

# The Price Equation

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## Abstract

The Price equation is a mathematical model of an evolutionary process. Its abstract nature allows it to be applied to evolutionary processes of different kinds, both biological and nonbiological.

My aim here is to give, in one place, simple and rigorous derivations of Price's equation and its application to kin and group selection, in particular to altruism. The equivalence of kin and group selection follows immediately.

## Evolution = Selection + Transmission Bias

Assign a number  $z$  to each member of a set  $S$ . Let  $\bar{z}$  be the  $z$ -average over members of  $S$ .

Partition  $S$  into mutually exclusive and exhaustive subsets  $S_i$ . Let  $Z_i$  be the  $z$ -average in  $S_i$ . Set  $q_i = |S_i|/|S|$ .<sup>1</sup> Then  $\bar{z}$  will also be written  $\bar{Z} = \sum q_i Z_i$ , a weighted average of the  $Z_i$ . We still use  $\bar{z}$  when it is regarded as an average of  $z$ -values of members of  $S$ .

Partition a second set  $S'$  into an equal number of subsets  $S'_i$ , with analogous quantities  $z'$ ,  $\bar{z}'$ ,  $Z'_i$ ,  $q'_i$ . In general  $|S'| \neq |S|$ .

Set  $\Delta\bar{z} = \bar{z}' - \bar{z}$ ,  $\Delta Z_i = Z'_i - Z_i$ , and  $\Delta q_i = q'_i - q_i$ .

*Theorem* (Price equation). 
$$\Delta\bar{z} = \sum \Delta q_i Z_i + \sum q'_i \Delta Z_i. \quad (1)$$

The terms in the equation have intuitive names:

- $\Delta\bar{z}$  is the *evolution* of  $\bar{z}$  from  $S$  to  $S'$ .
- $\sum \Delta q_i Z_i$  is the *selection* part of the evolution of  $\bar{z}$ . It measures the “success” of  $z$  from  $S$  to  $S'$  in terms of the averages  $Z_i$ .
- $\sum q'_i \Delta Z_i$  is the *transmission bias* part of the evolution of  $\bar{z}$ . It is a weighted average of the  $z$ -average changes from the  $S_i$  to the  $S'_i$ .

*Proof:* 
$$\begin{aligned} \Delta\bar{z} &= \sum q'_i Z'_i - \sum q_i Z_i = \sum (q'_i - q_i) Z_i + \sum q'_i (Z'_i - Z_i) \\ &= \sum \Delta q_i Z_i + \sum q'_i \Delta Z_i. \end{aligned}$$

Price's equation is a trivial algebraic identity (a tautology). But it usefully separates the evolution  $\Delta\bar{z}$  into two parts in a very general setting.

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<sup>1</sup>Notation:  $|S|$  is the number of members of the set  $S$ .

## Covariance Form

Set  $W_i = |S'_i|/|S_i|$ , the *fitness* of  $S_i$ , and  $\bar{w} = |S'|/|S|$ , the *fitness* of  $S$ . Then<sup>2</sup>

$$\bar{w}q'_i = \frac{|S'|}{|S|} \frac{|S'_i|}{|S_i|} = \frac{|S_i|}{|S|} \frac{|S'_i|}{|S_i|} = q_i W_i.$$

Sum this:  $\bar{w} = \overline{W_i}$ . Use these to reformulate the right side of Price's Eq. (1):<sup>3</sup>

$$\begin{aligned} \bar{w} \sum \Delta q_i Z_i &= \bar{w} \sum q'_i Z_i - \bar{w} \sum q_i Z_i = \sum q_i W_i Z_i - \overline{W_i} \overline{Z_i} \\ &= \overline{W_i Z_i} - \overline{W_i} \overline{Z_i} = \text{Cov}(W_i, Z_i). \\ \bar{w} \sum q'_i \Delta Z_i &= \sum q_i W_i \Delta Z_i = \overline{W_i \Delta Z_i}. \end{aligned}$$

Substitute in Eq. (1):

$$\boxed{\bar{w} \Delta \bar{z} = \text{Cov}(W_i, Z_i) + \overline{W_i \Delta Z_i}.} \quad (2)$$

This is the *covariance form* of Price's equation. The selection  $\sum \Delta q_i Z_i$  in Eq. (1) translates to  $\text{Cov}(W_i, Z_i)/\bar{w}$  in Eq. (2). The better the  $Z_i$  covary with the fitnesses  $W_i$ , the stronger the selection for  $z$ . Intuitive!

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<sup>2</sup>One can also see directly that  $q'_i = q_i \frac{|W_i|}{\bar{w}}$ .

<sup>3</sup>A straightforward calculation shows that  $\overline{W_i Z_i} - \overline{W_i} \overline{Z_i} = \overline{(W_i - \overline{W_i})(Z_i - \overline{Z_i})}$ , just as with un-weighted averages. The right side shows the *meaning* of covariance.

## A Biological Interpretation

$S$  is a set of *individuals*, each with a value  $z$  of some *phenotypic* trait.

(Natural selection acts on phenotypes, regardless of their genetic basis.)

$S_i$  is the set of individuals with trait value  $z_i$ .

$S'$  is the set of *offspring* of the individuals, each with trait value  $z'$ .

