

Genetics and Natural Selection

Darwin did not have an understanding of the mechanisms of inheritance and thus did not understand how natural selection would alter the patterns of inheritance in a population. It took an understanding of genetics and an understanding of evolution to merge the two fields into the cornerstone of modern evolutionary theory – The Genetical Theory of Natural Selection – Sir Ronald Fisher was the first to begin to develop this theory.



Points to keep in mind:

Natural Selection \neq Evolution

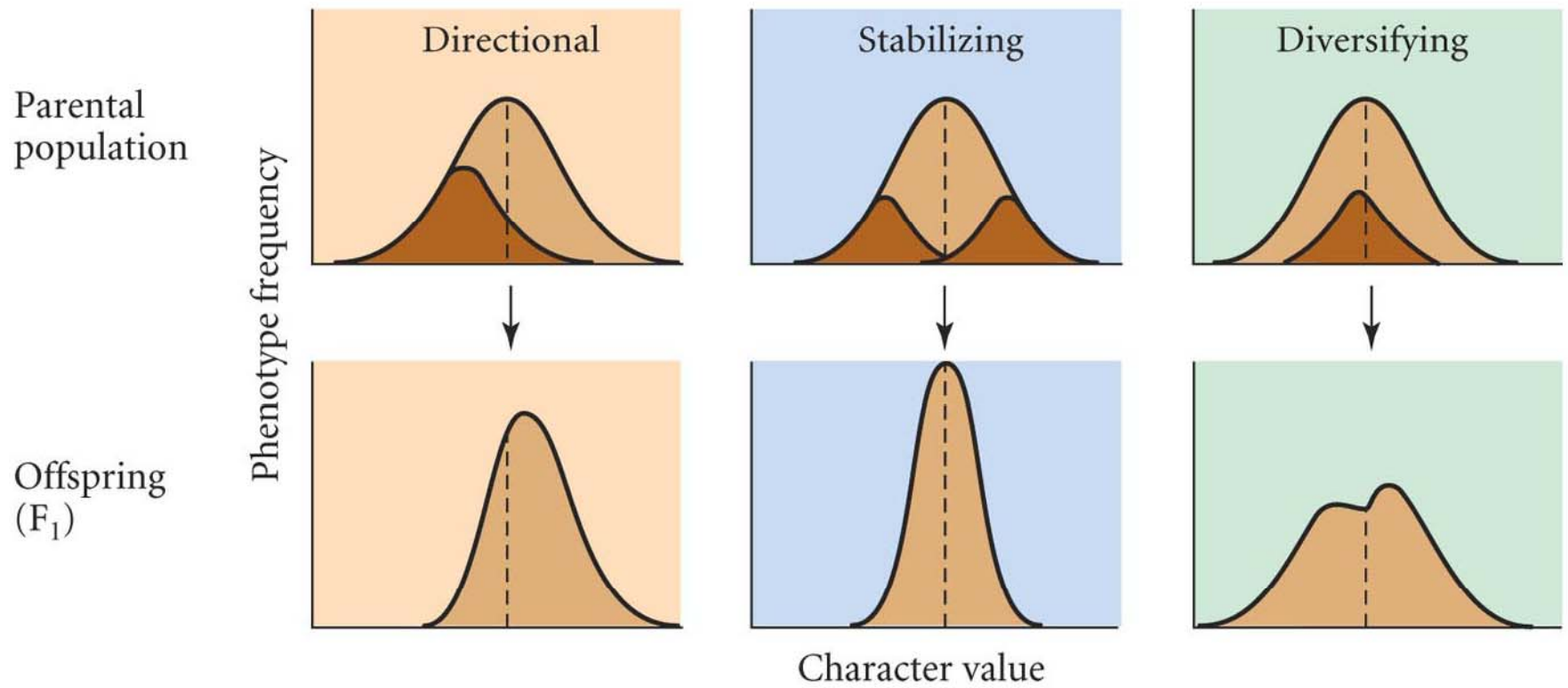
For natural selection to produce evolution selected traits must be heritable

Natural selection can not increase or decrease the frequency of a trait in a population unless the trait influences reproductive success.

