

Lecture Outline

1. Basics of Natural Selection
2. How to test for the key components of natural selection
 - a. Variation
 - b. Heritability
 - c. Can the trait respond to selection?
 - d. What are the selective forces?

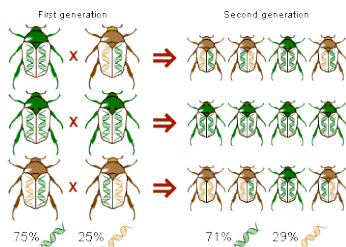
Darwin's Theory of Natural Selection

1. **Variation:** Individuals within a species differ in their characteristics (behavior, etc).
2. **Heritability:** Some characteristics can be passed from parents to offspring.
3. **Differential reproduction/fitness:** Some characteristics cause their bearers to reproduce more than others.
4. **The result:** Organisms become adapted to their environment. Adapted = better able to find food, attract mates, escape from predators, etc.

Modern Theory of Natural Selection

1. **Variation:** Genes can differ in DNA sequence (alleles). Alleles can code for different proteins.
2. **Heritability:** Genetic information (DNA) can be passed from parents to offspring.
3. **Differential reproduction:** Some alleles are spread more in a population, because the characters they code for are selectively advantageous.
 - a. Selection on genes is mediated by phenotypes.
4. **Definition of Evolution by natural selection:** Changes in the frequencies of alleles in a population due to differential survivorship and/or reproduction of their phenotypes.

Changes in frequencies of alleles



1. **Natural selection** = Non-random changes in allele frequencies.
2. **Genetic drift** = Random changes in allele frequencies.

Natural Selection on Crickets

1. Marlene Zuk and her colleagues (1991-2003) on Kauai.
2. The fly, *Ormia ochracea*, invaded Hawaii from North America.
3. One study observed 30% of crickets invested with flesh-eating parasitoid maggots, offspring of the fly.

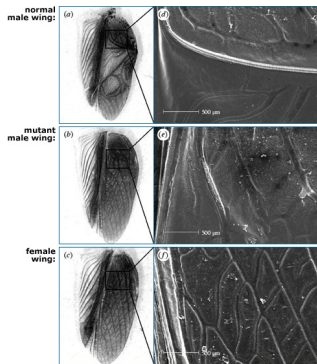


Natural Selection on Crickets

4. The flies follow the chirps of a calling cricket and deposit eggs on them.
5. By 2001 the island was virtually silent. Only heard 1 calling cricket!
6. The evolution of silent crickets only took about 20 cricket generations!



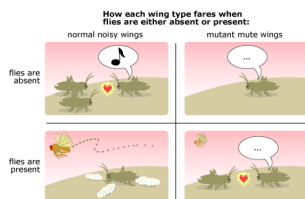
Natural Selection on Wings



http://evolution.berkeley.edu/evolibrary/news/061201_quietcrickets

Natural Selection on Crickets

7. Remaining calling males attract females. Non-calling males stay near callers to get females.
8. Ancestral females were tested for mate preferences: Some would mate with non-calling males.
9. What traits are naturally selected depends on the environment.



Facts about Natural Selection

1. Natural selection acts on individuals, but its consequences occur in populations (e.g. mean phenotype of the population changes).
2. Natural selection acts on phenotypes, but evolution consists of changes in allele frequencies.
3. Evolution is not forward looking. Adaptation is based on past selection, not future conditions.
4. Natural selection is nonrandom; it increases adaptation to the environment. Mutations (variation) is randomly generated.
5. Selection acts on individuals, not for the good of the species.

Testing Natural Selection

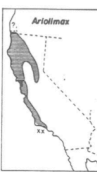
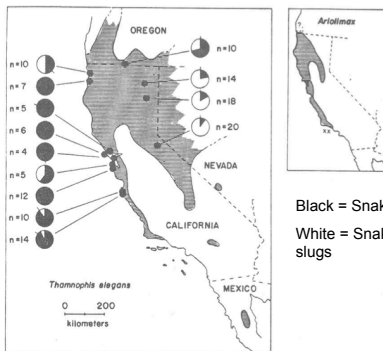
Observe variation within/among populations

Variation in Feeding Behavior



Geographic Variation in Garter snakes eating Banana Slugs

Data from Wild Caught Adult snakes, Steven Arnold 1981



Black = Snakes Eat Slugs
White = Snakes do not eat slugs

Test for slug feeding in newborn snakes

Arnold, S.J., 1981. The microevolution of feeding behavior

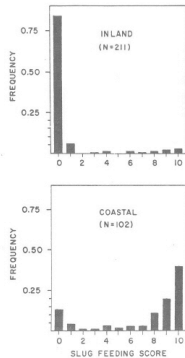


Figure 19-5. Frequency distributions of slug feeding scores in an inland and a coastal sample of naive, newborn snakes.

