Selection, part 2

BIOL 434/509

Mutation-selection balance

Mutation introduces many deleterious alleles; selection removes them.

The resulting equilibrium frequency of deleterious alleles is called the mutation-selection balance.

Mutation-selection balance

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

q : frequency of the deleterious allele

μ : mutation rate from high to low fitness alleles

Mutation-selection balance

$$p' = \frac{p\big(p + q(1 - hs)\big)}{\bar{w}}(1 - \mu)$$

$$\hat{p} = \frac{\hat{p}\big(\hat{p} + \hat{q}(1 - hs)\big)}{\bar{w}}(1 - \mu)$$

Some algebra gives:

$$\hat{q}hs(1 + \mu - 2\hat{q}) + \hat{q}^2 s = \mu$$

Complete dominance; $h = 0$

$$\hat{q}hs(1 + \mu - 2\hat{q}) + \hat{q}^2 s = \mu$$
$$\hat{q}^2 s = \mu$$

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

Partial dominance: $h > 0$

$$\hat{q}hs(1 + \mu - 2\hat{q}) + \hat{q}^2 s = \mu$$

Assuming $\hat{q}$ is small (which it will be if μ ≪ *hs*), then $\hat{q}^2 \ll \hat{q}$

$$\hat{q} \cong \frac{\mu}{hs}$$

Genetic load

Load is the reduction of mean fitness of a population due to some factor.

$$L = \bar{w}_{max} - \bar{w}$$

Some types of load

Mutation load : reduction in mean fitness caused by deleterious mutations.

Drift load : reduction in mean fitness caused by drift

Segregation load : reduction in mean fitness caused by segregation during meiosis (e.g., as would occur with overdominance.)

Mutation load

If the fitnesses of the three genotypes are 1: 1– *hs* : 1–*s*

$$\bar{w}_{max} = 1$$

$$\bar{w} = 1 - 2pqhs - q^2 s$$

So the mutation load is

$$L = \bar{w}_{max} - \bar{w} = 2pqhs + q^2 s$$

At mutation-selection balance, $\hat{q} \cong \frac{\mu}{hs}$ and $\hat{q}^2$very small:

$$L \cong 2\left(\frac{\mu}{hs}\right) hs = 2\mu$$

Load over many loci

$$L = 1 - e^{-\sum 2\mu}$$

genomic deleterious mutation rate : $U = \sum 2\mu$

$$L = 1 - e^{-U}$$

Load over many loci

In humans, U = ~2.2.

