Measuring natural selection in populations
Recall...

Evolution by natural selection will happen if these are true:

1. There is variation in natural populations
2. The variation is heritable
3. More offspring are produced than will survive each generation, because there is a struggle for existence

→ Natural selection tries to maximize the fitness of a population (making the average individual really good at surviving and making babies)
How do populations of organisms evolve?

- A **population** is a group of organisms of the same species that live in a particular geographic area at the same time and interbreed.
- We can ask:
  - What causes natural selection to act?
  - Which traits are favored in a population?
  - What mode of natural selection is acting?
  - How strong is selection in a population?
  - What is the *average fitness* of a population?
  - What other evolutionary forces affect the population?
  - Is a trait in a population evolving?
What causes natural selection to act?

- Natural selection is the process by which organisms adapt to their environment.

How would natural selection act on a brown bear in the forest? A brown bear in the Arctic? Vice versa?
The origin and future of polar bears

- They evolved ~150,000 years ago from a brown bear ancestor
- Polar bears are specialized (highly adapted!) to their environment:
  - Hunt for seals with the "sit and wait" approach
  - They have not evolved to be efficient at walking long distances to hunt
- ...What now?
Modes of natural selection
Modes of selection: Formal definitions

- **Directional selection**
  - Individuals at one trait extreme are favored

- **Balancing selection**
  - Individuals with an intermediate trait value are favored
  - AKA stabilizing selection

- **Disruptive selection**
  - Individuals at both extremes are favored, i.e. selection against the mean
Continuous vs. discrete variation

Natural selection affects different types of traits differently, so we study them differently.

![Graph showing continuous variation](image1)

![Moth example](image2)
Modes of natural selection on continuous quantitative traits

Population before natural selection

Assume quantitative X-axis (mice shown for visual only)

Directional Selection

Disruptive Selection

Balancing Selection

Natural selection begins to act (why?)

Does variation remain in the populations?
Modes of natural selection on discrete traits (like alleles!)

Consider a population where a gene has two alleles, "A" and "a". At the beginning, all is equal: \( \frac{1}{3} \) are AA \( \frac{1}{3} \) are Aa \( \frac{1}{3} \) are aa

Table discussion: What happens to the frequency of genotypes after many generations experiencing...

- Directional selection?
- Balancing selection?
- Disruptive selection?
Modes of natural selection on discrete traits

- **Directional selection?**
  - Selection will make "AA" the most common genotype (or aa)
  - Eventually, all individuals will be homozygous

- **Balancing selection?**
  - Selection will make "Aa" the most common genotype

- **Disruptive selection?**
  - Selection will make "AA" and "aa" the most common, with very few "Aa"

Does variation remain in the populations?
Example: Directional selection

- DDT resistance in mosquitoes
  - RR = resistant genotype
    - mosquitoes survive DDT
  - R+ and ++ = susceptible genotypes
    - DDT kills mosquitoes
  - Which genotype is better for mosquito fitness?

Before (early stages of) selection pressure

After selection pressure is removed

Why the change?
Example: Disruptive selection
Example: Disruptive selection (could be viewed as directional too!)

Desert environment

Lava pit environment

Close match between phenotype and environment

https://www.ncbi.nlm.nih.gov/pmc/articles/PMC154334/
Example: Balancing selection

- Sickle cell anemia is a recessive genetic disorder caused by $S$ allele ($A$ is the “wild type”)
  - $SS = \text{sickle cell}$
  - $SA, AA = \text{healthy (but what is SA?)}$
- $SS$ is up to 20% in certain regions...?????
Quantifying selection in populations
How strong is natural selection in a population?

- We measure fitness using survival or fecundity.

Scenario:

There are 1,000 dragonflies in a population. Some dragonflies are blue and some are red. On average, birds eat 50% of blue dragonflies and 25% of red dragonflies.

→ 50% of blue survive. 75% of red survive.
We quantify selection using *relative fitness* and *selection coefficients*. 75% of red survive. 50% of blue survive.

<table>
<thead>
<tr>
<th></th>
<th>Red morph</th>
<th>Blue morph</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Absolute Fitness</td>
<td>0.75</td>
<td>0.50</td>
<td>The actual measurements</td>
</tr>
<tr>
<td>Relative fitness, (w) (normalized survivorship)</td>
<td>(0.75 / 0.75 = 1.0)</td>
<td>(0.5 / 0.75 = 0.67)</td>
<td>Divide by the largest value *in the population*</td>
</tr>
<tr>
<td>(s = 1 - w)</td>
<td>1 - 1 = 0</td>
<td>1 - 0.67 = 0.33</td>
<td>(s = 1 - w)</td>
</tr>
</tbody>
</table>

Survival of these two phenotypes, *relative to each other*. For every 10 surviving red dragonflies, we expect ~6.7 blue dragonflies will survive.

The strength of selection acting *against* the trait.

\(S = 0 \rightarrow relatively, \) no selection against the trait (most fit phenotype)

\(S = 1 \rightarrow complete \) selection against the trait (no survivors)
Imagine a population with 1 blue morph and 1 red morph. What is the mean fitness of the population?

\[
\frac{1.0 + 0.67}{2} = 0.833
\]

Imagine a population with 2 red morphs and 1 blue morph (so \(N=3\)). What is the mean fitness of the population?

\[
\frac{1.0 + 1.0 + 0.67}{3} = 0.89
\]
Mean fitness of populations

\[ \bar{w} = \sum_{i}^{N} F_i w_i \]

- \( N \) = total number of phenotype
- \( i \) = each phenotype (genotype)
- \( F \) = frequency of phenotype
- \( w \) = fitness of phenotype

Population with 2 red morphs and 1 blue morph. Fitness?

\[
(1.0 + 1.0 + 0.67) / 3 = 0.89
\]

Over time, natural selection will act to increase the POPULATION fitness.
A classic example: peppered moths (*Biston betularia*)

- Melanic form was first seen in 1848
  - Frequency of 1-10% in industrial areas by 1890
  - Frequency >99% in Manchester by 1948.
  - Typical form remained common in rural areas

- Kettlewell asked, “Does color affect survival?”
Kettlewell’s capture/recapture results (1955)

<table>
<thead>
<tr>
<th>Polluted Area</th>
<th>White</th>
<th>Black</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number released</td>
<td>137</td>
<td>447</td>
</tr>
<tr>
<td>Number recaptured</td>
<td>18</td>
<td>123</td>
</tr>
<tr>
<td>Percent recaptured</td>
<td>13.1%</td>
<td>27.5%</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Unpolluted Area</th>
<th>White</th>
<th>Black</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number released</td>
<td>393</td>
<td>406</td>
</tr>
<tr>
<td>Number recaptured</td>
<td>54</td>
<td>19</td>
</tr>
<tr>
<td>Percent recaptured</td>
<td>13.7%</td>
<td>4.7%</td>
</tr>
</tbody>
</table>

These survival measurements represent "ABSOLUTE FITNESS"