Microevolution 2 – mutation & migration
A recap:

Let \( p = A_1 \) and \( q = A_2 \)

<table>
<thead>
<tr>
<th>Genotype</th>
<th>( A_1A_1 )</th>
<th>( A_1A_2 )</th>
<th>( A_2A_2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fitnesses:</td>
<td>( w_{11} )</td>
<td>( w_{12} )</td>
<td>( w_{22} )</td>
</tr>
</tbody>
</table>

Fitness of \( A_1 \) allele = \( w_1 = pw_{11} + qw_{12} \)
Fitness of \( A_2 \) allele = \( w_2 = qw_{22} + pw_{12} \)

Mean population fitness = \( \bar{w} = pw_1 + qw_2 \)
An example of directional selection

Let $p = q = 0.5$

Genotype: $A_1A_1$ $A_1A_2$ $A_2A_2$
Fitness: $1$ $0.95$ $0.90$

\[
w_1 = pw_{11} + qw_{12} = 0.975
\]
\[
w_2 = qw_{22} + pw_{12} = 0.925
\]
\[
\overline{w} = pw_1 + qw_2 = 0.950
\]

\[
p' = p(w_1/\overline{w}) = 0.513
\]
\[
q' = q(w_2/\overline{w}) = 0.487
\]

In ~150 generations the $A_1$ allele will be fixed!
Conclusion:

Natural selection can cause rapid evolutionary change!
Natural selection and mean population fitness
Natural selection and mean population fitness

Question: How does $\bar{w}$ change during the process of directional selection?
Natural selection and mean population fitness

Question: How does $w$ change during the process of directional selection?

<table>
<thead>
<tr>
<th>Genotype</th>
<th>AA</th>
<th>Aa</th>
<th>aa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fitness</td>
<td>1</td>
<td>1</td>
<td>0.50</td>
</tr>
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</table>

Here, selection is favoring a dominant allele.
Directional selection always maximizes mean population fitness!

Selection against a recessive allele ($s = 0.5$) and for a dominant allele

Fraction surviving:

$$
\begin{align*}
AA & \quad 1.0 \\
Aa & \quad 1.0 \\
aa & \quad 0.5 
\end{align*}
$$

Figure 6-17a Evolutionary Analysis, 4/e
© 2007 Pearson Prentice Hall, Inc.
Natural selection and mean population fitness

Question: How does $\bar{w}$ change during the process of directional selection?

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<tbody>
<tr>
<td>Fitness</td>
<td>0.4</td>
<td>0.4</td>
<td>1</td>
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Here, selection is favoring a recessive allele.
Directional selection always maximizes mean population fitness!

Selection for a recessive allele and against a dominant allele \((s = 0.6)\)
Natural selection and mean population fitness

Question: How does $\bar{w}$ change during the process of balancing selection?
Natural selection and mean population fitness

Question: How does $\bar{w}$ change during the process of balancing selection?

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<tr>
<td>Fitness</td>
<td>1-s</td>
<td>1</td>
<td>1-t</td>
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Natural selection and mean population fitness

Question: How does \( \bar{w} \) change during the process of balancing selection?

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^

Results in stable equilibrium point at \( p = t/(s + t) \)
Natural selection and mean population fitness

Question: How does $\bar{w}$ change during the process of balancing selection?

Example: suppose $s = 0.40$ and $t = 0.60$
Natural selection and mean population fitness

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Natural selection and mean population fitness

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Stable equilibrium point at \( p = t/(s + t) \)
Natural selection and mean population fitness

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Stable equilibrium point at $p = t/(s + t)$

$= 0.60$
Balancing selection maximizes mean population fitness!

**Mean fitness as a function of $p$ for overdominance**

Equilibrium

![Graph showing mean fitness as a function of p for overdominance](Figure 6-20b) Evolutionary Analysis, 4/e © 2007 Pearson Prentice Hall, Inc.
Balancing selection maximizes mean population fitness!