$$L = 1 - e^{-2.2} = \sim 0.89$$

Load with compete dominance

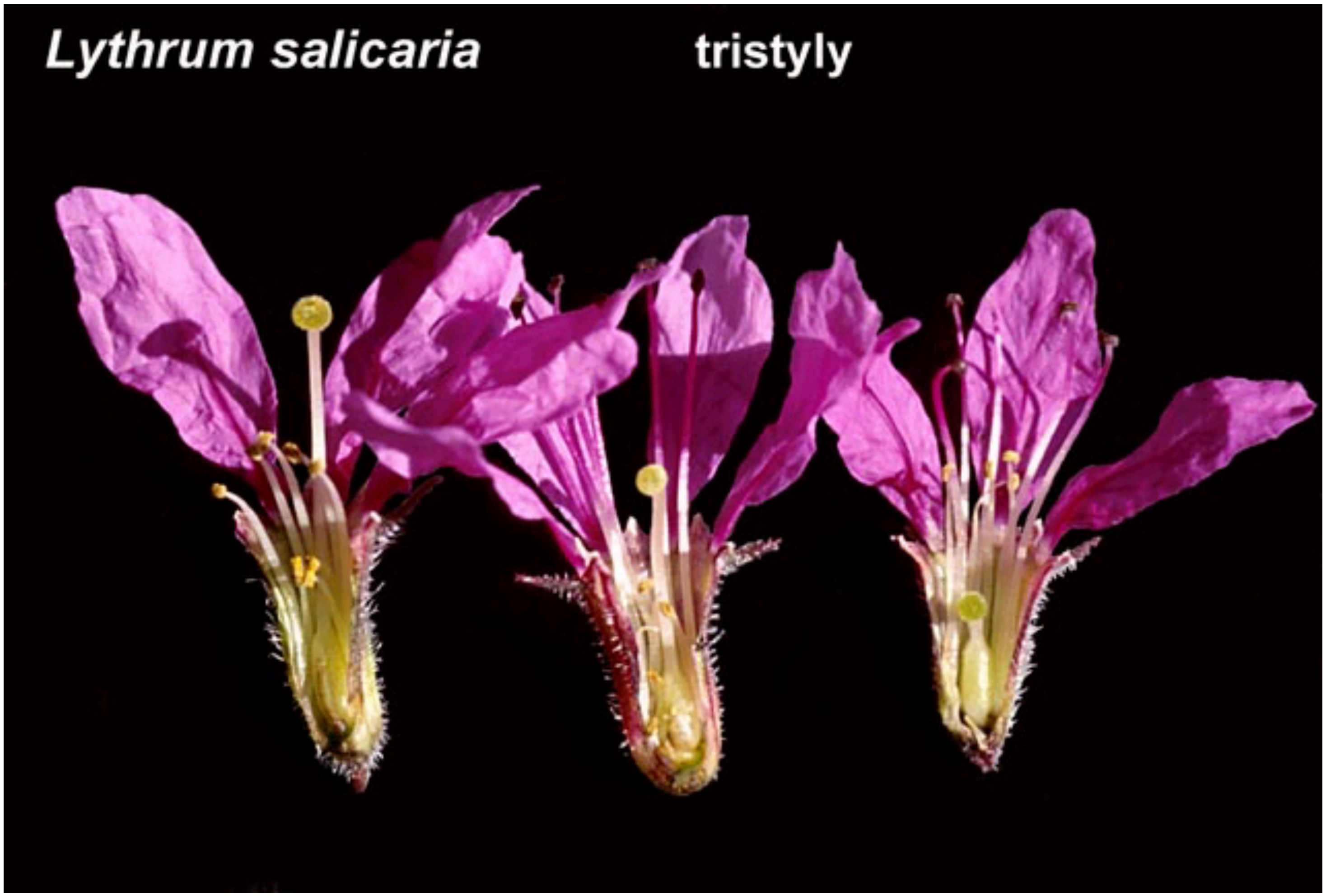
$$L = \mu$$

Frequency-dependent selection: fitness of a genotype depends on the genotype frequencies in the population

Positive frequency-dependence: Genotypes become more fit as they become more common.

Negative frequency-dependence: Genotypes become less fit as they become more common.

Tristyly



Fitness components

Selection can act at many stages of the life cycle:

