Lecture 7: Levels and Types of Selection

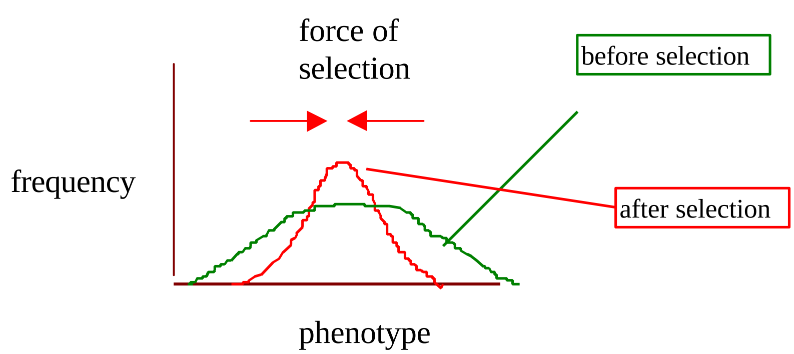
Outline

Types of selection
- Stabilizing
- Directional
- Disruptive

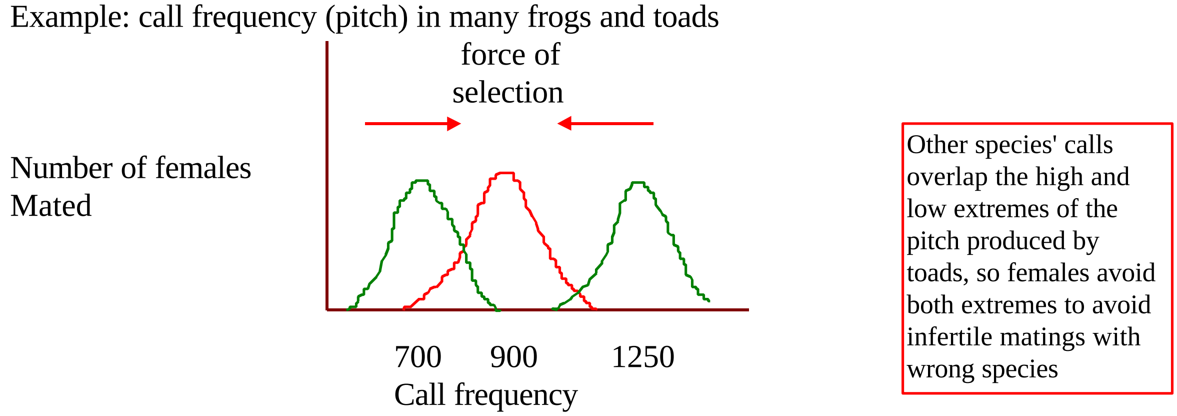
Levels of Selection
- Gene
- Individual
- Group
  - Problems with 'good of the group' arguments
- Kin
  - Measuring relatedness
  - Hamilton's rule
  - Inclusive fitness

Types of Selection (Fig. 7.1 Pianka)

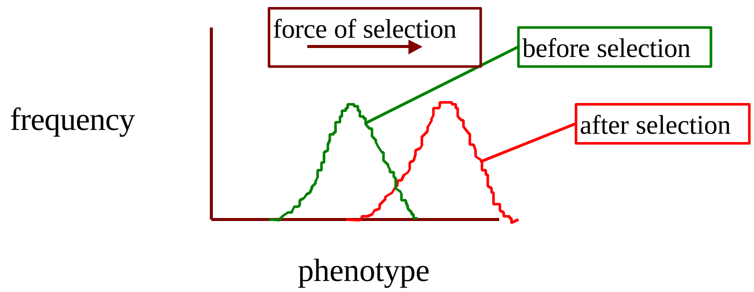
Stabilizing - under constant conditions, once population has reached local adaptive peak, then selection maintains mean trait value at optimum. Selection against phenotypes that differ from current mean in either direction. Reduces variability but does not change allele frequencies.



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



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.