$S'_i$  is the set of offspring of individuals in  $S_i$ .<sup>4</sup>

A special case of Eq. (2) occurs when each set  $S_i$  is an individual  $j$  in  $S$ . At this individual level biologists usually set the transmission bias to zero:<sup>5</sup>

$$\boxed{\bar{w}\Delta\bar{z} = \text{Cov}(w_j, z_j)}. \quad (3)$$

Here  $w_j$  is the fitness of individual  $j$  – the number of its offspring<sup>6,7</sup> – and  $z_j$  is the  $z$ -value of individual  $j$ . The covariance represents the natural selection part of evolution.

## Altruism

Many organisms exhibit *altruistic* behavior which benefits others' fitness at a potential cost to their own. For example, some animals give an alarm call to their neighbors when they see a predator, endangering themselves. This poses a challenge to the theory of natural selection, if understood as “survival of the fittest”: how can altruism evolve? Darwin was well aware of the challenge.

Two answers to the question are developed here: *kin selection* and *group selection*.

Kin and group selection both use the notion of a *group*. “A group is defined as a set of individuals that influence each other's fitness with respect to a certain trait but not the fitness of those outside the group.”<sup>8</sup> Geographically proximate individuals need not be a group, even if they interact socially. Groups will be represented by the sets  $S_i$  in our formalism.

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<sup>4</sup>For asexual reproduction. For sexual reproduction, each individual contributes  $\frac{1}{2}$  of its offspring to its  $S'_i$ .

<sup>5</sup>For asexual reproduction simply assume that there are no mutations. Then  $\Delta z_j = 0$ , so the transmission bias is zero. This doesn't work for sexual reproduction because we expect  $\Delta z_j \neq 0$  even with no mutations. According to Price, “If meiosis and fertilization are random with respect to [an altruistic gene], the [transmission bias] will be zero except for statistical sampling effects (random drift), and these will tend to average out to give [Eq. (3)].” G. Price, *Selection and Covariance*, Nature **227**, 520 (1970). I don't follow Price very well here.

Also: “[Eq. (3)] . . . concerns only selection itself, not the response to selection; the latter depends on the fidelity of transmission across generations, hence on facts about the inheritance mechanism etc. Throughout this paper, our concern will be with selection itself, hence the within-generation change in  $z$ , rather than the response to selection. So we do not need to worry about the genetic basis of  $z$ , whether it is heritable, and so on. This separation of selection from the response to selection is standard fare in quantitative genetics.” S. Okasha, *Multi-Level Selection, Price's Equation and Causality*.

[http://www.lse.ac.uk/CPNSS/pdf/DP\\_withCover\\_Causality/CTR13-03-C.pdf](http://www.lse.ac.uk/CPNSS/pdf/DP_withCover_Causality/CTR13-03-C.pdf)

<sup>6</sup>For asexual reproduction. For sexual reproduction divide by 2.

<sup>7</sup>So  $W_i$  is the  $w$ -average in  $S_i$  and  $\bar{w}$  is the  $w$ -average in  $S$ .

<sup>8</sup>E. Sober and D. Wilson, *Unto Others*, Harvard University Press, 1998, p. 92.

## Kin Selection

*Kin selection* theory points out that an altruistic trait can confer a group benefit (by means which might not be obvious) in addition to the cost to individuals. And under suitable conditions the trait will be favorably selected.

The theory is due to William Hamilton. He gave two, very different, versions.

Here is a caricature of the first (1964) version,<sup>9</sup> to help gain intuition. It omits important points. Here Hamilton interpreted survival of the fittest as survival of the fittest *genes*, not the fittest *individuals*.

By definition, an altruistic act entails a fitness cost  $c > 0$  to the altruist. Let the act confer a fitness benefit  $b$  to others in the altruist's group. Let  $r$  be the probability that others in the group exhibit the altruistic trait. Thus  $r = 1$  for identical twins,  $\frac{1}{2}$  for siblings or parent-child, . . . .

*Hamilton's rule* states that the trait will be selected for if and only if  $rb > c$ , i.e., the benefit of the act, discounted by  $r$ , exceeds its cost. Intuitive! It is one way to see that a trait unfavorable to its carrier can be selected for.

Hamilton: "An animal acting on this principle would sacrifice its life if it could thereby save more than two brothers"<sup>10</sup> (e.g.,  $b = 3c$ , so  $rb = \frac{1}{2}(3c) > c$ ).

Hamilton's second (1975) version is based on Price's equation. It is concerned with altruistic traits, not genes. One possibility for assigning trait values is to set  $z = 1$  if an individual possesses the trait and  $z = 0$  if not.

