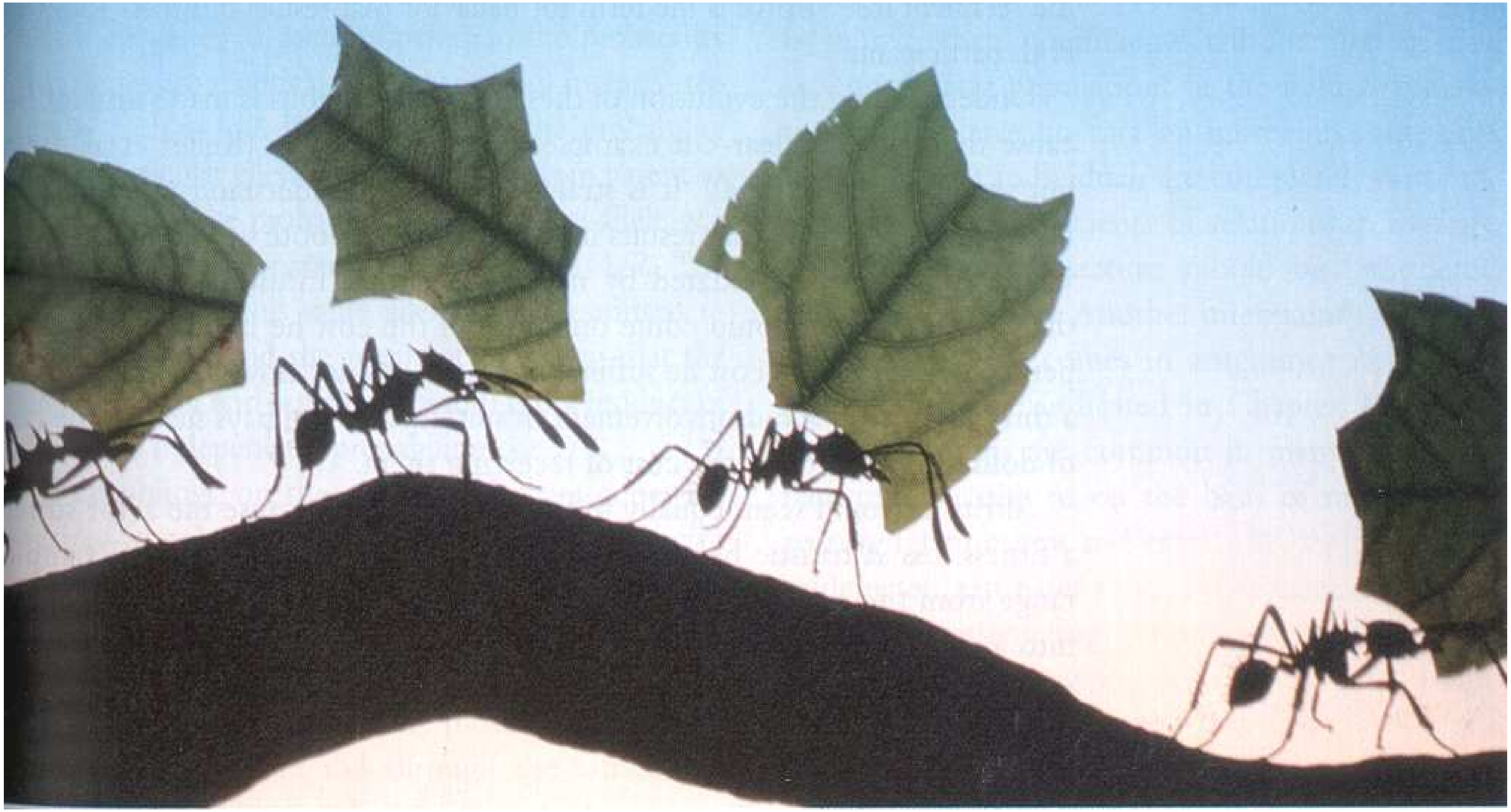
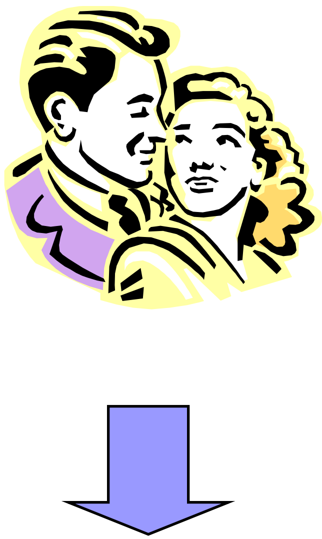
Evolution of socially affected traits

