Evolution at multiple loci

- Linkage
- Sex

- Quantitative genetics

Quantitative genetics

- Heritability
- Selection
- Evolutionary response to selection
- Modes of selection

Requirements of natural selection

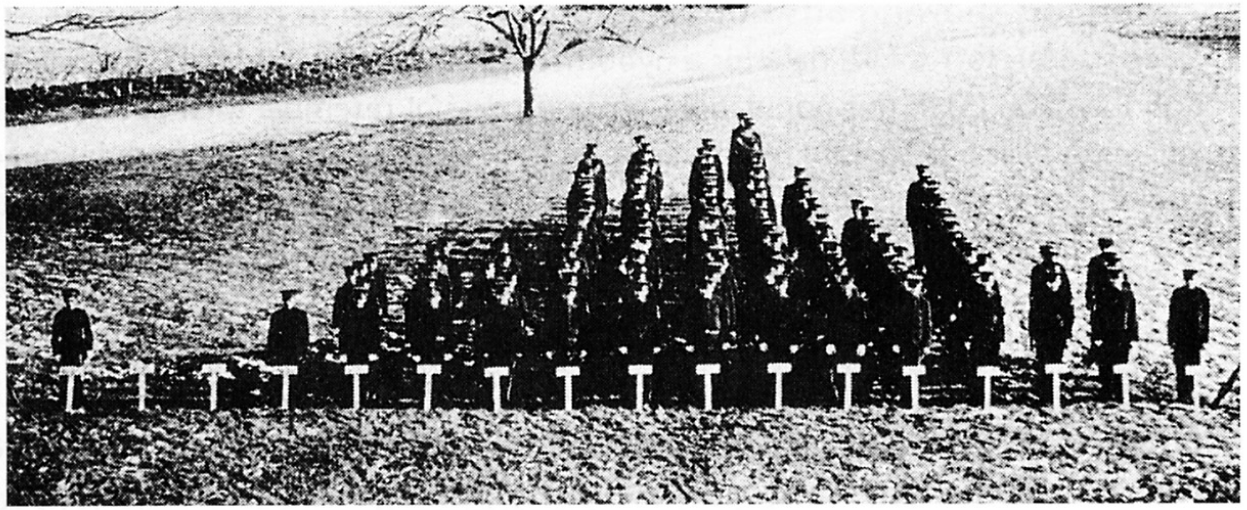
- Individuals vary
- Some of that variation is genetic
- More offspring are produced that can survive (reproduce)
- Survival (reproduction) not random

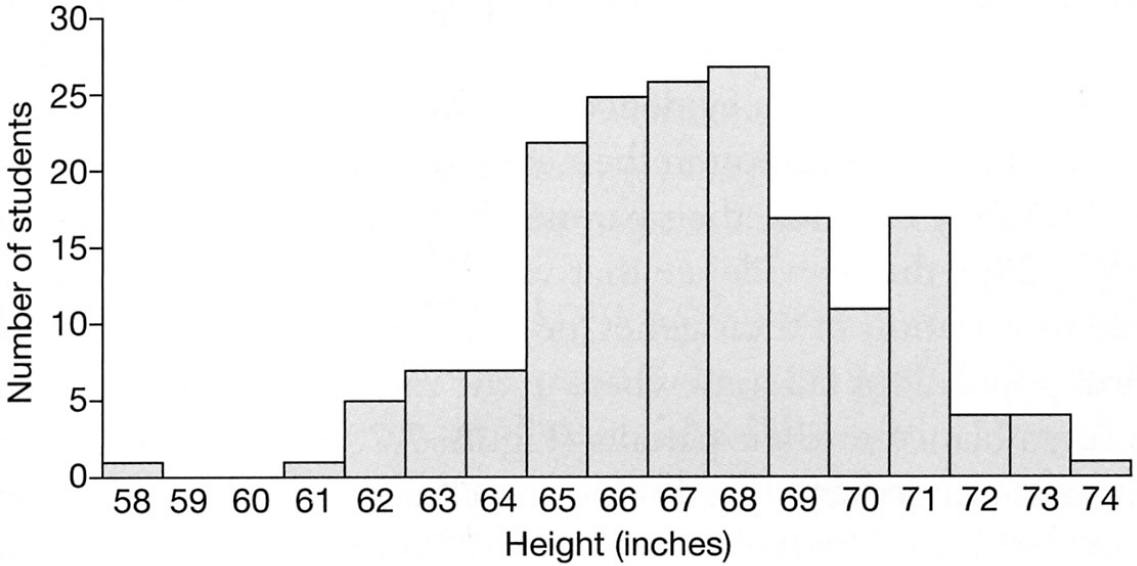
Selection on quantitative traits

- Most traits controlled by many many genes
- Phenotype produced also depends on environment

- Quantitative traits continuously distributed
  - Qualitative traits, either yes or no

Continuous variation





Phenotype due to

- Interaction of genes with environment
  - No trait is entirely genetic or entirely environmental
- But within a population, *differences* among individuals can be due to genes, environment, or both

Causes of variation

- Individuals vary, they are not all the same
- Total phenotypic variation in the population, symbolized Vp, is due to genetic variation, symbolized Vg, and variation due to the environment, symbolized Ve
- $Vp = Vg + Ve$