Figure 6-20b: Evolutionary Analysis, 4/e
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... but is only 0.75!
Conclusion:

Natural selection always acts to maximize mean population fitness
Natural selection and mean population fitness
Natural selection and mean population fitness

- Sewall Wright envisioned populations occupying “adaptive landscapes”.
Natural selection and mean population fitness

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Wright at the University of Chicago in 1925
Natural selection and mean population fitness

• Sewall Wright envisioned populations occupying “adaptive landscapes”.

Wright in 1965
Natural selection and mean population fitness

• Sewall Wright envisioned populations occupying “adaptive landscapes”.

• these landscapes were covered with multiple adaptive peaks separated by valleys of reduced fitness
A hypothetical adaptive landscape
Natural selection and mean population fitness

• Sewall Wright envisioned populations occupying “adaptive landscapes”.

• these landscapes were covered with multiple adaptive peaks separated by valleys of reduced fitness

• his shifting balance theory considered how populations could move from one peak to another.
A hypothetical adaptive landscape

How does a population move among peaks??
A hypothetical adaptive landscape

Maybe by random genetic drift?
### An example: Sickle-Cell

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<tr>
<th>Genotype</th>
<th>Fitness</th>
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<tbody>
<tr>
<td>AA</td>
<td>0.9</td>
<td>malarial susceptible</td>
</tr>
<tr>
<td>AS</td>
<td>1</td>
<td>malarial resistant</td>
</tr>
<tr>
<td>SS</td>
<td>0.2</td>
<td>severe anemia</td>
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</tr>
<tr>
<td>CC</td>
<td>1.3</td>
<td>malarial resistant</td>
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An example: Sickle-Cell

Hb^C_Hb^C

Hb^A_Hb^S
Mutation

• Let $p =$ frequency of $A_1$ allele
Mutation

• Let $p = \text{frequency of } A_1 \text{ allele}$

• Let $q = \text{frequency of } A_2 \text{ allele}$
Mutation

• Let $p$ = frequency of $A_1$ allele
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• Let $p = q = 0.50$
Mutation

- Let $p =$ frequency of $A_1$ allele
- Let $q =$ frequency of $A_2$ allele
- Let $p = q = 0.50$

\[ A_1 \xrightarrow{u} A_2 \]

- Let $u = 1 \times 10^{-5}$ (and ignore $v$)
Mutation

- Let $p =$ frequency of $A_1$ allele
- Let $q =$ frequency of $A_2$ allele
- Let $p = q = 0.50$

\[
\begin{array}{c}
A_1 \\
\overset{u}{\leftrightarrow}
\end{array}
\quad \begin{array}{c}
A_2 \\
\overset{v}{\leftrightarrow}
\end{array}
\]

- Let $u = 1 \times 10^{-5}$ (and ignore $v$)
Mutation

• denoting the change in A2 in one generation as $\Delta q$, 
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$$\Delta q = u \times p$$
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$$= (1 \times 10^{-5})(0.5)$$
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\[ \Delta q = u \times p \]
\[ = (1 \times 10^{-5})(0.5) \]
\[ = 0.000005 \]
Mutation

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$$= 0.000005$$

• the $A_2$ allele has increased in frequency to 0.500005.
Mutation

- denoting the change in A2 in one generation as $\Delta q$,
  
  $\Delta q = u \times p$
  
  $= (1 \times 10^{-5})(0.5)$
  
  $= 0.000005$

- the A2 allele has increased in frequency to 0.500005.
- it would take another 140,000 generations to reach 0.875
Mutation

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$$\Delta q = u \times p$$

$$= (1 \times 10^{-5})(0.5)$$

$$= 0.000005$$

• the $A_2$ allele has increased in frequency to 0.500005.
• it would take another 140,000 generations to reach 0.875

Conclusion: The rate of change due to mutation pressure is extremely small!
Some comments on mutation

1. Mutation is the “raw material” that fuels all evolutionary change.
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2. Mutations occur randomly!
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1. Mutation is the “raw material” that fuels all evolutionary change.