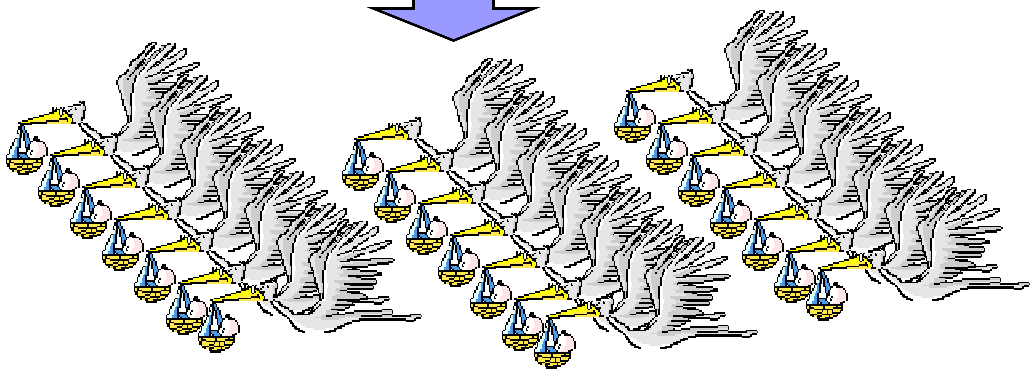
A quantitative genetic perspective



Why cooperate with thy neighbor?

Natural selection





Casanova’s have more offspring $\rightarrow$ frequency of the Casanova allele increases

In General:

Natural selection works to increase fitness

Fitness

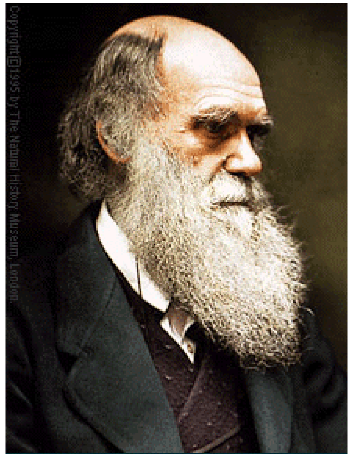
$\equiv$

number of offspring

The direction of natural selection: fitness

- Darwin: survival of the fittest
  - Natural selection targets reproductive output (fitness)
    - Struggle for life $\rightarrow$ competition increases
    - Maybe at the expense of others

- Questions
  - How can altruistic behaviors evolve?
  - How do populations avoid extinction due to competition?


Charles Darwin (colourized B&W print)

Alarm calling in squirrels

Squirrels warn each other when a hawk appears

Non-breeding helpers in naked mole-rats

Sterile workers in social insects

Worker bee

Blood sharing in vampire bats

Territory defense in lions

Why not let the others fight ?

Mechanisms for the evolution of altruism

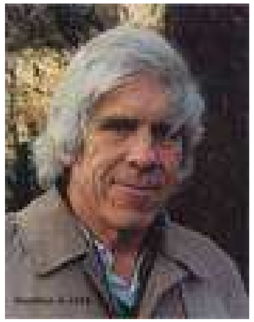
- Kin selection
  - Helping behavior is directed towards relatives
- Group selection
  - Behavior for the good of the group evolves because selection acts between groups
- Multilevel selection
  - Fitness depends on properties of others

Kin Selection & Hamilton's rule

If your gene
makes you help **somebody carrying the same gene**,
then this gene may increase its own fitness
at your expense

Helping behavior will evolve when
the relationship between helper and recipient
is higher than
the ratio of fitness cost to the helper over
fitness benefit to the recipient

