## Lecture 7: Levels and Types of Selection

### Outline
Types of selection
        Stabilizing
        Directional
        Disruptive
Levels of Selection
        Gene
        Individual
        Group
          Problems with 'good of the group' arguments
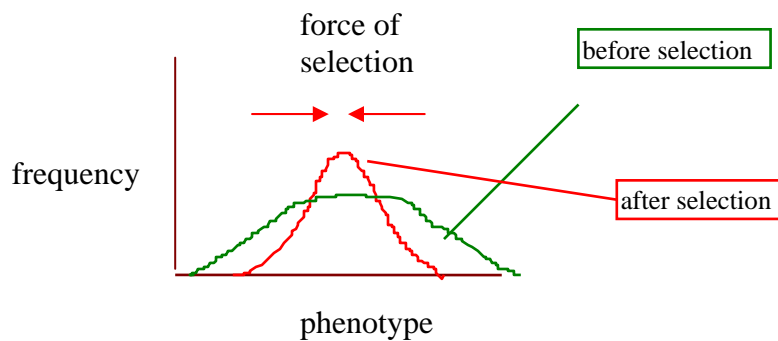        Kin
          Measuring relatedness
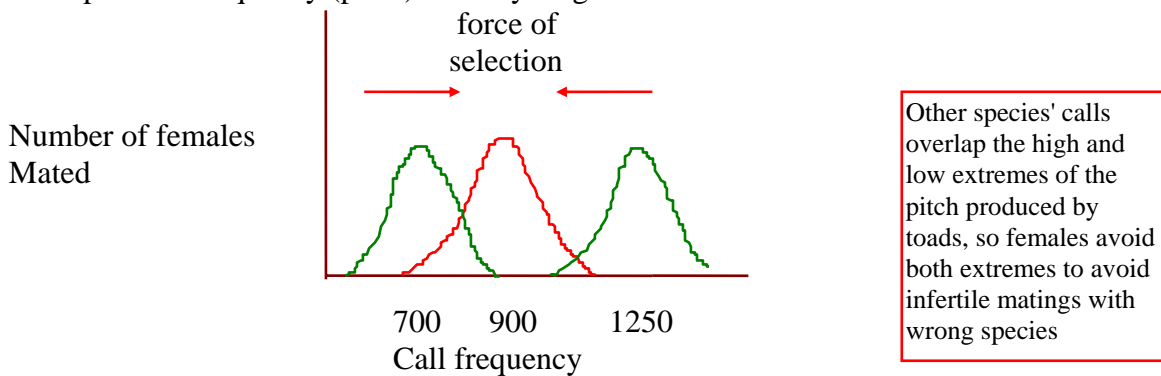          Hamilton's rule
          Inclusive fitness

### Types of Selection  (Fig. 7.1 Pianka)

*Stabilizing* - under constant conditions, once population has reached local adaptive peak, then selection maintains mean trait value at optimum.  Selection against phenotypes that differ from current mean in either direction.  Reduces variability but does not change allele frequencies.



Example: call frequency (pitch) in many frogs and toads



Other species' calls overlap the high and low extremes of the pitch produced by toads, so females avoid both extremes to avoid infertile matings with wrong species

*Directional* - under changing conditions, when current mean trait value differs from optimum.  Selection favors phenotypes that differ from current mean in direction of optimum.  Changes allele frequencies.
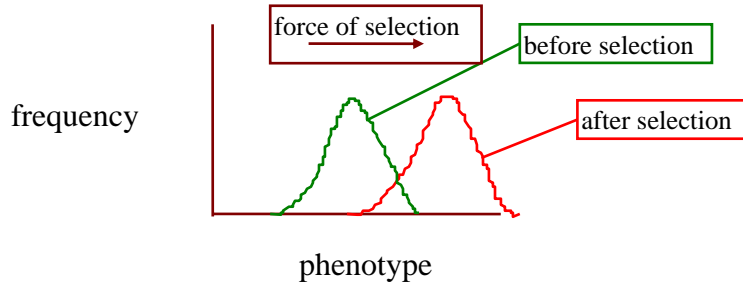


Example: sexual selection by female choice on tail length in widowbirds, experiments by Malte Andersson

Male widowbirds have spectacularly long tails that obviously impair flight performance, thus survival ↓.  Andersson hypothesized ↑ in reproductive success through female choice.  Tested in experiment w/4 groups

1. cut tail to 14 cm (experimental short)
2. banded only (procedural control)
3. cut tail off and reattached it (procedural control)
4.  lengthened tail by 25 cm
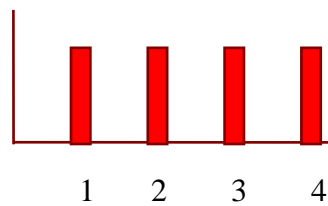


shorten tail - RS ↓
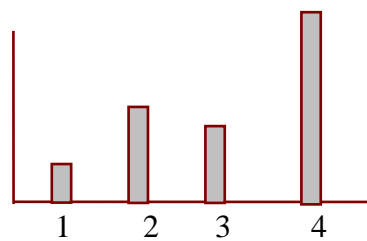lengthen tail - RS ↑
banding ←→
tail cut and restore, small ↓, but does not affect comparison of short/long

So female choice imposes directional sexual selection on tails, in favor of longer tails.

After tails reach a certain length, this is offset by natural selection acting against long tails due to effect on flight (survival).

