Natural Selection

- **HWE requires that there be no natural Selection.**

I) Introduction

- **NS is the differential survival and reproduction of genotypes in populations.**

A) Requirement for NS to operate

1) **Reproduction – generally modeled as discrete, not age structured, constant population size with no overlapping generations**

2) **Heritability – character that is responding to NS must be stably passed from one generation to the next.**

3) **Variation in fitness among phenotypes.**

B) Terms

1) **Fitness – average number of offspring produced by individuals of a specific phenotype (i.e., genotype). If sexually reproducing each parent get 50% of each offspring.**

2) **Overall fitness – the proportion of the offspring surviving to reproduction multiplied by average number of offspring produced by individual (i.e., viability and fertility)**

3) **Absolute fitness – the measured viability and fertility fitnesses.**

4) **Relative fitness – absolute fitness normalized to most fit phenotype (i.e., genotype).**

W_{ij} = fitness of the ij^{th} type

e.g., W_{11} = AA

e.g., W_{12} = Aa

e.g., W_{22} = aa

5) **Inclusive fitness – overall life time or reproductive life span fitness**

6) **Selection coefficient – s_{ij} = the magnitude of reduction in relative fitness of the ij^{th} type.**

$$W_{ij} = 1 - s_{ij}$$

C) Assumptions of the Classical Fitness Model

Hardy Weinberg Assumptions

1) **1 autosomal locus with 2 alleles**
2) **random mating**
3) **no migration**
4) **no mutation**
5) **infinite population size**
6) **discrete, nonoverlapping, nonage structured generations**
7) **each individual contributes an average of 2m gametes to the next generation (i.e., replaces itself in gametes)**
8) **In each generation, a constant proportion of zygotes, V_{ij} survives to reproduce (i.e., population size is stable)**
9) **Among the sexes there is equal genotype frequencies, fertilizations and viability.**

II) General Types of Natural Selection

- **Before we get into specific models, let's generally review basic types.**

OH 9.1

A) General Model

OH 9.2

B) Variables

1) **Mean Population Fitness ($\overline{W}$)**

$$\overline{W} = p^2W_{11} + 2pqW_{12} + q^2W_{22}$$

$$p' = \frac{p^2W_{11} + \frac{1}{2}(2pqW_{12})}{\overline{W}}$$

$$p' = \frac{pW_1}{\overline{W}}$$

Where $W_1 = pW_{11} + qW_{12}$

W_1 is the marginal fitness or the average fitness of the genotypes that contain the p allele weighted by their frequencies.

$$q' = \frac{qW_{21}}{\overline{W}}$$

Where $W_2 = pW_{12} + qW_{22}$

W_2 is the marginal fitness or the average fitness of the genotypes that contain the q allele weighted by their frequencies.

2) **Equilibrium allele frequencies – we will be dealing with equilibrium states extensively so it is often convenient to know the change in allele frequency over time (Δp). Equilibrium are when $\Delta p = 0.0$.**

OH 9.4

$$\Delta p = p' - p$$

$$= \frac{p^2W_{11} + pqW_{12}}{\overline{W}} - p$$

$$= \frac{p^2W_{11} + pqW_{12} - p\overline{W}}{\overline{W}}$$

$$= \frac{p^2W_{11} + pqW_{12} - p(p^2W_{11} + 2pqW_{12} + q^2W_{22})}{\overline{W}}$$

$$= \frac{p\left[(pW_{11} + qW_{12}) - (p^2W_{11} + 2pqW_{12} + q^2W_{22}\right]}{\overline{W}}$$

$$= \frac{p\left[pW_{11} + qW_{12} - p^2W_{11} - 2pqW_{12} - q^2W_{22}\right]}{\overline{W}}$$

$$= \frac{p\left[pW_{11} - p^2W_{11} + qW_{12} - pqW_{12} - pqW_{12} - q^2W_{22}\right]}{\overline{W}}$$

$$= \frac{p\left[pW_{11}(1-p) + qW_{12}(1-p) - pqW_{12} - q^2W_{22}\right]}{\overline{W}}$$

$$= \frac{p\left[pqW_{11} + q^2W_{12} - pqW_{12} - q^2W_{22}\right]}{\overline{W}}$$

$$= \frac{pq\left[(pW_{11} + qW_{12}) - (pW_{12} + qW_{22})\right]}{\overline{W}}$$

$$\Delta p = \frac{pq\left[W_1 - W_2\right]}{\overline{W}}$$

OH 9.4.5

C) No Selection Model: $W_{11} = W_{12} = W_{22}$ (s = 0.0)

Genotype	AA	Aa	aa
Frequency Before Selection	p^2	2pq	q^2
Fitness	W_{11}	W_{12}	W_{22}
Relative Fitness	1	1 – hs	1 – s
Frequency After Selection	p^2	2pq(1 – hs)	$q^2(1 – s)$

$0.0 \le h \le 1.0,\ 0.0 \le s \le 1.0$

Remember: $\overline{W} = p^2W_{11} + 2pqW_{12} + q^2W_{22}$

And: $p' = \dfrac{p^2W_{11} + pqW_{12}}{\overline{W}}$

Since: $W_{11} = W_{12} = W_{22} = W_x$

Then: $\overline{W} = W_x(p2 + 2pq + q^2)$

$\overline{W} = W_x$

And $p' = \dfrac{W_x(p^2 + pq)}{W_x} = p^2 + pq = p(p + q) = p$

OH 9.3 $\Delta p = p' - p = 0$

D) Directional Selection Model – three types: selection against dominant, recessive, and codominant.

