Selection

BIOL 434/509

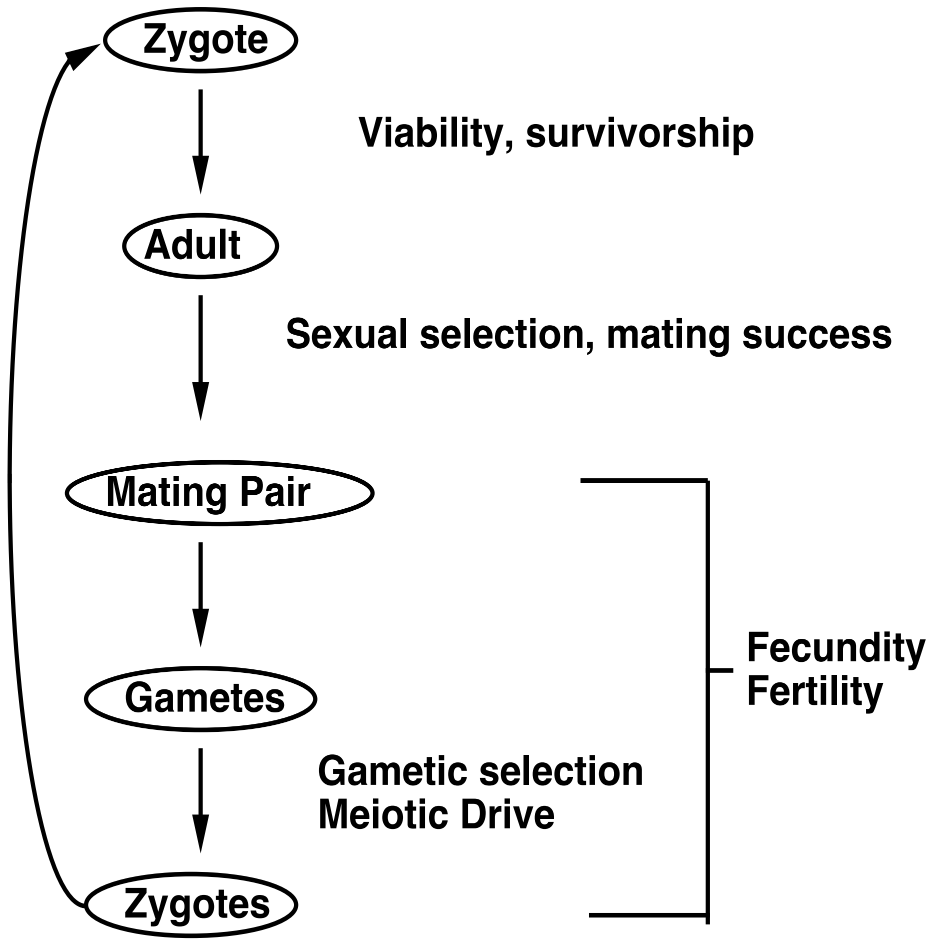
Fitness

The fitness of an individual is the expected number of offspring it will produce (a composite of its ability to survive and to reproduce).

Selection

Selection occurs when individuals (or other entities) with a particular attribute leave more or fewer offspring than other individuals.

Genotypes with higher fitness leave more offspring on average, therefore these genotypes increase in frequency.


Zygote
Viability, survivorship
Adult
Sexual selection, mating success
Mating Pair
Gametes
Fecundity
Fertility
Gametic selection
Meiotic Drive
Zygotes

Mean fitness

The mean fitness of a population is simply the mean over the expected fitness of all genotypes, weighted by the frequency those genotypes appear in the population.

w_i is the fitness of genotype *i*

P_i is the frequency of genotype *i*

$\bar{w}$ is the mean fitness:

$$\bar{w} = \sum_{all\ genotypes} (P_i w_i)$$

Relative fitness

The relative fitness of a genotype is its fitness divided by some standard.

The standard is often the fitness of a particular genotype (usually the ancestral genotype).

Genotype	Absolute Fitness	Relative Fitness
AA	1.4	$\frac{1.4}{1.4} = 1$
Aa	1.2	$\frac{1.2}{1.4} = 0.86$
aa	0.8	$\frac{0.8}{1.4} = 0.57$

Positive and purifying selection

Positive selection is selection for a new beneficial allele.

Purifying selection is selection removing deleterious mutations.