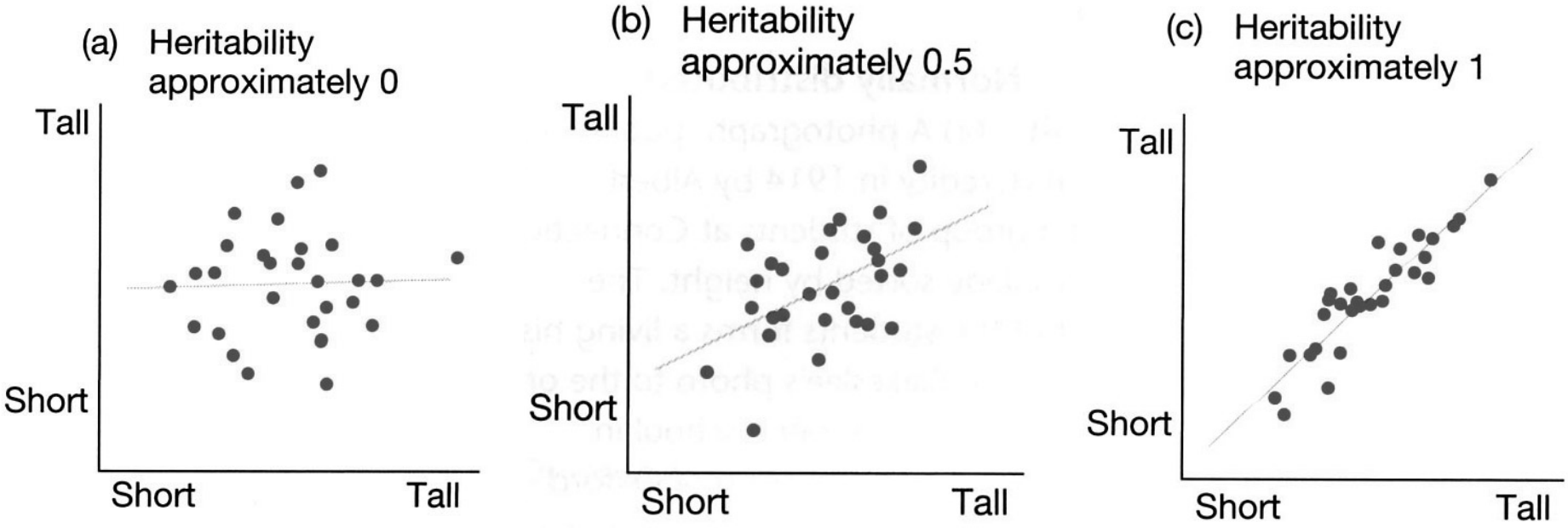
Heritability

- The fraction of phenotypic variation that is due to genetic variation
- Symbolized h^2
- $h^2 = Vg/Vp$
- It is a number, ranges from 0 to 1

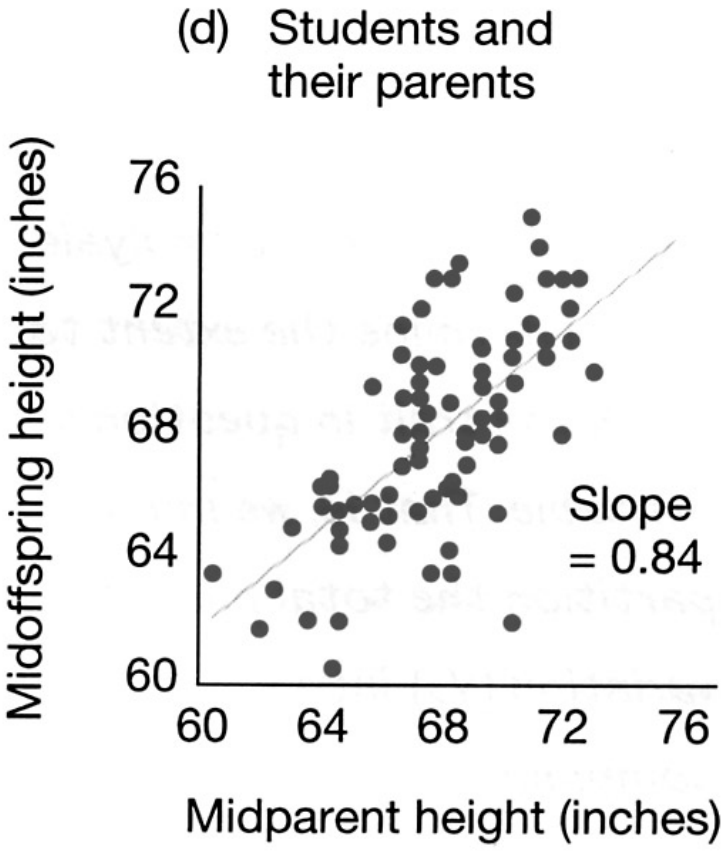
Intuition

- Suppose that differences among individuals are mostly genetic
- Then offspring will strongly resemble parents
- Suppose that differences are mostly due to environment
- If offspring environment not similar to parental environment, then offspring do not closely resemble parents