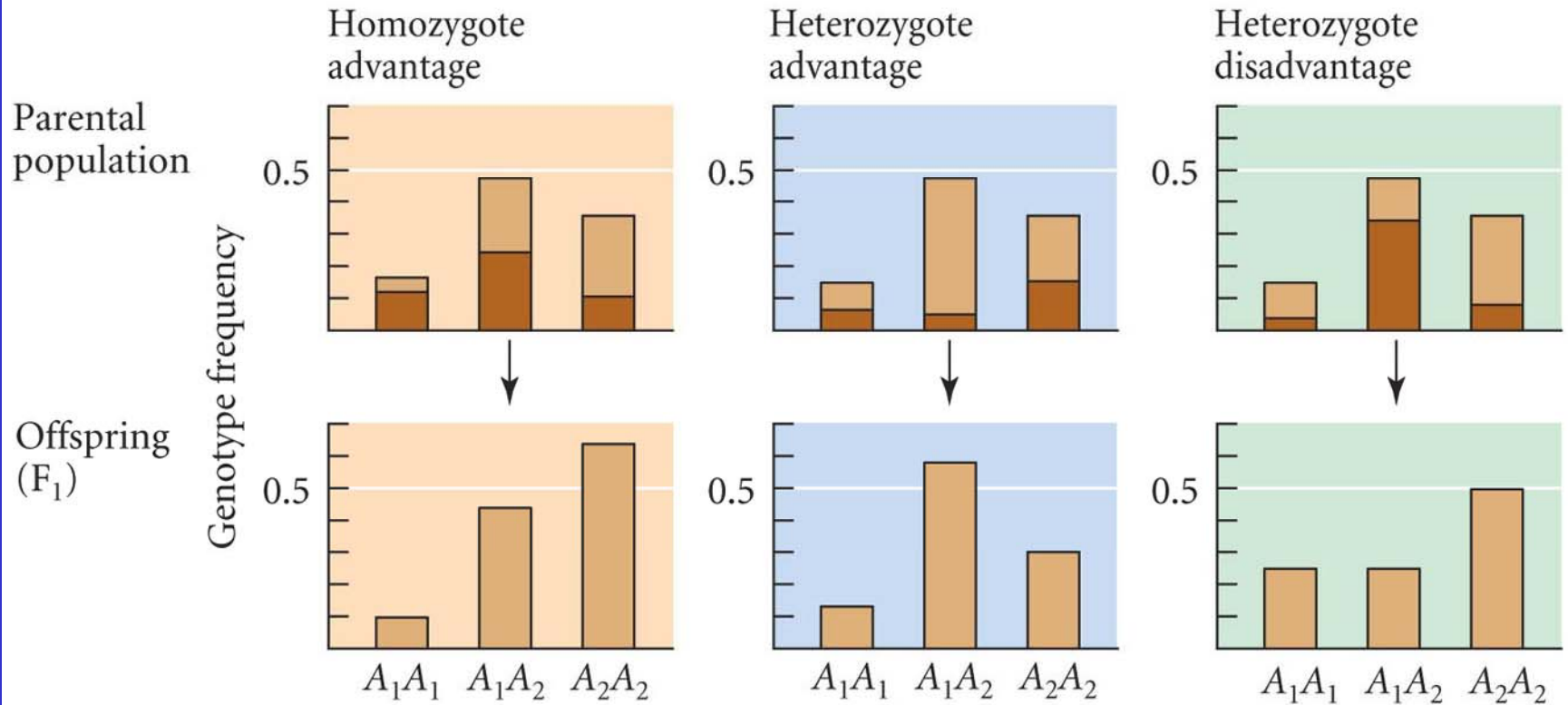


Modes of selection:

Quantitative trait



Polymorphism



Directional selection increases the proportion of genotypes with a more extreme value of the trait.

Stabilizing selection does not alter the mean, but may reduce the variance.

Diversifying selection is unlikely to be exactly symmetrical, and thus usually shifts the mean.

