

January, 2002

Genetics 453

Evolutionary Genetics

Population Genetics

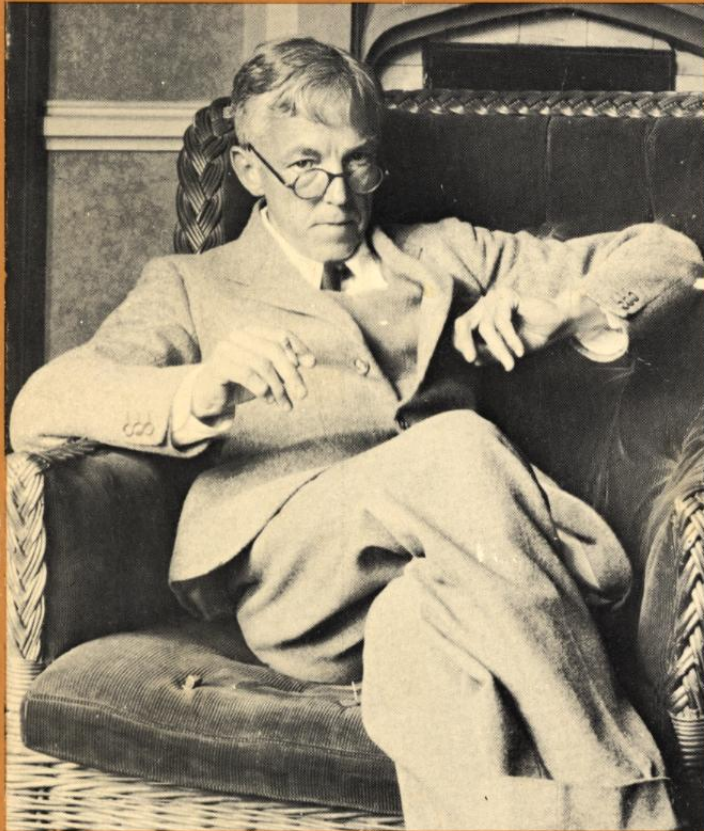
Joe Felsenstein

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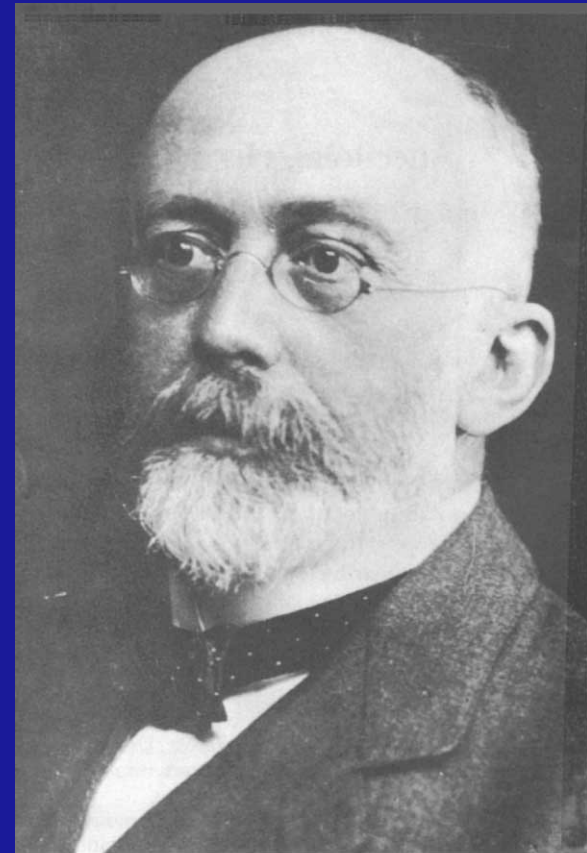
A MATHEMATICIAN'S APOLOGY

G.H. HARDY / Foreword by C.P. Snow



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Godfrey Harold Hardy (1877-1947)



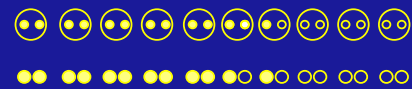
Nature Reviews | Genetics

Wilhelm Weinberg (1862-1937)

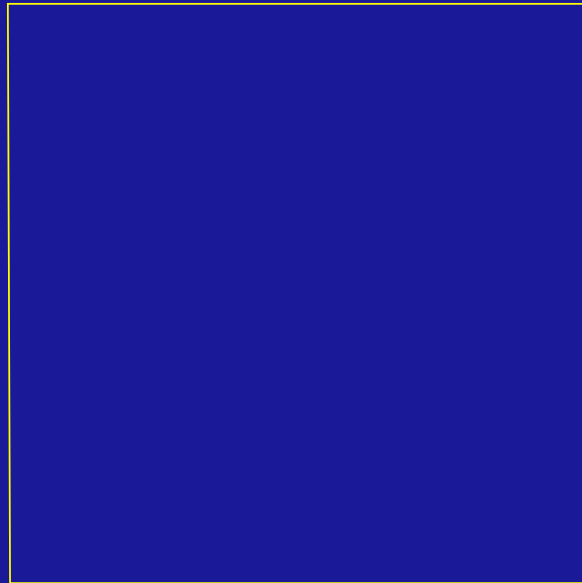
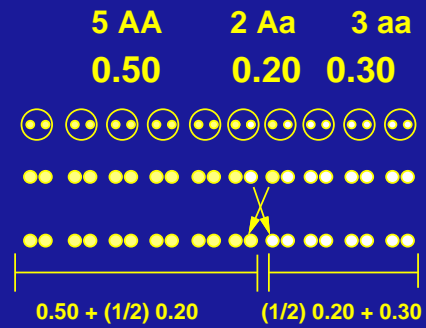
A Hardy–Weinberg calculation

5 AA 2 Aa 3 aa

0.50 0.20 0.30



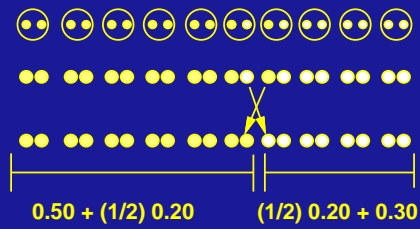
A Hardy–Weinberg calculation



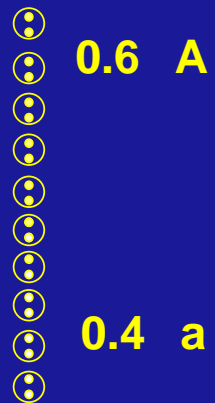
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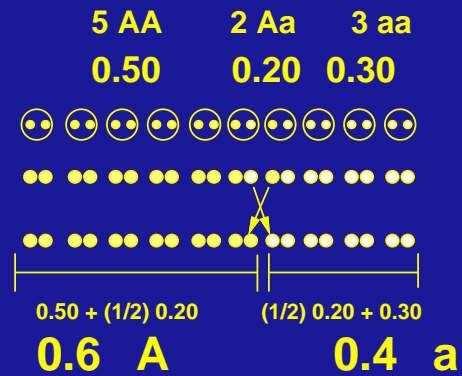
0.50 0.20 0.30



0.6 A **0.4 a**

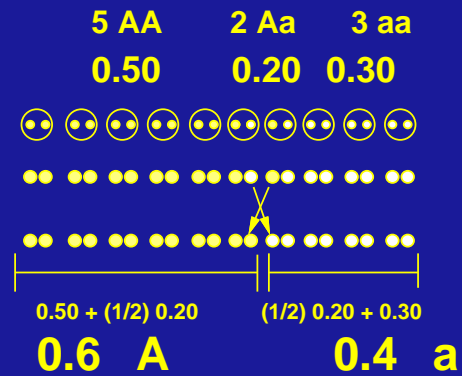
A 2x2 grid of blue squares with yellow borders. The grid is composed of four identical blue squares arranged in two rows and two columns. The squares are separated by thin yellow lines, and the entire grid is enclosed by a thicker yellow border.