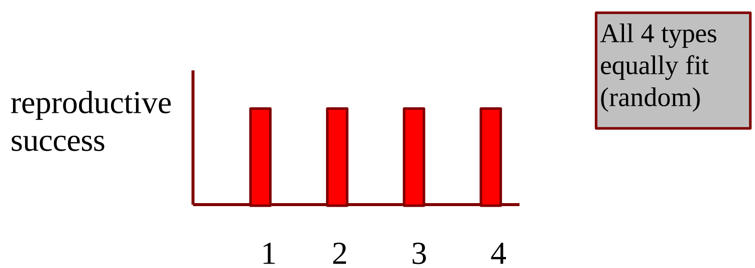


Example: sexual selection by female choice on tail length in widowbirds, experiments by Malte Andersson

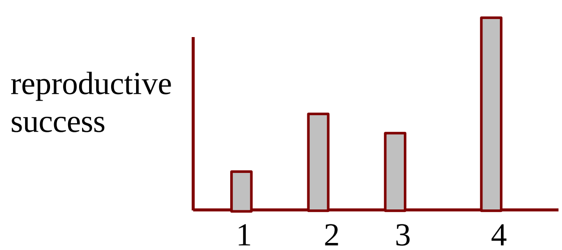
Male widowbirds have spectacularly long tails that obviously impair flight performance, thus survival ↓. Andersson hypothesized ↑ in reproductive success through female choice. Tested in experiment w/4 groups

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

Before manipulation:



After manipulation:



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).

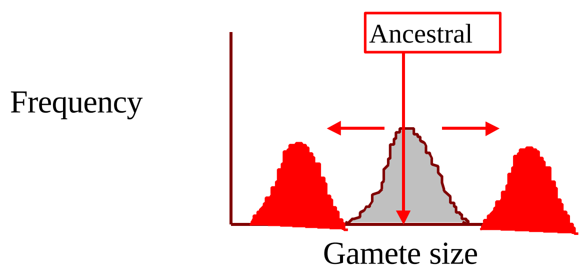
Balance of two directional selection pressures in opposition ⇒ *balancing selection*, not identical to stabilizing selection, though superficially the same outcome - individuals above or below optimum are disfavored.

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.



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
Individual
Family (kin)
Group

Hierarchy of levels at which selection might act simultaneously, in reinforcing 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

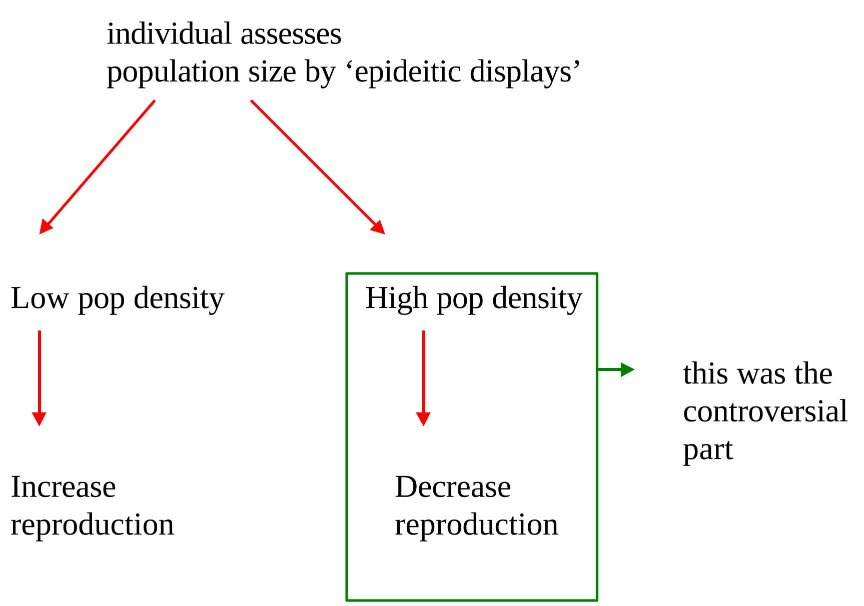
Very similar to individual-level analysis, but views individual simply as a carrier for gene, which is the self replicating entity that persists through time. Genes go unchanged through generations, but individuals are unique - they die and their total phenotype, due to many loci, does not pass on exactly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

Group Selection
'Old' group selection

Very different from gene/individual selection: argues that a trait can spread that benefits the group, even if it harms the individual bearing the trait.

Proposed by Wynne-Edwards (1962, 1963), who formalized popular 'good-of-the-species' arguments. He argued that animals will reduce reproductive rates or sacrifice access to resources (↓ survival) for the benefit of the population. In other words, a population is adapted to its resources, even if this leads individuals within the population to behave in ways that lower their own fitness.