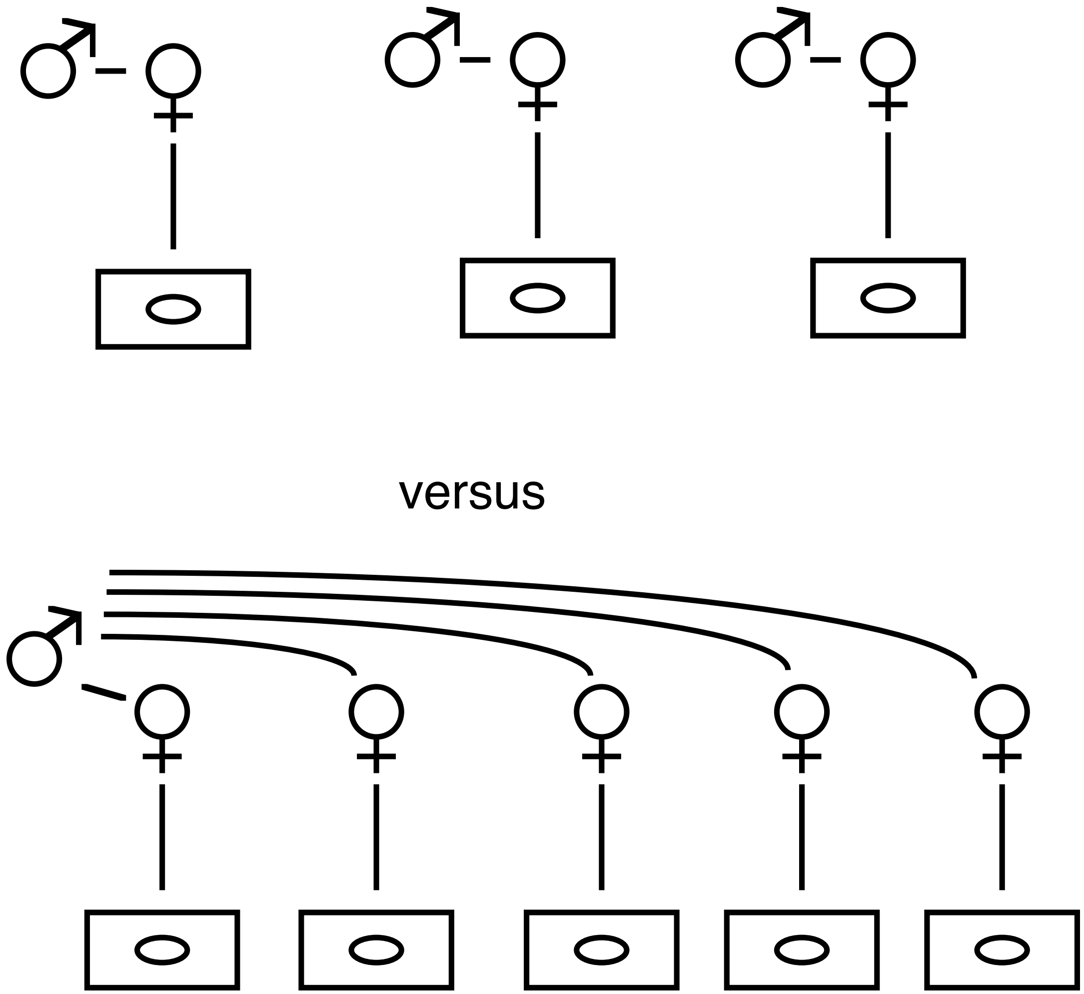
Survivorship, attracting mates, fecundity, meiosis, gamete selection, etc.

Correlations between fitness components

Sometimes selection for one fitness component for a trait or gene is opposed by selection on another fitness component.

This make measuring fitness extremely difficult.

Sex ratio



Why so many males?

All offspring have one male parent and one female parent.

If males are rare, then males will have a high fitness relative to females (males would contribute more of the genes of the next generation.

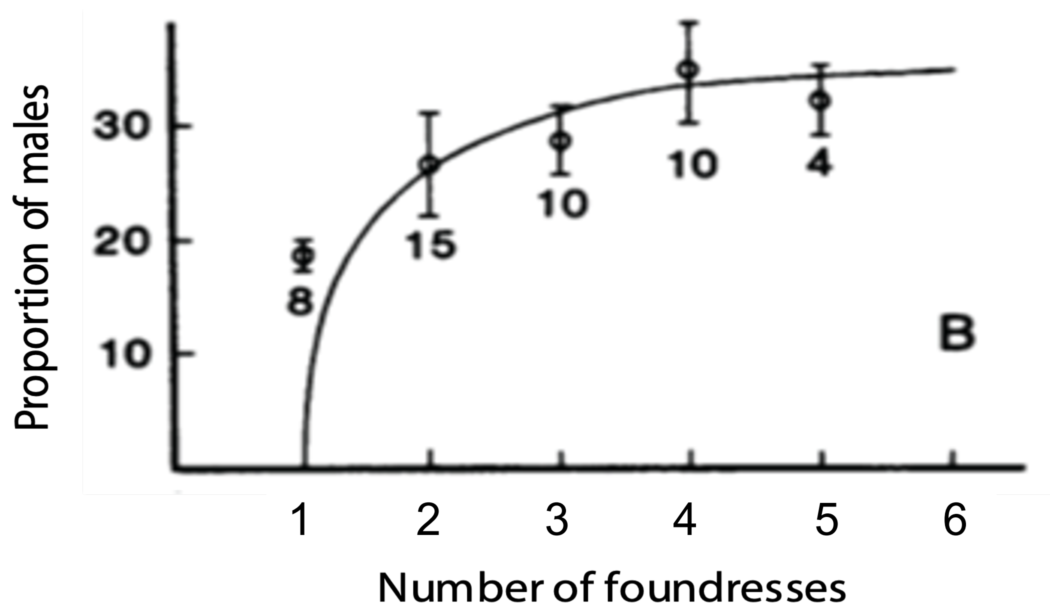
Same in reverse, if females are rare.