2. Mutations occur randomly!

3. Mutations occur too infrequently to cause significant allele frequency change.

4. Most mutations are deleterious and experience “purifying selection”.

5. A small (but unknown) proportion of mutations are beneficial and lead to adaptation.
Migration (gene flow)
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- gene flow is simply the movement of genes among populations.
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- it can occur by the movement of gametes, or by the movement (and successful breeding) of individuals.
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• its magnitude is determined by m
Migration (gene flow)

- gene flow is simply the movement of genes among populations.

- it can occur by the movement of gametes, or by the movement (and successful breeding) of individuals.

- its magnitude is determined by $m$

  \[ m = \text{the proportion of genes entering a population in individuals (genes) immigrating from a different population.} \]
Sewall Wright’s Continent-Island model
A simple model of migration
A simple model of migration

• let $p_1 = \text{frequency of } A_1 \text{ allele on island}$
A simple model of migration

- let $p_I = \text{frequency of } A_1 \text{ allele on island}$
- let $p_C = \text{frequency of } A_1 \text{ allele on continent}$
A simple model of migration

• let $p_I = \text{frequency of } A_1 \text{ allele on island}$

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A simple model of migration

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• let $p'_I = \text{frequency of } A_1 \text{ allele on island in the next generation}$
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- let $p'_I = \text{frequency of } A_1 \text{ allele on island in the next generation}$

\[ p'_I = (1-m)p_I + m(p_C) \]
A simple model of migration

- let $p_I$ = frequency of $A_1$ allele on island
- let $p_C$ = frequency of $A_1$ allele on continent
- let $m$ = proportion of $A_1$ alleles moving to island each generation
- let $p'_I$ = frequency of $A_1$ allele on island in the next generation

$$p'_I = (1-m)p_I + m(p_C)$$

↑ "resident"  "immigrant"
A simple model of migration

- let $\Delta p_i = \text{change in frequency of } A_1 \text{ allele on island from one generation to the next}$
A simple model of migration

• let $\Delta p_I = \text{change in frequency of } A_1 \text{ allele on island from one generation to the next}$

$$\Delta p_I = p'_I - p_I$$
A simple model of migration

• let $\Delta p_I = \text{change in frequency of } A_1 \text{ allele on island from one generation to the next}$

$$\Delta p_I = p'_I - p_I$$

$$= (1-m)(p_I) + m(p_c) - p_I$$
A simple model of migration

• let $\Delta p_i = \text{change in frequency of } A_1 \text{ allele on island from one generation to the next}$

$$\Delta p_i = p'_i - p_i$$

$$= (1-m)(p_i) + m(p_c) - p_i$$

$$= m(p_c - p_i)$$
An example:
An example:

\[ p_c = 0.75 \]
An example:

\[ \text{let } p_c = 0.75 \]
\[ \text{let } p_l = 0.25 \]
An example:

let $p_c = 0.75$

let $p_l = 0.25$

let $m = 0.10$
An example:

let $p_I = 0.25$

let $p_c = 0.75$

let $m = 0.10$

let $p_l = 0.25$

let’s ignore back-migration
An example:

let $p_c = 0.75$

let $p_I = 0.25$

let $m = 0.10$

$\Delta p_I = m(p_c - p_I)$
An example:

let $p_c = 0.75$

let $m = 0.10$

let $p_l = 0.25$

$\Delta p_l = m(p_c - p_l)$

$= 0.10(0.75 - 0.25)$
An example:

\[ \Delta p_I = m(p_c - p_I) \]
\[ = 0.10(0.75 - 0.25) \]
\[ = 0.050 \]
Now:

\[ p_c = 0.75 \]

\[ p_I = 0.30 \]

let \( m = 0.10 \)

Figure 7-4 Evolutionary Analysis, 4/e
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Now:

\[ p_c = 0.75 \]

\[ p_I = 0.30 \]

let \( m = 0.10 \)

\[ \Delta p_I = m(p_c - p_I) \]

\[ = 0.10(0.75 - 0.30) \]

\[ = 0.045 \]
Conclusions
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1. Gene flow can cause rapid evolutionary change.
Conclusions