Heritability graphs



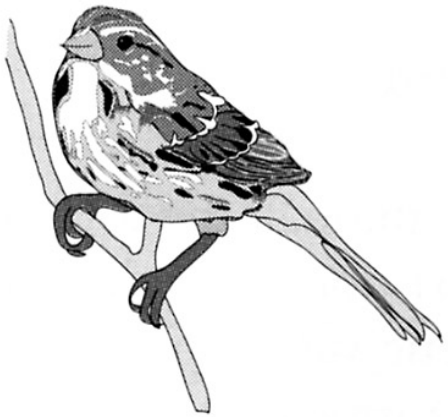
Human height heritability

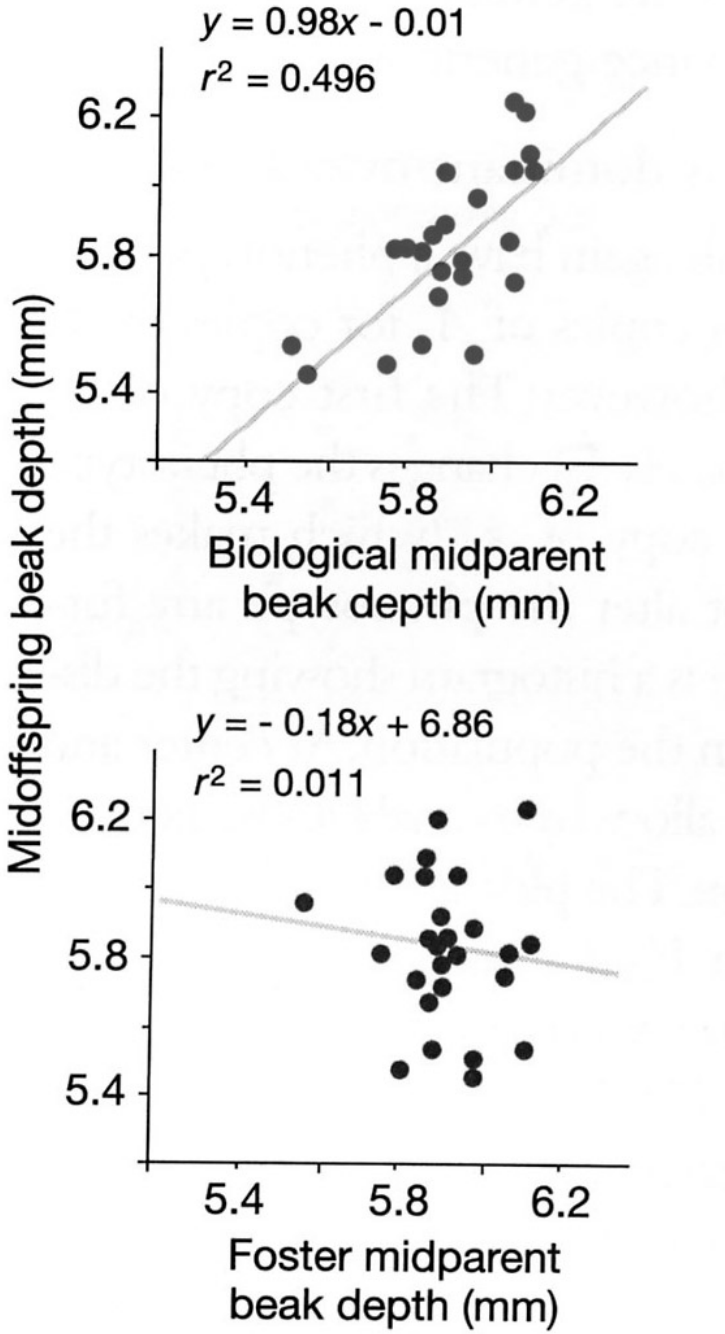


Environmental correlation

- offspring might resemble their parents because they have similar environments, not similar genes
- Important to eliminate effects of common environment
- Which is a better genetic estimator,
  - Identical twins reared together
  - Or identical twins reared apart