Modelling selection in haploids

Allele name	Growth rate	Number in population	Frequency
A	$1+a$	N_A	p_A
B	$1+b$	N_B	P_B
Total		$N = N_A + N_B$	$p_A + p_B = 1$

Ratio of allele numbers

$$N_{A,t+1} = (1 + a)N_{A,t}$$
$$N_{B,t+1} = (1 + b)N_{B,t}$$

Defining relative fitness:

$$w = \frac{1+a}{1+b}$$

Allele frequencies

$$p_A = \frac{N_A}{N_A + N_B}$$

$$p'_A = \frac{N'_A}{N'_A + N'_B}$$

$N'_A = (1 + a)N_A$ and $N'_B = (1 + b)N_B$, so

$$p'_A = \frac{(1 + a)N_A}{(1 + a)N_A + (1 + b)N_B} = \frac{wN_A}{wN_A + N_B}$$

$$p'_A = \frac{wp_A}{wp_A + p_B}$$

Allele frequencies

$$p'_A = \frac{wp_A}{wp_A + p_B}$$

Denominator of this equation is the mean relative fitness of the population:

$$\bar{w} = p_A(w) + p_B(1) = wp_A + p_B.$$

$$p'_A = \frac{wp_A}{\bar{w}}$$

Change in allele frequency

Δ denotes change

(so Δ*p* is the change in allele frequency over one generation):

$$\Delta p = p'_A - p_A = \frac{w p_A}{\bar{w}} - p_A$$

$$= \frac{p_A p_B (w - 1)}{\bar{w}}$$

Selection coefficients

A selection coefficient typically describes a difference in relative fitness between one genotype and another standard genotype.

The details of how selection coefficients are defined vary from case to case.

For example, if *A* has relative fitness *w* and *B* has relative fitness 1, then we might define the selection coefficient $s = w - 1$. Then we can say that *B* has fitness 1 and *A* has fitness $1+s$.

We can then write:

$$\Delta p = \frac{p_A p_B s}{\bar{w}}$$

where $\bar{w} = p_A(1+s) + p_B = 1 + p_A s$

Survivorship selection in diploids

Assume random mating; q = 1– p

Before selection: $p^2 : 2pq : q^2$

After selection: $w_{AA}p^2 : w_{Aa}2pq : w_{aa}q^2$

Renormalize so that frequencies add to 1:

$$\frac{w_{AA}p^2}{\bar{w}} : \frac{w_{Aa}2pq}{\bar{w}} : \frac{w_{aa}q^2}{\bar{w}}$$

where

$\bar{w} = w_{AA}p^2 + w_{Aa}2pq + w_{aa}q^2$ is the mean fitness.

Converting to allele frequency

$$p' = P'_{AA} + \frac{P'_{Aa}}{2} = \frac{p^2 w_{AA} + pq w_{Aa}}{\bar{w}}$$

$$= p\left(\frac{p w_{AA} + q w_{Aa}}{\bar{w}}\right)$$

$$q' = 1 - p'$$

Marginal fitness

The **marginal fitness** of an allele is the average fitness of that allele weighted by the frequency is appears in all genotypes.

With random mating…

$$w_A = pw_{AA} + qw_{Aa}$$

$$w_a = pw_{Aa} + qw_{aa}$$

Marginal fitness with multiple alleles

$$w_i = \sum p_j w_{ij}$$

Selection equations with marginal fitness

$$p_i' = p_i \frac{\sum p_j w_{ij}}{\bar{w}}$$

For two alleles this becomes:

$$p' = p \frac{p w_{AA} + q w_{Aa}}{\bar{w}}$$

as we calculated above.

Directional selection

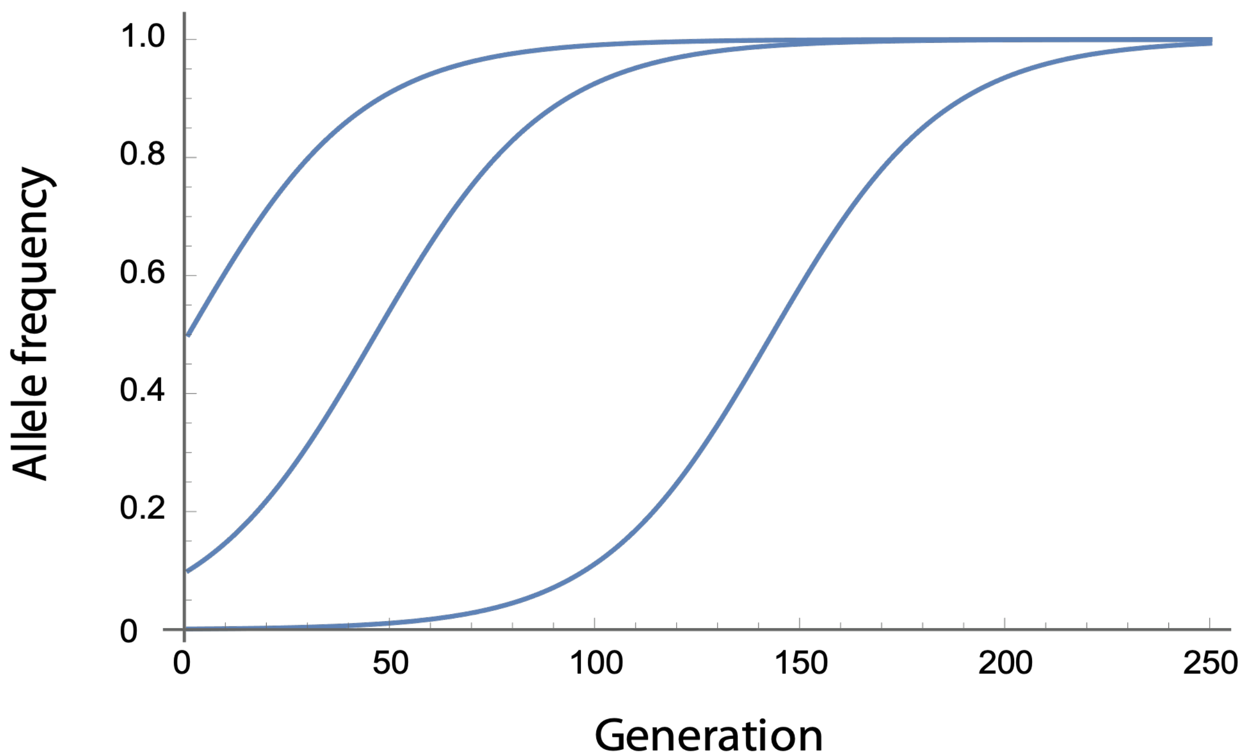
With directional selection, selection always acts to move the phenotype (or genotype) frequency in the same direction.