Fisher showed that selection for rarer sex causes an equal investment in sexes in a randomly mating population.

Local mate competition

If mating occurs among close relatives before mixing with the general population, this selects for female-biased sex ratios.

***Ficus popenoei* wasp, Herre 1985**



Kin selection

If selection acts by increasing the fitness of relatives, this is kin selection.

Hamilton's Rule

r = coefficient or relatedness of 2 individuals
(= $2F/(1+F)$ where *F* is the inbreeding coefficient of offspring of those two individuals)

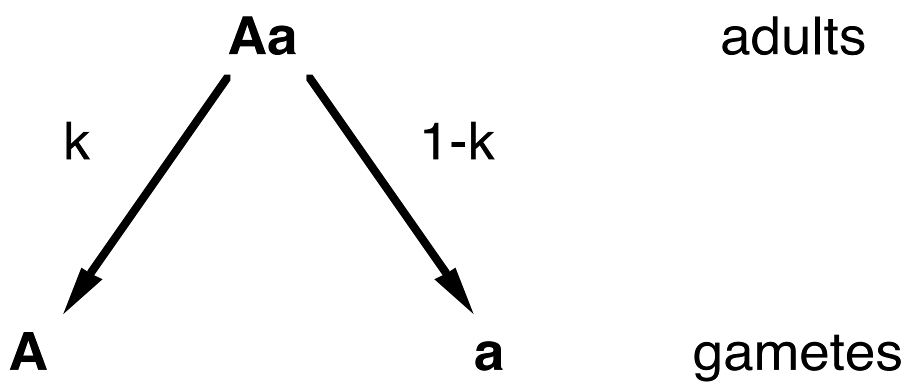
c: cost to its own fitness

b: benefit to relative's fitness

A trait will evolve by kin selection if

$$c < r\,b$$

Meiotic drive:
Non-Mendelian production of gametes by heterozygotes



$$p' = p^2 + 2kpq$$

Selection with non-random mating

Inbreeding depression

Inbred individuals usually have lower fitness than outbred individuals.

This reduction in fitness with inbreeding is called *inbreeding depression*.

$$\delta = \frac{w_{outbred} - w_{inbred}}{w_{outbred}}$$

Why does inbreeding depression exist?

(1) deleterious recessive alleles

(2) overdominance

In both cases, heterozygotes are more fit than the *average* of the homozygotes, and inbreeding increases homozygosity

Inbreeding depression via deleterious recessive alleles

Genotype	AA	Aa	aa
Frequency in outbred individuals	p^2	2pq	q^2
Frequency in inbred individuals	p^2 + fpq	2pq(1-f)	q^2+ fpq
Fitness	1	1	1–s

