Kin selection under blending inheritance

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Kin selection in *The Origin of Species*

- How to explain adaptations of neuters?
Kin selection in *The Origin of Species*

• How to explain adaptations of neuters?

“...these neuters often differ widely in instinct and in structure from both the males and fertile females, and yet, from being sterile, they cannot propagate their kind.”

“This difficulty, though appearing insuperable, is lessened, or, as I believe, disappears, when it is remembered that selection may be applied to the family... breeders of cattle wish the flesh and fat to be well marbled together; the animal has been slaughtered, but the breeder goes with confidence to the same family... Thus I believe it has been with social insects: a slight modification of structure, or instinct, correlated with the sterile condition of certain members of the community, has been advantageous to the community: consequently the fertile males and females of the same community flourished, and transmitted to their fertile offspring a tendency to produce sterile members having the same modification.”

Darwin (1859, Ch 7)

• The first kin selection argument
“The inclusion of kin selection here is dubious. Although Darwin was certainly aware that leaving progeny was important to the struggle for existence, *kin selection in the modern sense quantifies relatedness and the benefits of aiding kin a way that was not possible before the development of classical genetics*. Furthermore, it is formally selection between groups of kin.”

Borrello (2010, p8)

“The problem with the appeal to kin selection is that Darwin could not really have meant this, for he did not understand genetics... Because he didn’t know about genetics, we cannot read back into Darwin a perspective only available much later... He again brings out the notion of group selection.”

Cunningham (2010, p31)

• Does kin selection theory require an understanding of classical genetics?
Blending inheritance

• Informal model of inheritance, widely held prior to rediscovery of Mendelian genetics in 1900
• Blending inheritance implicitly underlies the arguments of Darwin (1859)
• Jenkin (1867) – “swamping argument”
• Popular account has it that this led Darwin to underplay natural selection, and emphasize use & disuse, in later editions of *The Origin of Species*
Paint-pot model

- Mathematical model of blending developed by Fisher (1930)
- Named the “paint-pot” theory of inheritance by Hardin (1959)
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\[ h = \frac{x + y}{2} + m \]

where:  
- \( h \) = heritable (i.e. “breeding”) value  
- \( x \) = mother’s heritable value  
- \( y \) = father’s heritable value  
- \( m \) = mutational effect

\[ \text{cov}(m,x) = \text{cov}(m,y) = E(m) = 0, \ E(x) = E(y) = E(h') \]
Blending inheritance under neutrality

• The change in the average heritable value is given by

\[
E(h) = \frac{E(x) + E(y)}{2} + E(m) = E(h')
\]

• Blending does not change the average heritable value in the population
• This refutes Jenkin’s (1867) “swamping argument” (cf Davis 1871; Bulmer 2004)
  - there is no tendency for the more common type to take over
The change in the heritable variance is given by

\[
\operatorname{var}(h) = \frac{1 + f}{2} \var(h') + \var(m)
\]

Where \( f = \frac{\operatorname{cov}(x,y)}{\sqrt{\operatorname{var}(x)\operatorname{var}(y)}} \), i.e. the coefficient of inbreeding.

Blending does reduce the heritable variance in the population, reducing the efficacy of NS (Fisher 1930).
• Assuming a constant input of mutational variation \((\text{var}(m))\) in every generation, the equilibrium variance is

\[
\text{var}(h) = \text{var}(h') = \frac{2\text{var}(m)}{1 - f}
\]

• i.e. assuming no inbreeding \((f = 0)\), half of the heritable variation is \textit{de novo}, and half is inherited from the previous generation
Kin selection under blending


• Fully general partition (Gardner et al. 2011, *J. Evol. Biol.* 24, 1020-1043)
Kin selection under blending


\[ \Delta_s E(h) = \text{cov}(v, h) \]

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\Delta_s E(h) = \text{cov}(v, h) = \beta_{v,h} \text{var}(h)
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\[
= [\beta_{v,h|H} + \beta_{v,H|h} \beta_{H,h}] \text{var}(h)
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Kin selection under blending


\[ \Delta_s E(h) = \text{cov}(v, h) \]
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\[ = [\beta_{v,h\mid H} + \beta_{v,H\mid h} \beta_{H,h}] \text{var}(h) \]

- Fully general partition (Gardner et al. 2011, *J. Evol. Biol.* 24, 1020-1043)
Relatedness (no mutation)

- Assume no inbreeding
- Full siblings are identical in the absence of *de novo* mutation

![Image showing relatedness]

- Individual values own life as equal to those of **one** sibling or **two** cousins
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**Blending**

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Blending

\[ r_{\text{SELF}} = 1 \]
\[ r_{\text{FULLSIB}} = 1 \]

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\[ r_{\text{SELF}} = 1 \]
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**Blending**

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\begin{align*}
    r_{\text{SELF}} &= 1 \\
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**Mendelian**

- $\rho_{\text{SELF}} = 1$
- $\rho_{\text{FULLSIB}} = \frac{1}{2}$
- $\rho_{\text{HALFSIB}} = \frac{1}{4}$
- $\rho_{\text{COUSIN}} = \frac{1}{8}$

- Individual values own life as equal to those of one sibling or two cousins
Relatedness (constant mutation)

- However, mutation erodes relatedness
- Full siblings need not be identical in the presence of *de novo* mutation

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- Individual values own life as equal to those of **two** siblings or **eight** cousins
Relatedness (constant mutation)

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\[ h = \frac{x + y}{2} + m \]

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\[ h = \frac{x + y}{2} + m \]

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1/2 of the variance between individuals

the other 1/2 of the variance

- Individual values own life as equal to those of two siblings or eight cousins
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Relatedness (variable mutation)

• Darwin believed that mutational input varied between generations

  “A change in the conditions of life, by specially acting on the reproductive system, causes or increases its variability.”
  Darwin (1859, Ch 4)

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\[ h = \sum_{l=1}^{2^n} \frac{x_{(l,n)}}{2^n} + \sum_{t=0}^{n-1} \sum_{l=1}^{2^t} \frac{m_{(l,t)}}{2^t} \]

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h = \sum_{l=1}^{2^n} \frac{x_{(l,n)}}{2^n} + \sum_{t=0}^{n-1} \sum_{l=1}^{2^t} \frac{m_{(l,t)}}{2^t} \quad r = \frac{v}{2^{2\mu}} \times \frac{\text{var}(h^{(\mu)})}{\text{var}(h^{(0)})} = \rho \times V
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    r &= \frac{\nu}{2^{2\mu}} \times \frac{\text{var}(h^{(\mu)})}{\text{var}(h^{(0)})} = \rho \times V \\
    \Delta_s E(h) &= [-c + br \text{var}(h)]
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- Individual values own life as equal to those of two siblings or eight cousins
Summary

- The rationale for social adaptation is **unaffected** by blending inheritance - e.g. the individual’s life is equal to those of two siblings or eight cousins
- Kin selection does **not** require genes
- Darwin **was** making a KS argument
- Eliminating the gene clarifies its role in the standard theory of kin selection - gene is not unit of selection: KS driven by **individual** fitness differences
- gene is not unit of adaptation: **individual** adapted to maximize her IF
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