A Hardy–Weinberg calculation



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	0.4 a	0.24 Aa	0.16 aa

A Hardy-Weinberg calculation



0.6 A
0.4 a

0.36 AA	0.24 Aa
0.24 Aa	0.16 aa

Result:

0.36 AA → 0.6 A
0.48 Aa $\xrightarrow{1/2}$ 0.6 A
0.16 aa $\xrightarrow{1/2}$ 0.4 a

Calculating the gene frequency (two ways)

Suppose that we have 200 individuals: 83 AA, 62 Aa, 55 aa

Method 1. Calculate what fraction of gametes bear A:

Genotype	Number	Genotype frequency	Fraction of gametes	
AA	83	0.415	all	0.57 A
Aa	62	0.31	1/2	
			1/2	0.43 a
aa	55	0.275	all	

Calculating the gene frequency (two ways)

Suppose that we have 200 individuals: 83 AA, 62 Aa, 55 aa

Method 2. Calculate what fraction of genes in the parents are A:

Genotype	Number	A's	a's	
AA	83	166	0	$\frac{228}{400} = 0.57$ A
Aa	62	62	62	$\frac{172}{400} = 0.43$ a
aa	55	0	110	
<hr/>				
228 + 172 =				400

The process of natural selection at one locus

●● genotypes are lethal in this case

gametes

●●●●●●●●●●●●●●●●○○○○○○

zygotes

●●●●●●●●●●○○●●○○●●○○

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gametes

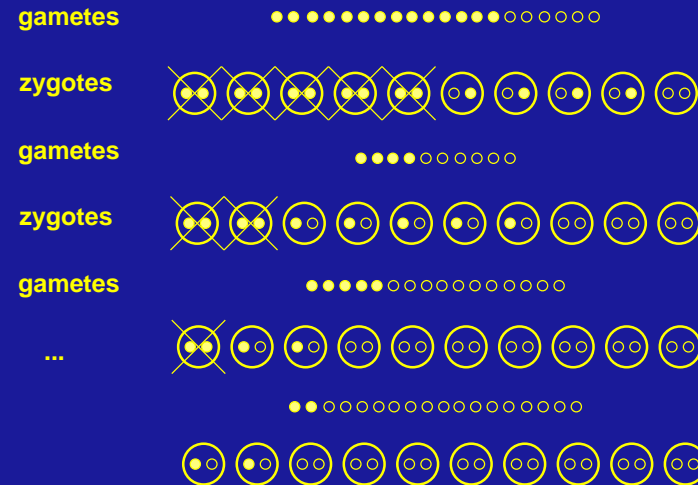
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The process of natural selection at one locus

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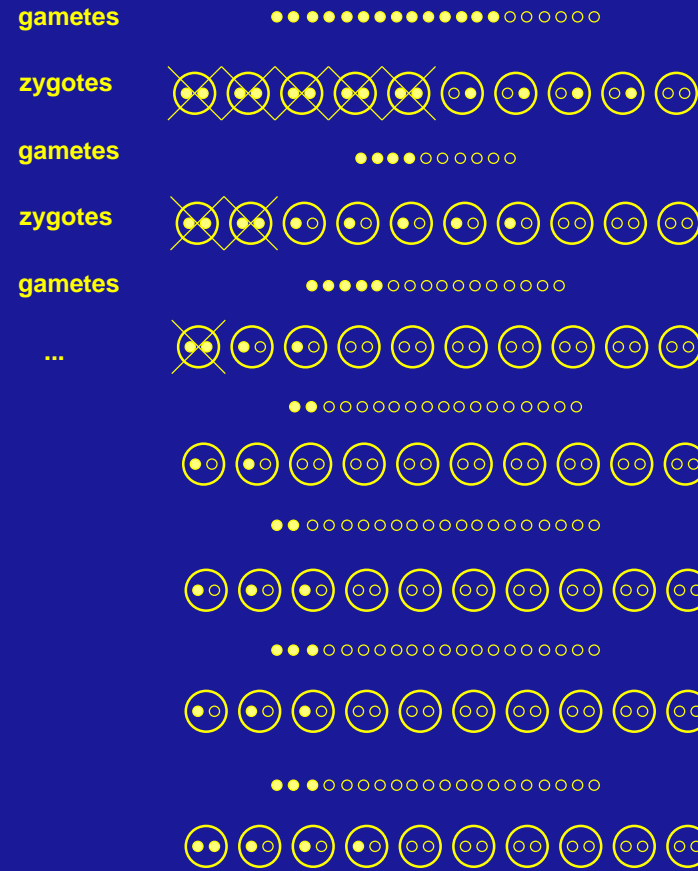
The process of natural selection at one locus

●● genotypes are lethal in this case



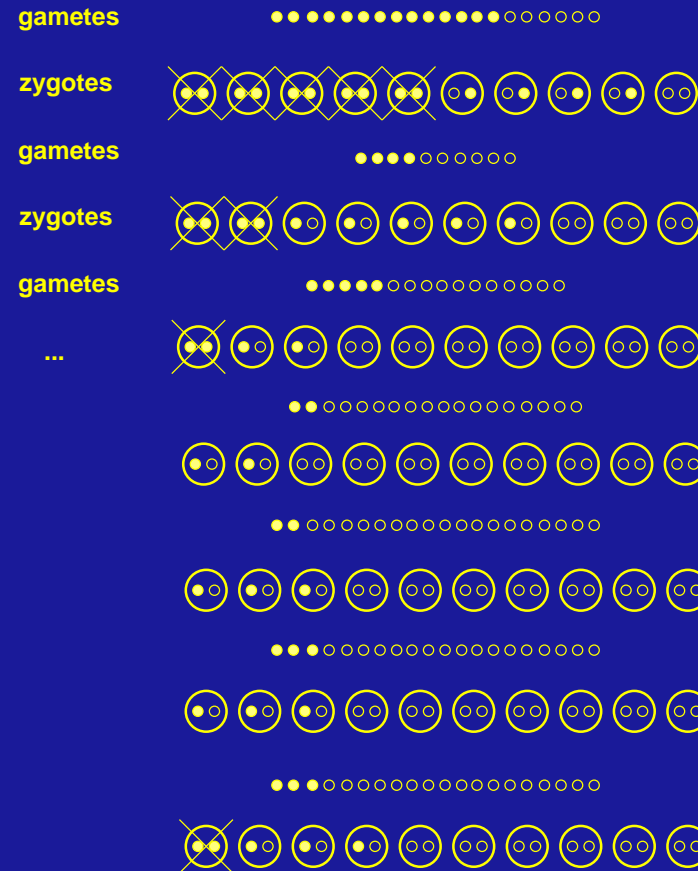
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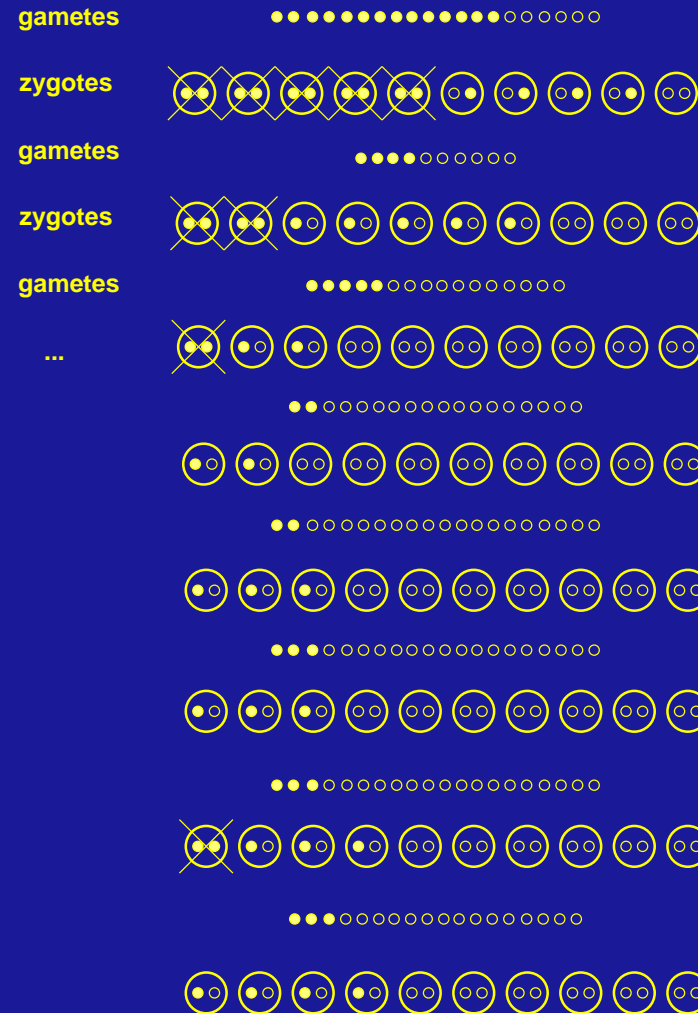
The process of natural selection at one locus