Selection can go on at different stages in the life cycle

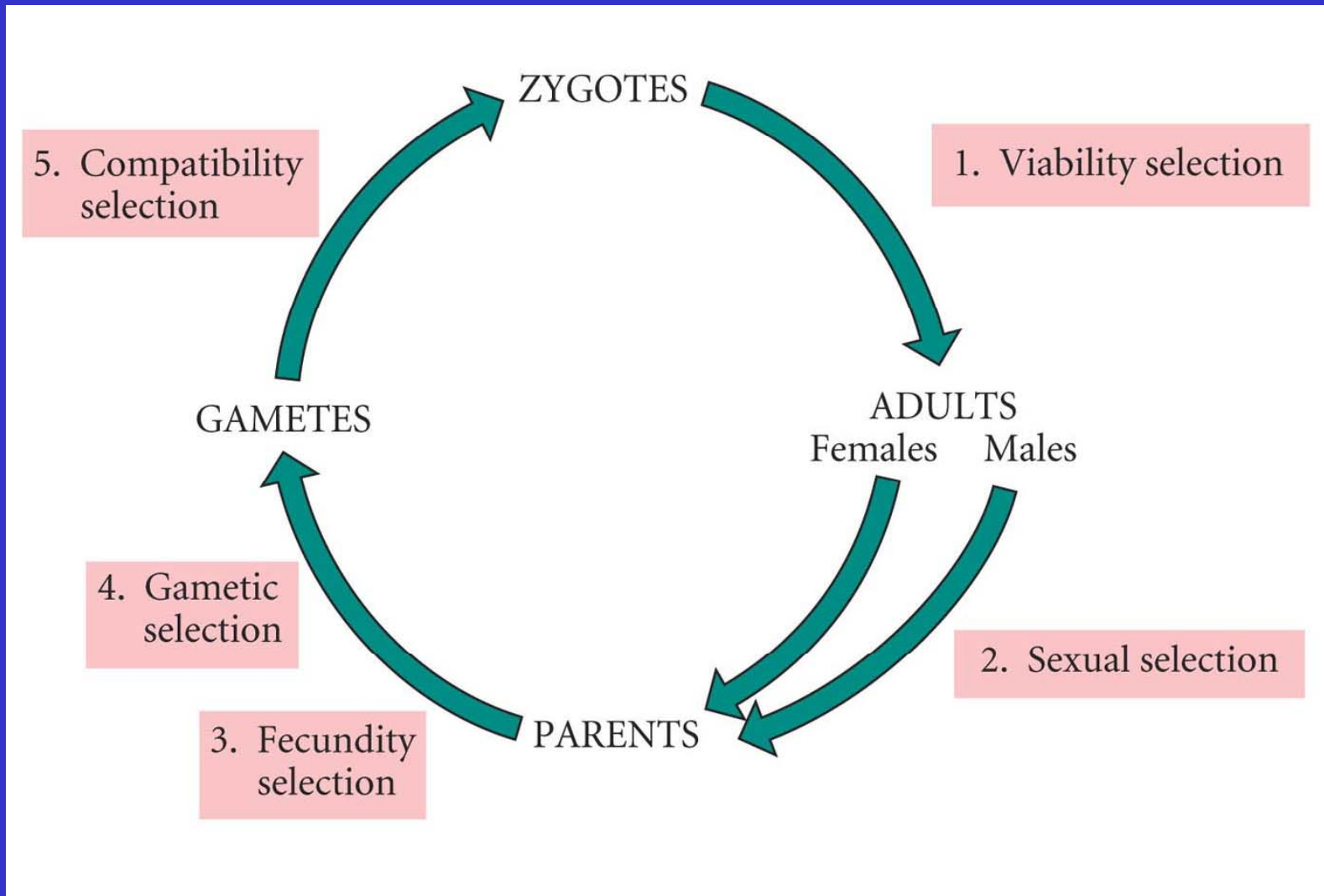


TABLE 12.1 *Components of selection in sexually reproducing organisms*

I. Zygotic selection

A. *Viability*. The probability of survival of the genotype through each of the ages at which reproduction can occur. After the age of last reproduction, the length or probability of survival does not usually affect the genotype's contribution to subsequent generations, and so does not usually affect fitness.

B. *Mating success*. The number of mates obtained by an individual. Mating success is a component of fitness if the number of mates affects the individual's number of progeny, as is often the case for males, but less often for females, all of whose eggs may be fertilized by a single male. Variation in mating success is the basis of sexual selection.

C. *Fecundity*. The average number of viable offspring per female. In species with repeated reproduction, the contribution of each offspring to fitness depends on the age at which it is produced (see Chapter 17). The fertility of a mating may depend only on the maternal genotype (e.g., number of eggs or ovules), or it may depend on the genotypes of both mates (e.g., if they display some reproductive incompatibility).

II. Gametic selection

D. *Segregation advantage* (meiotic drive or segregation distortion). An allele has an advantage if it segregates into more than half the gametes of a heterozygote.

E. *Gamete viability*. Dependence of a gamete's viability on the allele it carries.

F. *Fertilization success*. An allele may affect the gamete's ability to fertilize an ovum (e.g., if there is variation in the rate at which a pollen tube grows down a style).