$$w_{AA} > w_{Aa} > w_{aa}$$

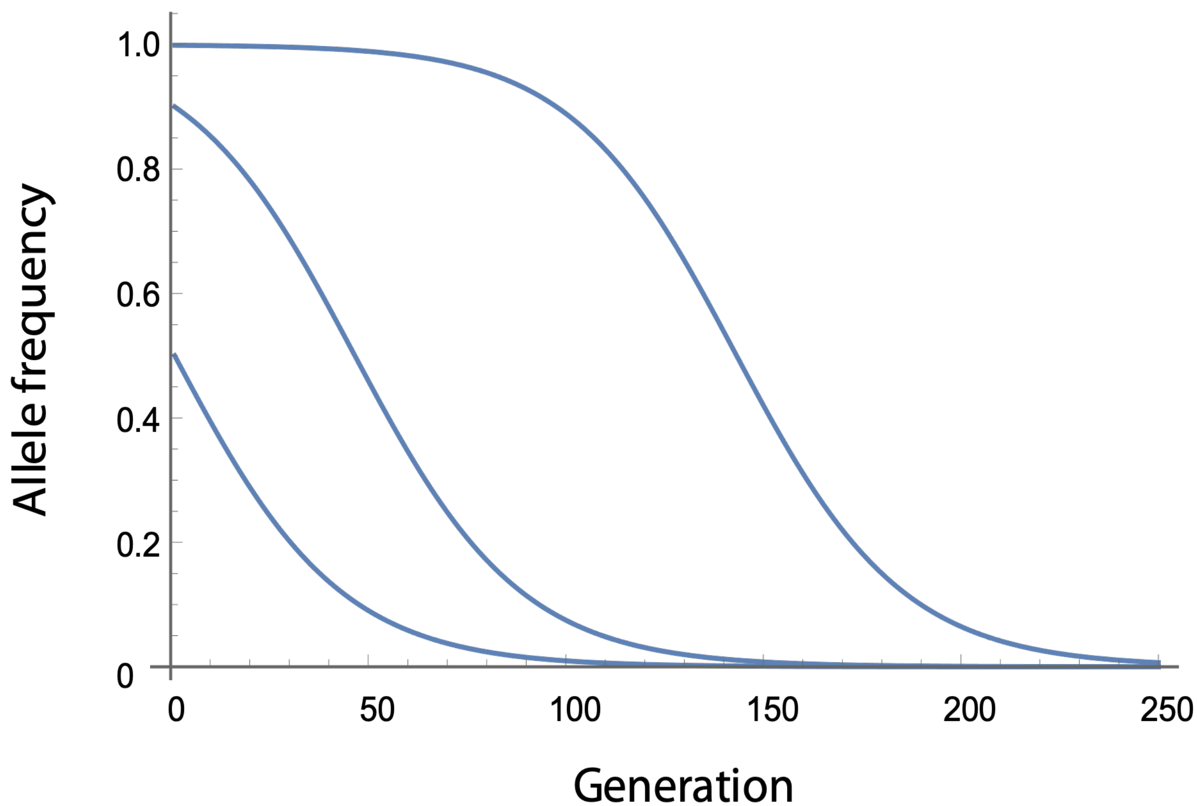
or

$$w_{AA} < w_{Aa} < w_{aa}$$

In this case the favored allele will go towards fixation.



$$w_{AA} = 1.1, w_{Aa} = 1.05, w_{aa} = 1.0$$



$$w_{AA} = 1.0, w_{Aa} = 1.05, w_{aa} = 1.1$$

https://keholsinger.shinyapps.io/Viability-selection/

Additive selection

Fitness is additive if the fitness of the heterozygote is exactly intermediate between the two homozygotes.