Individual  $j$  belongs to some group  $S_i$ . Let  $y_j$  be the  $z$ -average in  $S_i$ . Write a least squares approximation to  $w_j$ , including the residual  $\epsilon_j$ :

$$w_j = w_0 + by_j - cz_j + \epsilon_j. \quad (4)$$

Take the covariance with  $z_j$ :

$$\text{Cov}(w_j, z_j) = \text{Cov}(w_0, z_j) + b\text{Cov}(y_j, z_j) - c\text{Cov}(z_j, z_j) + \text{Cov}(\epsilon_j, z_j). \quad (5)$$

In this equation  $\text{Cov}(w_0, z_j) = 0$ , as  $w_0$  is constant;  $\text{Cov}(z_j, z_j) = \text{Var}(z_j)$ ; and  $\text{Cov}(\epsilon_j, z_j) = 0$ .<sup>11</sup> Define  $r = \text{Cov}(y_j, z_j) / \text{Var}(z_j)$ . Substitute, using Eq. (3):

$$\bar{w}\Delta\bar{z} = (rb - c)\text{Var}(z_j). \quad (6)$$

We have the second version of Hamilton's rule (assume  $\bar{w} \neq 0, \text{Var}(z_j) \neq 0$ ):

$$\boxed{\Delta\bar{z} > 0 \Leftrightarrow rb > c.} \quad (7)$$

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<sup>9</sup>W. Hamilton, *The Genetical Evolution of Social Behaviour, I & II*, Journal of Theoretical Biology **7**, 152 (1964).

<sup>10</sup>W. Hamilton, *The Evolution of Altruistic Behavior*, American Naturalist **97**, 354 (1963).

<sup>11</sup>See p. 14 for  $\text{Cov}(\epsilon_j, z_j) = 0$ .

The  $r = \text{Cov}(y_j, z_j) / \text{Var}(z_j)$  here is more general than the relatedness  $r$  in the first version of Hamilton’s rule. The covariance shows that  $r$  is “A statistical tendency for the recipients of altruism to be altruists themselves.”<sup>12</sup> Hamilton: “Kinship should be considered just one way of getting positive regression [i.e.,  $r$ ] of genotype in the recipient, and it is this positive regression that is vitally necessary for altruism.”<sup>13</sup>

The term *kin selection* does not accurately describe this second version of Hamilton’s rule. *Inclusive fitness* is better and often used. But the distinction is often not made.

Even  $r < 0$  (i.e.,  $\text{Cov}(y_j, z_j) < 0$ ) is possible, making possible the phenomenon of *spite*.<sup>14</sup> By definition, a spiteful trait has  $b < 0$  as well, so  $rb > 0$ . This makes  $rb > c$  possible. Then an individual possessing the trait harms itself and is harmed by others in its group. Yet such traits can be favorably selected!

Until recently, most discussions of kin selection have defined  $b$  as the fitness benefit bestowed *by* individuals *on* their group. Equation (4) is different: it defines  $b$  as the fitness benefit bestowed *on* individuals *by* their group. This is the *direct fitness* approach to inclusive fitness. “Direct fitness can be mathematically easier to work with and has recently emerged as the preferred approach of theoreticians.” And “These two approaches are computationally equivalent.”<sup>15</sup>

## Kin Selection Acceptance

Kin selection is widely accepted. Yet it is contentious. I cite several opinions.

Bourke<sup>16</sup> provides a list of successful tests of inclusive fitness theory.

There are cases where “a striking quantitative fit between the predictions of kin selection theory and the empirical patterns that are observed.”<sup>17</sup> Several studies are cited.

Gardner et al. provide a listing of and rebuttals to claims that kin selection is limited in its application.<sup>18</sup>

A pair of titles: *What’s wrong with inclusive fitness?* and *There is nothing wrong with inclusive fitness*.<sup>19</sup>

<sup>12</sup>Samir Okasha, *Evolution and the Levels of Selection* (2009), p. 182.

<sup>13</sup>Hamilton, *The Evolution of Altruistic Behavior*, p. 337. See also Okasha, *ibid.*

<sup>14</sup>W. Hamilton, *Selfish and spiteful behaviour in an evolutionary model*, *Nature* **117**, 228 (1970). S. West and A. Gardner, *Altruism, Spite, and Greenbeards*, *Science* **327**, 1341 (2010).

<sup>15</sup>P. D. Taylor et al, *Direct fitness or inclusive fitness: how shall we model kin selection?* *Journal of Evolutionary Biology* **20**, 301 (2007). But see minor caveats about equivalence.

<sup>16</sup>Andrew F. G. Bourke, *The validity and value of inclusive fitness theory*, *Proceedings of the Royal Society B*, **278**, 3313-32 (2011), Table 1.

<sup>17</sup>A Griffin and S. West, *Kin selection: fact and fiction*, *Trends in Ecology & Evolution* **17**, 15 (2002).

<sup>18</sup>A. Gardner et al., *The genetical theory of kin selection*, *ibid.*, Table 2.

<sup>19</sup>TRENDS in Ecology and Evolution **21**, 597-600 (2006).

“While many studies have provided qualitative support for Hamilton’s rule, quantitative tests have not yet been possible due to the difficulty of quantifying the costs and benefits of helping acts. Here we use a simulated system of foraging robots . . . over hundreds of generations of selection in populations with different  $c/b$  ratios, [and] show that Hamilton’s rule always accurately predicts the minimum relatedness necessary for altruism to evolve.”<sup>20</sup>

A criticism of this study: “Their study is based on computer simulations and is not an empirical test. No actual robots were used to generate the results concerning Hamilton’s rule. Moreover, the computer simulation is arranged such that altruistic behavior spreads if  $br > c$ . No other outcome would have been possible. It is not surprising that Hamilton’s rule holds in a computer simulation that is specifically designed to validate it.”<sup>21</sup>

A 2010 paper in *Nature* by M. Nowak, C. Tarnita, and E. O. Wilson claims that “kin selection almost never holds”.<sup>22</sup> The paper caused a furor. A rebuttal with 137 (!) signatures, followed by a reply by the original authors, was also printed in *Nature*.<sup>23</sup> The original authors have also posted a “brief statement”.<sup>24</sup>

In 2013 Nowak and Wilson continued their attack with *Limitations of inclusive fitness*, this time with B. Allen.<sup>25</sup> From the paper: “The dominance of inclusive fitness theory has held up progress in this area for many decades.” And “There is no problem in evolutionary biology that requires an analysis based on inclusive fitness.”