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The process of natural selection at one locus

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A numerical example of natural selection at one locus

Genotypes:	AA	Aa	aa
relative fitnesses:	1	1	0.7 (assume these are viabilities)

Initial gene frequency of $A = 0.2$

Initial genotype frequencies (from Hardy–Weinberg)
(newborns) 0.04 0.32 0.64

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Survivors (these are relative viabilities)

$$0.04 + 0.32 + 0.448 = \text{Total: } 0.808$$

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$$0.0495 \quad 0.396 \quad 0.554$$

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gene frequency

$$A: 0.0495 + 0.5 \times 0.396 = 0.2475$$

$$a: 0.554 + 0.5 \times 0.396 = 0.7525$$

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gene frequency

$$A: 0.0495 + 0.5 \times 0.396 = 0.2475$$

$$a: 0.554 + 0.5 \times 0.396 = 0.7525$$

genotype frequencies: (among newborns)

$$0.0613 \quad 0.3725 \quad 0.5663$$

The algebra of natural selection

New gene frequency is then

(adding up A bearers and dividing by everybody)

Genotype:	AA	Aa	aa
Frequency:	p^2	$2pq$	q^2
Relative fitnesses:	w_{AA}	w_{Aa}	w_{aa}
After selection:	$p^2 w_{AA}$	$2pq w_{Aa}$	$q^2 w_{aa}$

Note that these don't add up to 1

$$p' = \frac{p^2 w_{AA} + (1/2) 2pq w_{Aa}}{p^2 w_{AA} + 2pq w_{Aa} + q^2 w_{aa}}$$

$$p' = \frac{p (p w_{AA} + q w_{Aa})}{p^2 w_{AA} + 2pq w_{Aa} + q^2 w_{aa}} = p \frac{\bar{w}_A}{\bar{w}}$$

mean fitness of A

mean fitness of everybody

Is weak selection effective?

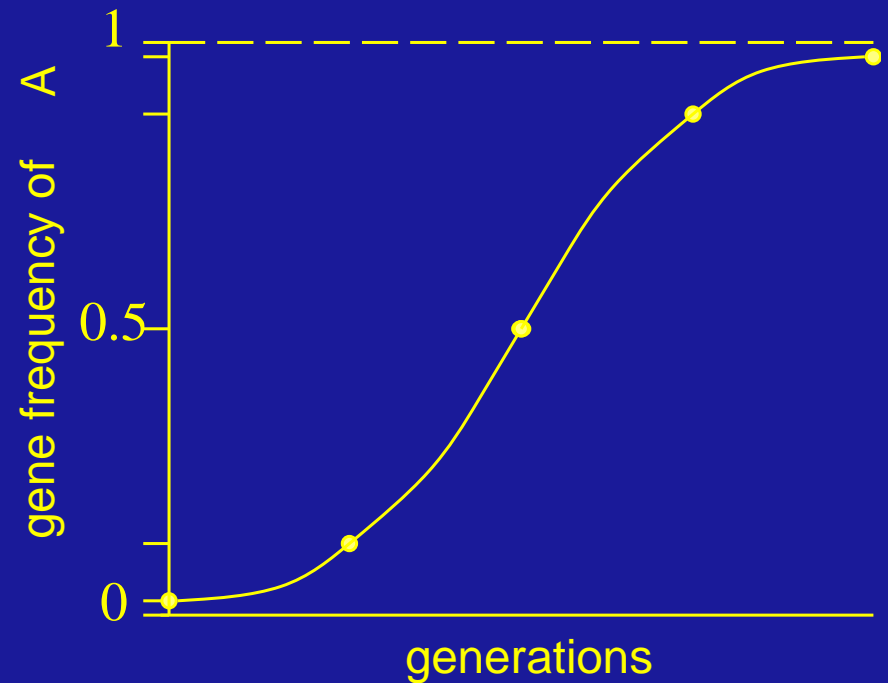
Suppose (relative) fitnesses are:

$$\begin{array}{ccc}
 AA & Aa & aa \\
 (1+s)^2 & 1+s & 1 \\
 \swarrow \quad \searrow & \swarrow \quad \searrow & \\
 \times (1+s) & \times (1+s) &
 \end{array}$$

So in this example each change of a to A multiplies the fitness by $(1+s)$, so that it increases it by a fraction s .

The time for gene frequency change, in generations, turns out to be:

s	change of gene frequencies			
	0.01 – 0.1	0.1 – 0.5	0.5 – 0.9	0.9 – 0.99
1	3.46	3.17	3.17	3.46
0.1	25.16	23.05	23.05	25.16
0.01	240.99	220.82	220.82	240.99
0.001	2399.09	2198.02	2198.02	2399.09