(E.g., adding another favored alleles changes fitness by the same amount).

e.g.: $w_{AA} = 1.1, w_{Aa} = 1.05, w_{aa} = 1.0$, as in the previous figures.

Additive selection

Defining a selection coefficient such that:

$$w_{AA} = 1 + 2s, w_{Aa} = 1 + s, w_{aa} = 1$$

the mean fitness would be

$$\begin{aligned}\bar{w} &= p^2(1 + 2s) + 2pq(1 + s) + q^2(1) \\ &= (p^2 + 2pq + q^2) + s(2p^2 + 2pq) \\ &= 1 + 2sp(p + q) \\ &= 1 + 2sp\end{aligned}$$

Therefore, new allele frequency would be

$$p' = p\,\frac{p(1+2s)+q(1+s)}{\bar{w}} = p\,\frac{(1+s+sp)}{1+2sp}$$

Change in allele frequency with additive fitness

The change in allele frequency over one generation is

$$\Delta p = p' - p = p\,\frac{(1+s+sp)}{1+2sp} - p = \frac{spq}{1+2ps}$$

If the strength of selection is small ($|s| \ll 1$), then this is approximately

$$\Delta p \approx spq$$

Response to selection

$$\Delta p \approx spq$$

Response to selection: Δp is a function of two aspects of biology: the strength of selection and the amount of genetic variation.

Selection with dominance

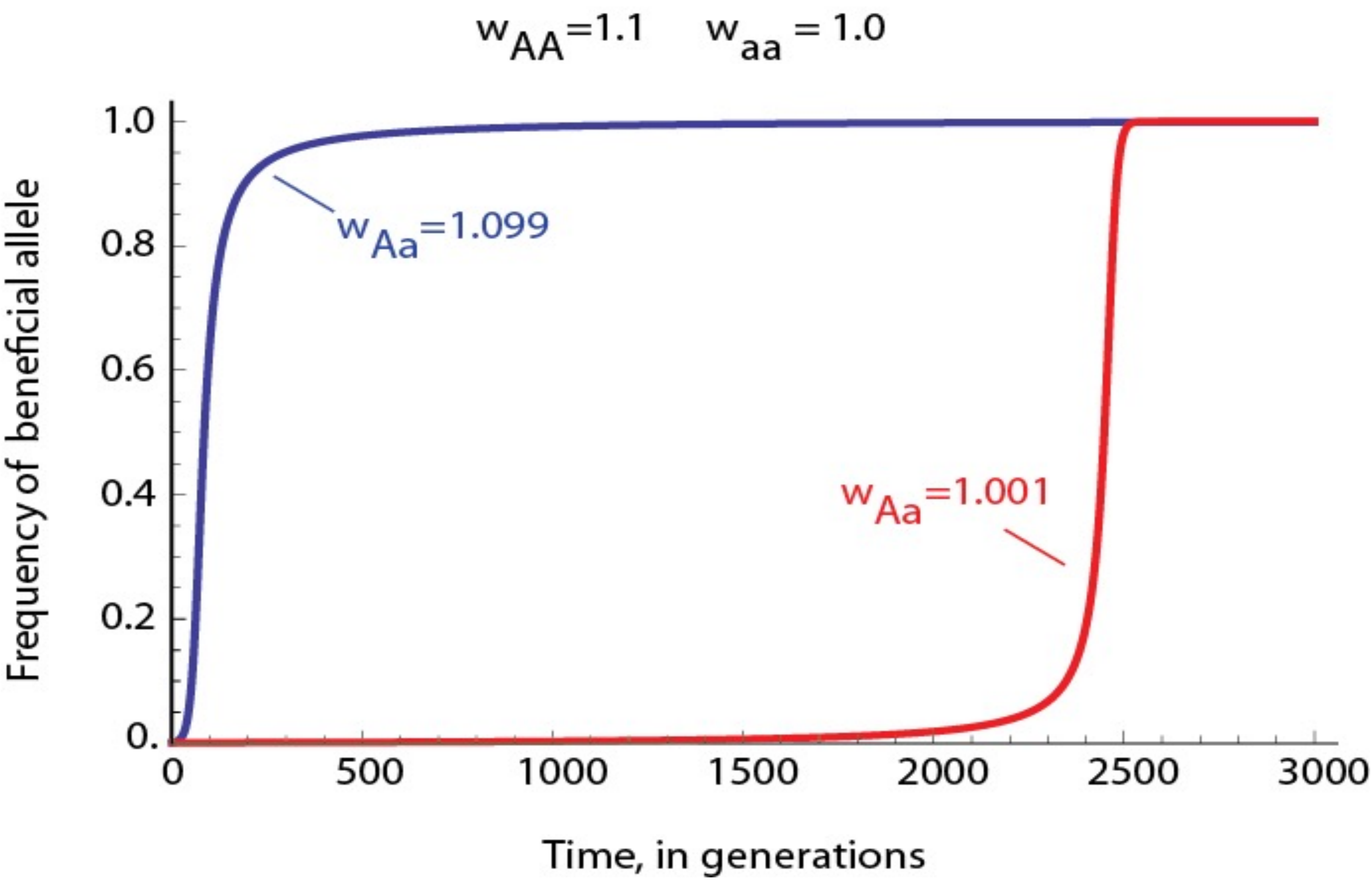
AA	Aa	aa	
$1+s$	$1+hs$	1	Relative fitnesses

