The Evolution of Altruism

Kin Selection through the eyes of a group selectionist!

Chapter 11
Switching Gears

Up to this point we have discussed:

What evolution is

The basics of the mechanics of evolution

What I want to turn to:

Modes of Adaptation
A Short history of Group Selection

V. C. Wynne-Edwards 1962
“Animal Dispersion in Relation to Social Behavior”

Animals choose not to reproduce for the good of the group
A Short history of Group Selection

Maynard- Smith 1964

Group Selection and Kin Selection (published in Nature)

Conditions under which an individual should give up fitness to help another are rare. The one exception is helping kin.
Principle of Parsimony

G. Williams 1974
“Adaptation and Natural Selection”

"In explaining adaptation, one should assume the adequacy of the simplest form of natural selection, that of alternative alleles in Mendelian populations, unless the evidence clearly shows that this theory does not suffice."

This book killed group selection as a viable model for evolution!
This view persists to this day

"Is there anything in evolution that can't be answered by Individual selection, that needs to be explained by selection acting on groups?" . . .

. . . "I can't think of any."

Jerry Coyne
Quoted in Science August 9, 1996

Your book does not even have group selection in the index!
Bottom line on Group Selection

How Effective is Group Selection?
The Simple Answer: VERY EFFECTIVE!

Group Photo Disasters
An Example: Wade 1977

- **Treatments**
  - 37 Day Interval
  - Data Gathered
  - Selection

- **Common Stock**
  - High Group Selection
    - 48 Populations
    - 16 Adults/Pop.
  - Low Group Selection
    - 48 Populations
    - 16 Adults/Pop.
  - No Group Selection
    - 48 Populations
    - 16 Adults/Pop.

- **Number of Adults in Each Population**
  - Redrawn from Wade 1977

- **Repeated 8 times**
Wade Experiment Results

There was a rapid response to Group Selection

*Tribolium castaneum*
Conventional Wisdom

“... extinction and recolonization have only a limited potential to create, or coexist with, strong genetic differentiation ... This implies that adaptive evolution is unlikely to occur by classic interdemic selection, a conclusion that has often been reached.”

Harrison and Hastings 1996

The Truth

The effectiveness of group selection surprises even group selection researchers.
Why is Group Selection So Effective?

The Simple Answer:

Genetically based interactions among individuals
Actually all interactions. (Interactions AGAIN?)
Evidence for Ecological Interactions

Responses to community selection in two species, *Tribolium* communities are dependent on the genetical identity of both strains (Goodnight 1991)

Four traits measured

- Population size in *T. castaneum*
- Population size in *T. confusum*
- Emigration rate in *T. castaneum*
- Emigration rate in *T. confusum*
Back to Kin Selection

W. D. Hamilton 1964.
The genetical evolution of
social behavior

Hamilton’s Rule:

\[
\frac{C}{B} < r \quad \text{and} \quad C < rB
\]

\[
\frac{\text{Cost}}{\text{Benefit}} < \text{relatedness} \quad \text{and} \quad \text{Cost} < \text{relatedness} \times \text{Benefit}
\]
Haldane said this a long time ago!

“Would I lay down my life to save my brother? No, but I would to save two brothers or eight cousins.” 

(see box 11.1, P. 421)

1/2 of genes shared 1/8 of genes shared
There are many examples of Kin Directed Altruism

Alarm calls (ground squirrels)
Helping at the nest (bee eaters, scrub jays)

Less obvious “altruism”
Directing cannibalism away from Kin
Offering yourself up for dinner.

*Tribolium* avoid eating age classes that might be their offspring.
Kin Selection as Group Selection

Hamilton’s Rule:

\[
\frac{\text{Cost}}{\text{Benefit}} < \text{relatedness}
\]

Hamilton’s Rule based on a Group selection Perspective:

\[
\text{Individual selection against trait} < \text{Variance Among Groups}
\]

\[
\text{Group selection in favor of trait}
\]

This is based on the statistical methods of Contextual Analysis

The “greenbeard” model – May actually be important in humans!
Hamilton and the Green Beard Model

Hamilton suggested:

If there was a gene that promoted altruism AND changed the phenotype (altruists had a “green beard”)

Then altruism might evolve IF altruists directed their behavior towards other altruists (those with “green beards”)

Problem: Altruism and phenotype must be the same gene.

Less of a problem for cultural inheritance!

The term “green-beard” was coined by Dawkins.
Kin Selection as Group Selection

Individual selection against trait  <  Variance Among Groups
Group selection in favor of trait

• Altruism: a trait favored by selection at the group level and opposed by selection at the individual level

• Hamilton’s rule is about the evolution of altruism, which is why the two levels are in opposition in the equation.

• Variance among groups = relatedness IF all heritable differences among groups are genetic, and all genes act additively. In many real situations variance among groups will be greater than relatedness.
Eusociality

Eusocial organisms: Colony living organisms in which there is a single (or a few) reproductives, with the majority of the colony forgoing reproductions.

Consider an individual human as a colony of individual cells

• The majority of cells are “somatic”
• A very few are reproductive.
• At a cellular level we are eusocial!
# Eusociality

Why would an individual cell choose to do this?