Hamilton's rule: $r > c/b$

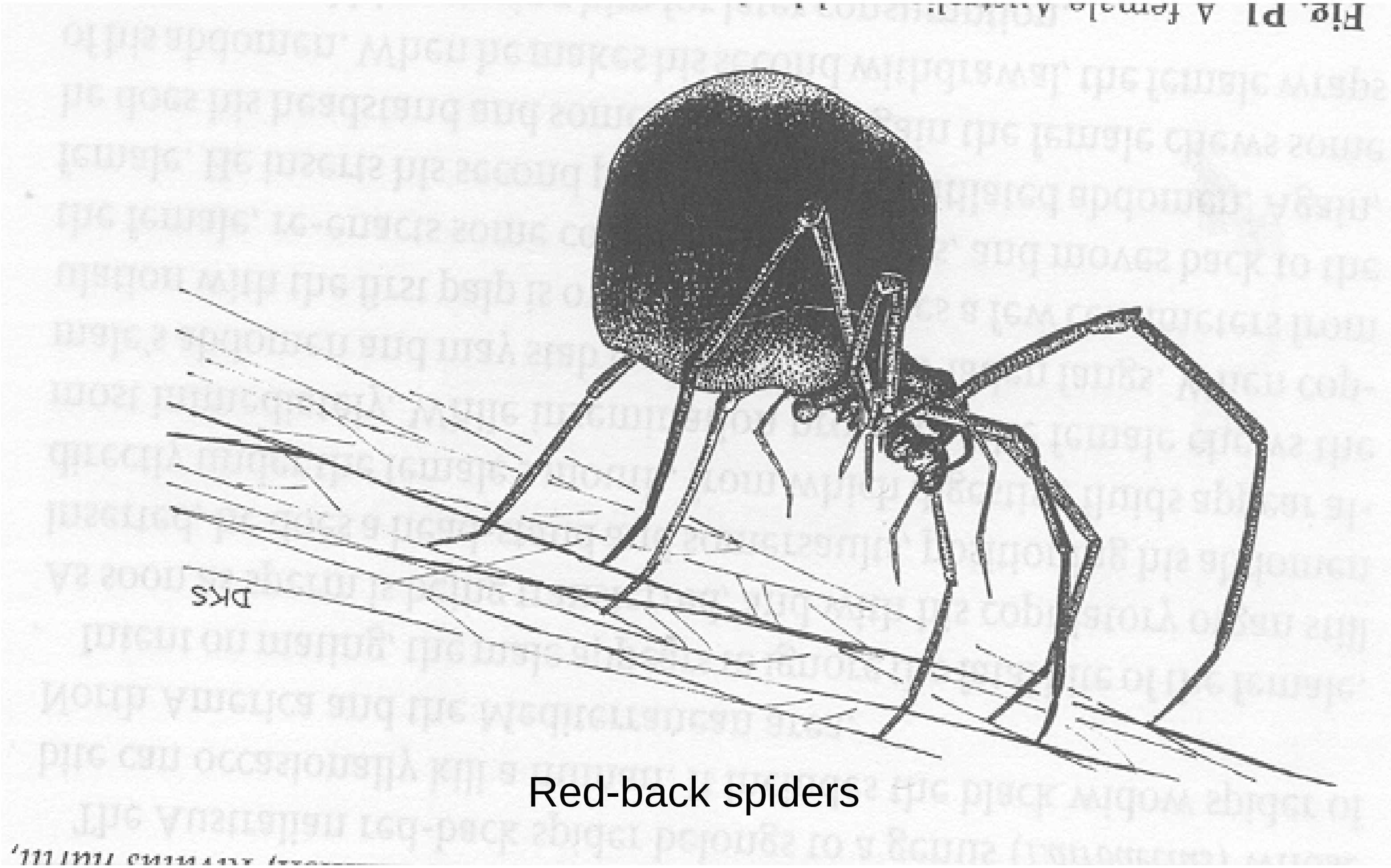


The Selfish Gene

Evolution of traits is determined by the fitness of the genes (alleles)

Not by fitness of individuals or phenotypes

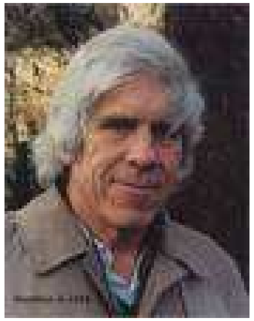
Great sex for girls: eat and breed



Red-back spiders

The direction of natural selection: Kin selection

- Hamilton: Kin Selection & evolution of social behaviors
  - Natural selection leads to organisms maximizing their Inclusive Fitness
  - IF = relatedness x benefit – cost (IF = rb – c)
    - This is fitness of the genes
  - Helping relatives has benefits for inclusive fitness (r > 0)
    - Social insects (bee's, ants & termites)
    - Kin selection can explain evolution of social behaviors



Key Factor: **relatedness**

- Relatives have the same genes

- Relatedness = correlation between genes in individuals

"Problem" with IF: this redefines fitness, a fundamental parameter in biology

Example of relatedness, cost and helping behavior

Blue-footed boobies

The older sib pushes the younger out of the nest
only with enduring food shortage.
i.e. when the cost is high, helping no longer benefits IF = rb-c

Group selection

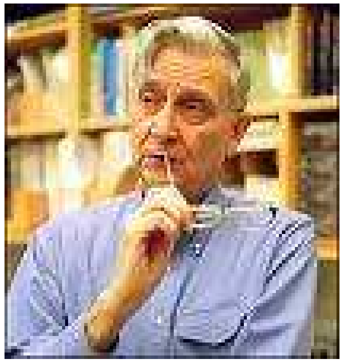
- In agriculture, animal breeders may (artificially) apply group selection
- In nature, natural selection may act between groups rather than individuals??