The dominance coefficient h indicates where the fitness of the heterozygote is between the fitnesses of the two homozygotes:

If $h = 1/2$, then these alleles are co-dominant with respect to fitness

If $h < 1/2$, then *A* is recessive (or partially recessive)

if $h > 1/2$ then *A* is dominant (or partially dominant)



wAA=1.1 waa = 1.0
1.0
0.8
0.6
0.4
0.2
0.
Frequency of beneficial allele
wAa=1.099
wAa=1.001
0
500
1000
1500
2000
2500
3000
Time, in generations

Calculating *h*

Genotype	*AA*	*Aa*	*aa*
Absolute fitness	1.80	1.32	1.20
Relative fitness	1.5	1.1	1
Fitness in terms of *h* and *s*	1 + s	1 + *hs*	1

$s = 0.5$

$1 + hs = 1 + h\,(0.5) = 1.1 \rightarrow h = 0.2$

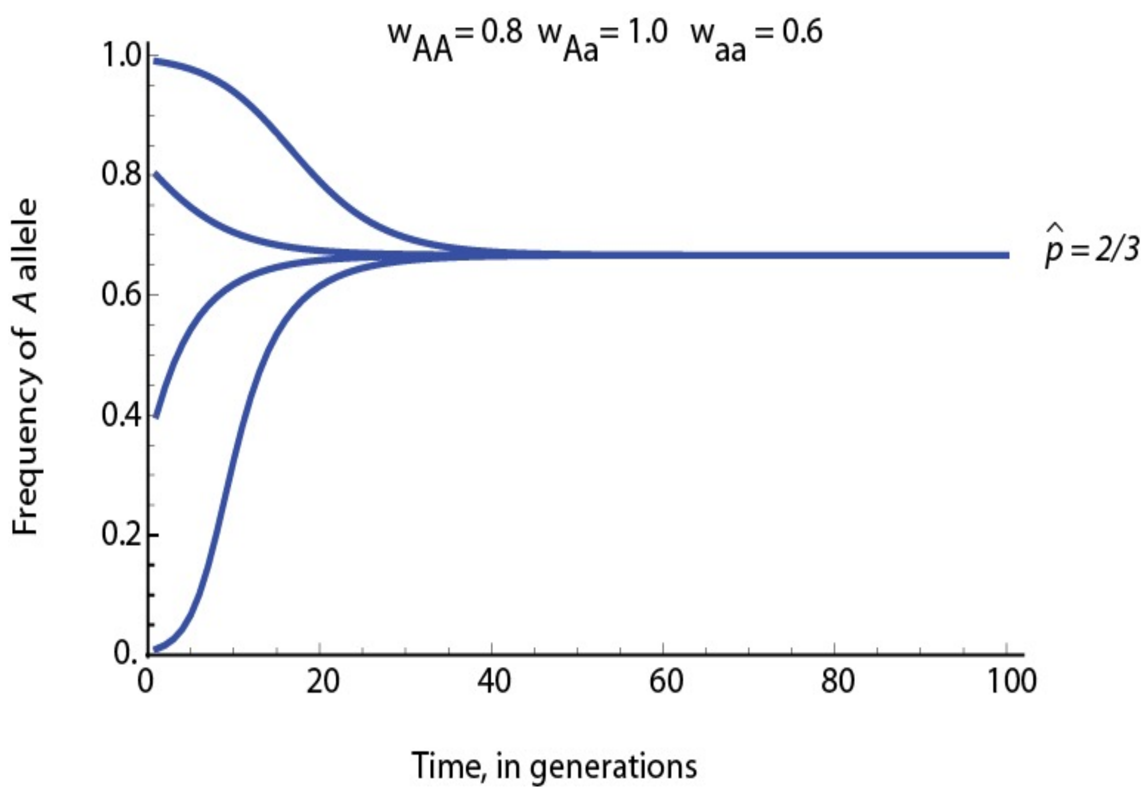
Overdominance

With overdominance, the heterozygote is the most fit genotype.