Eliminates possibility of slug preference in adults due to learning.

Testing Natural Selection

Observe variation within/among populations

Can it be acted upon by natural selection?

Test if the trait is heritable.

Genetic Basis of Behavior

1. There is a range in how genetically determined traits are.

100% Environmental ←-----→ 100% Genetic

2. **Heritability**: estimates the proportion of phenotypic variation in a population attributable to genetic variation among individuals.

3. Phenotype (P) = Genotype (G) + Environment (E).

4. Broad sense heritability = $\frac{V_G}{V_P} = \frac{\text{Variance (G)}}{\text{Variance (G) + Variance (E)}}$

Heritability

1. Narrow-sense heritability (h^2) = proportion of all phenotypic variation that is due to additive effects of genes.

2. Natural selection acts on the additive genetic variation.

3. h^2 affects how quickly a trait can evolve in response to natural selection.

$$h^2 = \frac{V_A}{V_P}$$

100% Environmental ←-----→ 100% Genetic
 $h^2 = 0$ $h^2 = 1$

Broad vs. Narrow Sense Heritability

Broad sense heritability = $\frac{V_G}{V_P}$

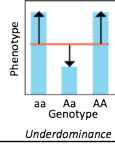
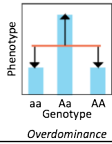
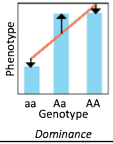
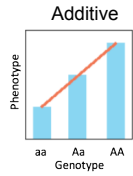
Narrow sense heritability $h^2 = \frac{V_A}{V_P}$

$Var(G) = V_A + V_D + V_I$

V_A = additive genetic variance

V_D = dominance genetic variance

V_I = epistatic genetic variance



Estimating heritability

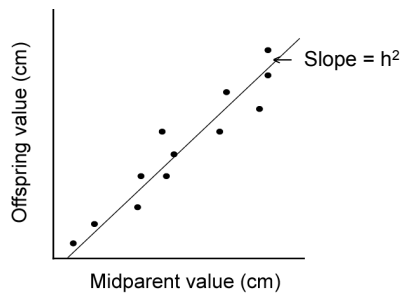
- compare phenotypic scores of **parents** and their **offspring**:

Cross Midparent value Offspring value

$F_1 \times M_1$	4.34	4.73
$F_2 \times M_2$	5.56	5.31
$F_3 \times M_3$	3.88	4.02

Three matings

Regress offspring value on midparent value



- Slope = 0, Parents do not predict offspring. $h^2 = 0$
- Slope = 1, Parents perfectly predict offspring. $h^2 = 1$

Heritability estimates from other regression analyses

Comparison	Slope
Midparent-offspring	h^2
Parent-offspring	$1/2h^2$
Half-sibs	$1/4h^2$
First cousins	$1/8h^2$

***as the groups become less related, the precision of the h^2 estimate is reduced.

Heritability of IQ

1. Devlin et. al analyzed 212 IQ studies based on 50,470 distinct pairings of relationships (i.e. Familial correlations for IQ scores).

