Lecture 8: Selection (Cont’d)

- Basic selection model
- Selection and Polymorphism
- Balancing selection
- Underdominance & Overdominance
- Mutation as an evolutionary force
Selection against $B_2$

- Adaptive landscape for $B_1$: the variation in average fitness over the range of allele frequencies

Genotype: $B_1B_1$ $B_1B_2$ $B_1B_2$
Fitness (Abs): 1.0 0.75 0.5

\[ \bar{w} = p^2w_{11} + 2pqw_{12} + q^2w_{22} \]
Selection against $B_2$

"adaptive landscape"

Mean fitness, $w$

All $B_2 B_2$, $w = 0.5$

All $B_1 B_1$, $w = 1.0$

Frequency of $B_1$ allele ($p$)
Selection against $B_2$

Mean fitness vs. Frequency of $B_1$ allele ($p$)
Rate of evolution

Genotype: \( B_1B_1 \quad B_1B_2 \quad B_1B_2 \)

Fitness (Abs): \( 1.0 \quad 0.75 \quad 0.5 \)

\[ \Delta p = \left( \frac{p}{\bar{w}} \right) \left( pw_{11} + qw_{12} - \bar{w} \right) \]
Selection: a recessive lethal

Genotype: \( B_1B_1 \) \( B_1B_2 \) \( B_2B_2 \)

Fitness: 1.0 1.0 0.0

\( B_2 \): a recessive lethal

\( s \) = selection coefficient = -1.0

- difference in selection of one genotype versus others
Selection: a recessive lethal

Genotype: \begin{tabular}{c} B_1B_1 \ B_1B_2 \ B_2B_2 \end{tabular}

Fitness: \begin{tabular}{c} 1.0 \ 1.0 \ 0.0 \end{tabular}

\[
q' = q^2w_{22} + pqw_{12} / \bar{w}
\]

- Substitution

\[
q' = q / (1+q)
\]
Why does the rate of evolution slow down?

- $w_{11} = 1.00$
- $w_{12} = 1.00$
- $w_{22} = 0.00$
  
  ($s_{22} = 1.0$)

Frequency of recessive allele after 500 generations = 0.002
### Tribolium example

<table>
<thead>
<tr>
<th>Gen</th>
<th>Fr(lethal)</th>
<th>% in het's</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.500</td>
<td>50.0</td>
</tr>
<tr>
<td>10</td>
<td>0.091</td>
<td>90.9</td>
</tr>
<tr>
<td>100</td>
<td>0.010</td>
<td>99.0</td>
</tr>
<tr>
<td>1000</td>
<td>0.001</td>
<td>99.9</td>
</tr>
</tbody>
</table>

- \( w_{11} = 1.00 \)
- \( w_{12} = 1.00 \)
- \( w_{22} = 0.00 \)
  - \( s_{22} = -1.0 \)

Frequency of recessive after 500 gens = 0.002

“masked” from selection
Tribolium example

- As lethal allele becomes rare, rate of evolution slows
Selection and polymorphism

- Selection against alleles: leads to “fixation” of favored allele
- Polymorphism: A population, locus, or trait with more than one allele or phenotype
How can selection maintain polymorphism?

Maintained by selection

- Heterozygote advantage
- Frequency-dependent selection
- Mutation/selection balance
- Variable selection in time
- Variable selection in space (+ immigration)

Balancing Selection
Selection on heterozygotes

Selection on one homozygote and heterozygote the same:

\[ w_{11} = w_{12} > w_{22} \]

leads to fixation
Selection on heterozygotes

- Heterozygote advantage: overdominance
  \[ w_{11} < w_{12} > w_{22} \]

- Heterozygote disadvantage: underdominance
  \[ w_{11} > w_{12} < w_{22} \]
Selection on heterozygotes

Allele frequencies: \( Fr(A) = p \) \( Fr(a) = q \)

Genotype: \( AA \) \( Aa \) \( aa \)

Frequency (z): \( p^2 \) \( 2pq \) \( q^2 \)

Fitness (abs): \( w_{11} \) \( w_{12} \) \( w_{22} \)

Fitness (abs): \( 1+S \) \( 1 \) \( 1+T \)

\( S, T < 0: \) Overdominance

\( S, T > 0: \) Underdominance

Box 5.8
Selection on heterozygotes

Allele frequencies: \[ \text{Fr}(A) = p \quad \text{Fr}(a) = q \]

Genotype: \[ AA \quad Aa \quad aa \]

Frequency (z): \[ p^2 \quad 2pq \quad q^2 \]

Fitness (abs): \[ w_{11} \quad w_{12} \quad w_{22} \]

Fitness (abs): \[ 1 + S \quad 1 \quad 1 + T \]

\[ \Delta p = \frac{p}{\bar{w}}(pw_{11} + qw_{12} - \bar{w}) \]

When will \( \Delta p = 0? \)

\( p = 0, \quad p = 1, \) or \( p = \hat{p} \)

\[ \hat{p} = \frac{T}{S + T} \]
## Overdominance

### Allele frequencies:
- Fr(A) = p
- Fr(a) = q

### Genotype:
- AA
- Aa
- aa

### Frequency (z):
- p²
- 2pq
- q²

### Fitness (abs):
- $w_{11}$
- $w_{12}$
- $w_{22}$

### Fitness (abs):
- $1 + S$
- 1
- $1 + T$

\[
S = -0.4 \text{ and } T = -0.6
\]

\[
\hat{p} = \frac{-0.6}{-0.4 + -0.6} = 0.6
\]
Adaptive Landscape: Overdominance

Equilibrium (stable)

Fig 5.20
Stability of equilibrium allele frequency

\[ \Delta p \]

Fig 5.20

\[ p = 0.0 \quad p = 0.6 \quad p = 1.0 \]

\[ p = Fr(A) \]
Heterozygote advantage in *Drosophila*

\[ w_{VV} = 0.735 \]
\[ w_{VL} = 1.0 \]
\[ w_{LL} = 0.0 \]
\[ S = -0.265 \]
\[ T = -1.000 \]

\[ \hat{p} = \frac{T}{S + T} \]
\[ \hat{p} = 0.791 \]
Heterozygote advantage in *Drosophila*

- $w_{VV} = 0.735$
- $w_{VL} = 1.0$
- $w_{LL} = 0.0$
- $S = -0.265$
- $T = -1.000$
- $\hat{p} = \frac{T}{S + T}$
- $\hat{p} = 0.791$

**Figure 5.18**
Adaptive Landscape: Underdominance

Fig 5.20

$S = 0.4$ and $T = 0.6$

Equilibrium (unstable)
• Evolution under selection is slow when recessive alleles reside in heterozygotes
  - Leads to fixation
• Selection favoring heterozygotes (overdominance) can maintain polymorphism (underdominance leads to fixation)