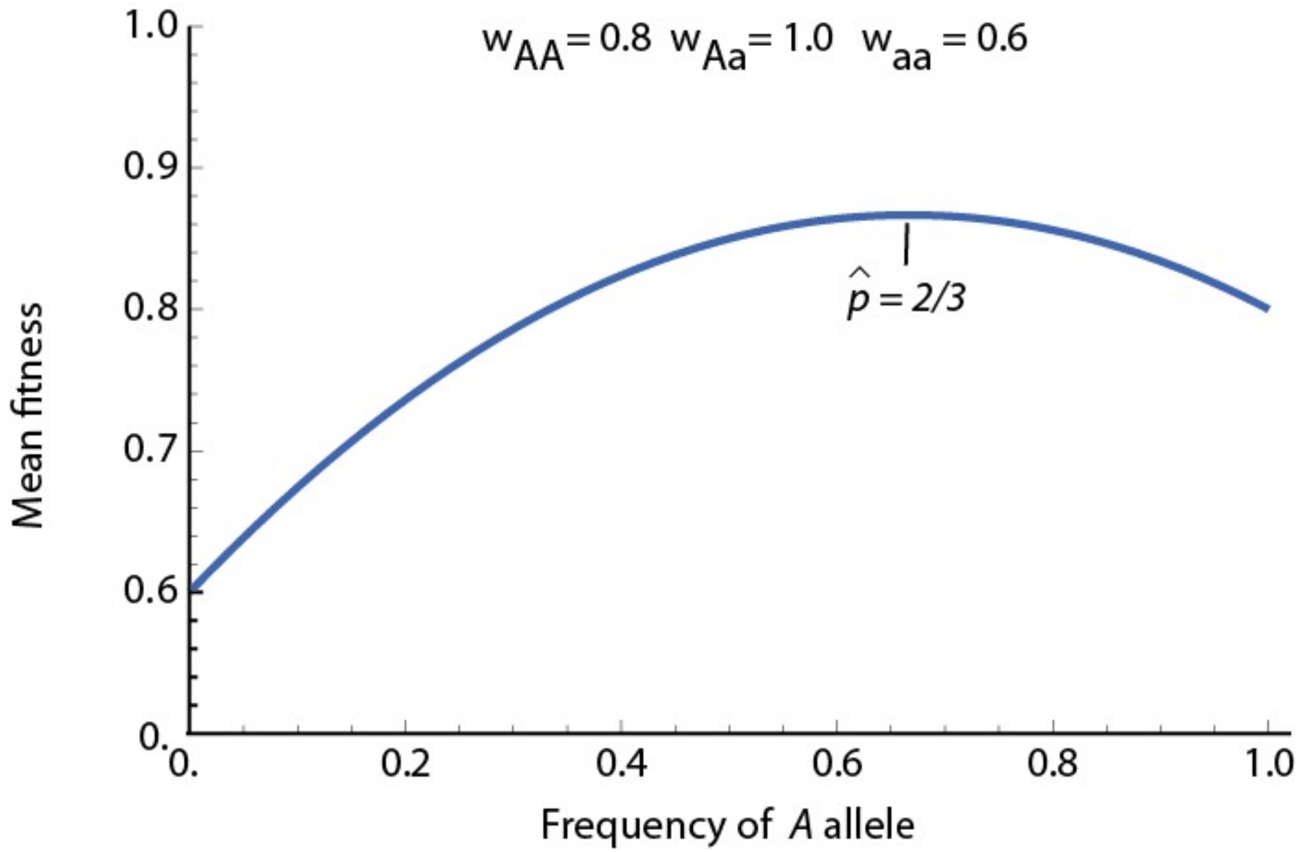
AA	*Aa*	*aa*	
1–*s*	1	1–*t*	Relative fitnesses