1) Selection against Dominant allele (h = 1, s > 0.0):

Genotype	AA	Aa	aa
Frequency Before Selection	p^2	2pq	q^2
Fitness	W_{11}	W_{12}	W_{22}
Relative Fitness	1	1 – hs	1 – s
Frequency After Selection	p^2	2pq(1 – hs)	$q^2(1 - s)$

$$W_{11} > W_{12} = W_{22}$$

In this case, a is the dominant allele and both the Aa and aa genotypes are selected against (alternatively you can view this as selection FOR the recessive allele).

NOTE: We know that $p^2 + 2pq + q^2 = 1.0$

SO: $p^2 + 2pq(1 - hs) + q^2(1 - s) < 1.0$

$$\overline{W} = p^2 + 2pq(1 - s) + q^2(1 - s)$$

$$\overline{W} = p^2W_{11} + 2pqW_{12} + q^2W_{22}$$

Normalized Frequency After Selection	$\frac{p^2}{\overline{W}}$	$\frac{2pq(1 - hs)}{\overline{W}}$	$\frac{q^2(1 - s)}{\overline{W}}$

$$\Delta p = \frac{pq[W_1 - W_2]}{\overline{W}}$$

Movie: Directional Selection

OH 9.5

OH 9.6

2) Selection against Recessive allele

Genotype	**AA**	**Aa**	**aa**
Frequency	p^2	2pq	q^2
Rel. Fitness	1	1	1 – s

$$W_{11} = W_{12} > W_{22}$$

In this case, a is the recessive allele and aa genotype is the only one selected against (alternatively you can view this as selection FOR the dominant allele).

OH 9.7

$$\overline{W} = p^2 + 2pq + q^2(1 - s)$$

$$\overline{W} = 1 - q^2s$$

OH 9.8

3) Codominant alleles

Genotype	AA	Aa	aa
Frequency	p^2	2pq	q^2
Rel. Fitness	1	1 – hs	1 – s

where $0 < h < 1$, $W_{11} > W_{12} > W_{22}$

In this case, all genotypes have unique fitness value. When h = 0.5 this is a perfectly additive situation.

OH 9.9

$$\overline{W} = p^2 + 2pq + q^2(1 - s)$$

$$\overline{W} = 1 - q^2 s$$

OH 9.10

4) Summary Directional Selection.

- **Mean population fitness ALWAYS increases**

OH 9.11

- **Time to fixation decreases with increasing selection pressure**
- **Time to fixation decreases with increasing selection against the heterozygote**

OH 9.12

- **Codominant generally fixes faster and has a more linear increase in mean population fitness.**

E) Heterozygote Disadvantage (Underdominant Selection)

Genotype	AA	Aa	aa
Frequency	p^2	2pq	q^2
Rel. Fitness	1 + s	1	1 + t

$$W_{11} > W_{12} < W_{22}$$

$$\hat{p} = p_t = p$$

$$\hat{p} = \frac{W_{12} - W_{22}}{2W_{12} - W_{11} - W_{22}} = \frac{t}{s + t}$$

In the case where t = s, the population will be in equilibrium at p = 0.5. All other values the population goes to fixation of one allele or the other depending on which side of 0.5 the population starts on.

OH 9.13

In all cases except at the equilibrium, mean population fitness is maximized at 1.0. The rate is dependent on the selection coefficient. At equilibrium, the magnitude of the mean population fitness (which is unstable) depends on the magnitude of the selection coefficient.

OH 9.14

At equilibrium, the mean population fitness is minimized. The magnitude of the mean population fitness depends on the magnitude of the selection coefficient.

OH 9.16
OH 9.16.5
Movie: Underdominant Selection
OH 9.16.6

F) Heterozygote Advantage (Overdominant Selection)

Genotype	AA	Aa	aa
Frequency	p^2	2pq	q^2
Rel. Fitness	1 – s	1	1 – t

$$W_{11} < W_{12} > W_{22}$$

$$\hat{p} = p_t = p$$

$$\hat{p} = \frac{W_{12} - W_{22}}{2W_{12} - W_{11} - W_{22}} = \frac{t}{s+t}$$

In all cases (i.e., all values of p), the population will be in equilibrium at $\frac{t}{s+t}$.

OH 9.15

In all cases, the mean population fitness is maximized. The rate is dependent on the selection coefficient. At equilibrium (which is stable), the magnitude of the mean population fitness depends on the magnitude of the selection coefficient.

OH 9.17
Movie: Overdominant Selection
OH 9.18

Remember: $\hat{P} = \frac{pq[p(W_{11} - W_{12}) + q(W_{12} - W_{22})]}{\overline{W}}$

If: $W_{11} < W_{12} > W_{22}$

Then: $W_{11} - W_{12} < 0.0$

$W_{12} - W_{22} > 0.0$

And **Sign of Δp is affected by the magnitude of p and q**

G) Summary

1) **For all forms of selection, mean population fitness increases ($\overline{W}$).**
2) **For heterozygote disadvantage, $\overline{W}$ is minimum at unstable equilibrium.**
3) **Except for heterozygote advantage, populations tend to be fixed for most fit allele.**
4) **Heterozygote advantage is only stable polymorphic population conditions so far derived.**