Cross fostering

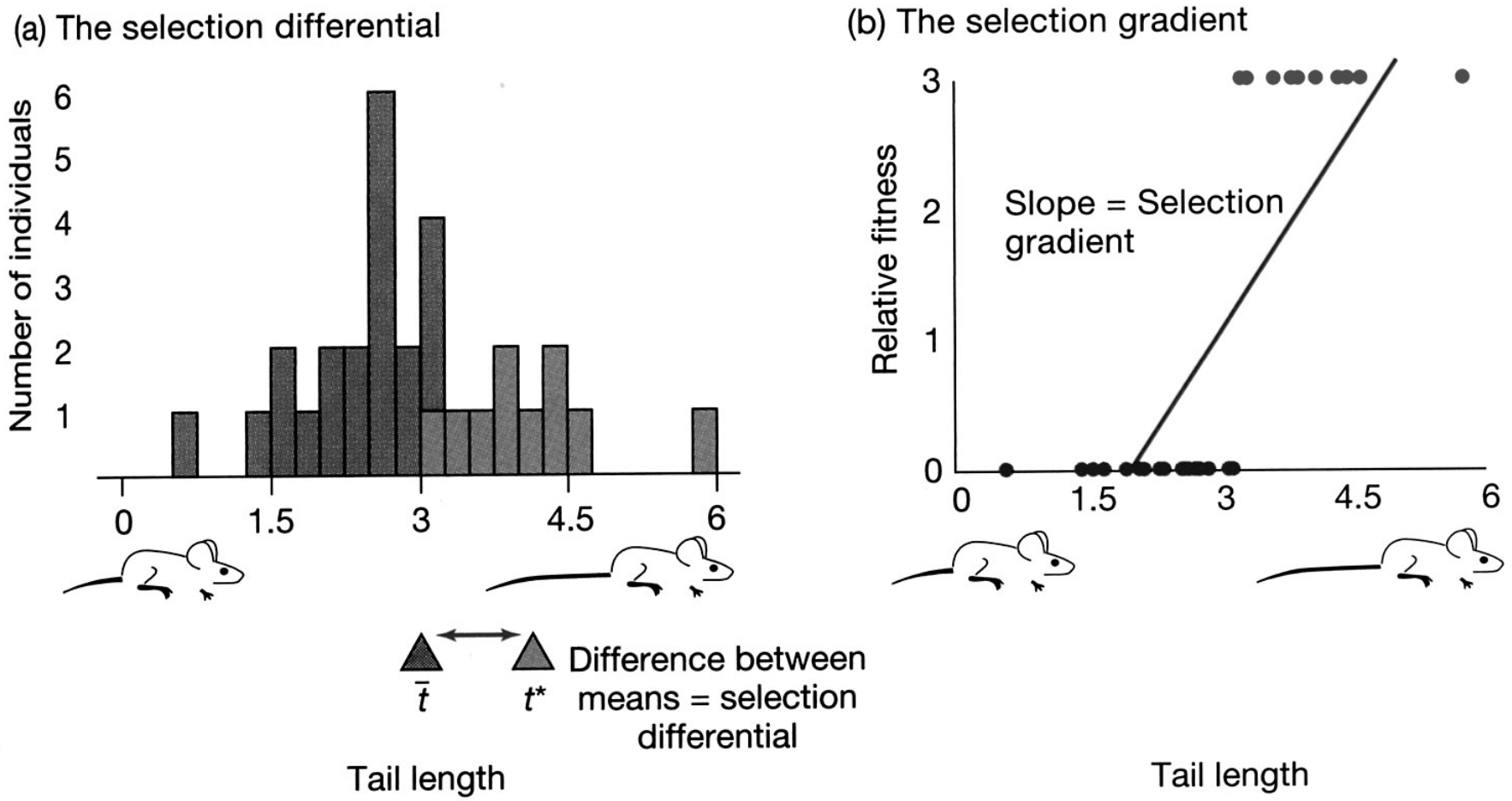




Measuring selection

- Selection differential = S
  - The difference between the average survivor (or reproducer) and the entire population
- Selection gradient
  - Slope of relative fitness on the trait value