Several authors have issued rebuttals.

In 2015, David Queller and colleagues claimed that the conclusions of the 2010 paper are wrong, and in fact their “modeling strategy yields results that confirm important insights from kin selection and inclusive fitness.”<sup>26</sup>

Bourke’s paper<sup>27</sup> is a response.

Birch and Okasha<sup>28</sup> have provided a balanced (to me) commentary on the dispute. They carefully distinguish between the kin selection and inclusive fitness versions of Hamilton’s rule and claim that the controversy is caused by Nowak et al. using the kin selection version and their opponents the inclusive fitness version.

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<sup>20</sup>M. Weibel, et al., *A Quantitative Test of Hamilton’s Rule for the Evolution of Altruism*, PLoS Biology, e1000615 (2011).

<sup>21</sup>*A brief statement about inclusive fitness and eusociality*, [www.ped.fas.harvard.edu/IF\\_Statement.pdf](http://www.ped.fas.harvard.edu/IF_Statement.pdf).

<sup>22</sup>*The evolution of eusociality*, *Nature* **466**, 1057 (2010).

<sup>23</sup>Inclusive fitness theory and eusociality. *Nature* **471**, E1, Issue 7339 (2011).

<sup>24</sup>*A brief statement about inclusive fitness and eusociality*, *ibid*.

<sup>25</sup>PNAS **110** 20135 (2013).

<sup>26</sup>Liao X, Rong S, Queller DC, *Relatedness, Conflict, and the Evolution of Eusociality* PLoS Biol **13**(3): e1002098. Their references [14-22] have “extensively criticized [Nowak et. al] as depending on multiple misconceptions.” See <http://phys.org/news/2015-03-duel-mathematical-theory-genetics-altruism.html> for a good summary.

<sup>27</sup>, *loc. cit*.

<sup>28</sup>J. Birch and S. Okasha, *Kin Selection and Its Critics*, *BioScience* **65**, 22-32 (2015). The paper is freely downloadable at <http://bioscience.oxfordjournals.org/content/65/1/22>.

## Group Selection

Kin selection theory models both the individual cost  $c$  of an altruistic trait and its group benefit  $b$  (Eq. (4)). It shows that under suitable conditions the trait will be favorably selected.

*Group selection* theory does the same. But it looks at the situation in a different way.

Recall Price's Eq. (2) for the groups  $S_i$ :

$$\bar{w}\Delta\bar{z} = \text{Cov}(W_i, Z_i) + \overline{W_i\Delta Z_i}. \quad (8)$$

Call the selection  $\text{Cov}(W_i, Z_i)$  *between-group selection*.

Now apply Eq. (3) to each  $S_i$  (not  $S$  as before):  $W_i\Delta Z_i = \text{Cov}_i(w_j, z_j)$ . Take the weighted average over  $i$ :  $\overline{W_i\Delta Z_i} = \overline{\text{Cov}_i(w_j, z_j)}$ . Call this selection average  $\overline{\text{Cov}_i(w_j, z_j)}$  *within-group selection*. It is negative for an altruistic trait, as such a trait is by definition disadvantageous to an individual bearing it.

Substitute into Eq. (8):

$$\bar{w}\Delta\bar{z} = \text{Cov}(W_i, Z_i) + \overline{\text{Cov}_i(w_j, z_j)}. \quad (9)$$

Thus (assume  $\bar{w} \neq 0$ )

$$\boxed{\Delta\bar{z} > 0 \iff \text{Cov}(W_i, Z_i) + \overline{\text{Cov}_i(w_j, z_j)} > 0.} \quad (10)$$

This equation shows that the trait is favored if and only if the between-group selection  $\text{Cov}(W_i, Z_i)$  overpowers the negative within-group selection  $\overline{\text{Cov}_i(w_j, z_j)}$ . Intuitive! It is one way to see that a trait can be favored despite being unfavorable to its carriers.

The term *multilevel selection* is a better description than *group selection*. It emphasizes that the between-group and within-group selection terms in Eq. (9) act at different *levels* – groups and individuals, respectively.

Kin selection and group selection divvy up the same  $\bar{w}\Delta\bar{z}$  on the left sides of Eqs. (6) and (9) in different ways on their right sides. For kin selection, the right side comes from applying Price's equation to individuals  $j$  in  $S$ . For group selection, it comes from applying the equation to the groups  $S_i$ .<sup>29</sup>

"[Group selection] is a partitioning of selection into between-group and within-group components. The expectations and covariances are all weighted by group size, however, making clear that this is a different viewpoint [from kin] selection acting at the level of individuals."<sup>30</sup>

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<sup>29</sup>Both right sides use the approximation Eq. (3) at the individual level, i.e., they set the transmission bias at the individual level to zero.