V.C. Wynne Edwards

- Wynne Edwards: Group Selection
  - “Individuals may behave for the good of the group”
  - Highly controversial
    - Are group units of selection?
    - Opposing selection within groups
      - Why not cheat?

Multilevel selection

- Fitness of individuals may depend on other individuals
  - less extreme variant of group selection
  - groups are not enduring entities of selection



EO Wilson

Artificial group selection has been very successful (M.J. Wade and co-workers)

Key Factor: **Level of selection**
- The origin of fitness differences between individuals (group vs. individual)

Intermezzo: Price' Theorem

- Response to selection: ΔA = Cov(A,w)/w_{avg}
  - (There is a second term relating to non-additivity)

The derivation:

$$\Delta A = \overline{A}^* - \overline{A}$$

$$\overline{A}^* = \frac{1}{n}\sum_n A_i \frac{w_i}{\overline{w}}$$

$$\rightarrow \Delta A = \frac{1}{n}\sum_n A_i \frac{w_i}{\overline{w}} - \overline{A}\frac{\overline{w}}{\overline{w}}$$

$$= \left[\overline{Aw} - \overline{A}\,\overline{w}\right] / \overline{w} = Cov(A, w) / \overline{w}$$

Response in a trait equals
the additive genetic covariance of
the trait with relative fitness

If higher breeding values go together with more offspring, then the trait value increases over generations

Powerful starting point for derivations

A quantitative genetic approach

- Fitness models
  - Consequences of social interactions for the evolution of <u>fitness</u>
- Trait models
  - Consequences of social interactions for the evolution of <u>traits</u>
  - Without social effects on trait values
  - Including social effects on trait values
    - Terminology
      - Social breeding values, competitive effects (animal breeders)
      - Indirect Genetic Effects (IGEs, Moore, Cheverud,..)
      - Associative effects (Griffing)

Fitness model of social effects

Polygenic quantitative model of Hamilton's rule

- Treat **fitness** as a quantitative trait
- Fitness is affected by
  - Properties of the individual (direct effects, D)
  - Properties of others (social effects, S)

$$W_i = A_{D,i} + E_{D,i} + \sum_{j \neq i} \left(A_{S,j} + E_{S,j} \right)$$

- When Cov(A_D,A_S) is negative, being social (A_S > 0) has a fitness disadvantage
  - Helping has a fitness cost on average, A_D is like "cost", A_S is like "benefit"
- Evolution of Altruism: $\Delta A_S > 0$ while Cov(A_D,A_S) < 0
  - Social "behavior" evolves while it is detrimental to the individual

Fitness model of social effects

- Note: This is a fitness model $\rightarrow$ it specifies reproductive success $\rightarrow$ you cannot model group selection on top of this model !

- Response to selection

$$W_i = A_{D,i} + E_{D,i} + \sum_{j \neq i} \left(A_{S,j} + E_{S,j} \right) \rightarrow$$

$$\Delta \overline{W} = \Delta \overline{A}_D + (n-1)\Delta \overline{A}_S \rightarrow$$

$$TBV_i = A_{D,i} + (n-1)A_{S,i}$$

- Price's Theorem: ΔA = Cov(w,A)/w_{avg} $\rightarrow$

$$\Delta \overline{A}_D = Cov(W_i, A_{D,i}) / \overline{W}$$

$$\Delta \overline{A}_S = Cov(W_i, A_{S,i}) / \overline{W}$$

Fitness model of social effects

- Evolution of Altruism ($\Delta A_S > 0$ while $Cov(A_D, A_S) < 0$)

$$\Delta \bar{A}_S = Cov(W_i, A_{S,i}) / \bar{W}$$
$$= Cov(A_{D,i} + \sum_{n-1} A_{S,j}, A_{S,i}) / \bar{W}$$
$$= \underbrace{\sigma_{A_{DS}}}_{\text{"}-c} + \underbrace{r(n-1)\sigma^2_{A_S}}_{rb\text{"}}$$

Hamilton's rule

$$\sigma_{A_{DS}} + r(n-1)\sigma^2_{A_S} > 0$$

This is empirically powerful !