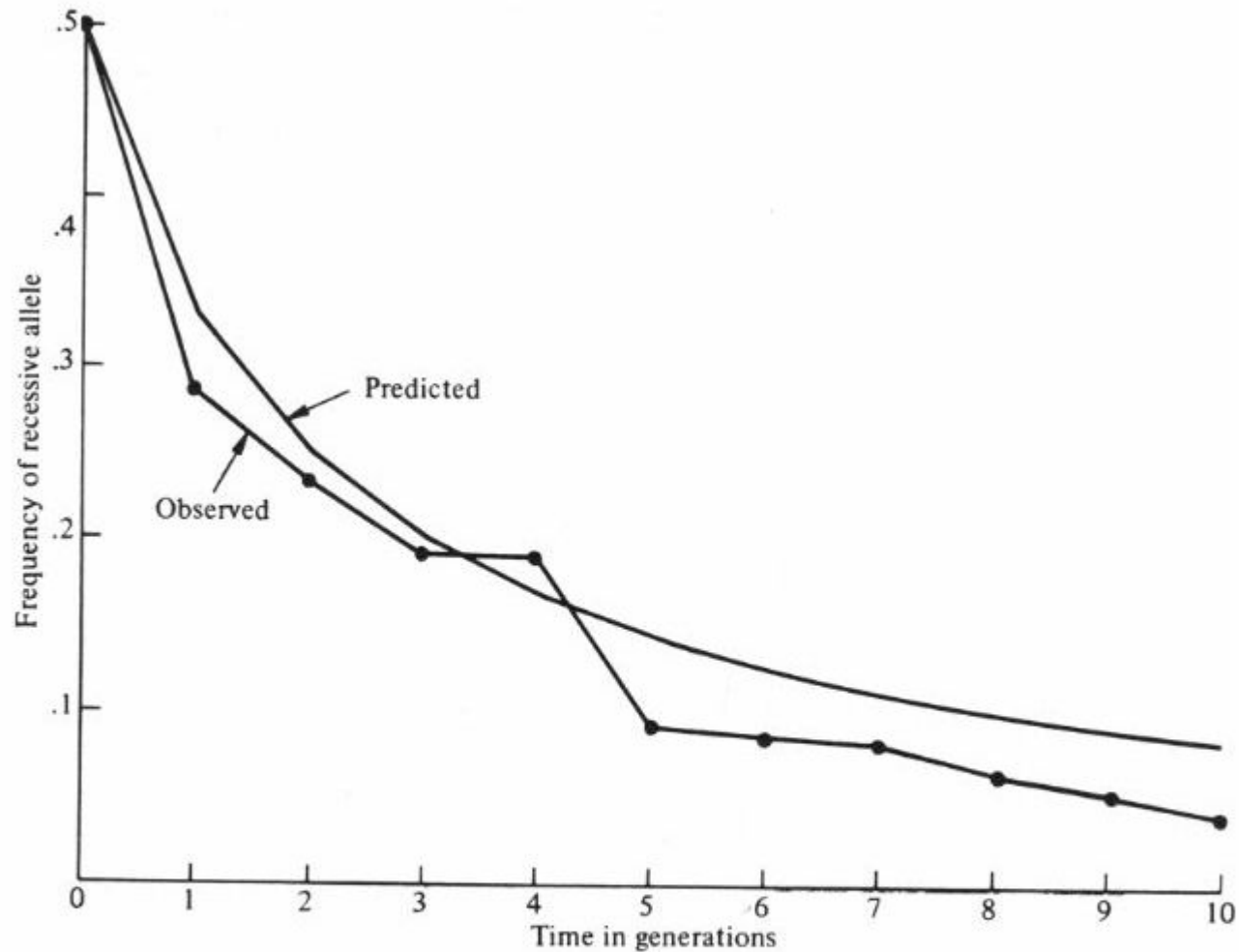
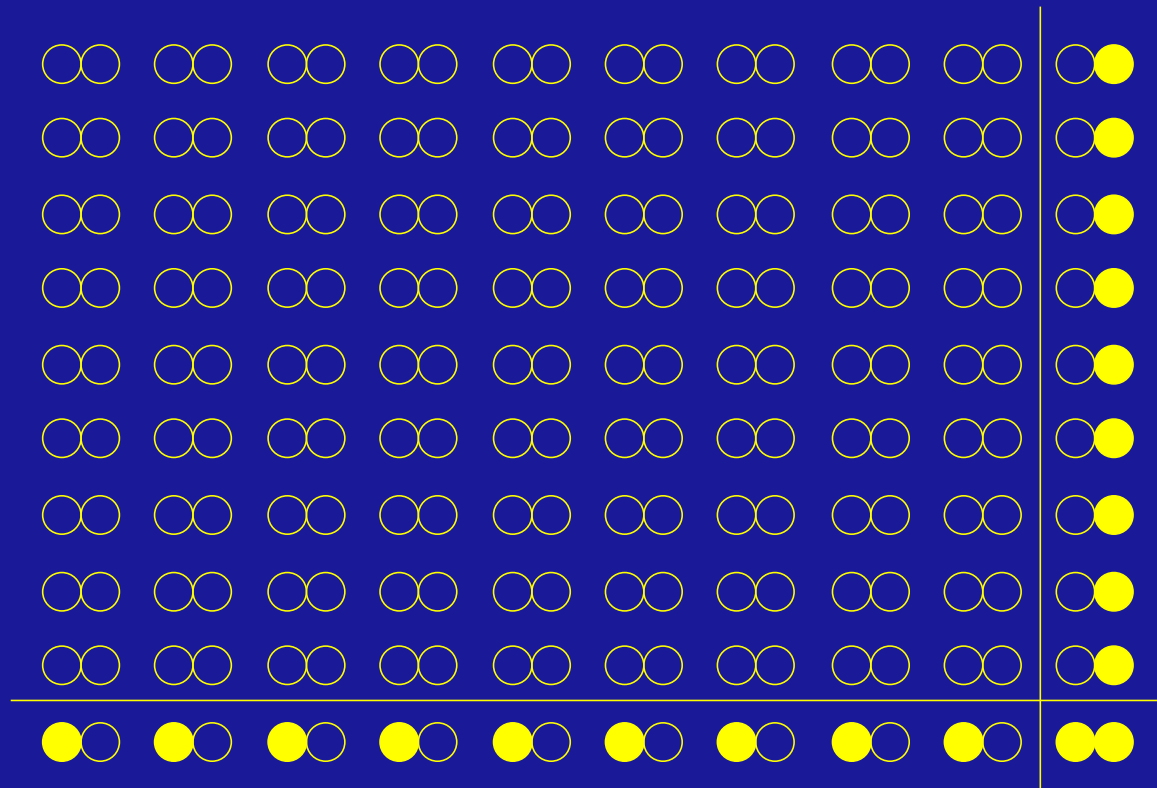


FIGURE 3.4. Experiment illustrating selection against a recessive lethal gene. The frequency of the recessive allele is on the vertical axis, time in generations is on the horizontal axis. [Data from B. Wallace (1963), The elimination of an autosomal lethal from an experimental population of *Drosophila melanogaster*, *Amer. Natur.* **97**: 65–66.]

Rare alleles occur mostly in heterozygotes



This shows a population in Hardy–Weinberg equilibrium

at gene frequencies of $0.9 A : 0.1 a$

Genotype frequencies:

$0.81 AA : 0.18 Aa : 0.01 aa$

Note that of the 20 copies of a ,

18 of them, or $18 / 20 = 0.9$ of them are in Aa genotypes

Overdominance and polymorphism

AA	Aa	aa
$1 - s$	1	$1 - t$

when A is rare, most A 's are in Aa , and most a 's are in aa

The average fitness of A -bearing genotypes is then nearly 1

The average fitness of a -bearing genotypes is then nearly $1 - t$

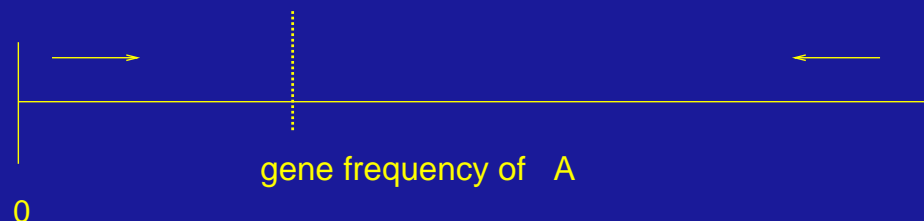
So A will increase in frequency when rare

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The average fitness of a -bearing genotypes is then nearly 1

