Lecture Overview: Targets of selection

- candidates: individuals, groups, genes
- the problem of altruism
- gene-centric view of fitness
  - inclusive fitness
  - kin selection and Hamilton's rule
  - when should altruism evolve?
    - Special cases:
      - paternal uncertainty-not all cousins are created equal
      - eusocial insects- cooperation and conflict

What is the 'target' of selection?

- why does natural selection occur?
- population genetic models often assume selection acts directly on individuals (phenotypes) and only indirectly on genotypes
  - individual-based view
- there are other levels at which selection can and does act

Selection below the individual level

- meiotic drive allele D, 'regular' allele d
- in Dd individuals, D 'disobeys' law of equal segregation and is overrepresented (>>50%) in gametes
- but this seems pretty rare… why?
- 'driving' alleles (D) either quickly fixed due to advantage in segregation, or lost due to low heterozygote fitness

Selection above the individual level?

- Some behaviours appear to reduce the individual's survival and reproductive success, instead helping other individuals or the group as a whole
  - 'altruism'
- is it 'altruistic' to help your direct descendants (eg offspring)?

Selection above the individual level?

- just as individuals within a group compete and vary in fitness, groups of individuals compete with other such groups (some go extinct, others persist and/or give rise to new groups)
- group selection:
  - some traits spread not because they increase individual's fitness but because they increase success of the group

- Group selection widely accepted until 1960s as the clear explanation for alarm calls, predator mobbing, sterile worker castes forgoing reproduction…
- formalized by Wynne-Edwards
- refuted by Williams
  - a group of altruists will ALWAYS be vulnerable to 'invasion' by non altruists
  - even if group level selection favours self-sacrifice, individual level selection will oppose it
  - individual level selection much stronger than group level (why?)
  - So, why do 'altruistic' traits persist?

Hamilton's solution: *inclusive* fitness

- more than one way 'your' alleles can get into the next generation
  - direct fitness
    - through your direct descendants
  - indirect fitness
    - through your non-descendant kin… nieces/nephews etc
    - # of extra offspring your kin produce as a result of your help
  - inclusive fitness = direct + indirect

Seemingly 'altruistic' traits favoured not by group selection, but by kin selection

- consider rare allele A (altruistic)
- individual bearing A helps its relative to reproduce, at some cost to itself
- this relative also likely to carry allele A, and transmit it
- So, A can increase in frequency despite the cost to the 'altruist'
- kin selection: helping relatives reduces your direct fitness but increases indirect fitness

Hamilton's Rule Br > C

- describes when selection favours helping relatives
- B = benefit to recipient
  - eg # of additional offspring produced thanks to the 'altruist' helping
- C = cost to 'altruist's direct fitness
  - # of offspring the altruist would otherwise have been able to produce had it not helped
- r = coefficient of relatedness
  - chance that recipient also bears the altruistic allele

Calculating r from pedigrees

- In diploid organisms, $r = \Sigma (1/2)^n$
  - n = # of pedigree steps to link the two individuals
  - if there are more than one shared ancestor (eg full siblings have same mom AND same dad) r is summed over each shared ancestor (each path)

A young warbler can either leave its parents and try to breed on its own, or stick around and help its mother produce more offspring… what should it do?

- Average breeding success of experienced adults with no helpers: 2
- Average breeding success of experienced adults with a helper: 5
- Average breeding success of young warblers: 1

Ecology and the evolution of 'altruism'

- Altruism favoured if Br > C
- How might these affect B, r or C?
  - Nest site limitation: young warbler is unlikely to successfully breed on its own
  - Age effects: the warbler's mother happens to be so old and weak that she's unlikely to produce many eggs
  - Relationship uncertainty: females often lay eggs in one another's nests, so the young warbler is not 100% sure its 'mother' is really its mother

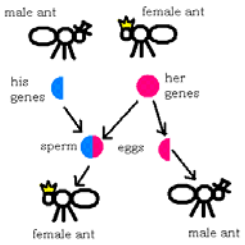
Hamilton's rule and uncertain relationships

- calculating r from pedigrees assumes the pedigree is accurate!
- but pedigree errors can occur
  - egg laying animals may be uncertain of maternity
  - animals with internal fertilization face uncertain paternity
- All other things being equal, would you expect people to behave MOST helpfully to their:
  - father's brother's children?
  - father's sister's children?
  - mother's brother's children?
  - mother's sister's children?

Eusocial insects: the ultimate 'altruists'

- in many Hymenoptera (wasps, bees, ants…) many individuals forego reproducing entirely
  - instead, help their mother (the queen) to reproduce
  - sterile 'worker' females
  - why would selection favour this behaviour?

Answer: these insects are haplodiploid



- unfertilized egg → (haploid) male
- fertilized egg → (diploid) female

Relatedness in haplodiploids

- two sisters share approx 25% of their alleles via mom, plus exactly 50% of their alleles via dad (haploid)
- $r_{sissis} = 0.75$
- $r_{sismom} = 0.5$
- $r_{sisbro} = 0.25$
- Females are more closely related to their sisters than to their potential offspring
- So, helping mom to produce sisters is selectively favoured

but even haplodiploids can have conflicting interests…

- workers and queen often 'disagree' over what sex ratio of offspring the colony should produce (sex ratio conflict)
  - mostly daughters, just enough males to keep things going?
  - equal proportions sons and daughters?

Summary: levels of selection

- Selection can act at many levels (genes, individuals, groups…)
  - group-level selection usually much weaker than gene- or individual-level, thus it can't explain apparent altruism
- Much apparent altruism can be explained by taking a gene's eye view
  - inclusive fitness
- Whether or not helpful ('altruistic') behaviour is likely to evolve depends on the species' ecology
  - Altering B, r and/or C affects payoff to 'altruism'