Example



Selection gradient = selection differential/trait variance

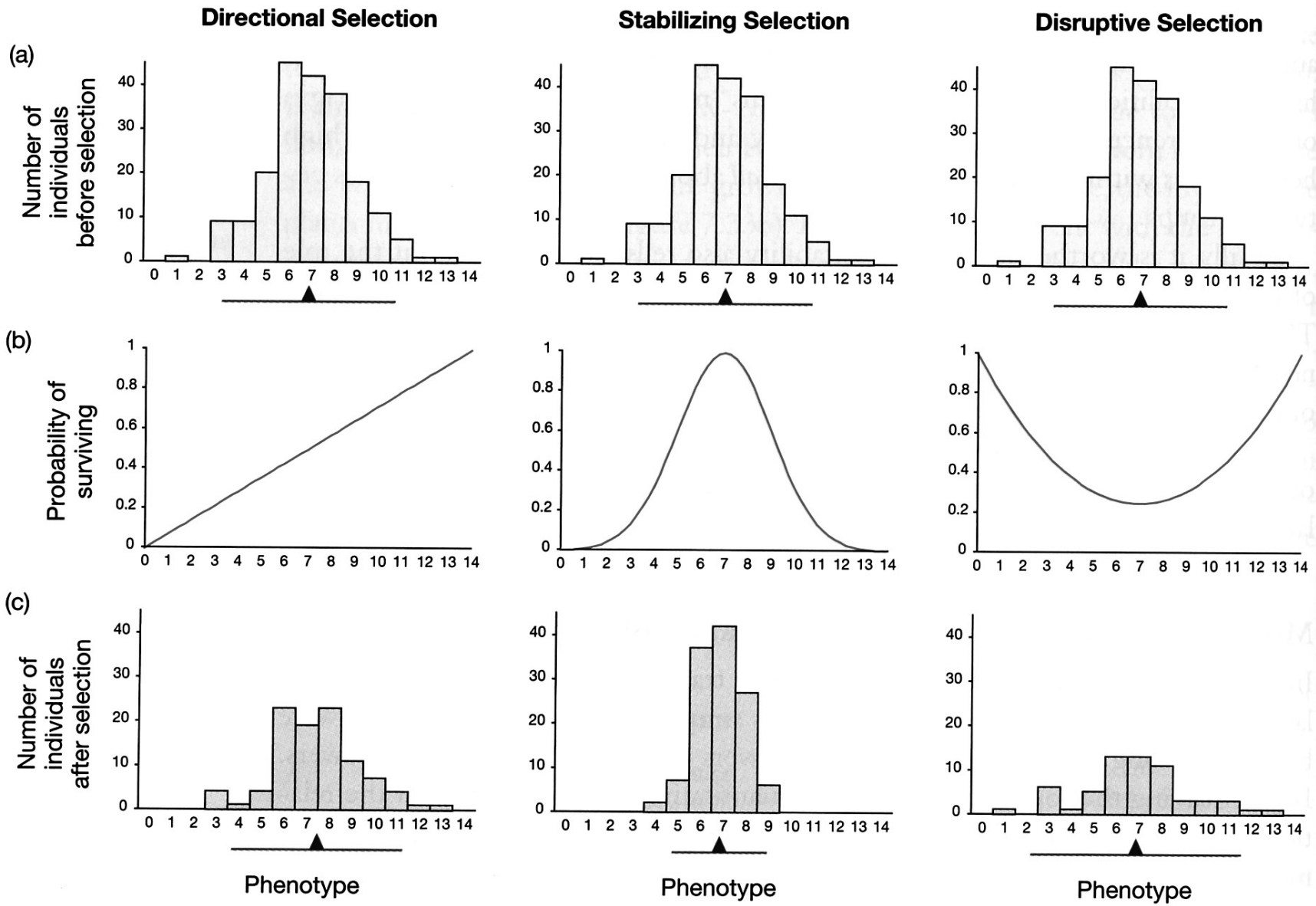
Response to selection

- Recall that evolution by natural selection happens if
  - Individuals vary
  - Variation is genetic (at least partially)
  - Not everyone reproduces
  - Reproduction not random
- The evolutionary change requires genetic variation

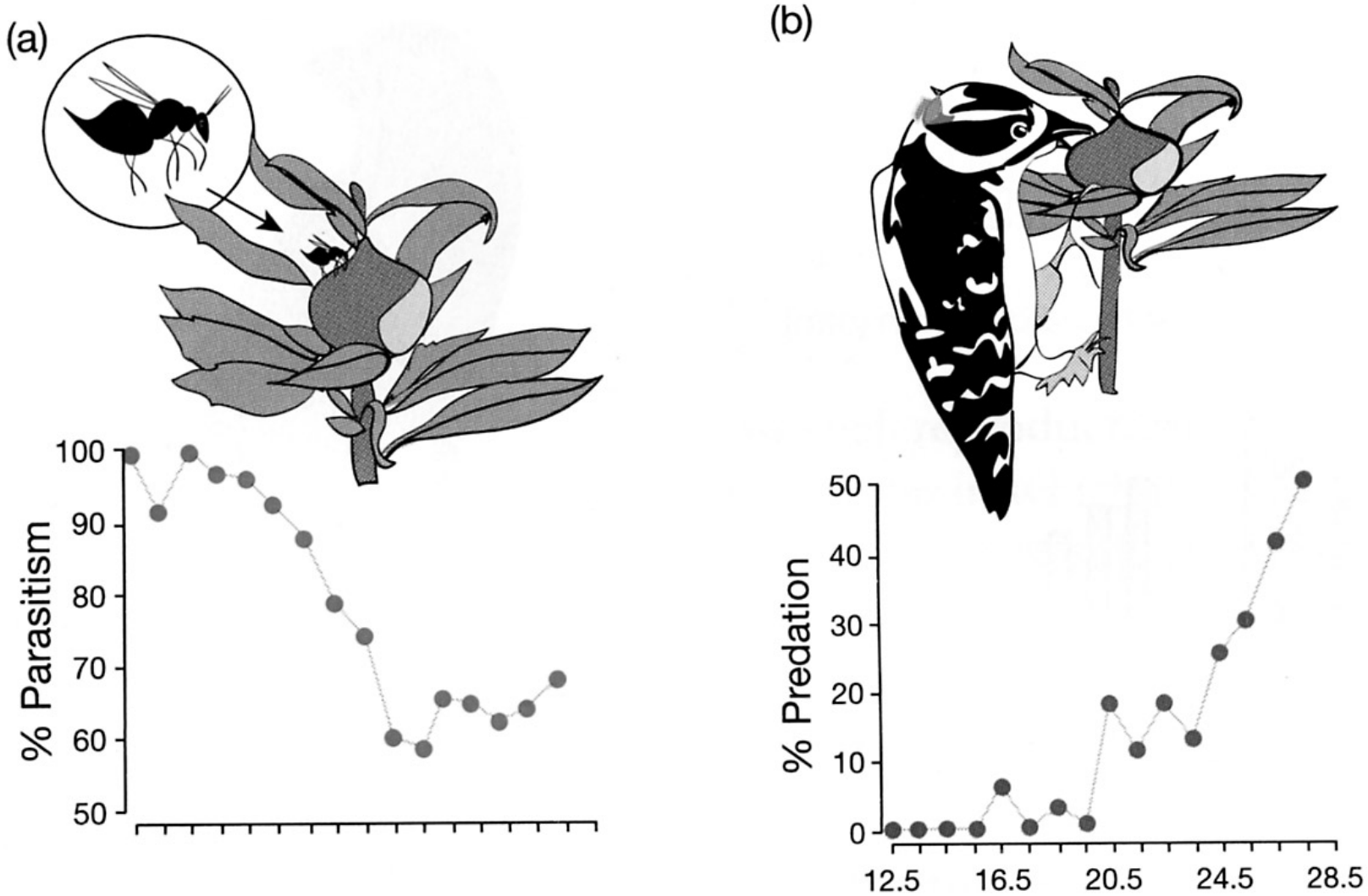
Calculating response to selection

- $R = h^2S$
- Response = heritability*selection differential
- If heritability = 1, response to selection = selection differential
- If heritability = 0, response to selection = 0
- Usually heritability intermediate, response proportional