From Devlin et al., The heritability of IQ

Relationship	Raised	Predicted	Weighted average
		correlation	correlation
Monozygotic twins	Together	1.0	0.85 Share genes, womb, rearing env.
Monozygotic twins	Apart	1.0	0.74 Share genes, womb
Dizygotic twins	Together	0.5	0.59 In womb and reared at same time
Siblings	Together	0.5	0.46 In womb and reared at different times
Siblings	Apart	0.5	0.24 Different rearing environment
Midparent/child	Together	1.0	0.5 Rearing environment may be different or culturally transmitted
Single-parent/child	Together	0.5	0.41 Single parent estimate less reliable
Single-parent/child	Apart	0.5	0.24 Eliminates a household env. effect
Adopting parent/child	Together	0	0.2 No genes shared, all environmental

Heritability of IQ

1. Broad-sense heritability = 48%
Narrow-sense heritability = 34%
2. 20% of twin and 5% of sibling covariance may be attributable to maternal effects.
3. IQ can be affected by prenatal (maternal) environment
Substantial brain growth in utero
IQ is positively correlated with birth weight
Alcohol, drug and cigarette consumption may lower IQ

Lessons from the Heritability of IQ

1. Both genes and environment play large roles.
2. Heritability estimates are dependent on the environment they were measured in. More env. variation = lower heritability.
3. There is error associated with the estimates.
4. Maternal effects may confound estimates of heritability.
Normally variation due to maternal effects is assigned to genes.

Testing Natural Selection

1. Observe variation in/among populations
2. Can it be acted upon by natural selection?
Test if the trait is heritable.
3. **Can the trait respond to selection?**
Test: Do an artificial selection experiment.

Can Use Artificial Selection Experiment to Estimate Heritability

Breeder's Equation = $R = h^2S$

S = selection differential
R = response to selection

\bar{x}_0 = mean value of trait in original population

\bar{x}_1 = mean of selected population after selection event passes

$\bar{x}_{\text{offspring}}$ = mean value in offspring of selected individuals

$S = \bar{x}_1 - \bar{x}_0$

$R = \bar{x}_{\text{offspring}} - \bar{x}_0$

$h^2 = R/S$

Example of an artificial selection experiment

$R = h^2S$

$S = \bar{x}_1 - \bar{x}_0$

$x_0 = 5$

$x_1 = 7$

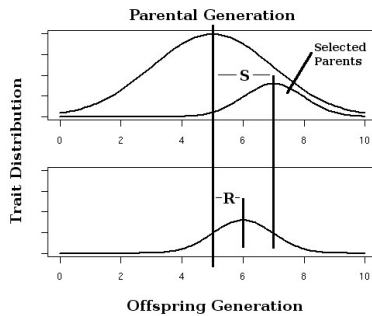
$x_{\text{offspring}} = 6$

$R = h^2S$

$(6-5) = h^2(7-5)$

$1 = h^2(2)$

$h^2 = 0.5$



Artificial Selection on Nesting in Mice

1. Carol Lynch, 1980.
2. Selected mice for high and low amounts of nest-building behavior.
3. Nesting scores = total weight of cotton pulled through the cage in four days of testing.
4. After 15 generations there was an 8 fold difference between the high and low lines.

Artificial Selection on Nesting Behavior in Mice

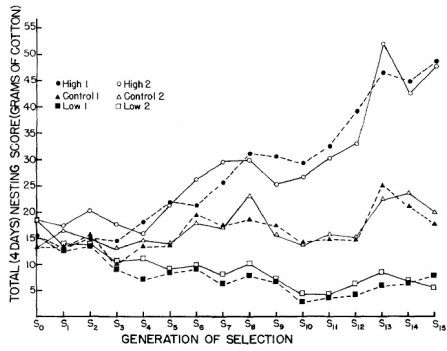


FIGURE 1.—Mean nesting scores across generations of selection for mice from the high, low and control lines of two replicate experiments.

Data from Carol Lynch, 1980

Lesson's from Lynch's experiment

1. Nesting behavior responded to selection in the lab. Predicted to respond to natural selection in the wild.
2. Response to selection may decrease over time.
 - a. Additive genetic variation gets used up. Selection has less to work with.
 - b. Could be tradeoffs of selection. Need a minimum amount of nesting material for offspring survival.
3. Average estimated heritability of high lines = .15
of low lines = .23

Testing Natural Selection

1. Observe variation in/among populations
2. Can it be acted upon by natural selection?
Test if the trait is heritable.
3. Can the trait respond to selection?
Test: Do an artificial selection experiment.
4. **What are the selective forces in nature?**
Test: observe who survives and reproduces. Determine the mode of selection.

