Natural selection...

a difference, on average, in the survival or fecundity of individuals with certain phenotypes compared to individuals with alternative phenotypes

Four tenets of natural selection...

(1) Individuals within populations are variable
(2) Variation is heritable
(3) Organisms differ in their ability to survive and reproduce
(4) Survival & reproduction are non-random
Divergent Induced Responses to an Invasive Predator in Marine Mussel Populations

Mytilus edulis, Blue mussel

Respond to presence of predators by thickening shells – defense response is inducible –

Hemigrapsus sanguineus
Asian shore crab

Carcinus maenas
European green crab
Anolis sagrei typically terrestrial
(longer legs ~ faster escape from predators)

Invasion by Leiocephalus carinatus causes
Anolis sagrei to be arboreal

...predicted that leg length would DECREASE in arboreal populations of Anolis sagrei lizards following invasion by Leiocephalus carinatus
Rapid Temporal Reversal in Predator-Driven Natural Selection

Jonathan B. Losos,† Thomas W. Schoener, R. Brian Langerhans, David A. Spiller

All Anolis sagrei individuals tagged / measured
Leiocephalus carinatus were introduced on 6 islands
Censused after 6 (and 12) months to record survival

Six INTRODUCTION islands

Six CONTROL islands

CONTROL
INTRODUCED

Longer legs
Shorter legs
Components of natural selection

Gamete recognition systems

Probability of survival before and during the reproductive period

1. Viability selection

Segregation distortion

2. Sexual selection

Mating success

3. Fecundity selection

Average number viable offspring

4. Gametic selection

5. Compatibility selection

ZYGOTES

PARENTS

GAMETES

ADULTS

Females

Males
Natural selection is an average difference in the survival or fecundity of individuals with certain phenotypes.

**Demonstrating adaptation**

What is a trait for? Do individuals that possess the trait contribute more offspring to future generations? How does a trait develop? Who has it?

**Adaptation**

Any heritable trait (structure, physiological ability, behavior) that makes an organism better able to survive & reproduce.

The *evolutionary process* leading to the persistence of such a trait in populations.
Natural selection is the differential contribution of offspring to the next generation by certain genotypes.

Demonstrating adaptation

What is a trait for? Do individuals that possess the trait contribute more offspring to future generations? How does a trait develop? Who has it?

Adaptation

Any heritable trait (structure, physiological ability, behavior) that makes an organism better able to survive & reproduce.

The evolutionary process leading to the persistence of such a trait in populations.
NATURAL SELECTION ALONG AN ENVIRONMENTAL GRADIENT: A CLASSIC CLINE IN MOUSE PIGMENTATION

Lynne M. Mullen\textsuperscript{1,2} and Hopi E. Hoekstra\textsuperscript{1,3}

Evolution 62-7: 1555–1570
The genetic basis of adaptive melanism in pocket mice

Michael W. Nachman*, Hopi E. Hoekstra, and Susan L. D’Agostino

5268–5273 | PNAS | April 29, 2003 | vol. 100 | no. 9

(Upper) Collecting localities, substrate color, and mouse color. Sample sizes at each site are given.

Pie charts are the proportion of light and dark mice at each site. Rectangles indicate substrate color.

(Lower) Light and dark C. intermedius from the Pinacate locality on light and dark rocks.
The genetic basis of adaptive melanism in pocket mice

Michael W. Nachman*, Hopi E. Hoekstra, and Susan L. D’Agostino

5268–5273  |  PNAS  |  April 29, 2003  |  vol. 100  |  no. 9

Coat color variation well studied in mammals

Association studies using markers in candidate pigmentation genes (Agouti & Mc1r)

Genotype-phenotype association between Mcr1 alleles & coat color in animals from Pinacate.
The Genetic Basis of Phenotypic Convergence in Beach Mice: Similar Pigment Patterns but Different Genes

Cynthia C. Steiner,* Holger Römler,†‡,†+1 Linda M. Boettger,* Torsten Schöneberg,† and Hopi E. Hoekstra‡

