Review of
Marshall 2011:

“Group selection and kin selection: formally equivalent approaches”

Eric Bolo, last edited 3/26/2013
OUTLINE

• **Definitions**: group selection & inclusive fitness

• **Argument**: formal equivalency of both models
  - Deriving the two models from Price equation
  - In defense of IFT
DEFINITIONS: Group Selection

• Group selection predates inclusive fitness theory: Darwin, Kropotkin

• Early models focused on differential survival/reproduction of groups. Requires:
  (1) reproductive isolation;
  (2) differential survival
  (3) genetic drift

=> Probably rare because of “cheaters” and need for small groups (Maynard Smith 1964)
DEFINITIONS: Group Selection

• Later definitions are less restrictive:
  • Selection divided into two components: between-group and within-group
  • Altruism favored when within-group selection against altruism is less than between-group selection for altruism.

• Most contemporary models of group selection use this approach

• *(But is this really natural selection on groups?)*
DEFINITIONS: Inclusive Fitness

- Inclusive Fitness Theory (IFT) is natural selection applied to social behavior
- Extends individual fitness to include effects on others weighed by relatedness to focal individual
- What is relatedness?
  - Early formulations based on pedigree. $R = \frac{1}{2}$ for siblings; $R = \frac{1}{8}$ for cousins. Restricted to weak selection
  - Broader definition based on genetic association, not kinship, e.g. greenbeard altruism. (*But doesn't relatedness then lose its true meaning?*)
DEFINITIONS: Inclusive Fitness

- Hamilton's rule: altruism selectively favored when
  \[ R > \frac{c}{b} \]
- Hamilton's rule is a product of IFT but should not be conflated with the theory itself.
- More sophisticated models are compatible with IFT.
ARGUMENT

• Central claim: the modern definitions of IFT and group selection are equivalent formally.
• Can derive both IFT and group selection from the Price equation

$$\Delta E(G) \propto \text{Cov}(G, W) + E(W\Delta G)$$

Where: E is population average
G is value for trait
W is individual fecundity

• If no transmission bias $\Delta G = 0$ so $E(W\Delta G) = 0$, then trait favored if $\text{Cov}(G,W) > 0$
Deriving IFT from Price Eq.

• Break down fitness into individual effects and effects on social partners, based on genetic association ("greenbeard" approach)
  \[ W = G'B - GC \]

• For trait to be favored, assuming no transmission bias, we need \( \text{cov}(W,G) > 0 \), which can be rewritten as:
  \[ \frac{\text{Cov}(G,G')}{\text{Var}(G)} > \frac{E(C)}{E(B)} \]
  \[ \Rightarrow \text{that's Hamilton's rule with relatedness defined as genetic association (not kinship!)} \]
Deriving group sel. from Price Eq.

• Again, with no transmission bias, we need $\text{Cov}(G,W) > 0$ for trait to be favored

• Fitness effects depend on group size, $N$. Introducing $N$ using the law of total covariance, we obtain:

$$\text{Cov}(G,W) = \text{Cov}(\mathbb{E}(G|N), \mathbb{E}(W|N)) + \mathbb{E}(\text{Cov}(G,W|N))$$

$\Rightarrow$ that's the Price equation divided into between-group and within-group components
ARGUMENT ctd.

- The Price equation is a general model of cross-generation transmission of heritable traits.
- IFT and group selection as specified by Marshall conform to this general model.
- Therefore, they are formally equivalent to each other (and to natural selection as a whole).
ARGUMENT ctd.: in defense of IFT

- Marshall uses the generality of the Price equation to counter following criticisms of IFT:
  - **IFT is only valid for pairwise interactions.**
  - **IFT can only be applied for cases of weak selection (small fitness differences) on rare genes.**
  - **IFT ignores retroactive effects on altruist actor from its benefactors.**
  - **IFT cannot deal with cumulative effects.** False: if we use correct definitions of b and c we can account for non-additivity. (Note: I don't understand Marshall's proof of that last point)
DISCUSSION

- Marshall: “Drawing false dichotomies is not helpful for the theory of social evolution”
- Marshall uses the broadest, most general available definitions of IFT and group selection
- There is a clear disagreement on what group selection and IFT exactly are. Does group selection require reproductive isolation/differential survival? Should relatedness used in IFT models be based on kinship or some other measure?
- Should we favor restrictive or broad definitions?
References