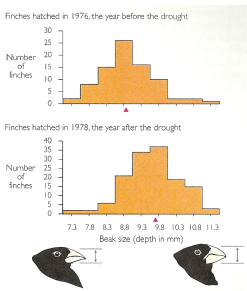
Directional Selection

1. Favors individuals at one end of a distribution of variation.
2. Changes the average value of the trait in the population.
3. Example: Directional selection for lots of nesting occurred in the high line of mice in Lynch's experiment.



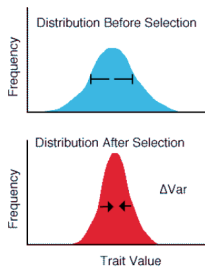
Directional Selection

Example: Selection in Darwin's finches during drought conditions.



Stabilizing Selection

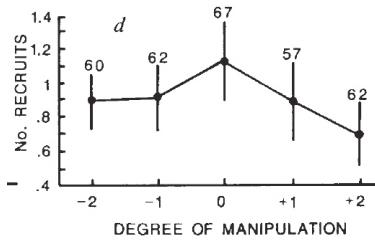
1. Favors individuals with intermediate values of a trait.
2. Does not alter the average value of the trait in the population.
3. Reduces variation at the tails of the distribution.



Stabilizing Selection

Example: Clutch size of the collared flycatcher

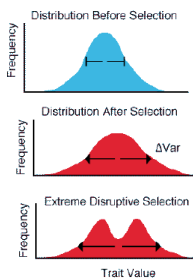
- a. Gustaffson and Sutherland (1988)
- b. Manipulated clutch size: added and subtracted eggs.



Best clutch size was no manipulation!

Disruptive Selection

1. Favors individuals at both extremes of a trait's distribution.
2. Does not alter the average value of the trait in the population.
3. Reduces variation at the middle of the distribution.



Disruptive Selection

Example: Black-bellied seed cracker (Smith, 1993)

- a. Birds have distinct beak sizes: large and small
- b. They specialize on different sized seeds.

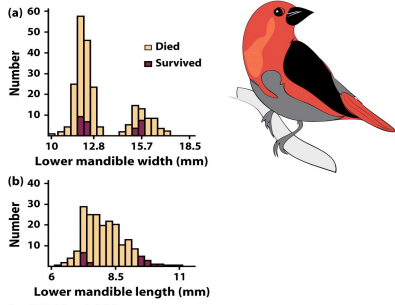
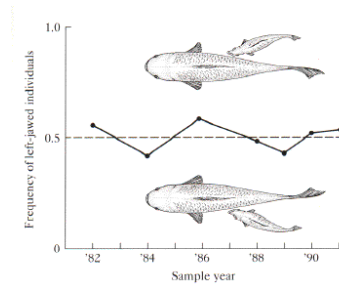


Figure 9.27 Evolutionary Analysis, 4/e
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Frequency Dependent Selection

1. When the relative fitnesses of genotypes are not constant but vary with their frequencies in the population.
2. Is a type of balancing selection; it maintains variation in the population.
3. Example: Handedness in scale-eating fish *Perissodus microlepis* (From Hori (1993) Science)

Frequency-dependent selection



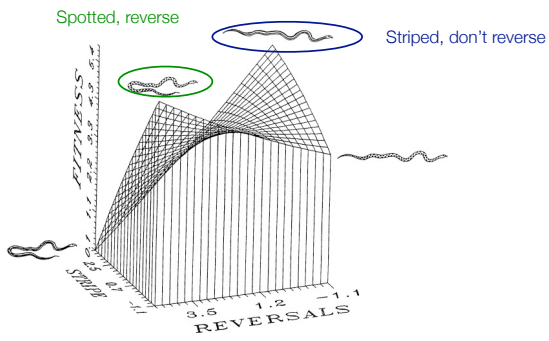
Example: Handedness in scale-eating fish *Perissodus microlepis*

From Hori (1993) Science

Correlational Selection

1. When two traits interactively affect fitness. Some combinations work together well, some do not.
2. Example: Escape behavior in Garter Snakes (Brodie, 1992)
Color traits: Striped, Blotched
Escape behavior: Reverse, Don't reverse

Correlational Selection



Correlational Selection

3. Combo of Striped, Don't reverse is fit
4. Combo of Blotched, Reverse is fit
5. Other combos are not fit.
6. Correlation is disrupted because of random mating.
7. Preferential mating could link behavior and phenotype.