Inclusive fitness and MLS

1. What is MLS and kin selection?
2. Averaging fallacy versus an expanded framework.
   - What is individual selection?
3. What is “r” and is it useful?
4. Predictive versus explanatory frameworks.

What is the actual selection pressure behind kin selection?

- Consider a single family
- Consider multiple families
- Now, what is responsible for altruism?
- Is relatedness important or is selection at the group level important?
- Why did Hamilton miss this?

Averaging fallacy

- George Price (1970, 1972) \( \Delta z = \frac{\text{Cov}(W, z)}{N} + \frac{\text{Cov}(W, Z)}{N} \)

- Price equation partitions total gene frequency change into within and between group components.
- Hamilton later recalled of Price: “I am pleased to say that, amidst all else that I ought to have done and did not do, some months before he died I was on the phone telling him enthusiastically that through a “group-level” extension of his formula I now had a far better understanding of group selection acting at one level or at many than I had ever had before.” (Hamilton 1996).

Averaging fallacy

Did Darwin write the *Origin* backwards?

Philosophical Essays on Darwin’s Theory

Elliot Sober

Expanded versus reductionist frameworks

<table>
<thead>
<tr>
<th>Figure 5.4</th>
<th>An individual’s fitness depends on its own phenotype and on the phenotype of its partner</th>
</tr>
</thead>
<tbody>
<tr>
<td>the individual is</td>
<td>Altruistic</td>
</tr>
<tr>
<td>swift</td>
<td>x - ( c )</td>
</tr>
<tr>
<td>selfish</td>
<td>x</td>
</tr>
</tbody>
</table>

(1) There is group selection favoring altruism and individual selection favoring selfishness, and the former is stronger when the latter is weaker.

(2) Preytarget is 4 (individual is 4) | Preytarget is 4 (individual is 4) > c *b.

(3) \( w(x) = \text{Prey target is 4} \) (individual is 4) + \( w(y) = \text{Prey target is 4} \) (individual is 4) = \( w(x) + w(y) = \text{Prey target is 4} \) (individual is 4) = \( w(t) = \text{Prey target is 4} \) (individual is 4).

Let \( \text{Prey target is 4} \) (individual is 4) and \( \text{Prey target is 4} \) (individual is 4). Then \( w(x) > w(y) \) (prey target is 4) (individual is 4).

\[ p(x) = \frac{1}{2} (p(x) + p(y)) \geq \frac{1}{2} (p(x) + p(y)) \]

**Note that any distinction between fitness within and between groups is now lost in the inclusive fitness formulation**
Why “r” may be different

• If the gene in question is close to fixation in the population, full sibs will still be r = 0.5
• If the gene in question is dominant.

<table>
<thead>
<tr>
<th>Individual is A, A is rare</th>
<th>Individual is A, A is common</th>
<th>Probability in the population</th>
</tr>
</thead>
<tbody>
<tr>
<td>aa</td>
<td>aa</td>
<td>0</td>
</tr>
<tr>
<td>aa</td>
<td>aa</td>
<td>1</td>
</tr>
<tr>
<td>aa</td>
<td>aa</td>
<td>0.75</td>
</tr>
</tbody>
</table>

What is “r” now and do we care?

• Hamilton noted this issue and realized in 1975, that “r” is not what is important, it is merely that altruists interact with other altruists.
• “r” changed to the probability of sharing the gene (not necessarily IBD)
• “r” then changed again to now to represent phenotypic correlation. Thus “kin” is no longer a necessary part of kin selection. (Genes are not even necessary).
• Relatedness (kinship) is merely a way to partition variance amongst groups, however other partitioning process also achieve this.

In a nutshell

“There is only difference between inclusive fitness [and MLS] is that instead of calculating the effects from a focal individual to its reproduction and that of neighbors, fitness accounting is done all in terms of effects to the focal individual’s reproduction from itself and its neighbors.”

Predictive value of the frameworks

• “r” provides no value at point of inquiry, but useful when interpreting results (Gardner).
• “Hamilton’s rule is at worst superfluous and at and best ad hoc” (Nowak et al. 2010)
• When only considering net outcomes, all traits are classified as acting in self-interest.

Eusociality: Origin and consequences

- Close relatedness either precursor or result.
- Evidence from presocial species suggest low relatedness in colony founding queens.

“In inclusive fitness [posits] that individuals are “trying” to maximize the representation of their genes in future generations, where it is recognized that an individual’s genes can be found in her genetic relatives (non-relatives) as well as in her own offspring... The net result is that any helping behavior that evolves gets viewed as a form of genetic self-interest. This may seem like a pleasing consequence until it is realized that “self-interest” has now become an all-encompassing category. When altruism evolves, this is consistent with the heuristic idea of self-interest, since altruists are getting their altruistic genes into the next generation by helping other altruists. The idea that altruism is good for the group but bad for the individual has been lost. The way to recovery is to set aside the metaphor of “trying” and focus on the fact that there can be conflicts of interest between different levels of organization. What is good for the individual can conflict with what is good for the group. Our concept of adaptation should reflect this fact. Rather than use “individual adaptation as an all-encompassing label that is defined so that it applies to all adaptations regardless of whether they evolve by group or individual selection.”

- Elliot Sober (2010)
Why is group selection still stigmatized?

- Hamilton acknowledged inclusive fitness was group selection in 1975, so why are his disciples unwilling to make this leap?
- What is group selection? Few know
  - Artifact of the widespread rejection in the 60s.
  - Understanding GS, came a distant second to the fact that it is impossible.
- Lead to the reemergence of GS under other names (pluralism).
  - Direct and indirect reciprocity, social selection, costly signalling, byproduct mutualism, etc...

Field dominated by within group selection

- Experiments typically take place within a single group OR disregarding group differences.
- These experiments demonstrate drastic population level consequences to this conflict (evolutionary suicide).
- Why are natural population entrenched in sexual conflict not going extinct?
- In multigroup populations, groups with less sexual conflict will contribute more offspring to the next generation than higher conflict groups, countering the local advantage of harmful males.
- Similar to the conflict between selfishness and altruism.

Water strider *Aquarius remigis*

<table>
<thead>
<tr>
<th></th>
<th>Pools</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Matings</td>
<td>Low</td>
<td>46</td>
<td>30</td>
</tr>
<tr>
<td>Overall eggs laid</td>
<td>Low</td>
<td>450</td>
<td>300</td>
</tr>
<tr>
<td>Overall hatching success</td>
<td>Low</td>
<td>76.75</td>
<td>78.78</td>
</tr>
<tr>
<td>Overall nymphs hatched</td>
<td>Low</td>
<td>607</td>
<td>807</td>
</tr>
<tr>
<td>Female survival</td>
<td>Low</td>
<td>80.00</td>
<td>60.00</td>
</tr>
<tr>
<td>Nymph survival</td>
<td>Low</td>
<td>14.81</td>
<td>8.14</td>
</tr>
</tbody>
</table>

Selection within groups vs. population

- Maximize variation in aggression within groups, eliminate variation between groups.
- Allow individuals to disperse in a multi group population.
- Compares fitness differentials within groups to what occurs in a naturalistic population.
• Selection within groups does not correspond to overall selection in the population.
• What is missing?

What can be predicted from this outcome?

Summary
• Group selection cannot be evaluated based on the net outcome alone.
• Group selection can only be evaluated when within and between group selection differentials are calculated.
• Predictive value of calculating within and between group differentials.