- Cost and benefits translate into variance components
  - The covariance between direct and social effects is a measure of cost of social behavior, $c \to Cov(A_D, A_S)$.
  - The variance in social effects is a measure of the benefits of social behavior, $b \to (n-1)Var(A_S)$.

Fitness model of social effects

- Response to selection in fitness
  - Price's Theorem: $\Delta W = \mathrm{Cov}(TBV_i, W_i) \rightarrow$

$$\Delta \overline{W} = \left\{ [1-r] \underbrace{[\sigma^2_{A_D} + (n-1)\sigma_{A_{DS}}]}_{\text{This term can be negative}} + r\sigma^2_{TBV} \right\} / \overline{W}$$

Relatedness among interacting individuals prevents a decline in fitness due to competition

The relationship between Hamilton’s IF and Fisher’s FTNS

- Hamilton: natural selection targets IF
- Fisher FTNS: $\Delta W = Var_A(w)/w_{avg}$
- Previous page: ΔW can be negative

- How are we to interpret these conflicting statements?

- Solution
  - FTNS refers to IF: $\Delta IF = Var_A(w)/w_{avg} = \Delta(rb\text{-}c)$
  - “Full” change in fitness: $\Delta W = \Delta A_D + (n\text{-}1)\Delta A_S = \Delta(b\text{-}c)$
- Conclusion
  - FTNS and IF are in agreement
  - FTNS ignores a proportion (1-r) of the response in social effects
  - With social interactions, natural selection can drive a population to extinction

Conclusion on fitness models

- With social interactions, fitness depends on genes in others
  - Problem: Who's fitness is this?
- Hamilton solved this by defining inclusive fitness as a function of genes in the individual itself
  - Problem: This redefines fitness, how to measure IF?
- With social effects we can use a direct fitness model
- The response in fitness with social interactions can be expressed in measureable VC
  - By considering social breeding values, we get rid of frequency dependency $\rightarrow$ We can use the "usual" quantitative genetic framework
  - By introducing social breeding values, we make a non-additive problem additive
- The result is an expression of Hamilton's rule that can be applied empirically

Trait models for natural populations

- Consequences of social interactions for the evolution of trait values

- Objective
  - Compare group and kin selection approaches
  - Either with or without social effects

Kin selection approach (n = 2)

- Kin selection models focus on the effect of trait values of an individual on fitness of another individual
  - "neighbor-modulated approach"

$$W_i = constant + \beta_{W_D,P} P_i + \beta_{W_S,P} P_j + e_i$$

- The Beta's are so-called selection gradients
  - Regression coefficients of fitness on trait values
  - Direct selection gradient $\beta_{W_D,P}$
    - Effect of own trait value on own fitness
    - This is like cost
  - Social selection gradient $\beta_{W_S,P}$
    - Effect of trait value of neighbor on fitness of individual
    - This is like benefit

Group selection approach (n = 2)

- Group selection models specify fitness as a function of the mean trait value of the group and the individual deviation thereof:

$$W_i = constant + \beta_{W,\overline{P}_g} \overline{P}_g + \beta_{W,\Delta P} \Delta P_i + e_i$$

  - Mean trait value of the group: $\overline{P}_g = (P_i + P_j)/2$
  - Deviation of the individual from the mean: $\Delta P_i = P_i - \overline{P}_g$
  - Effect of group mean on fitness: $\beta_{W,\overline{P}_g}$
  - Effect of individual deviation on fitness: $\beta_{W,\Delta P}$

The relationship between both approaches

- The relationship between group selection and “cost and benefit”

$$\beta_{W,\overline{P}_g} = \beta_{W_D,P} + \beta_{W_S,P} = c + b$$

$$\beta_{W,\Delta P} = \beta_{W_D,P} - \beta_{W_S,P} = c - b$$

Conclusion

Cost and benefit in kin selection models relate directly to within and between group selection

Specifying cost and benefit means specifying group selection

Response to selection

- Response depends on both group selection and relatedness (kin)

$$\Delta\overline{G} = \tfrac{1}{2}\left[\beta_{W,\overline{P}_g}(1+r) \;+\; \beta_{W,\Delta P}(1-r)\right]Var(G)$$