The average fitness of A -bearing genotypes is then nearly $1 - s$

So a will increase in frequency when rare



Overdominance and unstable equilibrium

AA	Aa	aa
$1+s$	1	$1+t$

when A is rare, most A 's are in Aa , and most a 's are in aa

The average fitness of A -bearing genotypes is then nearly 1

The average fitness of a -bearing genotypes is then nearly $1+t$

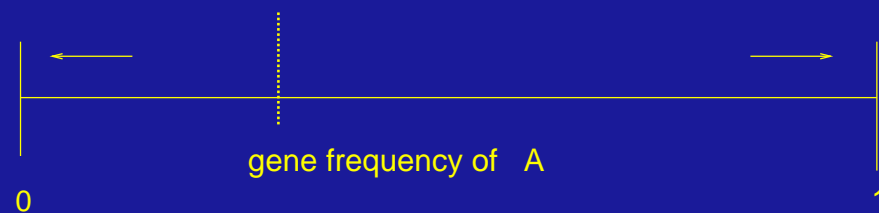
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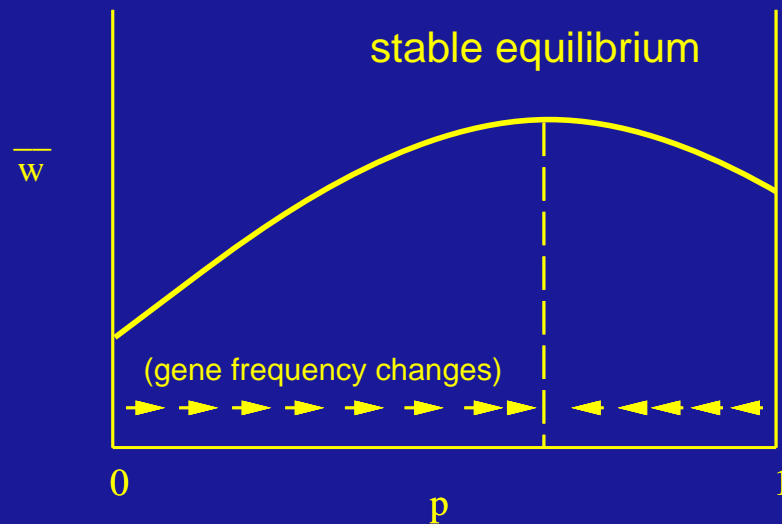
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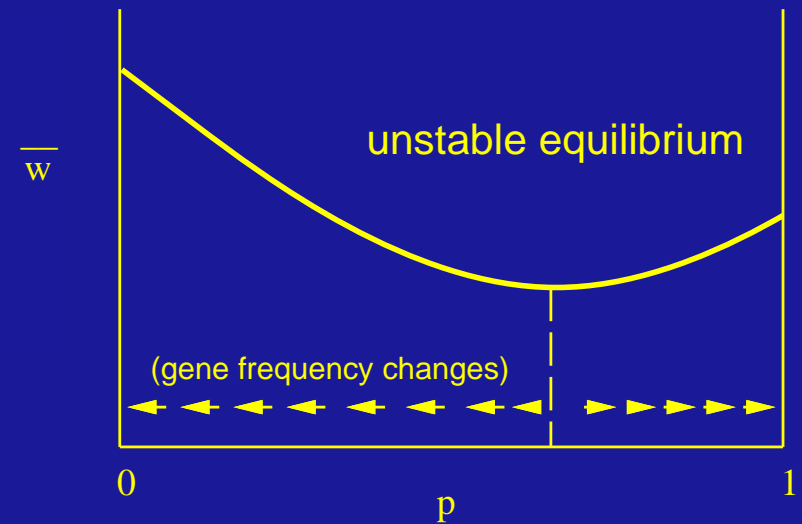


Fitness surfaces (Adaptive landscapes)