Biochemical studies indicate a different molecular mechanisms for the derived mutations (Rosenblum et al. PNAS 2010)

- Integration of receptor into membrane
- Receptor signaling

Derived amino acid replacements (1 in each species) are statistically associated with blanched coloration (Rosenblum et al. Evolution 2004)

Implications for convergence...
Derived amino acid replacements (1 in each species) are statistically associated with blanched coloration (Rosenblum et al. Evolution 2004)
How the Horned Lizard Got Its Horns

Kevin V. Young,1 Edmund D. Brodie Jr.,1 Edmund D. Brodie III2*

www.sciencemag.org SCIENCE VOL 304 2 APRIL 2004
Evolution of shorter horns (decrease)

Evolution of longer horns (increase)

Medium-sized horns in the MRCA
A pre-adaptation is an existing feature that serves a novel function.
Figure 13.4 There are two main groups of bony fish: the Actinopterygians (which include nearly all modern fish) and the Sarcopterygians (from which humans, and all other tetrapods) evolved. Cartilaginous fish are a related group. Modified from Strickberger (1990). Reprinted by permission of the publisher.
The **fitness** of a genotype is the average lifetime contribution of individuals of that genotype to future generations

(1) probability of survival to reproductive age
(2) average number of offspring produced

Probability and average refer to **groups of organisms**, thus fitness is usually defined for a set of individuals (e.g., members of a particular genotype)

---

**Absolute fitness**

Lifetime total fitness (= total number of offspring)

**Relative fitness**

Degree to which individuals with a particular genotype fare compared to other genotypes in the population
GENETIC ESTIMATES OF ANNUAL AND LIFETIME REPRODUCTIVE SUCCESS IN MALE RED-WINGED BLACKBIRDS

PATRICK J. WEATHERHEAD AND PETER T. BOAG

Fig. 1. True annual reproductive success (no. fledglings sired) relative to apparent annual reproductive success (no. young fledged from territory) for male Red-winged Blackbirds for all six years.

Fig. 5. True lifetime reproductive success (no. fledglings sired) relative to apparent lifetime reproductive success (no. young fledged from territory) for males.
Generalized notation...

<table>
<thead>
<tr>
<th>Absolute $\bar{w}$</th>
<th>Relative $\bar{w}$</th>
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<tbody>
<tr>
<td>$AA = 10$</td>
<td>$10/10 = 1.0$</td>
</tr>
<tr>
<td>$Aa = 8$</td>
<td>$8/10 = 0.8$</td>
</tr>
<tr>
<td>$aa = 8$</td>
<td>$8/10 = 0.8$</td>
</tr>
</tbody>
</table>

1  1  1−s  1−hs  1

Modeling natural selection...

Allele frequencies among gametes

Genotype frequencies among zygotes

$$\bar{w}_{pop} = p^2\bar{w}_{AA} + 2pq\bar{w}_{Aa} + q^2\bar{w}_{aa}$$

Genotype frequencies among surviving adults

$$AA = \frac{p^2\bar{w}_{AA}}{\bar{w}_{pop}}$$
$$Aa = \frac{2pq\bar{w}_{Aa}}{\bar{w}_{pop}}$$
$$aa = \frac{q^2\bar{w}_{aa}}{\bar{w}_{pop}}$$

Allele frequencies among mating adults

Genotype frequencies among offspring

See also F&H, box 6.3
Patterns of natural selection

Strength of selection (selection coefficients)

Allele frequencies

Dominance relationships

Heterozygotes & Homozygotes

Frequency dependence (positive & negative)

*Interactions with other evolutionary forces (coming up…)*
Strength of selection – selection coefficients

Time to fixation

\[
s = 0.2
\]

\[
s = 0.02
\]