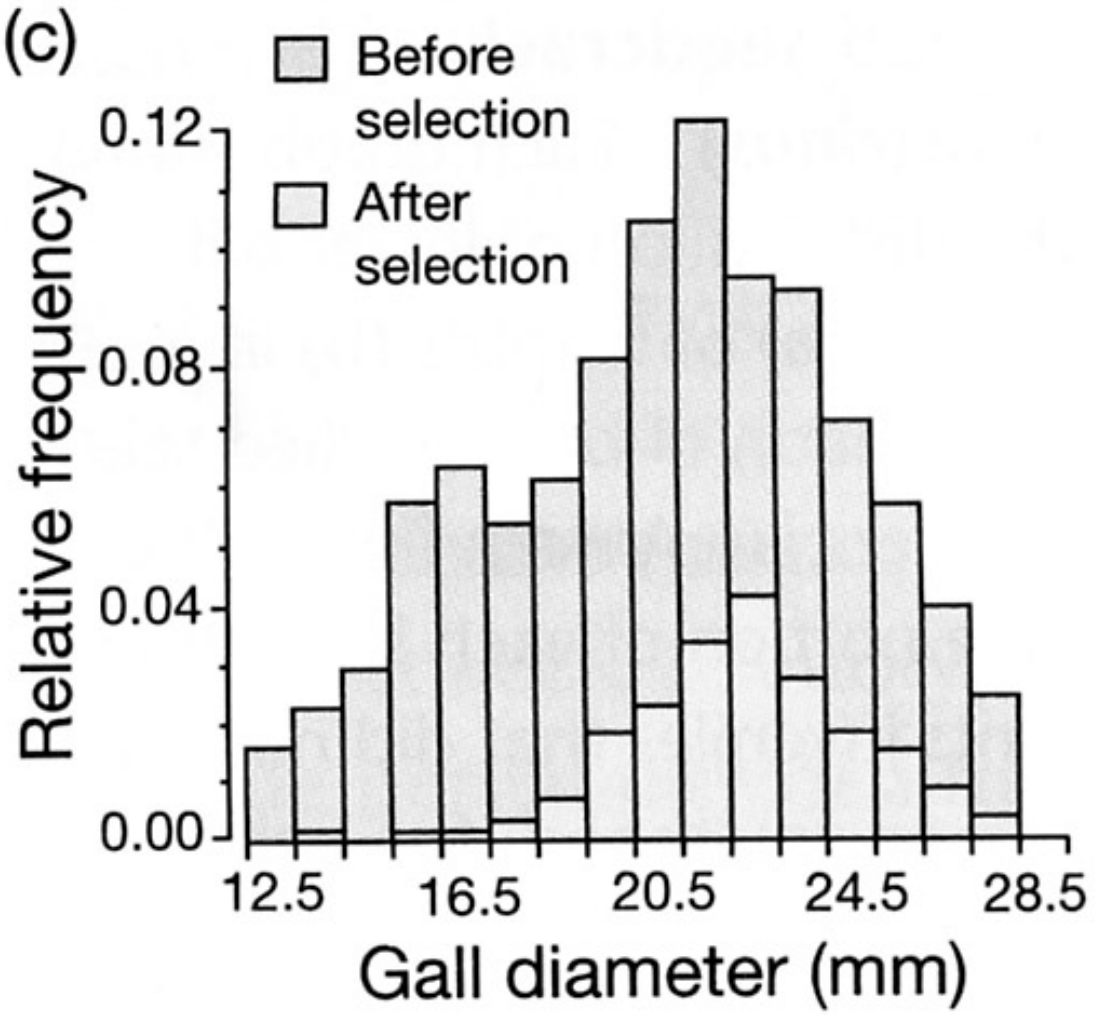
Modes of selection



Net stabilizing selection example



Net stabilizing selection



Selection and genetic variation

- Change in mean fitness is a function of genetic variation in fitness
- "Rate of increase in fitness of any **[*population of*]** organism**[*s*]** at any time is equal to its genetic variance in fitness at that time"
- Fisher's *fundamental theorem of natural selection*
- Selection removes genetic variation

Scaling up to quantitative traits

- $R = h^2S$
- But selection depletes genetic variation so h^2 changes…because Va changes

- A response to selection continues *initially* because of recombination, and allele frequency change