<table>
<thead>
<tr>
<th>No choice (policing)</th>
<th>liver cells are not capable of becoming reproductive. This just pushes back the problem. They could evolve to be capable of sexual reproduction!</th>
</tr>
</thead>
<tbody>
<tr>
<td>Relatedness (no heritability within body)</td>
<td>All of the cells in our body are genetically the same. It makes no difference whether the “liver” cell or a “gonad” cell produces the gametes the genetic outcome is the same.</td>
</tr>
<tr>
<td>No opportunity to reproduce (group selection)</td>
<td>Individual cells would not succeed in reproducing effectively, whereas a cooperating group (a human) can be quite effective</td>
</tr>
</tbody>
</table>
Eusociality

The evolution of “eusociality” for individual humans is easy BUT it is not so obvious for groups of organisms and “real” eusociality.

Nevertheless eusociality has evolved multiple times.

Dictyosetlium? (proto eusociality at best)
Ants, bees, wasps
Termites
Homoptera
Beetles
Thrips
Naked mole rats
Haplo-diploidy

Early on it was noted that many of the most obvious eusocial organisms are haplo-diploid

Haplo-diploid: females are diploid (2N) males are haploid (1N)

Wasps, bees, and ants are haplodiploid
Males exist only for reproduction
Queens and sterile casts are all workers
Sisters (sharing the same father) in haplo-diploid systems are more related than sisters in diplo-diploid systems
Haplo-diploidy and Eusociality

is haplo-diploidy important in the evolution of eusociality?

Many argue yes, because the higher relatedness of sisters. Data argues against this.

Honey bee queens (haplo-diploid) are multiply inseminated eliminating the relatedness advantage.

Hymenoptera (haplo-diploid) are only one of many groups that are eusocial.
More likely explanation for the evolution of eusociality

There are HUGE fitness advantages to group living.

• Ants are one of the most successful insect groups in the world

• Mole rats live in harsh environments were few other rodents can survive

• Bees can kill a human, they are not to be attacked lightly, even though insect larvae (not to mention honey) are extremely valuable food stores.
Eusociality

My guess on the evolution of eusociality (part 1)

Termites need to live communally because of their gut flora. This allows them to live on a food source few other species can eat (wood)

Ants, bees, and wasps can exploit the world in a way solitary species cannot.

Excess resources can be stored for future generations.

Bottom line: there are big advantages to cooperation and group living. In Hamilton’s rule: Benefits are large.
Eusociality

My guess on the evolution of eusociality (part 2)

The survivorship of an individual would be low.

It is unlikely that an individual mole rat could survive in the harsh environment in which they live.

Reproduction would be low.

Wasp nests are regularly attacked because the larvae are valuable as food. An individual could not both protect the nest and forage.

Bottom line: single individuals have low fitness
In Hamilton's rule: costs are low (since individual fitness is near zero)
Eusociality

My guess on the evolution of eusociality (part 3)

Reproduction strategy results in relatives living together
This makes colony members genetically similar and amplifies differences among colonies

Many (all?) species have behaviors enforcing conformity
Honey bees “police” each other, selectively destroying eggs not laid by the queen

Bottom line: Great genetic and behavioral similarity within groups, magnified differences among groups
In Hamiltons rule: Variance among groups is large
Eusociality

My guess on the evolution of eusociality

Individual selection against trait
Group selection in favor of trait
< Variance Among Groups

costs are low
Benefits are large
< Variance Among Groups is large

Viewed this way, it is hardly surprising that eusociality has evolved multiple times!
Egrets usually lay 3 eggs, all usually hatch. Usually the the two oldest siblings gang up on the youngest and kill it.

Parents to not interfere, and physiologically give the youngest sibling a disadvantage to make it easy to kill.
Siblicide

Why would siblings want to kill each other?

They share half their genes!
They also share half their food.

Why would parents allow their children to be killed?

Reproduction is the best measure of fitness.
*Live* children are the best measure of fitness!
If there is not enough food for three, somebody must die.
Siblicide: The generally accepted explanation

Parents perspective:

• At the start of the season parents cannot predict if it will be a good or bad year.

• They produce as many offspring as they can raise in a good year, but more than they can raise in an average year.

• They allow one (or two) to die if the year is average.

• Biasing the competition (asynchronous hatching) minimizes the danger of injury to the surviving offspring.
Siblicide: The generally accepted explanation

Offspring perspective:

• If you are full go to sleep.

• If you are hungry get food when offered.

• Sharing is strictly secondary to surviving.

• Relatedness means nothing WITHIN the nest.

• Killing siblings is the best way to ensure your own survival.
Parent Offspring Conflict

This raises an interesting point: The interests of the parents are not the same as the interests of the offspring.

Parents:

- Produce as many offspring as possible in life time
- Provide the minimum amount resources to each offspring that insures survival.
- Equally provide for each offspring (or in proportion to their chance of survival)

Offspring:

- Maximize the chance or your survival.
- Get as many resources from your parents as possible.
- Support siblings ONLY if impact on your own fitness obeys Hamilton’s rule.