<table>
<thead>
<tr>
<th>Selection scheme</th>
<th>Percent surviving</th>
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<tbody>
<tr>
<td>( B_1B_1 )</td>
<td>100</td>
</tr>
<tr>
<td>( B_1B_2 )</td>
<td>90.0</td>
</tr>
<tr>
<td>( B_2B_2 )</td>
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</table>

\[
s = 0.2
\]

\[
s = 0.02
\]
Antibiotic Selection Pressure and Resistance in *Streptococcus pneumoniae* and *Streptococcus pyogenes*

Werner C. Albrich,* Dominique L. Monnet,† and Stephan Harbarth‡

Figure 1. Total antibiotic use in the outpatient setting (vertical axis) versus prevalence of penicillin-nonsusceptible *Streptococcus pneumoniae* (horizontal axis) in 20 industrialized countries. A regression line was fitted with 95% confidence bands ($r = 0.75$, $p < 0.001$).

Figure 2. A. Relationship between macrolide use in the outpatient setting (horizontal axis) and prevalence of macrolide-resistant *Streptococcus pneumoniae* (vertical axis) in 16 industrialized countries. A regression line was fitted with 95% confidence bands ($r = 0.88$; $p < 0.001$). B. Relationship between macrolide use in the outpatient setting (horizontal axis) and prevalence of macrolide-resistant *S. pyogenes* (vertical axis) in 14 industrialized countries. A regression line was fitted with 95% confidence bands ($r = 0.71$; $p = 0.004$).
Dominance relationships interact with allele frequencies

An adaptive landscape graphs the mean fitness of a population as a function of allele frequency

- where is a population is heading -
Allele A is eventually lost (and allele a fixed) in the population.

Once the frequency of A declines and is intermediate in frequency, selection is rapid against the dominant A allele.

A allele is very common (0.99).

Most individuals are AA, so the A allele is maintained initially.

Once the frequency of A declines and is intermediate in frequency, selection is rapid against the dominant A allele.

Allele A is eventually lost (and allele a fixed) in the population.

An adaptive landscape graphs the mean fitness of a population as a function of allele frequency – where is a population is heading –
Fig. 3. Dominance relationships of \( M c 1 r \) alleles. Dorsal coloration (mean and standard deviation for area under the spectral curve) for \( M c 1 r \) genotypes showing the derived allele is dominant in \( S. \text{ undulatus} \) and recessive in \( A. \text{ inornata} \). \( n \), number of alleles sampled; "light" and "dark" refer to statistically distinguishable groups.

Fig. 4. Spatial distribution of \( M c 1 r \) alleles in the wild for \( S. \text{ undulatus} \) (derived \( M c 1 r \) allele dominant) and \( A. \text{ inornata} \) (derived \( M c 1 r \) allele recessive). Proportion of wild-type (black) and derived (white) alleles across dark soil, ecotone, and white sand habitat. \( n \), number of alleles sampled.
Selection for heterozygotes

Heterozygote advantage • Overdominance

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<tbody>
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<td>$Aa$</td>
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</tr>
<tr>
<td>$aa$</td>
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</table>

<table>
<thead>
<tr>
<th></th>
<th>$\hat{p}$</th>
<th>$p$</th>
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<td>1-s</td>
</tr>
<tr>
<td>$Bb$</td>
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<td>1</td>
</tr>
<tr>
<td>$bb$</td>
<td>0.8</td>
<td>1-t</td>
</tr>
</tbody>
</table>

$s = t = 0.2$

Equilibrium frequency of $p$ given by...

$$\hat{p} = \frac{t}{s + t}$$
Selection against heterozygotes
Heterozygote inferiority • Underdominance

\[ \bar{W} \]

<table>
<thead>
<tr>
<th>Allele</th>
<th>Mean Fitness</th>
<th>Selection Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>AA</td>
<td>1.4</td>
<td>1-s</td>
</tr>
<tr>
<td>Aa</td>
<td>1.0</td>
<td>1</td>
</tr>
<tr>
<td>aa</td>
<td>1.6</td>
<td>1-t</td>
</tr>
</tbody>
</table>