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2. The long-term outcome will be the elimination of genetic differences between populations!
Conclusions

1. Gene flow can cause rapid evolutionary change.

2. The long-term outcome will be the elimination of genetic differences between populations!

But… natural selection act to oppose gene flow
Example: Lake Erie water snakes (*Nerodia sipedon*)
Example: Lake Erie water snakes (*Nerodia sipedon*)
Example: Lake Erie water snakes (*Nerodia sipedon*)

![Bar charts showing distribution of water snakes in different regions.](Figure 7-7 Evolutionary Analysis, 4/e © 2007 Pearson Prentice Hall, Inc.)
Random genetic drift
Random genetic drift

Definition: random changes in the frequencies of neutral alleles from generation to generation caused by “accidents of sampling”
Random genetic drift

Definition: random changes in the frequencies of neutral alleles from generation to generation caused by “accidents of sampling”

Q: What is a neutral allele?
Random genetic drift

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Q: What is a neutral allele?
A: A neutral allele has no affect on fitness.
Random genetic drift

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Q: What is a neutral allele?
A: A neutral allele has no effect on fitness.

Q: How can alleles be neutral?
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1. Mutations among very similar amino acids
How can alleles be neutral?

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(leu) → (val)
CUC → GUC
How can alleles be neutral?

1. Mutations among very similar amino acids

(\text{leu}) \rightarrow (\text{val})

\text{CUC} \quad \rightarrow \quad \text{GUC}

2. Mutations involving silent (synonymous) changes
How can alleles be neutral?

1. Mutations among very similar amino acids

   (leu)  →  (val)
   CUC    GUC

2. Mutations involving silent (synonymous) changes

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How can alleles be neutral?

1. Mutations among very similar amino acids

   (leu) → (val)
   CUC       GUC

2. Mutations involving silent (synonymous) changes

   (leu) → (leu)
   CUC       CUU

3. Mutations in non-coding (nonfunctional) DNA
Codon bias shows that silent changes may not be neutral!
Random genetic drift

white = $p = 0.50$
red = $q = 0.50$

Sample 40,000,000 balls
Random genetic drift

white = $p = 0.50$
red = $q = 0.50$

\[ \downarrow \]

20,000,167 white
19,999,833 red
Random genetic drift

white = \( p = 0.50 \)
red = \( q = 0.50 \)

\[
\begin{align*}
\downarrow \\
20,000,167 \text{ white} \\
19,999,833 \text{ red}
\end{align*}
\]

now \( p = 0.5000042 \)
\( q = 0.4999958 \)
Random genetic drift

white = \( p = 0.50 \)
red = \( q = 0.50 \)

↓

Sample 200 balls
Random genetic drift

white = $p = 0.50$
red = $q = 0.50$

94 white
106 red
Random genetic drift

white = $p = 0.50$
red = $q = 0.50$

\[\downarrow\]

94 white
106 red

now $p = 0.470$
$q = 0.530$
Some properties of random genetic drift
Some properties of random genetic drift

1. Magnitude inversely proportional to effective population size ($N_e$).
Some properties of random genetic drift

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2. Ultimately results in loss of variation from natural populations.
Some properties of random genetic drift

1. Magnitude inversely proportional to effective population size \( (N_e) \).

2. Ultimately results in loss of variation from natural populations.

3. The probability of fixation of a neutral allele is equal to its frequency in the population.
Some properties of random genetic drift

1. Magnitude inversely proportional to effective population size ($N_e$).

2. Ultimately results in loss of variation from natural populations.

3. The probability of fixation of a neutral allele is equal to its frequency in the population.

4. Over time, random drift will cause isolated populations to diverge.
What is effective population size?
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• in any one generation, $N_e$ is roughly equivalent to the number of breeding individuals in the population.
What is effective population size?

• in any one generation, $N_e$ is roughly equivalent to the number of breeding individuals in the population.

• this is equivalent to a contemporary effective size.
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• effective population size is also strongly influenced the long-term history.
What is effective population size?

• in any one generation, $N_e$ is roughly equivalent to the number of breeding individuals in the population.