$$\bar{w}_{outbred} = p^2 + 2pq + q^2(1-s) = 1 - sq^2$$

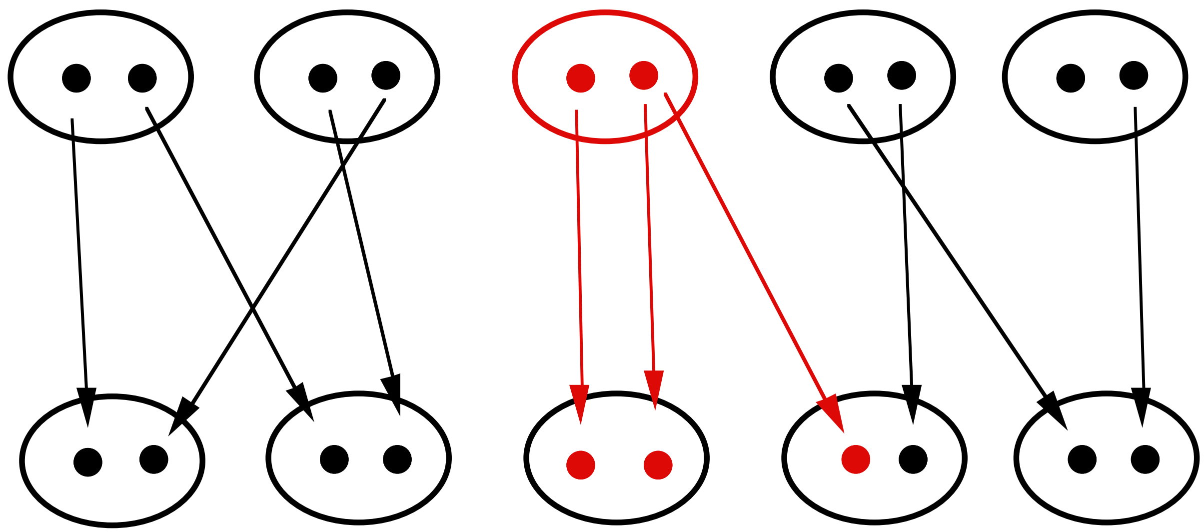
$$\bar{w}_{inbred} = p^2 + fpq + 2pq(1-f) + (q^2 + fpq)(1-s) = 1 - s(q^2 + fpq)$$

$\bar{w}_{inbred}$ is $sfpq$ smaller than $\bar{w}_{outbred}$.

Evolution of selfing

Advantages of selfing:

- Reproductive assurance
- Cost of outcrossing



When does selfing increase fitness?

The fitness of an individual which selfs at rate r in a population that selfs on average $\bar{r}$:

$$w(r) = rw_s + \frac{1}{2}(1-r)w_O + \frac{1}{2}(1-\bar{r})w_O$$

w_S = fitness of selfed offspring, w_O = fitness of outbred offspring

When does selfing increase fitness?

$$w(r) = rw_s + \frac{1}{2}(1 - r)w_O + \frac{1}{2}(1 - \bar{r})w_O$$

$$\frac{\partial w}{\partial r} > 0$$

$$\frac{\partial w}{\partial r} = w_s - \frac{w_O}{2}$$

So selfing increases fitness when $w_s > \frac{w_o}{2}$

or

$\delta < \frac{1}{2}$

Effects of inbreeding on selection

Inbreeding alone does not affect allele frequency; but it can influence the outcome of selection…

…because selection on homozygotes can be different from selection on heterozygotes.

A fraction *S* of a population selfs each generation, and 1–*S* outcross (mate at random).

Let *x*, *y*, and *z* be the frequencies of *AA*, *Aa*, and *aa*:

$$x' = \frac{\left\{(1-S)p^2 + S\left[x + \frac{y}{4}\right]\right\}w_{11}}{\overline{w}}$$

