Multilevel Selection

Merging Individual Selection and Group Selection
“Although a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe... an advancement in the standard of morality will certainly give an immense advantage to one tribe over another.”

--Charles Darwin, *The Descent of Man*
Group Selection

- When individual traits help one group outcompete other groups.
Individual Selection & Cooperation

Cooperator

Defector
Individual Selection & Cooperation

Defection is always locally advantageous!
Kin Selection

- Your relatives carry similar genes.
- Helping your relatives is helping your genes.

<table>
<thead>
<tr>
<th>Relative</th>
<th>Genetic Similarity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parent</td>
<td>.5</td>
</tr>
<tr>
<td>Sibling</td>
<td>.5</td>
</tr>
<tr>
<td>First Cousin</td>
<td>.25</td>
</tr>
<tr>
<td>Second Cousin</td>
<td>.125</td>
</tr>
</tbody>
</table>
Kin Selection
Direct Reciprocity

- Helping someone else provided they will help you later.
Direct Reciprocity
Conditional Cooperation

- Tit-for-Tat strategy only cooperates with other cooperators.
Conditional Cooperation

Behavior as a Second Mover:
Playing with a Cooperator

Behavior as a Second Mover:
Playing with a Defector
Tit-for-Tat in Nature: Birds
Tit-for-Tat in Nature: Fish
Tit-for-Tat in Nature: Primates
Indirect Reciprocity

- Reputation, gossip and other signals can be used to determine whether to cooperate or not.
Indirect Reciprocity
Group Selection

- Variation between Groups
- Competition between Groups
Defection is always locally advantageous!

But cooperative groups can beat non-cooperative groups!
Why Cooperate?
Why Cooperate?
Why Cooperate?
Multilevel Selection

- A framework that combines selection at all levels, from the gene to the group.
- Considers two things:
  - Level benefited by a trait’s operation.
  - If that level is being selected for by the environment.
Advantages of Multilevel Selection

- All other examples are just specialized cases of groups!
- Accounts for all evolutionary pressures and estimates their interplay.
Advantages of Multilevel Selection

Eusociality

Individual Selection

Individualism

Group Selection
Other Theories

Eusociality

Individualism