<sup>30</sup>J. Marshall, *Group selection and kin selection: formally equivalent approaches*, Trends in Ecology and Evolution **26**, 325 (2011), p. 327.

## Group Selection Examples

George Williams believed that group selection is rare. He did accept one example in his 1966 book: the “only convincing evidence for the operation of group selection” was a study on house mice.<sup>31</sup> But then from *The Dawn of Darwinian Medicine* (1991): “The evolutionary outcome will depend on relative strengths of within-host and between-host competition in pathogen evolution. This is a clear example of group vs. individual (clone) selection for altruism.”<sup>32</sup>

Many thousands of species have female biased sex ratios. Colwell (1981) explained unbiased and biased sex ratios in group selection terms.<sup>33</sup> Williams (1992): “I think it is desirable ... to realize that selection in female-biased Mendelian populations favors males, and that it is only the selection among such groups that can favor the female bias.”<sup>34</sup> According to Avilés (2012), “Although the initial reaction to Colwell’s interpretation was rather negative, his views are now generally accepted among those close to the field of sex ratios.”<sup>35</sup>

D. S. Wilson and E. O. Wilson (2008) give several examples of group selection: the Portuguese man-of-war, the cellular slime mold *Dictyostelium discoideum*, meiotic drive, and eusocial insect colonies.<sup>36</sup>

Chuang et al. (2009) give a vivid description of laboratory group selection experiments with controlled parameters.<sup>37</sup>

From a 2014 paper about social spiders: “Our study shows group selection acting in a natural setting, on a trait known to be heritable, and that has led to a colony-level adaptation.”<sup>38</sup> This assertion has been criticised and defended.<sup>39</sup>

The opinion (first?) expressed by Williams, that group selection requires special conditions and so must be rare, is widespread. However, simulations have shown that “group selection is able to override counteracting individual selection under a much broader range of conditions than previously believed”<sup>40</sup> and that “under general assumptions and a wide range of parameter values, predatory restraint may evolve as a group adaptation.”<sup>41</sup>

<sup>31</sup>G. Williams, *Adaptation and Natural Selection*, p. 117.

<sup>32</sup>G. Williams and R. Nesse, *The Quarterly Review of Biology* **66**, 1 (1991).

<sup>33</sup>R. Colwell, *Group Selection is Implicated in the Evolution of Female-Biased Sex Ratios*, *Nature* **190**, 401 (1981).

<sup>34</sup>G. Williams, *Natural Selection: Domains, Levels and Challenges*, p. 49.

<sup>35</sup>L. Avilés, *Sex Ratio Evolution in Subdivided Populations*,

<http://domingo.zoology.ubc.ca/isc350/DarwMedAnnotBiblio.html>.

<sup>36</sup>*Evolution “for the Good of the Group”*, *American Scientist* **96**, 380 (2008).

<sup>37</sup>J. S. Chuang et al., *Simpson’s Paradox in a Synthetic Microbial System*, *Science* **323**, 272 (2009). The term “group selection” is not used, but see the group selection criterion Eq. (10) at the end of the caption for Figure 1. The figure is quite instructive.

<sup>38</sup>J. Pruitt, C Goodnight, *Site-specific group selection drives locally adapted group compositions*, *Nature October 2014*. T. Linksvayer, *Survival of the fittest group*, *Nature October 2014*. A. Wild, *Elusive Form of Evolution Seen in Spiders*, *Quanta Magazine*, <http://www.simonsfoundation.org/quanta/20141002-in-social-spiders-evidence-that-groups-evolve/>.

<sup>39</sup>*Nature* 27 August 2015, **524** E1 (2015).

<sup>40</sup>*Simulation of group selection models*, <http://www.agner.org/evolution/groupsel/>.

<sup>41</sup>*Multilevel Selection and the Evolution of Predatory Restraint*, In *Artificial Life VIII*, Standish, Abbass, Bedau (eds.) (MIT Press) 2002. pp. 146-152.



## Old vs. New Group Selection

Group selection was the generally accepted explanation of altruism into the 1960's, culminating with the publication of V.C. Wynne-Edwards' book *Animal Dispersion in Relation to Social Behavior* (1962). The mathematics in the book is limited to graphs.

Hamilton's kin selection (1964) provided an alternative mathematical explanation. J. Maynard Smith's *Group selection and kin selection* (1964)<sup>42</sup> and George Williams' *Adaptation and Natural Selection* (1966) both advocated kin selection and rejected group selection. Richard Dawkins' semi-popular *The Selfish Gene* (1976) followed in the same vein. They were such powerful voices that mention of group selection became pretty much forbidden.

Except for Hamilton, who accepted group selection. He writes (1998) of "telling [Price] enthusiastically [in 1974] that through a 'group level' extension of his formula I now had a far better understanding of group selection and was possessed of a far better tool for all forms of selection acting at one level or at many than I had ever had before."<sup>43</sup>

Experiments with flour beetles by Wade (1977) showed strong group selection.<sup>44</sup> Wade: "Group selection might very well be one of the greatest creative forces for evolutionary change".