Overdominance

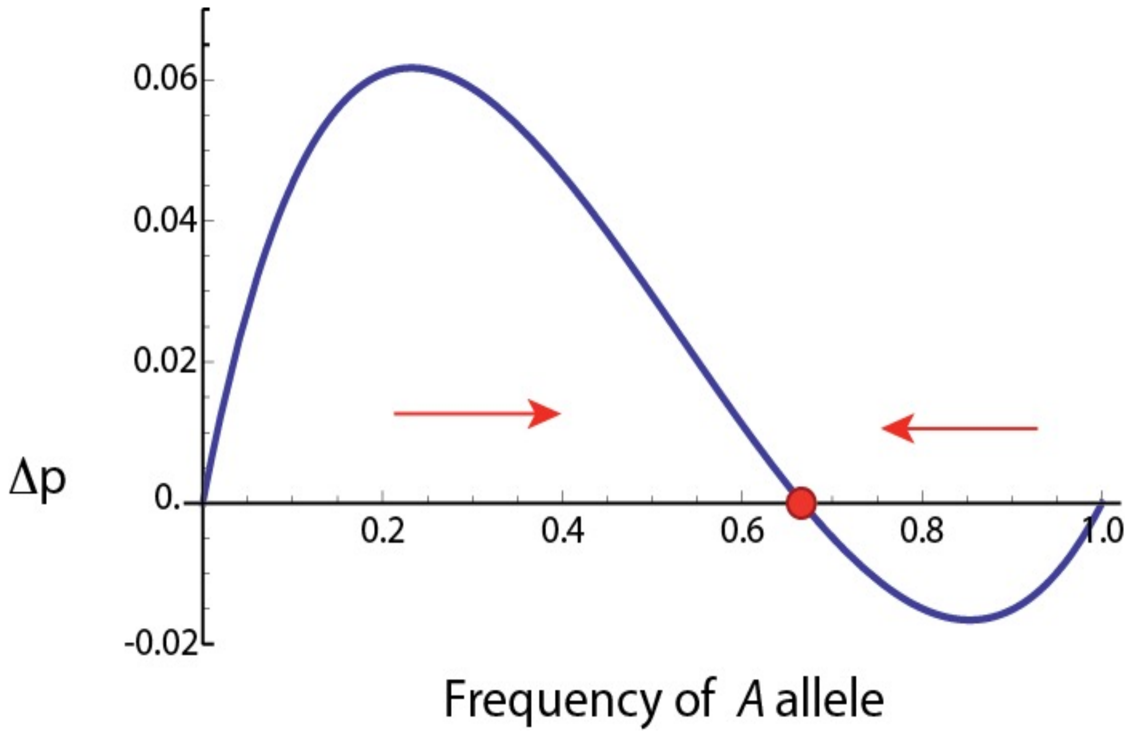
Equilibrium allele frequency: $\hat{p} = \frac{t}{s+t}$



Mean fitness with overdominance



Allele frequency change with overdominance



Overdominance can maintain genetic variation.

Hemoglobin

Relatively few examples of overdominance are known.

The classic example of overdominance is β hemoglobin in humans:

			Fitness
AA	"normal"	sensitive to malaria	0.89
AS	heterozygote	resistant to malaria, slight sickling of red blood cells	1
SS	sickle cell	sickle cell anemia	0.2

Marginal fitness with overdominance

$$w_A = p(1-s) + q = 1 - ps$$
$$w_a = p + q(1-t) = 1 - qt$$

At equilibrium, $w_A = w_a$:

$$1 - \hat{p}s = 1 - \frac{t}{s+t}s$$

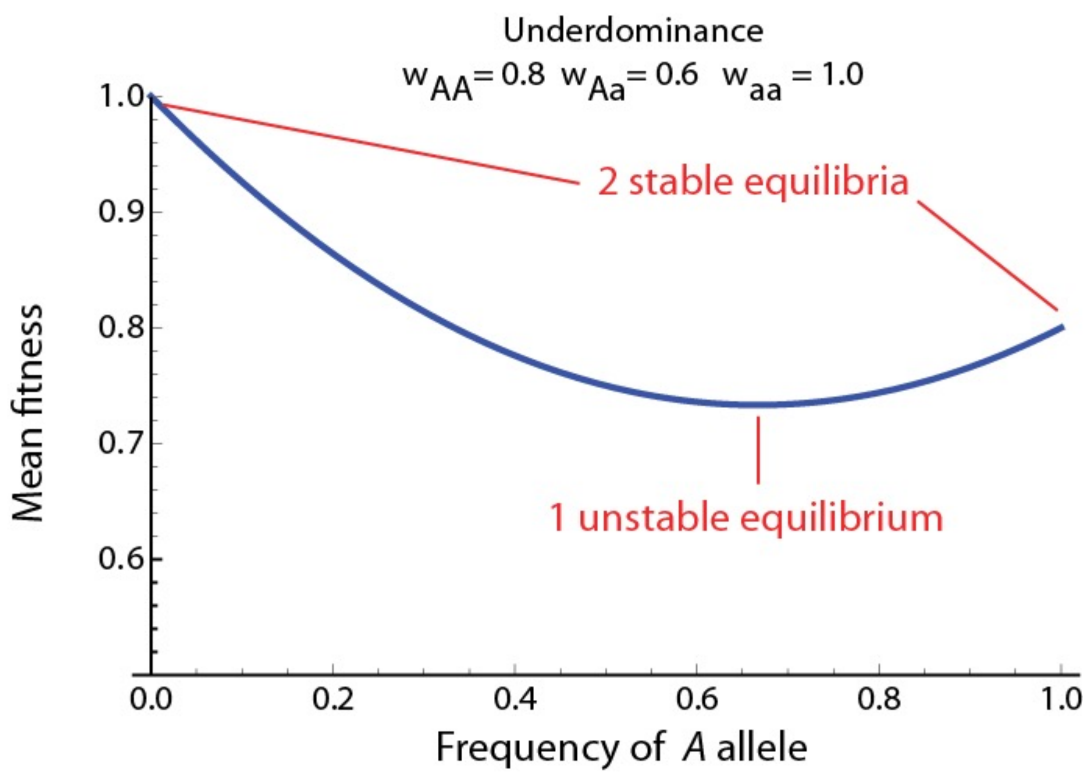
Same

$$1 - \hat{q}t = 1 - \frac{s}{s+t}t$$

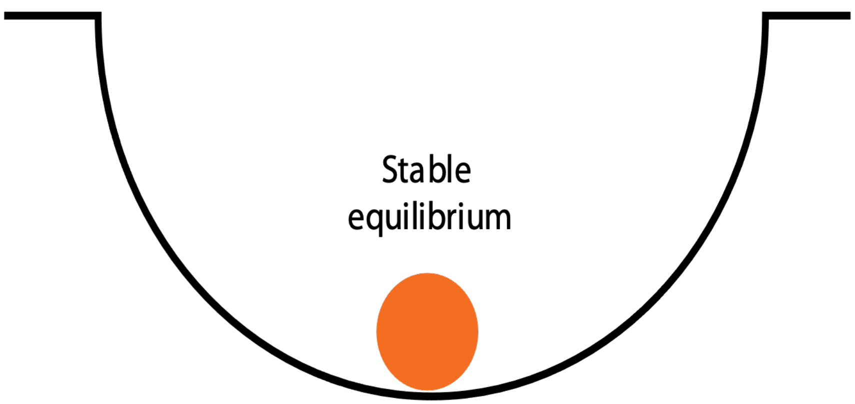
Underdominance

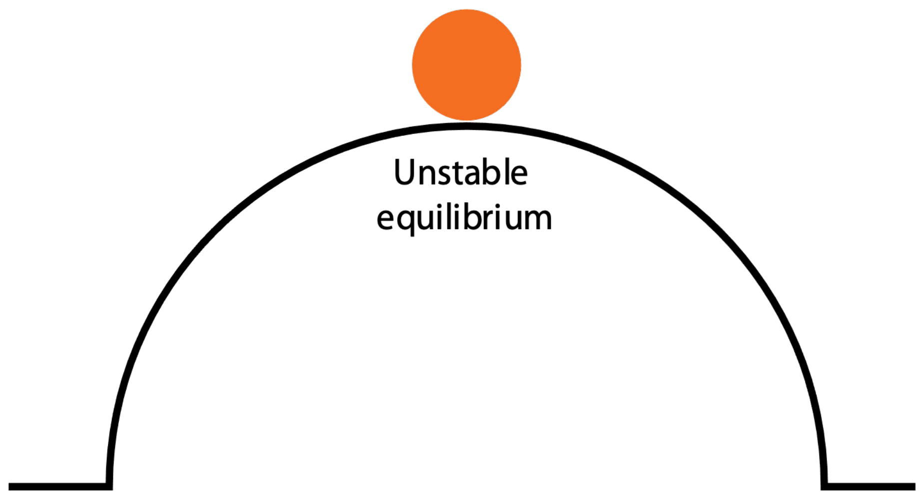
With **underdominance**, the heterozygote is the least fit genotype.

$$w_{AA} > w_{Aa} < w_{aa}$$



Equilibria





Equilibria

In the absence of migration or mutation, p =0 and p =1 are always equilibria, but whether they are stable or unstable depends on the genotype fitnesses.

If $w_{AA} < w_{Aa} < w_{aa}$ then p → 0;
p = 0 is stable equilibrium and p =1 is unstable equilibrium.

If $w_{AA} > w_{Aa} > w_{aa}$ then p → 1;
p = 0 is unstable equilibrium and p =1 is stable equilibrium.

Equilibria

In the absence of migration or mutation, p =0 and p =1 are always equilibria, but whether they are stable or unstable depends on the genotype fitnesses.

If $w_{AA} < w_{Aa} > w_{aa}$ then there will be a stable intermediate allele frequency;

p = 0 is unstable equilibrium and p =1 is unstable equilibrium

(overdominance)

If $w_{AA} > w_{Aa} < w_{aa}$ then p → 1 or p → 0, depending on the initial allele frequency;

p = 0 is stable equilibrium and p =1 is stable equilibrium;

there is an unstable equilibrium between 0 and 1.

(underdominance)

Additive genetic variance for fitness

The additive genetic variance for fitness contributed by a locus is the variance of the sum of average effects of the alleles in each the genotype.

The average effect of the *A* allele is equal to $\alpha = w_A - w_a$.

$$V_A = 2pq\alpha^2$$

Fisher's fundamental theorem

The rate of increase of mean relative fitness is equal to the additive genetic variance for relative fitness (capturing only effects of selection)

$$\Delta\bar{w} = \mathrm{V_A}$$