Rebuttals by Maynard-Smith (1964), Perrins (1964), Williams (1966)

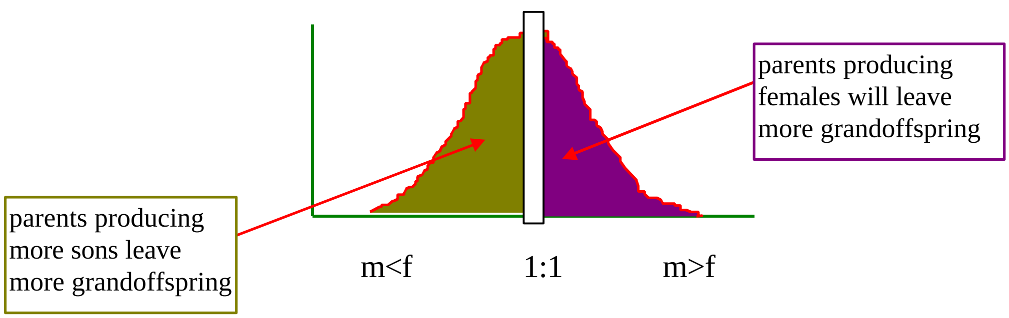
Group selection is possible in theory, but three reasons why it will be very weak and slow relative to individual selection:

1. Turnover rate or 'generation time' is low for groups relative to individuals. So if group selection operates in one direction and individual selection favors the opposite direction, the individual selection will be much faster, swamping the effects of group selection.
2. Genetic variation is higher among individuals than among groups, especially large groups. As groups becomes large, they are likely to hold most alleles at population-wide frequency, so there is little variation among groups.
3. Heritability is not great for many traits even at level of individual (0.1 - 0.3 is common). For groups, heritability is lower still.

Because of low turnover, variation and heritability, group selection will generally be a slow and weak force in nature, relative to individual selection..

Sex-ratio evolution is an example in which individual and group selection would act in opposition, so this can test which level of selection is more important.

⇒ Individual selection predicts 50:50 sex ratio (Fisher 1931). Every offspring has 1 mother and 1 father, so value of sons = value of daughters, (if sexes are equally costly to produce and raise). If one sex is in short supply, individuals producing that sex will have more offspring that reproduce, these kids inherit tendency to produce sex in short supply →→ SR returns to 50:50.



⇒ group selection predicts female bias. One male can fertilize many females, so under group selection, the reproduction of the group would be highest if the sex ratio was female biased

Most species have a sex ratio near 1:1 as predicted by individual selection, (with exceptions explained unequal costs of producing and rearing each sex).

Do not see the extreme female bias predicted by group selection, except under rare conditions discussed by Maynard Smith (1964) and developed by DS Wilson as "new group selection".

An example that meets these rare conditions: Orange mites in lab study (Wilson & Colwell 1981) did show the expected female biased SR.

Colonize orange and trait harmful to individual but good for group means that % of group carrying the trait ↓, but group size ↑ at rate that means total number of individuals with trait ↑, at least initially. Groups break up before % carrying trait drops to zero (when orange rots) and individuals disperse to form new groups on uncolonized oranges. (All groups break up about the *same time*, to *unoccupied* patches (oranges), *randomly* (individuals from same orange do not move together). This will not occur often enough for group selection to be widely important evolutionary force.

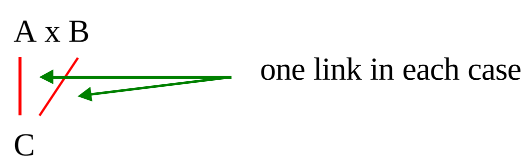
Kin Selection

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

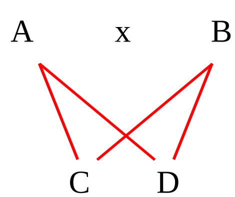
Kin selection is an extension of gene/individual selection that takes into account that selection can act through effects of an allele (trait) on relatives (kin), who are also likely to carry the allele.
Takes into account that one's relatives are likely to carry the same genes as oneself.
Wright's coefficient of relationship measures proportion of genes that an individual carries that are *identical by descent* (IBD).