Equilibrium frequency of \( p \) given by...

\[ \hat{p} = \frac{t}{s + t} \]
Equilibrium

Mean fitness vs. p

Δp as a function of p

Red: $s = 0.4; t = 0.6$

Blue: $s = -0.4; t = -0.6$
Selection for heterozygotes

Sickle cell anemia

- Normal RBC (A)
- Sickled RBC (S)

Malaria (Plasmodium falciparum)

- Vector-borne infectious disease caused by protozoan parasite
- Complex life cycle: reproduces inside human RBCs
- Critical public health concern

Genotypes:

- Normal: A/A (Susceptible to malaria)
- Slightly afflicted by SCA: A/S (Slightly protected from malaria)
- Afflicted by SCA: S/S (Protected from malaria)
Ward Watt, *Colias* butterflies

Phosphoglucose isomerase (PGI) plays a key role in allocating carbohydrates among biochemical pathways.

Butterflies are ectothermic & fly only when body temperature is high.

Selection should favor PGI variants with high catalytic efficiency (i.e., those that enable butterflies to metabolize glucose efficiently & allow them to fly quickly).

**Allozymes differ in their functional properties & are correlated with the prevalence of genotypes in different environments.**

**Do the allozyme alleles affect the fitness of *Colias* butterflies?**

Colias meadii (high elevation sp.)
- alleles 2, 3 common

2/2 & 2/3 relatively high activity @ low temps., but lose activity @ high temps.

heterozygous genotypes (esp. 3/4) had high efficiencies

Colias philodice, C. eurytheme (lower elevations)
- alleles 3, 4 common

Tested enzyme activity of genotypes @ various temperatures (10–50°C)
Allozymes differ in their functional properties & are correlated with the prevalence of genotypes in different environments.

Do the allozyme alleles affect the fitness of Colias butterflies?

Given biochemistry, 3/4 genotypes should...

1. fly more frequently
2. fly a greater span of the day

Captured flying females, let them have babies & genotyped all offspring

3/4 males made up 44% of population, but accounted for 69% of all matings
Frequency dependent selection

When the fitness values (of genotypes) varies depending on the FREQUENCY of the genotype in a population

- **Positive frequency dependence**
  
  the MORE COMMON a genotype in a population, the GREATER its fitness

- **Negative frequency dependence**
  
  the RARER a genotype in a population, the GREATER its fitness
Positive frequency dependence

**Heliconius erato**

Unpalatable species with many distinctive geographic varieties, each variety is monomorphic

Adjacent varieties breed in zones only a few kilometers wide

**Mallet & Barton (1989)** suggested that gene flow between races is countered by positive frequency dependence

Mark & recapture

Predators learn to avoid butterflies of the most COMMON pattern, but attack (eat?) butterflies of UNCOMMON patterns they do not recognize
Negative frequency dependence

Four tenets of natural selection...

1. Individuals within populations are variable
2. Variation is heritable
3. Organisms differ in their ability to survive and reproduce
4. Survival & reproduction are non-random
**Dactylorhiza sambucina**

Pollinated by bumblebees, but flowers are *rewardless*

Orchids make pollinia (making pollen unavailable) & there is no nectar

– *pollination by deceit* –

What does such movement mean for the number of times each type (color) is visited?

On average, which morph will receive more visits?

How will such visitation affect fitness?
Multiple niches & polymorphism

Contrasting selection can maintain genetic diversity

Figure 83.24: Multiple-niche polymorphism in the black-bellied seedcracker. (A) Probability of survival to adulthood of juvenile birds in relation to their lower mandible width, a measure of bill size. These curves are based on the data in (B), which shows the number of banded juveniles that survived (solid bars) and that did not survive (open bars). The distribution of lower mandible width among adults (C) is bimodal. The peak centered at 12.8 mm corresponds to recessive homozygotes, the other peak to heterozygotes and dominant homozygotes. (After Smith 1993.)