Fitness can be defined for a single genotype as **the average contribution of individuals of that genotype to the population after one or more generations.**

Relative fitness - W – the average contribution of individuals of a given genotype to the population relative to the fitness of the genotype with the highest fitness.

Coefficient of selection – s – the amount fitness of a genotype is reduced relative to the genotype with the highest fitness.

The rate of genetic change in a population depends on the relative fitness of genotypes.

The mathematics of a selection model

For simplicity assume that selection acts through differences in viability and otherwise the population satisfies all of the Hardy-Weinberg conditions (large population size, random mating, etc.)

For a single gene with two alleles (A,a) there are three genotypes AA, Aa, and aa. Each genotype has a fitness W (W_{AA} , W_{Aa} , and W_{aa}). Fitness is the relative probability of successful survival and reproduction. Fitness will have a value between 0 and 1. If a genotype has a fitness of 1 this means that genotype has the highest relative fitness. A fitness of 0 means that genotype has no chance of survival to reproduction. A fitness of 0.5 means that genotype has a chance of survival and reproduction that is half that of the genotype with the highest fitness.

Example 1: Selection against a recessive phenotype.

In this model $W_{AA} = W_{Aa} > W_{aa}$. For example $W_{AA} = 1.0$, $W_{Aa} = 1.0$ and $W_{aa} = 0.5$. We can start with any initial genotypic frequencies. Here we'll start with the frequency of $AA = 0.36$, the frequency of $Aa = 0.48$, and the frequency of $aa = 0.16$ among the newborn, newly hatched, newly sprouted, or newly established generation. We'll allow survival to reproductive age using the fitness values of each genotype. This is shown in the table on the next slide. To calculate the frequency of each genotype at reproductive age, we first multiply the initial frequency of each genotype and its fitness. The sum of the three products gives the average fitness (\bar{W}). Dividing each product by \bar{W} gives the frequency of each genotype at reproduction. Allele frequencies after selection (p' and q') can be calculated from the genotypic frequencies. If there is random mating the frequency of offspring in the next generation as a binomial distribution of the allele frequencies:

Genotypes:	AA	Aa	aa	Alleles:	A	a
Initial Frequencies	0.36	0.48	0.16		$p = 0.36 + 0.48/2 = 0.6$	$q = 0.16 + 0.48/2 = 0.4$
Fitness (W)	1.0	1.0	0.5	\bar{W}		
Product	0.36	0.48	0.08		$= 0.36 + 0.48 + 0.08 = 0.92$	
Frequencies after selection, or at reproduction (with rounding)	$0.36/0.92 = 0.39$	$0.48/0.92 = 0.52$	$0.08/0.92 = 0.09$		$p' = 0.39 + 0.52/2 = 0.65$	$q' = 0.09 + 0.52/2 = 0.35$
Frequencies among offspring of the next generation	$(p')^2 = 0.42$	$2p'q' = 0.46$	$(q')^2 = 0.12$		0.65	0.35

The process can be repeated in each generation indefinitely to follow changes in genotypic and allele frequency change through time.

If we say that selection against the recessive is equal to 1 minus its fitness ($s = 1 - W$) we can use algebra to determine how much the frequency of the A will change in each generation. The algebraic treatment in your text (Box 12.A) shows that the change in the frequency of the A allele for this case is

$$\Delta p = \frac{spq^2}{1 - sq^2}$$

A check of this formula for the example:

$$\Delta p = p' - p = 0.65 - 0.6 = 0.05$$

$$spq^2/1 - sq^2 = 0.5 * 0.6 * 0.4 * 0.4 / (1 - 0.5 * 0.4 * 0.4) = .048 / 0.92 = 0.05.$$

The algebraic formula can be applied to all cases of fitness difference (survival difference, reproductive difference, or a combination). The change will continue until the a allele is no longer in the population.

Example 2: Selection against a dominant phenotype.

In this model $W_{AA} = W_{Aa} < W_{aa}$. For example $W_{AA} = 0.5$, $W_{Aa} = 0.5$ and $W_{aa} = 1.0$. Here we'll start with the frequency of AA = 0.36, the frequency of Aa = 0.48, and the frequency of aa = 0.16 among the newborn, newly hatched, newly sprouted, or newly established generation.