• this is equivalent to a contemporary effective size.

• effective population size is also strongly influenced the long-term history.

• this is equivalent to a species’ evolutionary effective size.
Factors affecting effective population size
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1. Fluctuations in population size
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- here, $N_e$ is equal to the harmonic mean of the actual population numbers:
Factors affecting effective population size

1. Fluctuations in population size

- here, $N_e$ is equal to the **harmonic mean** of the actual population numbers:

$$\frac{1}{N_e} = \frac{1}{t}(\frac{1}{N_1} + \frac{1}{N_2} + \frac{1}{N_3} + \ldots + \frac{1}{N_t})$$
Factors affecting effective population size

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- here, $N_e$ is equal to the **harmonic mean** of the actual population numbers:

\[
\frac{1}{N_e} = \frac{1}{t} \left( \frac{1}{N_1} + \frac{1}{N_2} + \frac{1}{N_3} + \ldots + \frac{1}{N_t} \right)
\]

**Example**: Over 3 generations, $N = 2000, 30, 2000$
Factors affecting effective population size

1. Fluctuations in population size

- here, $N_e$ is equal to the **harmonic mean** of the actual population numbers:

$$\frac{1}{N_e} = \frac{1}{t}(\frac{1}{N_1} + \frac{1}{N_2} + \frac{1}{N_3} + \ldots + \frac{1}{N_t})$$

Example: Over 3 generations, $N = 2000, 30, 2000$

Arithmetic mean = 1343.3
Factors affecting effective population size

1. Fluctuations in population size

- here, \( N_e \) is equal to the harmonic mean of the actual population numbers:

\[
\frac{1}{N_e} = \frac{1}{t} \left( \frac{1}{N_1} + \frac{1}{N_2} + \frac{1}{N_3} + \ldots + \frac{1}{N_t} \right)
\]

**Example**: Over 3 generations, \( N = 2000, 30, 2000 \)

- Arithmetic mean = 1343.3
- Harmonic mean = 87.4
Factors affecting effective population size

2. Unequal numbers of males and females
Factors affecting effective population size

2. Unequal numbers of males and females

• let $N_m = \text{No. of males}$, $N_f = \text{No. of females}$:
Factors affecting effective population size

2. Unequal numbers of males and females

- let $N_m = \text{No. of males}$, $N_f = \text{No. of females}$:

$$N_e = \frac{4N_m N_f}{N_m + \bar{N}_f}$$
Factors affecting effective population size

2. Unequal numbers of males and females

• let $N_m =$ No. of males, $N_f =$ No. of females:

$$N_e = \frac{4N_mN_f}{N_m + N_f}$$

Example: Breeding populations of northern elephant seals:
Factors affecting effective population size

2. Unequal numbers of males and females

• let $N_m =$ No. of males, $N_f =$ No. of females:

$$N_e = \frac{4N_mN_f}{N_m + N_f}$$

Example: Breeding populations of northern elephant seals:

• 15 alpha males each controlling a harem of 20 females:
Factors affecting effective population size

2. Unequal numbers of males and females

- let \( N_m = \) No. of males, \( N_f = \) No. of females:

\[
N_e = \frac{4N_mN_f}{N_m + N_f}
\]

Example: Breeding populations of northern elephant seals:

- 15 alpha males each controlling a harem of 20 females:

  census size (N) = 315
Factors affecting effective population size

2. Unequal numbers of males and females

• let $N_m = \text{No. of males}, N_f = \text{No. of females}$:

$$N_e = \frac{4N_mN_f}{N_m + N_f}$$

Example: Breeding populations of northern elephant seals:

• 15 alpha males each controlling a harem of 20 females:

  census size ($N$) = 315
  effective size ($N_e$) = 57.1
Genetic Bottlenecks

• genetic bottlenecks refer to severe reductions in effective population size.
Genetic Bottlenecks

- genetic bottlenecks refer to severe reductions in effective population size.

**Examples:** the cheetah (*Acinonyx jubatus*) and the northern elephant seal (*Mirounga angustirostris*).