Starting in the late 1980's a "new" group selection, based mathematically on Price's equation, has emerged. It is different from the "old" group selection of Wynne-Edwards.

"One way of conceptualizing the difference between the old and new group selection models is that the new group selection models rely on within population group selection, whereas old group selection theory worked on between population group selection."<sup>45</sup>

"Most formal [new] group selection models . . . aim to explain the evolution of an *individual* character, often altruism, in a group-structured population."<sup>46</sup> The emphasis (in the original) on *individual* character is opposed to *group* character. The quote exactly describes Eq. (10), with  $\Delta\bar{z}$  over individuals on the left, and group quantities on the right.

"Everyone agrees that group selection occurs."<sup>47</sup> "Unfortunately", O. Eldakar and D. S. Wilson add, "'everyone' refers only to those who seriously study the subject."<sup>48</sup> (I'll come to Dawkins later.)

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<sup>42</sup>J. Maynard Smith, *Nature* **201**, 1145 (1964).

<sup>43</sup>W. Hamilton, *Narrow Roads of Gene Land: The Collected Papers of W. D. Hamilton Volume 1* (1998), p. 173.

<sup>44</sup>M. J. Wade, *An Experimental Study of Group Selection*, *Evolution*, **31**, 134-153 (1977).

<sup>45</sup>S. West, A. Griffen, A. Gardner, *Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection*, *Journal of Evolutionary Biology* **20**, 415 (2007).

<sup>46</sup>Okasha, *ibid.*, p. 179.

<sup>47</sup>A. Gardner, quoted in *The needs of the many*, *Nature* **456**, 296 (2008).

<sup>48</sup>*Eight Criticisms Not to Make about Group Selection*, *Evolution* **65**, 15 (2011).

## Kin and Group Selection are Equivalent

Starting with  $z$  values on partitioned sets  $S$  and  $S'$  we defined  $\Delta\bar{z} = \bar{z}' - \bar{z}$ . Then using the biological interpretation on Page 3 we derived two conditions, each equivalent to  $\Delta\bar{z} > 0$ : the condition for kin selection in Eq. (7) and the condition for group selection in Eq. (10). Conclusion: *kin selection and group selection are equivalent*. If you accept one, then you must accept of the other. Don't just take my word calculations for it:

“There is widespread agreement that group selection and kin selection ... are formally equivalent.”<sup>49</sup>

“The mathematical equivalence of [inclusive fitness and group selection theories] has long been known.”<sup>50</sup>

“The inclusive-fitness and group-selection models presented here do not represent alternative processes. Nor is one a subset of the other. Instead, they are simply alternative ways of viewing the same selection process.”<sup>51</sup>

“It has long been understood that the kin selection and multilevel [group] selection approaches to social evolution are mathematically equivalent, and merely represent different partitions of the same evolutionary process.”<sup>52</sup>

“Kin selection and group selection are now broadly understood to describe the same evolutionary process from complementary perspectives.”<sup>53</sup>

A choice between kin and group selection depends on technical convenience and insight obtained, which might differ from application to application. Opinions:

“At one level, kin selection and group selection are just different ways of doing the maths or conceptualizing the evolutionary process. However, from a practical point of view, it could not be clearer that the kin selection approach is the more broadly applicable tool that we can use to understand the natural world.”<sup>54</sup> This is the prevailing view.

Group selection “provides valuable insights into the evolution of social behavior that are not so easy to see when selection is viewed as an individual-level or gene-level process.”<sup>55</sup>

With a kin selection explanation, Eq. (7), “the idea that altruism is good for the group but bad for the individual has been lost. ... What is good for the individual can conflict with what is good for the group [Eq. (9)]. The concept of adaptation should reflect this fact.”<sup>56</sup>

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<sup>49</sup>The needs of the many, Nature **456**, 296 (2008).

<sup>50</sup>Marshall, *ibid*.

<sup>51</sup>D. Queller, *Quantitative Genetics, Inclusive Fitness, and Group Selection*, The American Naturalist **139** 540 (1992), p. 554.

<sup>52</sup>A. Gardner et al., *The genetical theory of kin selection*, *ibid*.

<sup>53</sup>A. Wild, *ibid*.

<sup>54</sup>S. West, A. Griffen, A. Gardner, *Social semantics: how useful has group selection been?*, Journal of Evolutionary Biology **21**, 374 (2008).

<sup>55</sup>R. McElreath and R. Boyd, *Mathematical Models of Social Evolution*.

<sup>56</sup>E. Sober and D. S. Wilson, *Adaptation and Natural Selection revisited*, Journal of Evolutionary Biology **24**, 462 (2011).

J. Birch and S. Okasha point out that multilevel selection sometimes gives a better *causal* account of selection.<sup>57</sup> Imagine a segregation distorter allele having deleterious effects on the fitness of its bearer. “It is very natural to describe the selection pressures operating on this allele in multilevel terms: At the gene level, there is selection in its favor, but at the organism level, there is selection against it.” The equivalent inclusive fitness description misses this causal structure. “When we are looking at selection occurring both between and within organisms, a multilevel description seems clearly more apt, causally speaking.” In other examples inclusive fitness gives a better causal account.

### Coyne, Pinker, and Dawkins

They deserve no space here, as they have contributed nothing but confusion about group selection. But they are outspoken and heard, so I address them.