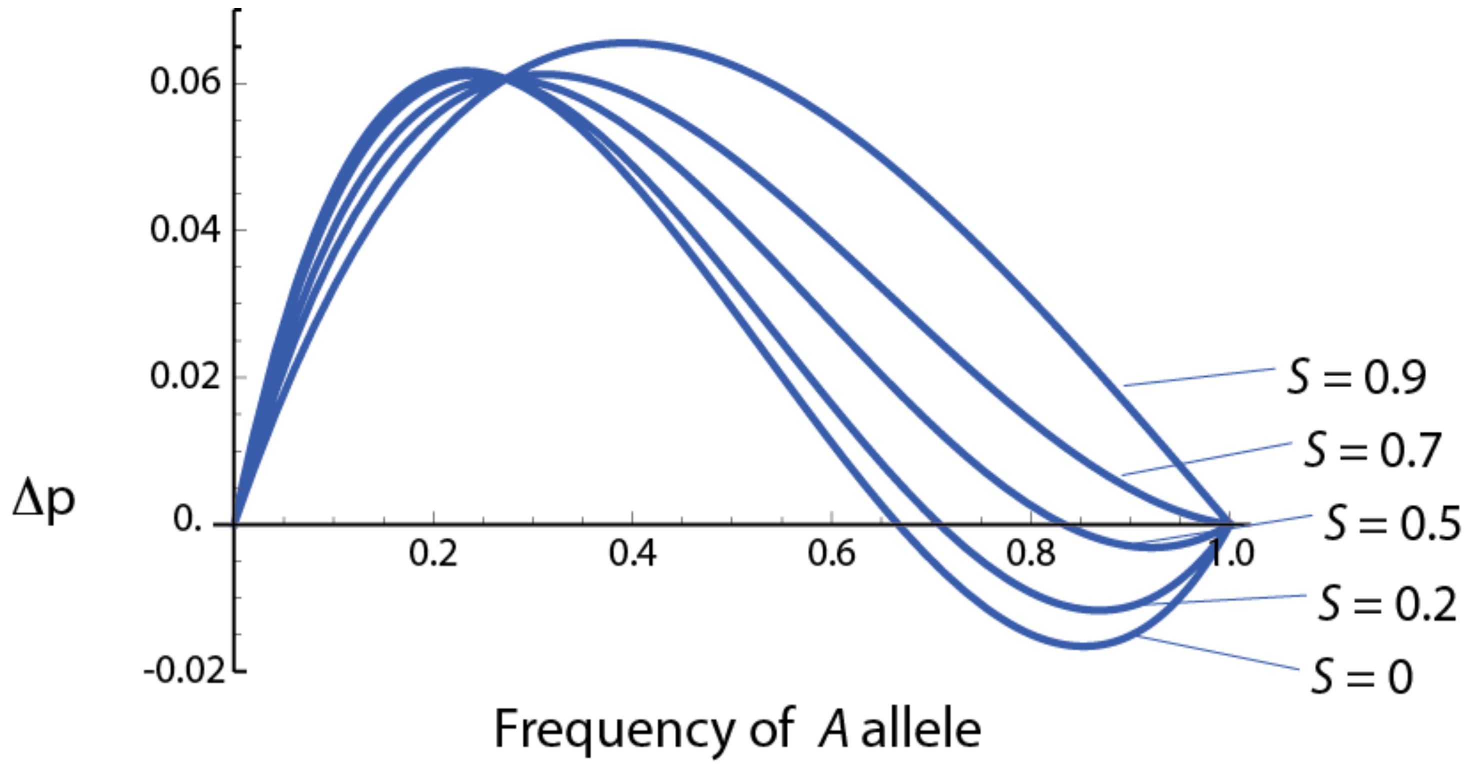
$$y' = \frac{\left\{(1-S)2pq + S\left[\frac{y}{2}\right]\right\}w_{12}}{\overline{w}}$$

$$z' = \frac{\left\{(1-S)q^2 + S\left[z + \frac{y}{4}\right]\right\}w_{22}}{\overline{w}}$$

$$\overline{w} = (1 - S)\overline{w}_{outbred} + S\,\overline{w}_{inbred}$$

$$\overline{w}_{inbred} = w_{11}\left(x + \frac{y}{4}\right) + w_{12}\left(\frac{y}{2}\right) + w_{22}\left(z + \frac{y}{4}\right)$$