Balance of two directional selection pressures in opposition $\Rightarrow$ *balancing selection*, not identical to stabilizing selection, though superficially the same outcome - individuals above or below optimum are disfavored.

If no balancing selection, directional selection becomes *runaway selection* - proceeds until genetic variation in favored direction is exhausted.  Any new mutation in favored direction would rapidly spread to fixation


*Disruptive* - Under conditions with two local optima that yield greater fitness than current mean trait value.  Selection favors phenotypes near these peaks, disfavors intermediate phenotypes.  Changes allele frequencies and increases variability.

Example:  gamete size  Parker 1972 JTB

Why have sperm and eggs differentiated, given that ancestral condition was similar-sized male and female gametes.

Frequency

Ancestral

Gamete size
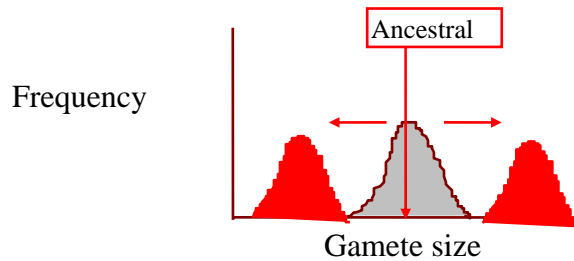
Selective advantage of divergence:
- small gamete specializes in motility, increasing odds that fertilization will occur
- large gamete specializes in nutrient storage, increasing survival of zygotes

**Levels of Selection**

On what units does selection act?

Gene                                    Hierarchy of levels at which selection
Individual                              might act simultaneously, in reinforcing
Family (kin)                            or opposing directions

*Individual Selection*

Most common unit in evolutionary analyses:  trait spreads if it increases bearer's fitness (survival and reproduction).  Survival and reproduction combine to determine ***Lifetime Reproductive Success,*** a property of individuals.

Individuals express phenotypes, ie. a gene is selected +/- because of effects on *phenotype.*   Individuals express phenotypes, so alleles at one locus are selected for or against on the basis of the complete genetic "background" formed by all the other loci in that individual.

Emphasis on *bearer*, in the combination of gene and its bearer.

*Gene Selection*

Very similar to individual-level analysis, but views individual simply as a carrier for gene, which is the self replicating entity that persists through time.  Genes go unchanged through generations, but individuals are unique - they die and their total phenotype, due to many loci, does not pass on exactly to their offspring.

*Gene & individual level selection are two ways of describing the same process, namely that an allele spreads if it raises the lifetime reproductive success of the individual that bears it*.

*Kin Selection*

Haldane (1932) " I would gladly lay down my life for 8 of my cousins".

Kin selection is an extension of gene/individual selection that takes into account that selection can act through effects of an allele (trait) on relatives (kin), who are also likely to carry the allele.

Takes into account that one's relatives are likely to carry the same genes as oneself. Wright's coefficient of relationship measures proportion of genes that an individual carries that are *identical by descent* (IBD).
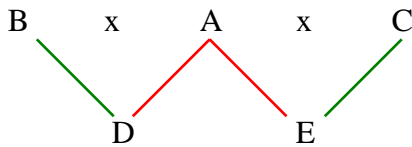
$$r = \Sigma 0.5^L$$

where L = # of steps between two individuals in a genealogy.  (At each step is a meiosis, so genes in common cut in half at each step).
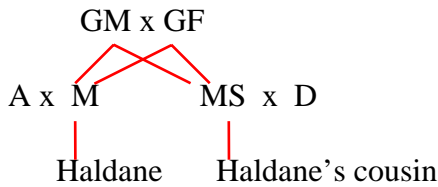
A x B

one link in each case

C
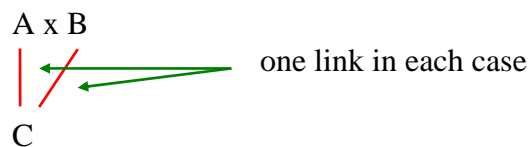
One link between offspring and parent (A & C or B & C), $r = 0.5^1 = 0.5$.  Parent and offspring have 50% of genes IBD.

A     x     B

C     D
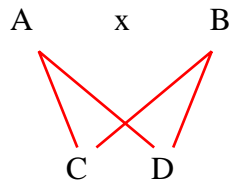
Siblings (C & D): one link up and one link down so $r = 0.5^2 = 0.25$ for each parent. Sum across two parents, $0.25 + 0.25 = 0.50$.

B     x     A     x     C

D               E

Half siblings (D & E):  $r = 0.5^2 = 0.25$

GM x GF

A x  M          MS  x  D

Haldane        Haldane's cousin

$$r = 2(0.5^4) = 2 * (^1/_{16}) = {}^1/_8$$

If r is $^1/_8$, then $r * 8 = 1$.  In genetic terms, saving eight cousins from death is equivalent to surviving yourself.

***Thus, kin selection can explain the evolution of traits that are harmful to the bearer such as sterility in worker hymenoptera (wasps, bees, termites).***

Hamilton's rule (1963, 1964) for spread of a rare 'altruism allele' for trait harmful to donor and helpful to recipient.
g = nonaltruist ,  G =altruist

$rb - c(1) > 0$

r = coefficient of relationship (probability that recipient carries the *G* allele)
b  = benefit of help to recipient
c = cost of help to donor

In the reading assignment (Hamilton 1963), this was written $k > {}^1/_r$, where $k = {}^b/_c$

$$^b/_c > {}^1/_r$$

rb > c          (multiply both sides by rc)
rb-c > 0        (subtract c from both sides)