Overdominance

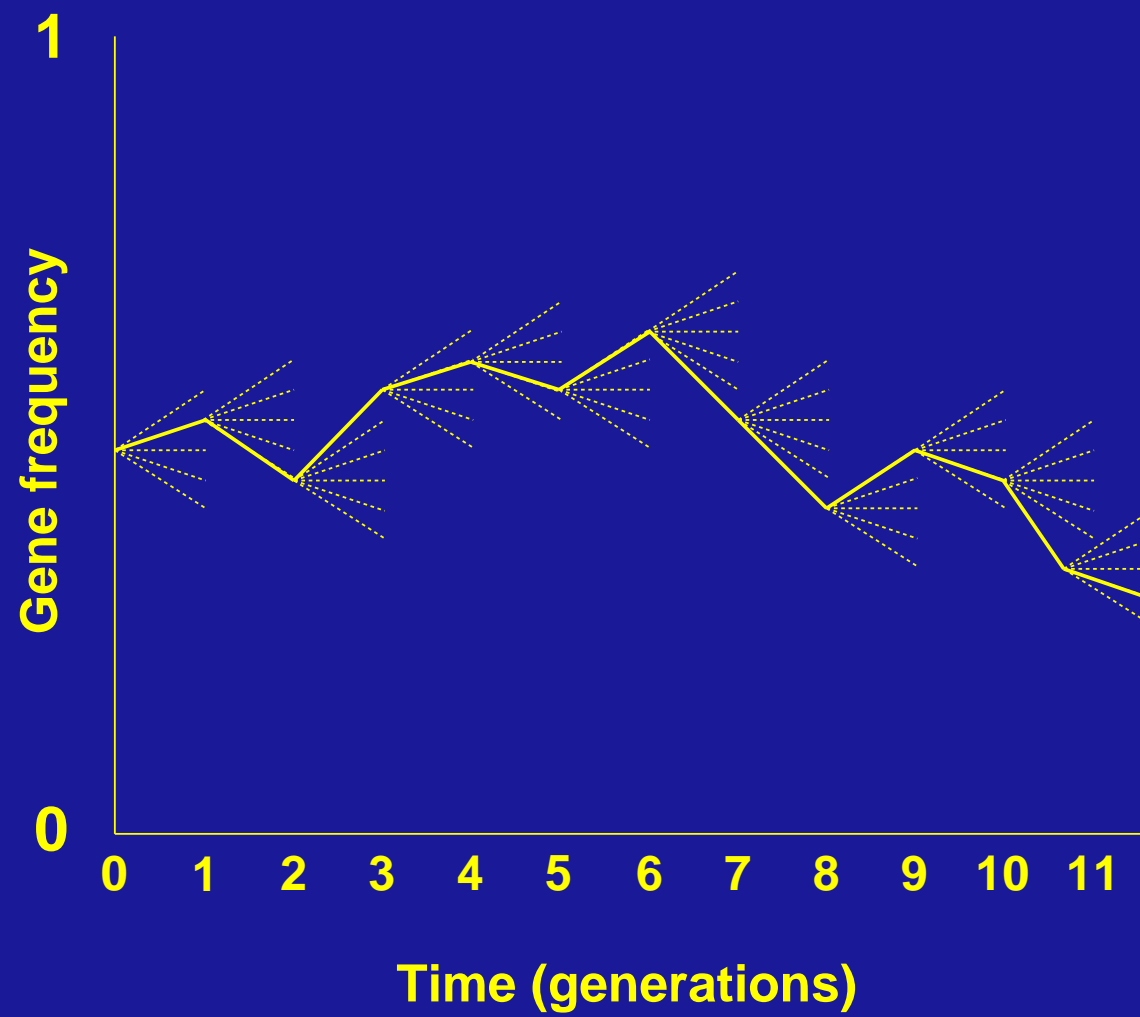


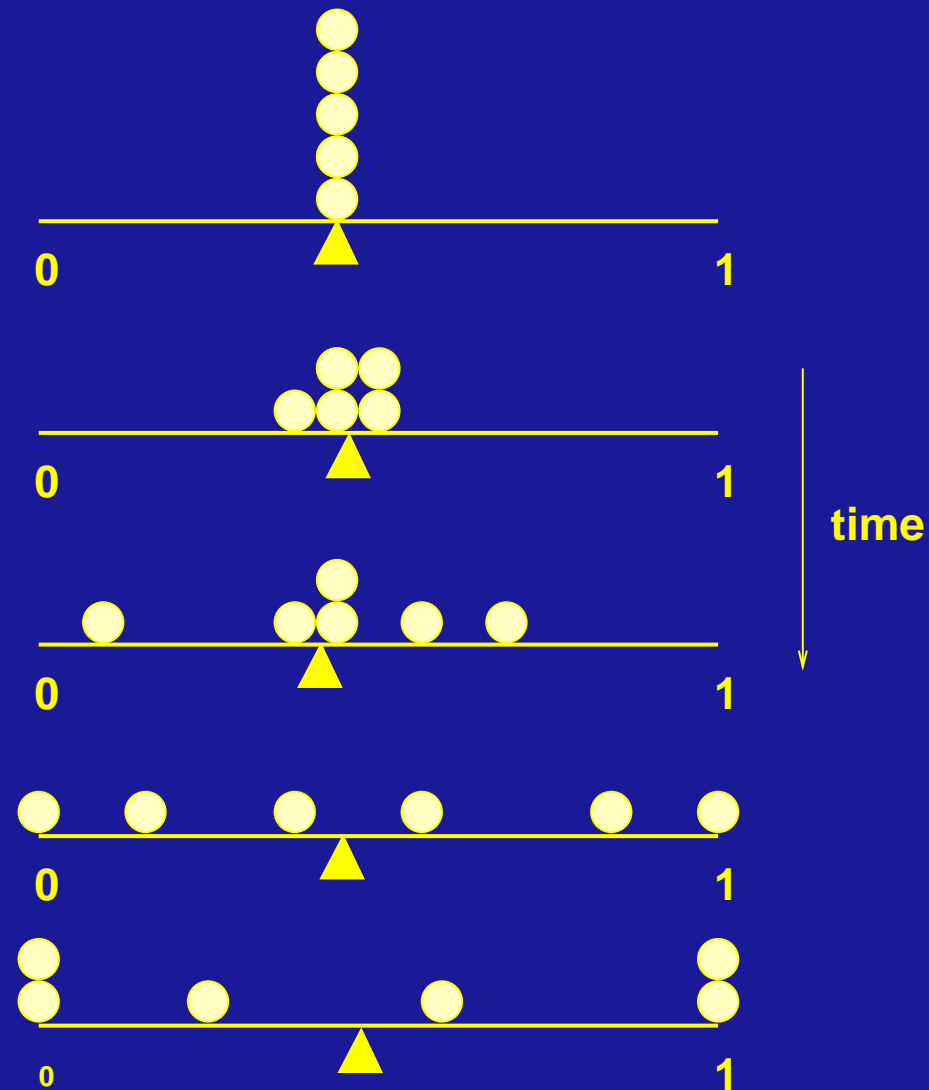
Underdominance



Is all for the best in this best of all possible worlds?

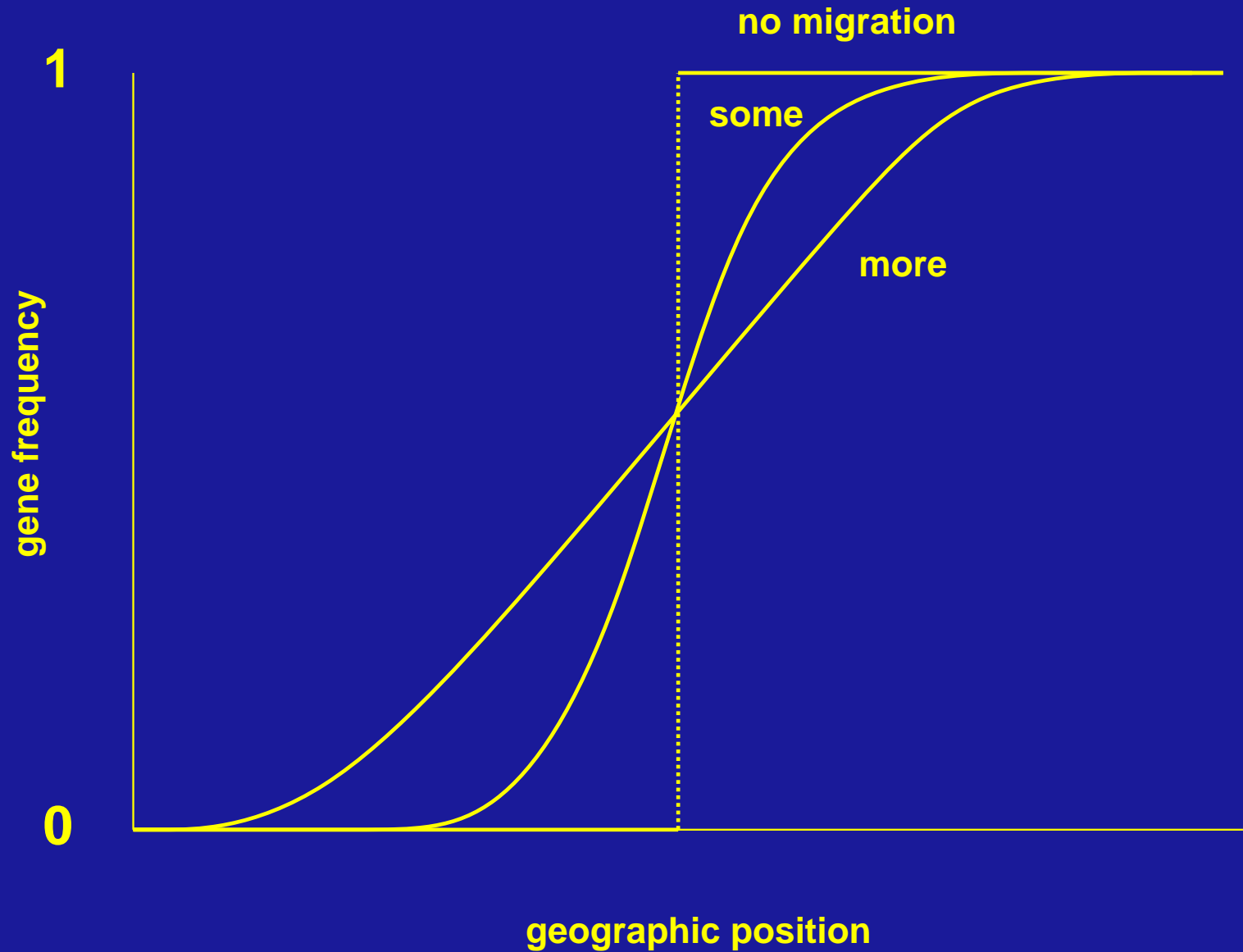
Can you explain the underdominance result in terms of rare alleles being mostly in heterozygotes?