- Interpretation:
  - Relatedness increases response due to between-group selection
    - (1+r)Var(G) is genetic variance between groups
  - Relatedness decreases response due to within-group selection
    - (1–r)Var(G) is genetic variance within groups
- Kin and group selection, rather than kin or group selection

Conclusion: Kin vs group selection theory

- Kin selection models implicitly have a group selection component
  - The cost and benefit specify the group selection process
- Group selection models implicitly have a relatedness (kin) component
  - Genetic variance within and between groups are determined by relatedness
- Each school denies the component of the other school

Response to selection: another parameterization

- The neighbor-modulated approach has a group selection interpretation

$$W_i = constant + \beta_{W_D,P} P_i + \beta_{W_S,P} P_j + e_i$$

$$= constant + \beta_{W_D,P} \left[P_i + \frac{\beta_{W_S,P}}{\beta_{W_D,P}} P_j \right] + e_i$$

$$= constant + \beta_{W_D,P} \left[P_i + g P_j \right] + e_i, \quad where\ g = \frac{\beta_{W_S,P}}{\beta_{W_D,P}} = b/c$$

g = 0 $\rightarrow$ individual selection
g = 1 $\rightarrow$ group selection
g is the degree of group selection
The ratio of benefits over costs corresponds to the degree of group selection

Response to selection: another parameterization

- Response to selection

$$\Delta\overline{G} = \beta_{W_D,P}\,\sigma^2_{A_D}\left[1+(n-1)gr\right]$$

- It is the product gr that determines the impact of kin&group selection on response
  - Group selection is equally important (in theory) as relatedness
  - When either g or r is zero, response reduces to $\Delta G = h^2 S$
- Evolution of altruism means $\Delta G > 0$ while $\beta_D < 0$
  - This requires that $1 + (n-1)gr < 0$
  - Which requires that both g and r are non-zero, that their product is negative, and that $|(n-1)gr| > 0$
  - This is a version of Hamilton's rule, illustrating both the relatedness and the group selection component of evolution of altruism.

Conclusion group and kin selection

- Response deviates from the breeder's equation when
  - Fitness differs among groups (g ≠ 0)
  - Groups consist of relatives (r ≠ 0)

$$\Delta\overline{G} = \beta_{W_D,P}\,\sigma^2_{A_D}\left[1+(n-1)gr\right]$$

Extension to social genetic effects on trait values (IGE's)

- Without IGEs: P = A + E, with IGEs:

$$P_i = A_{D,i} + E_{D,i} + \sum_{i \neq j}^{n-1} A_{S,j} + \sum_{i \neq j}^{n-1} E_{S,j}$$

$$\Delta \overline{G} = \beta_{W_D,P} \left\{ [g + r + (n-2)gr] \sigma^2_{TBV} + (1-g)(1-r) \left[\sigma^2_{A_D} + (n-1)\sigma_{A_{DS}} \right] \right\}$$

This is the same result as before, in the animal breeding approach

Response is symmetric in g and r

Relatedness and group selection have the same impact

Both g and r act directly on the TBV $\rightarrow$ adaptation

Extension to social genetic effects on trait values (IGE's)

$$\Delta\overline{G} = \beta_{W_D,P}\left\{[g+r+(n-2)gr]\sigma^2_{TBV} + (1-g)(1-r)\left[\sigma^2_{A_D} + (n-1)\sigma_{A_{DS}}\right]\right\}$$

- Three factors determine response to social selection
  - Relatedness (r)
  - Multilevel selection (g)
  - Indirect genetic effects (Var(A_S))
- IGE's in itself can reverse the direction of response to selection

$$\Delta\overline{G}_{g,r=0} = \beta_{W_D,P}\left[\sigma^2_{A_D} + (n-1)\sigma_{A_{DS}}\right]$$

Altruism can evolve without group selection or relatedness

$$\Delta\overline{G}_{g,r=0} > 0 \text{ when } \beta_{W_D,P} < 0 \text{ and } \left[\sigma^2_{A_D} + (n-1)\sigma_{A_{DS}}\right] < 0$$

Conclusions on social evolution

- Quantitative genetic models can explain social evolution, and are empirically powerful
- Key components
  - Relatedness
    - Correlation between genes in interacting individuals
  - Multilevel selection
    - Dependency of fitness on others
  - IGE's
    - Dependency of trait values on others
- Without IGE's
  - Both relatedness and group selection are required for response to deviate from h^2S
- With IGEs
  - You need neither relatedness nor group selection to explain altruism