Genotypes:	AA	Aa	aa	Alleles:	A	a
Initial Frequencies	0.36	0.48	0.16		$p = 0.36 + 0.48/2 = 0.6$	$q = 0.16 + 0.48/2 = 0.4$
Fitness	0.5	0.5	1.0	\bar{W} $= 0.18 + 0.24 + 0.16 = 0.58$		
Product	0.18	0.24	0.16			
Frequencies after selection, or at reproduction (with rounding)	$0.18/0.58 = 0.31$	$0.24/0.58 = 0.41$	$0.16/0.58 = 0.28$		$p' = 0.31 + 0.41/2 = 0.515$	$q' = 0.28 + 0.41/2 = 0.485$
Frequencies among offspring of the next generation	$(p')^2 = 0.27$	$2p'q' = 0.5$	$(q')^2 = 0.24$		0.515	0.485

If we say that selection against the dominant is equal to 1 minus its fitness ($s = 1 - W$) we can use algebra to determine how much the frequency of the A will change in each generation. An algebraic treatment similar to that in your text (Box 12.A) shows that the change in the frequency of the A allele for this case is:

$$\Delta p = \frac{-spq^2}{1 - sp(2 - p)}$$

Checking this formula against our example

$$\Delta p = p' - p = 0.515 - 0.6 = -0.085$$

$$spq^2 / 1 - sp(2 - p) = -0.5 * 0.6 * 0.4 * 0.4 / (1 - (0.5 * 0.6)(2 - p)) = -0.048 / 0.55 = -0.087.$$

Example 3: Selection favoring the heterozygote.

In this model $W_{AA} < W_{Aa} > W_{aa}$. For example $W_{AA} = 0.5$, $W_{Aa} = 1.0$ and $W_{aa} = 0.4$. We can start with any initial genotypic frequencies. Here we'll start with the frequency of $AA = 0.36$, the frequency of $Aa = 0.48$, and the frequency of $aa = 0.16$ among the newborn, newly hatched, newly sprouted, or newly established generation.

Genotypes:	AA	Aa	aa	Alleles:	A	a
Initial Frequencies	0.36	0.48	0.16		$p = 0.36 + 0.48/2 = 0.6$	$q = 0.16 + 0.48/2 = 0.4$
Fitness	0.5	1.0	0.4	\bar{W}		
Product	0.18	0.48	0.064		$= 0.18 + 0.48 + 0.064 = 0.724$	
Frequencies after selection, or at reproduction (with rounding)	$0.18/0.724 = 0.25$	$0.48/0.724 = 0.66$	$0.064/0.724 = 0.09$		$p' = 0.25 + 0.66/2 = 0.58$	$q' = 0.09 + 0.66/2 = 0.42$
Frequencies among offspring of the next generation	$(p')^2 = 0.34$	$2p'q' = 0.49$	$(q')^2 = 0.18$		0.58	0.42

If we say that selection against the AA phenotype is equal to 1 minus its fitness ($s = 1 - W_{AA}$) and **selection against** the aa phenotype is 1 minus its fitness ($t = 1 - W_{aa}$) we can use algebra to determine how much the frequency of the A will change in each generation. An algebraic treatment similar to that in your text (Box 12.A) shows that the change in the frequency of the A allele for this case is:

$$\Delta p = \frac{pq(tq - sp)}{1 - sp^2 - tq^2}$$

Checking this formula against our example

$$\Delta p = p' - p = 0.58 - 0.6 = -0.02$$

$$pq(tq - sp) / (1 - sp^2 - tq^2) = 0.6 * 0.4 (0.4 * 0.6 - 0.6 * 0.5) / (1 - (0.5 * 0.6 * .06) - (0.6 * 0.4 * 0.4)) = -0.0144 / 0.724 = -0.02.$$

In this case the allele frequencies will change until an equilibrium is reached.

At equilibrium the frequency of the A allele will be:

$$p = \frac{t}{s + t}$$

and the frequency of the a allele will be: .

$$q = \frac{s}{s + t}$$

In this case both allele will remain in the population indefinitely. This is a **balanced polymorphism**.

Selection against a dominant phenotype or selection against a recessive phenotype will remove deleterious alleles from a population or at least reduce their frequencies to very low levels.

Mutation can reintroduce alleles into a population. At equilibrium the rate of introduction of alleles into a population by mutation should equal the rate of loss of alleles from the population due to selection. For a deleterious recessive allele:

$$\mu p = \frac{spq^2}{1 - sq^2}$$

If the recessive allele is rare, the denominator is ~ 1 . And the equation simplifies to:

$$\mu = sq^2$$

So, at equilibrium the recessive allele should have the frequency:

$$\hat{q} = \sqrt{\frac{\mu}{s}}$$