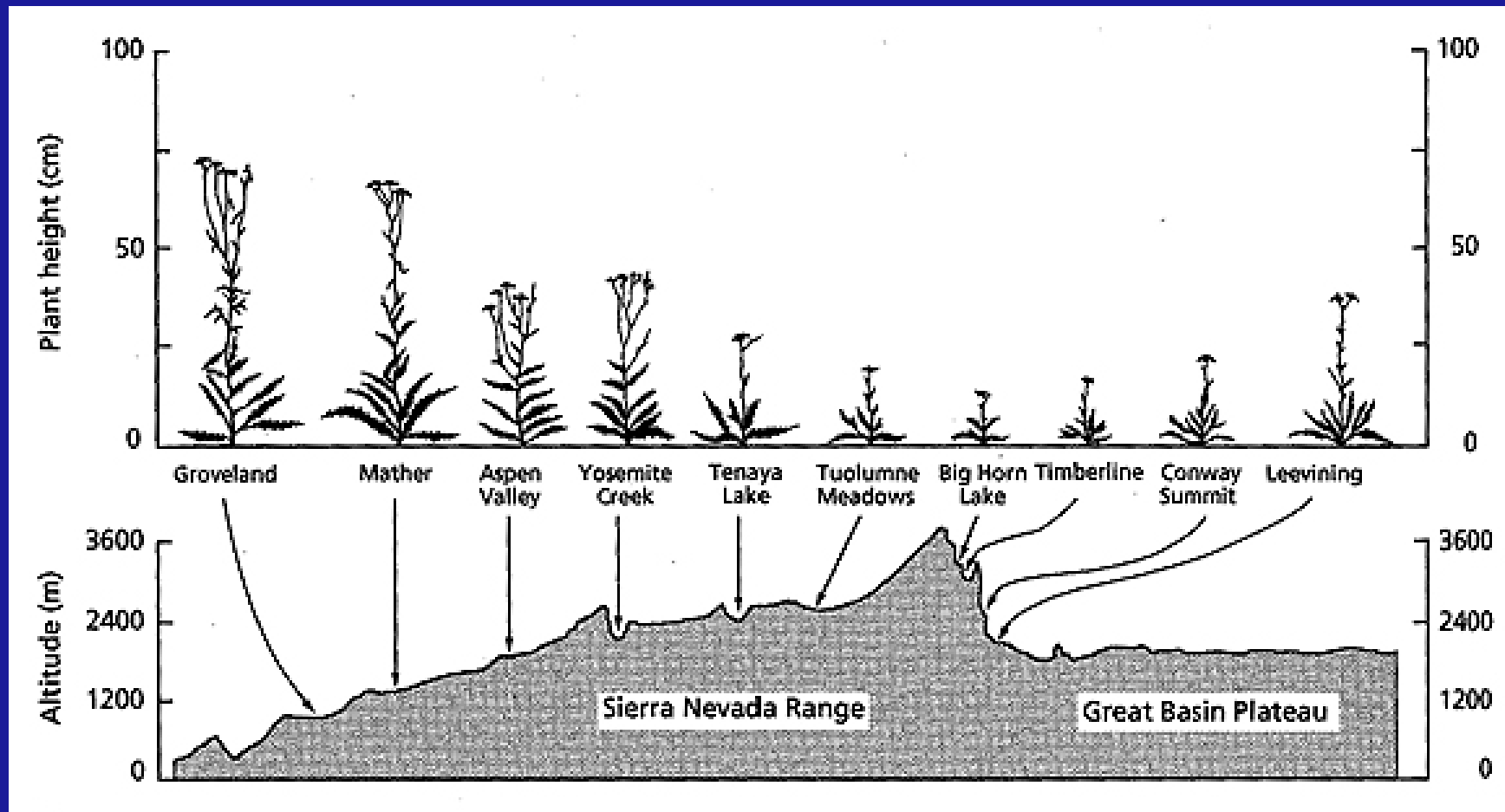




Note that although the individual populations wander their average hardly moves (not at all when we have infinitely many populations)

A cline (name due to Julian Huxley)





Clausen, Keck and Hiesey's (1949) common-garden experiment in *Achillea lanulosa*

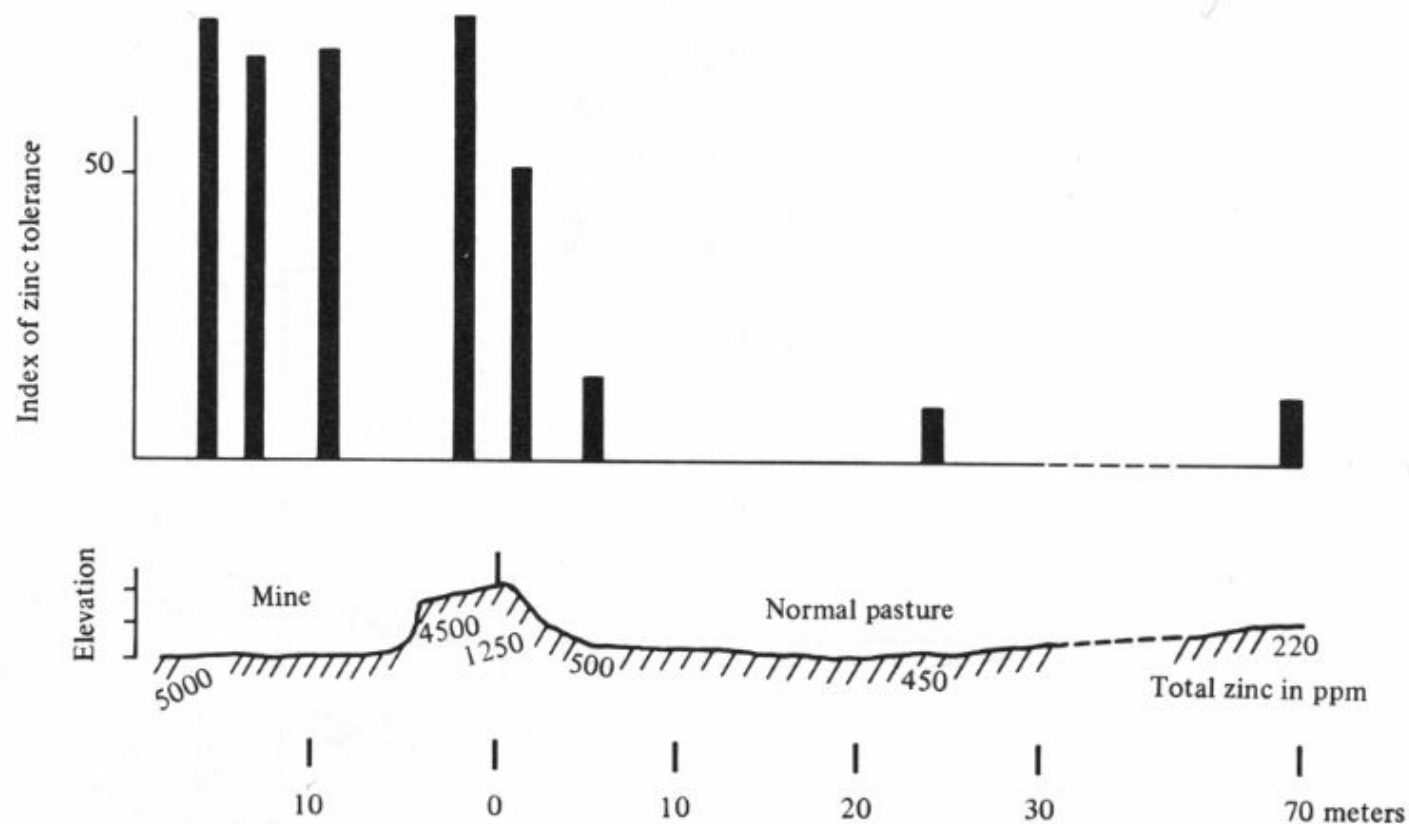


FIGURE 0.5. *The evolution of zinc resistance in grasses over a very fine spatial scale. The top graph illustrates the degree of zinc tolerance exhibited by plants collected from several places along a transect of approximately 100 meters in length. The lower graph illustrates the amount of zinc in the soil along the transect. Note the abrupt drop in zinc concentration at the boundary between the mine and the pasture. [From S. K. Jain and A. D. Bradshaw (1966), Evolutionary divergence among adjacent plant populations I, *Heredity* **21**: 407–441.]*

