Evolutionary Genetics
Population Genetics
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University of Washington, Seattle

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Godfrey Harold Hardy (1877-1947)  Wilhelm Weinberg (1862-1937)
A Hardy–Weinberg calculation

<table>
<thead>
<tr>
<th></th>
<th>5 AA</th>
<th>2 Aa</th>
<th>3 aa</th>
</tr>
</thead>
<tbody>
<tr>
<td>P</td>
<td>0.50</td>
<td>0.20</td>
<td>0.30</td>
</tr>
</tbody>
</table>
A Hardy–Weinberg calculation

5 AA  2 Aa  3 aa
0.50  0.20  0.30

0.50 + (1/2) 0.20  (1/2) 0.20 + 0.30
A Hardy–Weinberg calculation

5 AA  2 Aa  3 aa
0.50  0.20  0.30

\[
0.50 + \left(\frac{1}{2}\right) 0.20 \quad \left(\frac{1}{2}\right) 0.20 + 0.30
\]

0.6 A  0.4 a
A Hardy–Weinberg calculation

5 AA  2 Aa  3 aa
0.50   0.20  0.30

\[ 0.50 + \frac{1}{2} \times 0.20 \quad \frac{1}{2} \times 0.20 + 0.30 \]

0.6 A  0.4 a

\[
\begin{array}{c|c}
0.36 AA & 0.24 Aa \\
0.24 Aa & 0.16 aa \\
\end{array}
\]
A Hardy–Weinberg calculation

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\[ \frac{1}{2} \times 0.20 + 0.30 \]

Result:

- 0.36 AA
- 0.48 Aa
- 0.16 aa

0.6 A

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:

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Number</th>
<th>Genotype frequency</th>
<th>Fraction of gametes</th>
</tr>
</thead>
<tbody>
<tr>
<td>AA</td>
<td>83</td>
<td>0.415</td>
<td>0.57</td>
</tr>
<tr>
<td>Aa</td>
<td>62</td>
<td>0.31</td>
<td>0.43</td>
</tr>
<tr>
<td>aa</td>
<td>55</td>
<td>0.275</td>
<td></td>
</tr>
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</table>
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:

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Number</th>
<th>A’s</th>
<th>a’s</th>
</tr>
</thead>
<tbody>
<tr>
<td>AA</td>
<td>83</td>
<td>166</td>
<td>0</td>
</tr>
<tr>
<td>Aa</td>
<td>62</td>
<td>62</td>
<td>62</td>
</tr>
<tr>
<td>aa</td>
<td>55</td>
<td>0</td>
<td>110</td>
</tr>
</tbody>
</table>

\[
\frac{228}{400} = 0.57 \quad \text{A} \\
\frac{172}{400} = 0.43 \quad \text{a}
\]

\[
228 + 172 = 400
\]
The process of natural selection at one locus

Genotypes are lethal in this case

Gametes

Zygotes
The process of natural selection at one locus

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Gametes

Zygotes
The process of natural selection at one locus

- genotypes are lethal in this case

<table>
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<tr>
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<th>zygotes</th>
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<tr>
<td><img src="image1" alt="Gametes" /></td>
<td><img src="image2" alt="Zygotes" /></td>
<td><img src="image3" alt="Gametes" /></td>
<td><img src="image4" alt="Zygotes" /></td>
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Genotypes are lethal in this case

Gametes

Zygotes

Gametes

Zygotes

Gametes

...
The process of natural selection at one locus

Genotypes are lethal in this case.
The process of natural selection at one locus

Mate genotypes are lethal in this case

gametes

zygotes

gametes

zygotes

gametes

...
The process of natural selection at one locus

Genotypes are lethal in this case
The process of natural selection at one locus

genotypes are lethal in this case
The process of natural selection at one locus

- genotypes are lethal in this case

Gametes: ..............................................
Zygotes: ..............................
Gametes: ..............................................
Zygotes: ..............................
Gametes: ..............................................
...
The process of natural selection at one locus

Genotypes are lethal in this case
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  =  Total:  0.808
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A: 0.0495 + 0.5 x 0.396 = 0.2475
a: 0.554 + 0.5 x 0.396 = 0.7525
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a: 0.554 + 0.5 x 0.396 = 0.7525

genotype frequencies: (among newborns)
0.0613  0.3725  0.5663
The algebra of natural selection

Genotype: \[ \begin{array}{ccc}
AA & Aa & aa \\
p^2 & 2pq & q^2
\end{array} \]

Frequency: \[ \begin{array}{ccc}
w_{AA} & w_{Aa} & w_{aa} \\
p^2 & 2pq & q^2
\end{array} \]

Relative fitnesses: \[ \begin{array}{ccc}
w_{AA} & w_{Aa} & w_{aa} \\
p^2 & 2pq & q^2
\end{array} \]

After selection: \[ \begin{array}{ccc}
w_{AA} & w_{Aa} & w_{aa} \\
p^2 & 2pq & q^2
\end{array} \]

Note that these don’t add up to 1

New gene frequency is then
\[ p' = \frac{p^2 w_{AA} + (1/2) 2pq w_{Aa} + 2pq w_{Aa} + q^2 w_{aa}}{p w_{AA} + 2pq w_{Aa} + q^2 w_{aa}} \]

(adding up A bearers and dividing by everybody)
Is weak selection effective?

Suppose (relative) fitnesses are:

\[
\begin{align*}
AA & \quad (1+s)^2 \\
Aa & \quad 1+s \\
aa & \quad 1 \\
\end{align*}
\]

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:

![Graph showing gene frequency change over generations]
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

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td>AA</td>
<td>0.81</td>
</tr>
<tr>
<td>Aa</td>
<td>0.18</td>
</tr>
<tr>
<td>aa</td>
<td>0.01</td>
</tr>
</tbody>
</table>

Note that of the 20 copies of $a$, 18 of them, or $18 / 20 = 0.9$ of them are in $Aa$ genotypes. 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

\[
\begin{array}{ccc}
\text{AA} & \text{Aa} & \text{aa} \\
1 - s & 1 & 1 - t
\end{array}
\]

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

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–s

So a will increase in frequency when rare
Overdominance and unstable equilibrium

<table>
<thead>
<tr>
<th>AA</th>
<th>Aa</th>
<th>aa</th>
</tr>
</thead>
<tbody>
<tr>
<td>$1+s$</td>
<td>$1$</td>
<td>$1+t$</td>
</tr>
</tbody>
</table>

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 decrease in frequency when rare

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 $1+s$

So $a$ will decrease in frequency when rare

<table>
<thead>
<tr>
<th>← gene frequency of $A$ →</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
</tr>
</tbody>
</table>
Fitness surfaces (Adaptive landscapes)

Overdominance

\[
\begin{align*}
\bar{w} & \quad \text{stable equilibrium} \\
0 & \quad p & \quad 1
\end{align*}
\]

Underdominance

\[
\begin{align*}
\bar{w} & \quad \text{unstable equilibrium} \\
0 & \quad p & \quad 1
\end{align*}
\]

(gene frequency changes)

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)