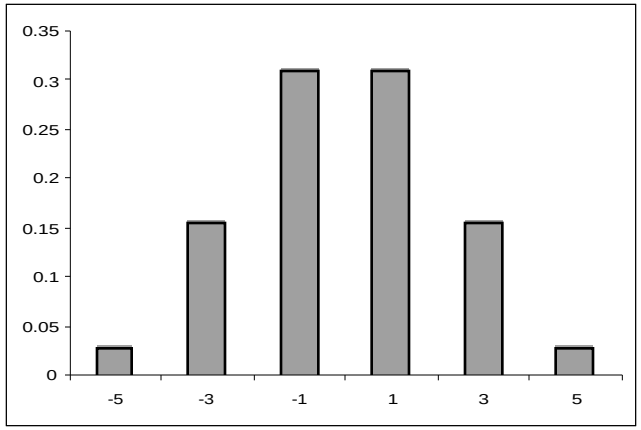
Example: Q-trait 5 loci, 10 alleles

LOCUS	ALLELE	EFFECT	FREQUENCY
A	A1	-1	0.5
A	A2	1	0.5
B	B1	-1	0.5
B	B2	1	0.5
C	C1	-1	0.5
C	C2	1	0.5
D	D1	-1	0.5
D	D2	1	0.5
E	E1	-1	0.5
E	E2	1	0.5

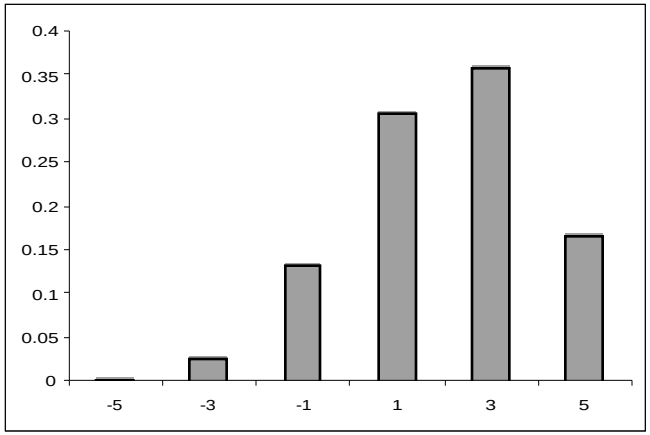
Example Cont.

PHENOTYPES	GENOTYPES									
-5	11111									
	0.031									
-3	11112	11121	11211	12111	21111					
	0.031	0.031	0.031	0.031	0.031					
-1	11122	11212	12112	21112	11221	12121	21121	12211	21211	22111
	0.031	0.031	0.031	0.031	0.031	0.031	0.031	0.031	0.031	0.031
1	11222	12122	21122	12212	21212	22112	12221	21221	22121	22211
	0.031	0.031	0.031	0.031	0.031	0.031	0.031	0.031	0.031	0.031
3	12222	21222	22122	22212	22221					
	0.031	0.031	0.031	0.031	0.031					
5	22222									
	0.031									