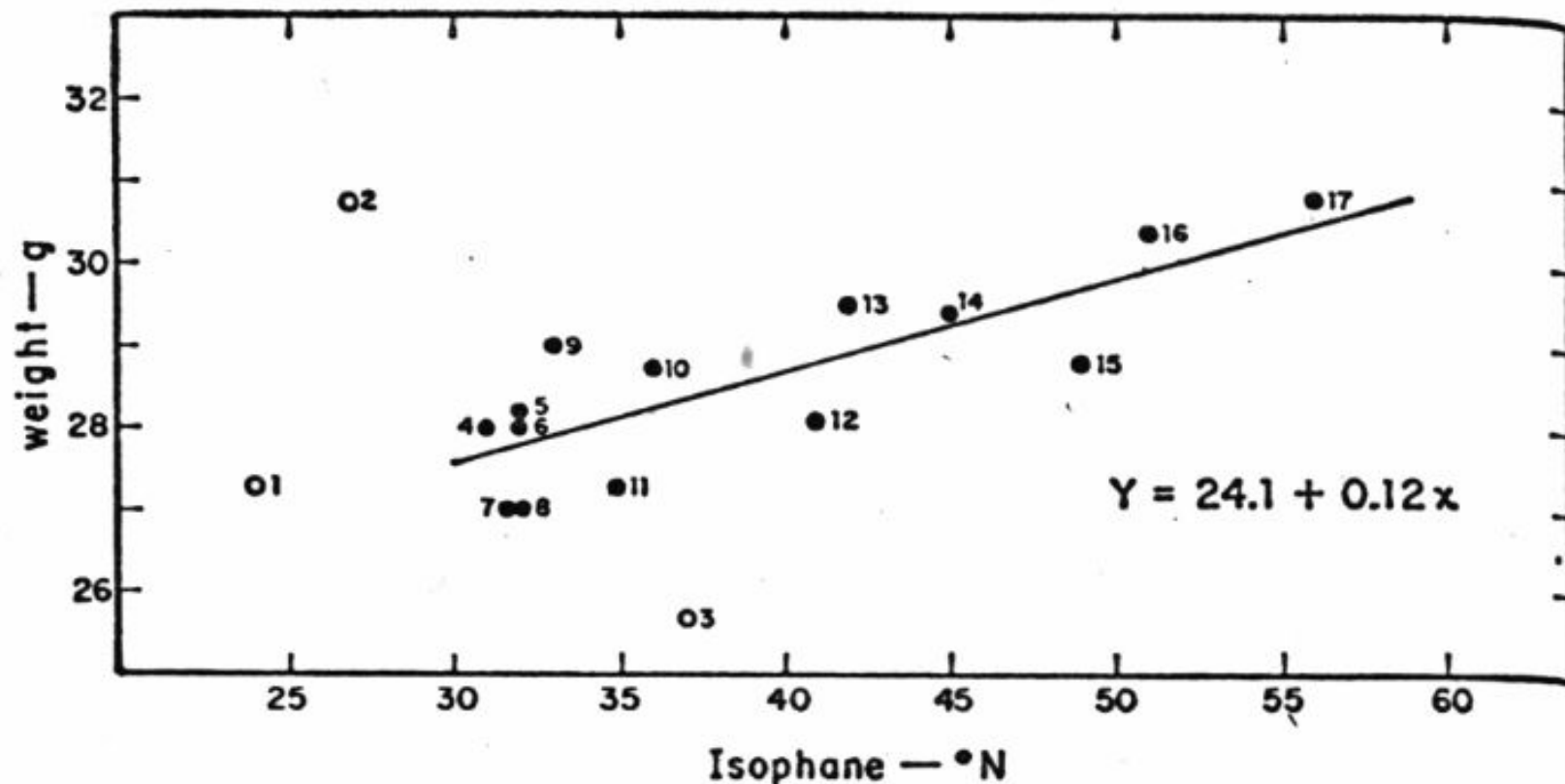
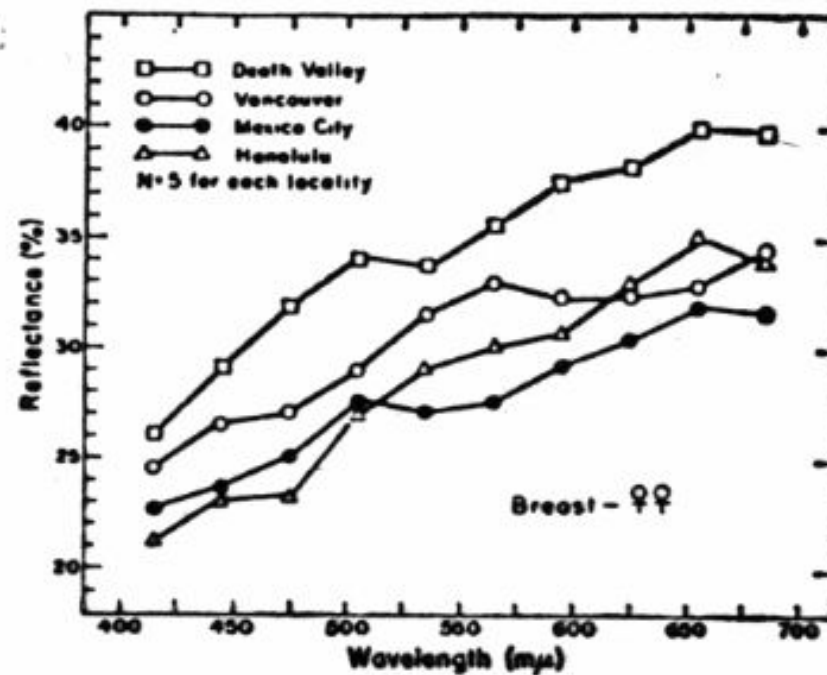


FIGURE 5. Mean body weights of adult male house sparrows plotted against isophanes (see text for explanation). Localities: 1, Oaxaca City, Mexico; 2, Progreso, Tex.; 3, Mexico City, Mexico; 4, Houston, Tex.; 5, Los Angeles, Calif.; 6, Austin, Tex.; 7, Death Valley, Calif.; 8, Phoenix, Ariz.; 9, Baton Rouge, La.; 10, Sacramento, Calif.; 11, Oakland, Calif.; 12, Las Cruces, N.M.; 13, Lawrence, Kan.; 14, Vancouver, B.C.; 15, Salt Lake City, Utah; 16, Montreal, Quebec; 17, Edmonton, Alberta. The regression line is based on data from localities 4 to 17.

FIGURE 2. Spectral reflectance curves for the breast of female house sparrows from Honolulu, Hawaii, and several North American localities.



This freeware-friendly presentation prepared with

- Linux (operating system)
- PDFLaTeX (mathematical typesetting and PDF preparation)
- Idraw (drawing program to modify plots and draw figures)
- Adobe Acrobat Reader (to display the PDF in full-screen mode)

(except that we had to use Microsoft Windows to project this as the X server I have in Linux is not too great)