Overdominance with selfing



Selection on multiple loci

Let P_{AB} and w_{AB} be the frequency and marginal fitness of the *AB* gamete (and similar for other gametes).

$$D = P_{AB}P_{ab} - P_{Ab}P_{aB}$$

Define D^* to be the LD after selection but before reproduction:

$$D^* = \left(\frac{P_{AB}w_{AB}}{\overline{w}}\right)\left(\frac{P_{ab}w_{ab}}{\overline{w}}\right) - \left(\frac{P_{Ab}w_{Ab}}{\overline{w}}\right)\left(\frac{P_{aB}w_{aB}}{\overline{w}}\right)$$

$$P'_{AB} = \frac{P_{AB}w_{AB}}{\overline{w}} - rD^*$$

$$P'_{Ab} = \frac{P_{Ab}w_{Ab}}{\overline{w}} + rD^*$$

$$P'_{aB} = \frac{P_{aB}w_{aB}}{\overline{w}} + rD^*$$

$$P'_{ab} = \frac{P_{ab}w_{ab}}{\overline{w}} - rD^*$$

If the marginal fitness of the *AB* and *ab* gametes are higher than the mean fitness of the population, then *D* will increase by selection. If fitnesses are additive among alleles, selection does not affect *LD*.

Chromosomal selection in *Moraba scurra*

Fitness

	BB	BB'	B'B'
AA	0.79	1.00	0.83
AA'	0.67	1.006	0.90
A'A'	0.66	0.66	1.07

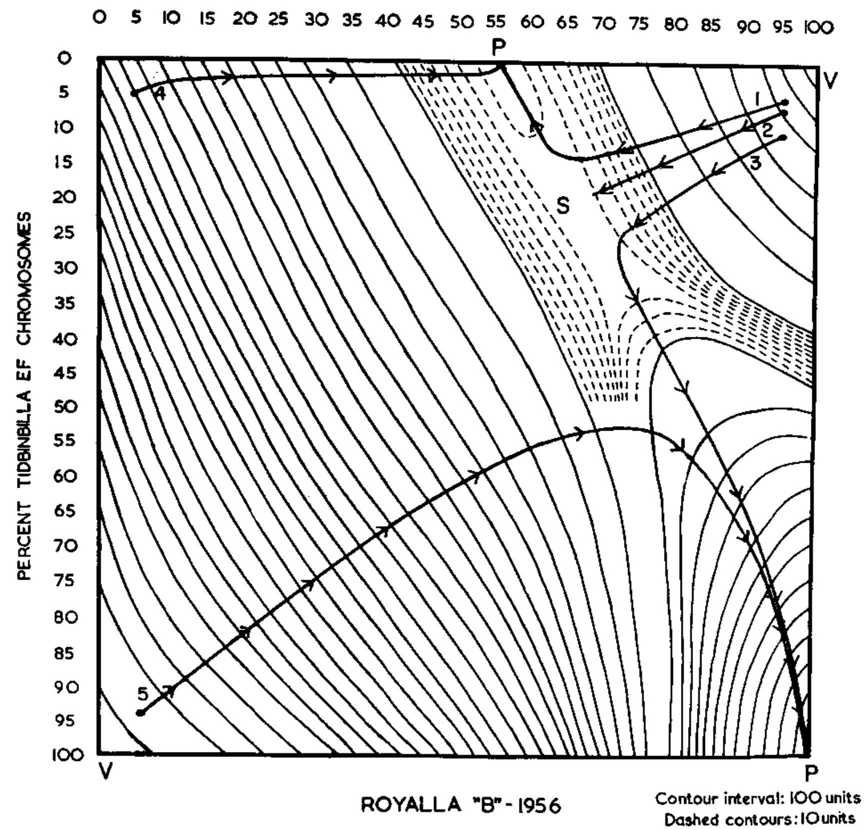


FIGURE 1

Fitness surface for two locus system estimated from field data on *Moraba scurra* [12].
Arrows show the direction of change in the gene frequencies from given starting points.