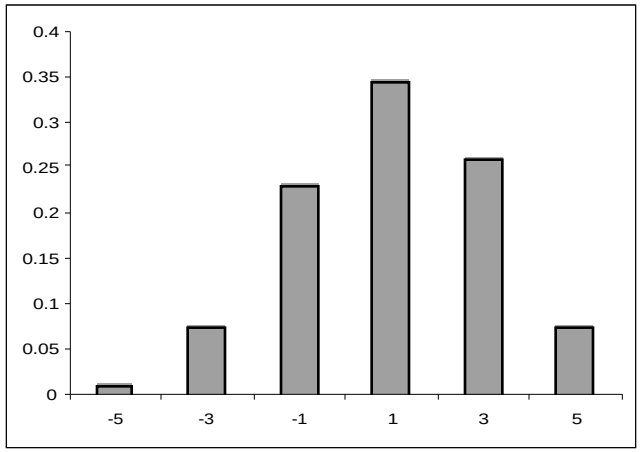
Phenotypic frequencies



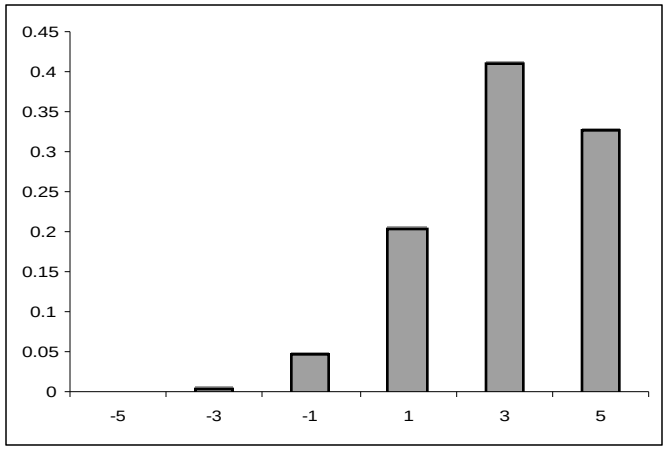
All loci $p = q = 0.5$



All loci $p = 0.7$ $q = 0.3$

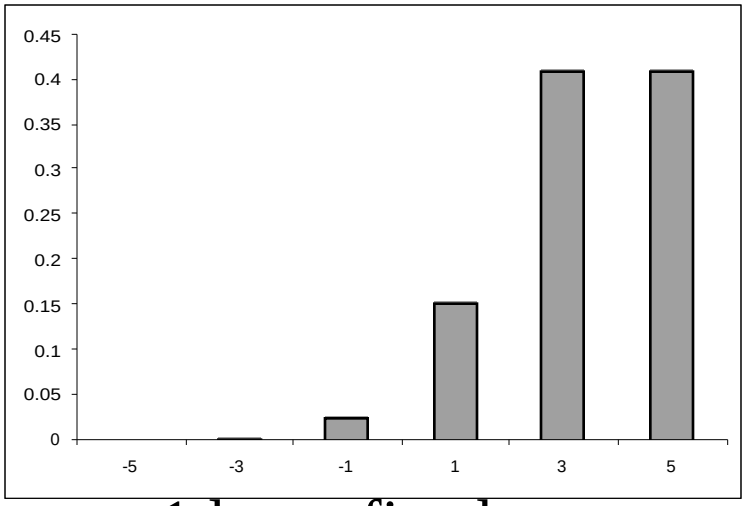


All loci $p = 0.6$ $q = 0.4$

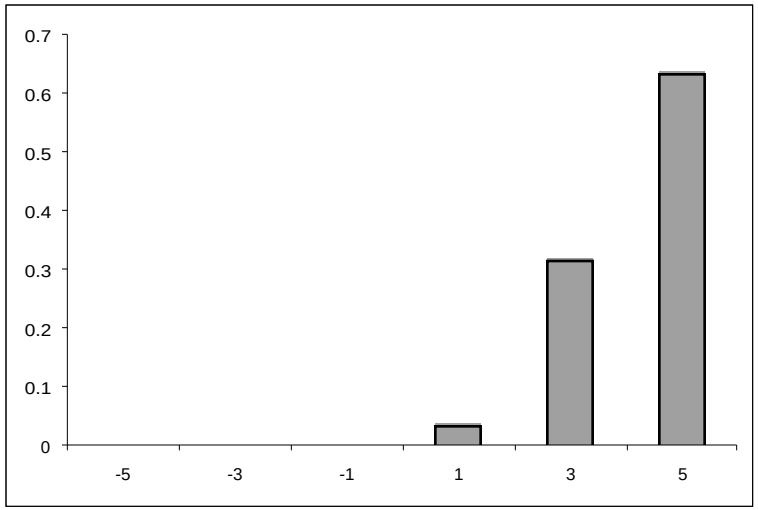


All loci $p = 0.8$ $q = 0.2$

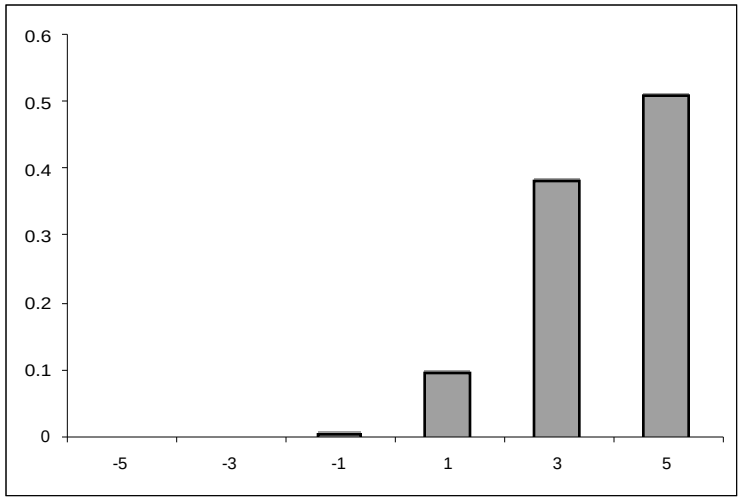
Alleles at loci reach fixation



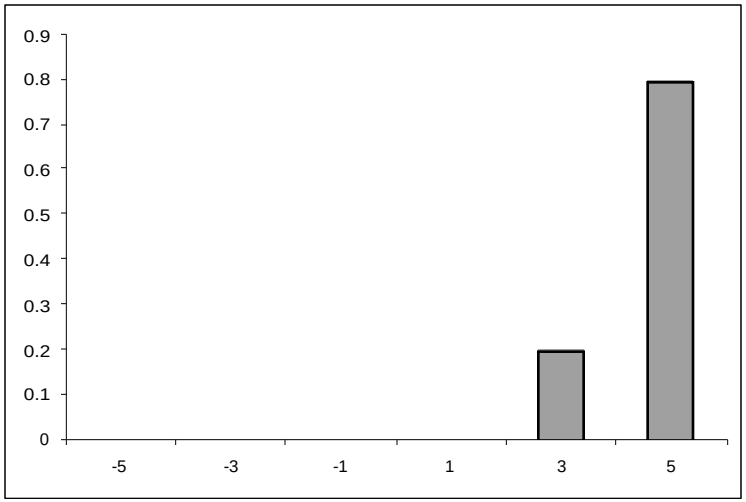
1 locus fixed



3 loci fixed



2 loci fixed



4 loci fixed

Maintenance of genetic variation

- Direction and stabilizing selection reduce genetic variation
  - Therefore Vg/Vp decreases,
  - R=h2*S, response decreases
- Mutation, mutation-selection balance
- Disruptive selection
- Fluctuating selection
  - Random
  - Cyclic