The Evolution of Eusociality

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Eusociality: A Definition

An overlap in generations

A reproductive division of labor

Cooperative brood care

Strange and Rare

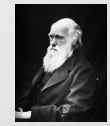
- Why / How could eusociality have evolved?

What Darwin had to say about it

•"…the one special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory" (1859)

•Darwin's solution:

- •Sterility can be carried but not expressed in some individuals.
- •Sterile individuals help reproductive relatives
- •Traits of sterile caste can persist and evolve.



The Origins of Inclusive Fitness and Kin Selection

- Darwin's solution that sterile castes can help their traits persist leads to inclusive fitness
- Inclusive Fitness:
  - An individual's fitness + the fitness of it's relatives

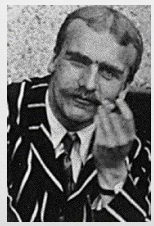
$F_i = F_o + [F_1(R_1) + F_2(R_2) + \ldots F_N(R_N)]$

What Fisher had to say about it (1930)

- Distasteful caterpillars travelling in sibling groups
- Aposematic coloration

What Haldane had to say about it (1950s)

- Would you lay down your life for your brother?
  - "No, but I would for two brothers or eight cousins!"



What Hamilton had to say about it (1964)

- Hamilton's Rule:
  - $C < R \times B$
- Kin Selection
  - Strategies that favor reproductive success of relatives even at expense to self

Haplodiploidy

- Hymenopteran females are diploid, males are haploid
- Sisters are more closely related to each other than they would be to their own offspring
- It is better to help your mother raise more sisters than to reproduce on your own

Who's Who: W. D. Hamilton (1936 – 2000)

B. S. at St. John's College, Cambridge
Ph.D. at London School of Economics and University College of London

Hamilton's Rule

Sex Ratios

Origins of Sex

Parasites

Contracted malaria in the Congo while researching the AIDs virus

Kin selection fails to explain:

- Eusocial organisms that are not haplodiploid
  - Naked Mole-Rats, Termites
- Haplodiploids that are not eusocial
  - Solitary wasps and bees
- Eusocialhaplodiploids with decreased relatedness
  - Multiple queens
  - Multiple matings

Shortcomings of the Kin Selection Explanation (Nowak et al., 2010)

- Assumes that fitness can be described by additive isolated interactions
- Assumes interactions are binary
  - Social insects often benefit from cooperation between many individuals

An Alternative Theory

- The 5 stages proposed by Nowak et al., (2010):
- 1: Formation of groups
- 2: Pre-adaptive traits
- 3: Mutations
- 4: Natural selection acts on emergent traits
- 5: Multi-level selection

Formation of Groups

- Related groups:
  - Parent-Offspring groups
- Unrelated groups:
  - Whenever cooperation is beneficial
- Living in a structured nest

Pre-adaptations

- Non-social bees act eusocial when forced experimentally
  - Evolutionary evidence for a pre-existing tendency toward social behavior
- Progressive Provisioning
  - Parental care → Cooperative brood care

Gene Level

- Mutations: Silencing of dispersal
- Monitoring the expression of genes
  - Switching on and off the gene for wing development can be influenced by diet

Natural Selection acts on Emergent Traits

- Once social living is established, natural selection acts on the emergent traits
  - Interactions of the individuals
- The colony is the extended phenotype of the queen
  - Establishes colony as a superorganism
- How does eusociality benefit the queen? Vs. Ho does it benefit the worker?
  - More time in the nest, less time looking for food

Multi-level Selection

- Between-Group Selection reinforces cooperation within groups
  - More cooperative groups out compete less cooperative ones

A combination of the theories?

- Relatedness is still important!
- The arguments continue…