variability would be most useful. Sexual reproduction is often associated with dispersal, and making it through an unfavorable season.

Think of a lottery example: if you know the winning number you should buy 1,000 tickets with that number. But if you don't, then you should 1,000 tickets with different numbers!

Completely asexual species have evolved, but they do not have large ranges and do not seem to last very long as species, so there may be a form of species selection operating to favor sex over the long term.

Sex as a fundamental example of division of labor:

isogamy -> anisogamy -> oogamy

Why is it nearly always female choice?

- gamete size, number, and cost to produce
- investment in producing offspring

The fundamental asymmetry of sex:

- Female fitness is limited by an ability to gain the resource required to produce eggs and rear young.
- Male fitness is limited by the ability to attract mates.

### **Why Natural Selection Cannot Fashion Perfect Organisms:**

Evolution is limited by historical constraints

Not every structure or function is adaptive

Adaptations are often compromises

Drift and natural selection interact

Selection can only edit existing variations

### **Questions relating to lecture on selection**

1. In Africa in an area where malaria is prevalent, 1,000 newborns and 1,000 adults are typed for the sickle-cell polymorphism:

Genotypes	AA	AS	SS	
Newborns (O)	780	204	16	Total: 1,000
Adults (O)	769	229	2	Total: 1,000

For both samples, determine the allele frequencies of the A and S alleles, and test fit to HWP. Comment on any differences, or not, between the allele frequencies and the test of HWP in the two samples.

2. For the following selection schemes, where the relative fitness values for each genotype are given, state whether one or the other allele will be fixed (and if so which allele) or whether a balanced polymorphism will be maintained:

	AA	AB	BB
(a)	0.8	0.9	1.0
(b)	0.2	1.0	0.6
(c)	1.2	1.1	1.0

3. Do self-quiz questions 2, 3, and 5 on page 486 of the 8th edition or self-quiz questions 4, 6, 7, and 10 on page 471 of the 7th edition.

**Answers to Problems** (don't peek till you try them!)

1. Among the newborns,  $f(A) = p = 0.8820$ ,  $f(S) = q = 0.1180$ , and in the adults  $f(A) = 0.8835$ ,  $f(S) = 0.1165$ .

Newborns (O)	780	204	16	Total: 1,000
Newborns (E)	777.9	208.2	13.9	Total: 1,000
Adults (O)	769	229	2	Total: 1,000
Adults (E)	780.6	205.9	13.5	Total: 1,000

The adult sample shows deviation from HWP, while the newborn sample does not. This reflects the fact that at birth (pre-selection) the genotype frequencies are expected to be in HWP, whereas after selection has acted (malaria and sickle-cell anemia), the adult population shows significant deviation from HWP. The fact that the allele frequencies are very similar in newborns and adults may indicate that the population is close to equilibrium.

2. (a) fixation of the B allele, loss of the A allele  
 (b) stable polymorphism  
 (c) fixation of the A allele, loss of the B allele