$r = S0.5^L$

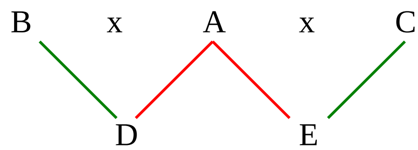
where L = # of steps between two individuals in a genealogy. (At each step is a meiosis, so genes in common cut in half at each step).



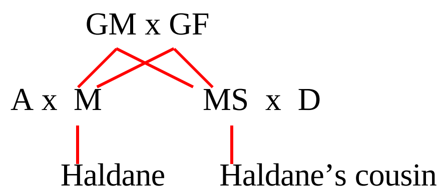
One link between offspring and parent (A & C or B & C), $r = 0.5^1 = 0.5$. Parent and offspring have 50% of genes IBD.



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



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



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

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

$rb - c(1) > 0$

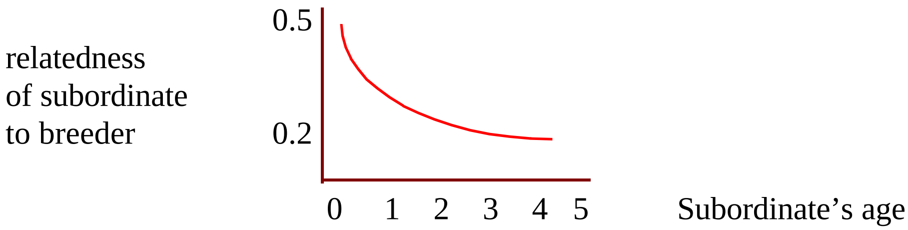
r = coefficient of relationship (probability that recipient carries the *G* allele)
b = benefit of help to recipient
c = cost of help to donor

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

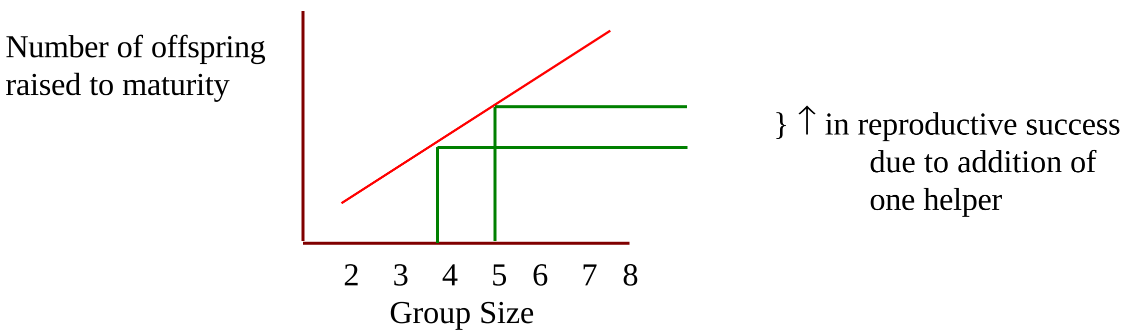
$^b/_c > ^1/_r$
$rb > c$ (multiply both sides by rc)
$rb-c > 0$ (subtract c from both sides)

Example: Cooperatively breeding birds (Florida scrub jays, red-cockaded woodpeckers) and mammals (wolves, African wild dogs, dwarf mongooses). Some offspring do not disperse at maturity

r = genetic relationship between helper (subordinate) and recipient (dominant) measured using DNA fingerprinting or microsatellites. Typically $0.25 < r < 0.35$ for subordinate-breeder pairs in cooperatively breeding species. decreases as subordinate ages, b/c parents more likely to have died as time goes by.



b = benefit of help to recipient
= slope of line relating dominant's reproductive success to group size



c = opportunity cost ≡ offspring helper could have had by pursuing other strategy, i.e. dispersing to breed elsewhere. Usually measured as reproductive success of first-time breeder (often low) devalued by risk of dying in dispersal (often high).

Inclusive fitness: an individual's Darwinian fitness (direct) plus effects on others' fitness, devalued by coefficient of relationship (indirect).

Inclusive fitness = direct fitness + indirect fitness.

Direct cost can be offset by indirect gain, in evolution of altruistic or harmful behavior.

Overheads - dwarf mongoose example.