Coyne, *The demise of group selection*,<sup>58</sup> and Pinker, *The False Allure of Group Selection*,<sup>59</sup> attack group selection, with Dawkins cheering them on.<sup>60,61</sup> They mostly beat the dead horse of old group selection.

Coyne, first sentences: “The idea that adaptations in organisms result from ‘group selection’ (selection among groups that differentially bud off subgroups, with those having good ‘group traits’ becoming more numerous), . . . has undergone a bit of resurgence in popular culture. This is in stark contrast to the views of most evolutionary biologists.” I don’t see subgroups budding off in Eq. (9). And “most evolutionary biologists” doesn’t include several I’ve quoted.

I quoted a paper endorsing the equivalence of kin and group selection, while finding kin selection “more broadly applicable”.<sup>62</sup> Coyne describes the paper as “three smart biologists taking group selection apart”. He suggests reading the paper starting at a specific paragraph. In it I find “We emphasized that the new group selection methodology is not only correct and a potentially useful tool”. I don’t read this as “taking group selection apart”. At least Coyne keeps the discussion at a high level, writing of “the intellectual vacuity of group selection.”

In February 2013 Coyne noticed a 2009 textbook claim that 1-1 sex ratios are evidence against group selection. He posted *Another case of individual selection trumping group selection* in his blog.<sup>63</sup> He cites only Fisher’s (1930) argument for a 1-1 ratio, mentioning only in passing “some exceptions”. But what about the exceptions? Coyne does not refer to the group selection explanation of unbiased *and* biased sex ratios cited above.

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<sup>57</sup>Birch and Okasha, *ibid*, p.30.

<sup>58</sup><https://whyevolutionistrue.wordpress.com/2012/06/24/the-demise-of-group-selection/>.

<sup>59</sup><http://edge.org/conversation/the-false-allure-of-group-selection>.

<sup>60</sup>[http://www.richarddawkins.net/news\\_articles/2012/6/24/the-demise-of-group-selection](http://www.richarddawkins.net/news_articles/2012/6/24/the-demise-of-group-selection).

<sup>61</sup>[http://www.richarddawkins.net/news\\_articles/2012/7/13/pinker-s-reply-on-group-selection](http://www.richarddawkins.net/news_articles/2012/7/13/pinker-s-reply-on-group-selection).

<sup>62</sup>S. West, A. Griffen, A. Gardner, *ibid*.

<sup>63</sup><https://whyevolutionistrue.wordpress.com/2013/02/27/another-case-of-individual-selection-trumping-group-selection>.

Pinker's essay is mostly about the application of kin and group selection to human behavior. These notes are about the mathematical foundation of kin and group selection, so I only address Pinker's comments about this.

Pinker writes: "The more carefully you think about group selection, the less sense it makes." He means the old group selection: "This brings us to the familiar problem which led most evolutionary biologists to reject the idea of group selection in the 1960s." He also writes of "groups budding off new groups". I still don't see this in Eq. (9).

Twenty-three comments follow the essay. David Queller, among others, defends group selection: "Modern group selection theory is as mathematically rigorous as individual selection or inclusive fitness theory. I say this despite being someone who favors the inclusive fitness approach and whose entire career has been based on it."<sup>64</sup>

Pinker then replies.<sup>65</sup> At the start he writes "The theory is mathematically equivalent to standard evolutionary theories based on gene selection or inclusive fitness, so the two theories make identical predictions and can never be empirically distinguished." He does not say that this is not the old group selection attacked in his essay. The discussion of "this new theory of group selection" begins about half way through the reply. What follows is too diffuse for me to summarize. Read it yourself. He seems to forget that the new group selection and kin selection "can never be empirically distinguished."

Dawkins deserves credit for helping to abolish the old group selection with his spectacularly influential *The Selfish Gene* (1976) and also *The Extended Phenotype* (1982). He deserves blame for helping to suppress the new group selection with his across-the-board rejection of all group selection.

Dawkins (1982): "The years [after] Darwin [saw] an astonishing retreat . . . , a lapse into sloppily unconscious group-selectionism. . . . It is only in recent years . . . that the stampede has been halted and and turned. We painfully struggled back, harassed by sniping from a Jesuitically sophisticated dedicated neo-group-selectionist rearguard, until we finally regained Darwin's ground."<sup>66</sup>

Whew! The word "stampede" is from Hamilton (1975), who Dawkins' quotes in support of his views: "Almost the whole field stampeded in the [group selection] direction where Darwin had gone circumspectly or not at all."<sup>67</sup> But Dawkins gets no support from Hamilton here. For Hamilton is writing about the old group selection. On the very next page we find "A recent reformulation of natural selection [by Price] can be adapted to show how two successive levels of the subdivision of a population contribute separately to the overall natural selection." He then derives the group selection Eq. (9).

Dawkins has not let up. In 2012 he wrote "Group selection: the poorly defined and incoherent view . . . ." D. S. Wilson has strong criticism under the heading "Holding Dawkins Accountable": [Click](#).

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<sup>64</sup><http://edge.org/conversation/the-false-allure-of-group-selection#dq>.

<sup>65</sup><http://edge.org/conversation/the-false-allure-of-group-selection#sp2>.

<sup>66</sup>Dawkins, *The Extended Phenotype*, 1982, p. 6.

<sup>67</sup>Hamilton, *Innate social aptitudes of man*, *ibid.*, p. 331

## Odds and Ends

Students must be disabused of wrongheaded group selection beliefs, which a biologist friend tells me are common. But it is wrong to tell them that group selection explanations are always wrong.

We have suffered two generations of a scientific scandal: everyone “knows” that group selection is bad science, making it impossible to benefit from its insights. How long will this wrongheaded meme ☺ persist?

“The range of circumstances in which inclusive fitness is known to apply is always being extended. . . . That range is still quite small, and there is a long way to go to cover the situations that most empirical biologists would consider usual.”<sup>68</sup>

If  $z = w$  in Eq. (3), i.e., the trait is fitness, then the equation becomes  $\bar{w}\Delta\bar{w} = \text{Var}(w)$ ; for a given  $\bar{w}$  the change in fitness due to natural selection<sup>69</sup> is proportional to its variance. This is *Fisher’s fundamental theorem of natural selection*. Fitness increases!

As is well known, the quantity  $r = \text{Cov}(y_j, z_j)/\text{Var}(z_j)$  in Eq. (6) is the slope of the least squares line  $y = rz + s$  for the points  $(z_j, y_j)$ . For the line is given by<sup>70</sup>

$$\begin{bmatrix} \sum z_j^2 & \sum z_j \\ \sum z_j & n \end{bmatrix} \begin{bmatrix} r \\ s \end{bmatrix} = \begin{bmatrix} \sum z_j y_j \\ \sum y_j \end{bmatrix}.$$

Solving by Cramer’s rule gives  $r = \text{Cov}(z_j, y_j)/\text{Var}(z_j)$ .

George Price led a fascinating life, which ended in suicide in 1975. For a biographical sketch see Gardner.<sup>71</sup> For a longer piece, see J. Schwartz, *Death of an altruist*.<sup>72</sup> For a full biography see O. Harman, *The Price of Altruism: George Price and the Search for the Origins of Kindness* (2011).

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<sup>68</sup>A. Grafen, *Formalizing Darwinism and Inclusive Fitness Theory*, Philosophical Transactions: Biological Sciences **364**, 3135 (2007).

<sup>69</sup>Recall that the transmission bias is not included in Eq. (3).

<sup>70</sup><http://mathworld.wolfram.com/LeastSquaresFitting.html>, Eq. (9).

<sup>71</sup>A. Gardner, *The Price equation*, Current Biology **18** R198 (2008).

<sup>72</sup><http://linguafranca.mirror.theinfo.org/0007/altruist.html>

## Least Squares

This page justifies the claim on Page 4 that  $\text{Cov}(\epsilon_j, z_j) = 0$ .

Least squares problems can be formulated using the matrix equation

$$\begin{bmatrix} y_1 \\ y_2 \\ \vdots \\ y_n \end{bmatrix} = \begin{bmatrix} 1 & x_{11} & x_{21} & \cdots & x_{m1} \\ 1 & x_{12} & x_{22} & \cdots & x_{m2} \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 1 & x_{1n} & x_{2n} & \cdots & x_{mn} \end{bmatrix} \begin{bmatrix} \beta_0 \\ \beta_1 \\ \vdots \\ \beta_m \end{bmatrix} + \begin{bmatrix} \epsilon_1 \\ \epsilon_2 \\ \vdots \\ \epsilon_n \end{bmatrix}.$$

Compactly:  $y = X\beta + \epsilon$ . The vector  $y$  and matrix  $X$  are given. A *least squares solution* is a vector  $\beta$  which minimizes  $\|\epsilon\|^2$ .

Let  $X'$  be the transpose of  $X$ . Compute:

$$\|\epsilon\|^2 = \epsilon \cdot \epsilon = (y - X\beta) \cdot (y - X\beta) = y \cdot y - 2\beta \cdot X'y + \beta \cdot X'X\beta.$$

Let  $c$  be a constant vector and  $C$  a constant matrix. Compute  $\partial(\sum_i c_i \beta_i) / \partial \beta_k$  and  $\partial(\sum_{ij} \beta_i C_{ij} \beta_j) / \partial \beta_k$  to show that

$$\nabla(\beta \cdot c) = c \quad \text{and} \quad \nabla(\beta \cdot C\beta) = (C + C')\beta.$$

Thus  $\nabla\|\epsilon\|^2 = -2X'y + 2X'X\beta$ . At a minimizing  $\beta$ ,  $\nabla\|\epsilon\|^2 = 0$ .<sup>73</sup> Then

$$X'X\beta = X'y = X'(X\beta + \epsilon) = X'X\beta + X'\epsilon.$$

Thus  $X'\epsilon = 0$ . The top entry of this vector equation says that  $\bar{\epsilon} = 0$ . Remembering this, the other entries say that  $\text{Cov}((x_{i1}, \dots, x_{in})', \epsilon) = 0$ ,  $i = 1, \dots, m$ .

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<sup>73</sup>If  $X$  is of full rank, then  $X'X$  is invertible. Then there is a unique minimizing  $\beta = (X'X)^{-1}X'y$ . (Usually  $m + 1 \leq n$ . Then full rank would be  $m + 1$ .)