

SHORT COMMUNICATION

Social semantics: toward a genuine pluralism in the study of social behaviour

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Abstract

Pluralism is the coexistence of equivalent theoretical frameworks, either because they are historically entrenched or because they achieve separate insights by viewing the same process in different ways. A recent article by West *et al.* [Journal of Evolutionary Biology (2007) vol. 20, 415–432] attempts to classify the many equivalent frameworks that have been developed to study the evolution of social behaviour. This article addresses shortcomings in the West *et al.*'s article, especially with respect to multilevel selection, in a common effort to maximize the benefits of pluralism while minimizing the semantic costs.

Scientific progress depends upon precise, reliable communication between scientists. In a recent article published in this journal, West *et al.* (2007) attempt to make sense of the semantic confusion that plagues the study of social behaviour from an evolutionary perspective. Although I laud their purpose and agree with some of their points, I think that their article does not yet achieve a genuine pluralism. In this article, I attempt to diagnose some of the unresolved problems in an effort to reach the common goal of maximizing the advantages of multiple theoretical frameworks while avoiding the semantic costs.

Why pluralism?

Science is typically imagined as a contest between theories that invoke different processes, such that one can be falsified and the other supported when tested against empirical evidence. An example is the contest between group and individual selection, as these terms were understood by Williams and others during the 1960s (e.g. Maynard Smith, 1964; Williams, 1966). Group selection was defined as a process of evolution based on the differential survival and reproduction of groups, whereas individual selection was defined as a process based on the differential survival and reproduction of individuals within groups. When Williams (1966, p. 151) used sex ratio to pit these two theories against

each other, he reasoned that within-group selection favours an even sex ratio based on Fisher's principle, whereas between-group selection could favour either a male-biased or female-biased sex ratio, depending upon whether group fitness is maximized by population regulation or by expanding the size of the group as fast as possible. He consulted the empirical literature and concluded that virtually all species have equal sex ratios, providing evidence *for* individual selection and *against* group selection (see Sober & Wilson, 1998, pp. 38–43 for a more detailed treatment).

Not all theories of social behaviour are like this, however. Consider selfish gene theory as described by Dawkins (1976), compared with inclusive fitness theory as described by Hamilton (1963, 1964, 1975). Dawkins never regarded selfish gene theory as an alternative to inclusive fitness theory, such that one might be falsified and the other supported based on empirical evidence. Instead, he regarded the 'gene's eye view' as a novel *perspective*, capable of achieving insights that might not be forthcoming from inclusive fitness theory, even if each and every result can be explained by both theoretical frameworks in retrospect. The optical illusion that graces the cover of *The Extended Phenotype* (Dawkins, 1982) perfectly captures the idea of different but equivalent theoretical frameworks that enable us to see the same world in different ways.

A more recent example is a new version of inclusive fitness theory based on calculating the effects of others on a focal individual's fitness, rather than the effect of a focal individual on the fitness of others (Taylor & Frank,

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1996; Taylor *et al.*, 2007). West *et al.* praise this new approach as having 'revolutionized social evolution theory' (p. 425), but the new insights come at a semantic cost, as the 'new' inclusive fitness theory uses terms such as 'direct fitness' in a different way than the 'old' inclusive fitness theory. How can we avoid the semantic confusion of using the same terms in different ways? Either we must coin different terms, or we must be careful to specify the framework and associated definitions that we are using at any particular time. When we consider that these are only two of many different frameworks for studying the evolution of social behaviour, the need to avoid semantic confusion becomes apparent (see also Foster, 2006).

Why should we tolerate multiple frameworks that all arrive at the same conclusions at the end of the day? The best reason has already been provided; a given framework deserves to exist to the extent that it leads to new insights not forthcoming from the others. Another reason is purely historical; a given definition might be so entrenched that we cannot get rid of it, even if we might want to. As an example, West *et al.* (p. 419–420) think that the term 'reciprocal altruism' is misleading because it does not count as altruism according to their favoured definition. Nevertheless, they acknowledge that the term is so entrenched that there is no likelihood of getting rid of it.

A foundational semantic polymorphism: absolute vs. relative fitness

Evolutionary altruism is typically defined as a behaviour that decreases the fitness of the actor while increasing the fitness of one or more recipients, but is fitness supposed to be measured in absolute or relative terms? The answer depends upon the theoretical framework. The bs and cs of inclusive fitness theory are defined in terms of absolute fitness, but group selection theory defines altruism in terms of relative fitness within groups. If we cannot understand and manage this foundational semantic polymorphism, then there is little hope of achieving the goal that West *et al.* have set out for themselves.

Both definitions and their associated theoretical frameworks can be traced to the very beginning of evolutionary thought. With respect to inclusive fitness theory and its absolute fitness criterion, Darwin realized that some individuals (such as worker bees) could evolve to sacrifice themselves on behalf of their relatives (such as the queen), in the same way that animal and plant breeders sacrifice some individuals and confidently breed from their relatives. With respect to group selection and its relative fitness criterion, consider the following famous passage from *Descent of Man* (Darwin, 1871, p. 166; *italics mine*):

It must not be forgotten that although a high standard of morality gives but a slight advantage to each individual man and his children *over the other men of the same tribe*, yet

that an increase in the number of well-endowed men and advancement in the standard of morality will certainly give an immense advantage *to one tribe over another*. There can be no doubt that a tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to aid one another, and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection.

It is clear from the first part of this passage that Darwin was perplexed by moral behaviours because *they do not provide a sufficient relative fitness advantage within groups*. He did not insist that they decrease the absolute fitness of the moral individual, although they might, as implied by the costly examples of altruism described in the second part of the passage.

Like Darwin, Haldane anticipated inclusive fitness theory in his famous quip that he would sacrifice his life for more than two siblings or more than eight cousins. He also elaborated upon Darwin's group selection scenario by describing altruism as a trait that declines in frequency within groups but causes the group to differentially contribute to the total population, for example by fissioning at a greater rate than nonaltruistic groups (Haldane, 1932, pp. 130–131, 207–210). When Wright (1945) built one of the first mathematical models of group selection, he assumed that altruistic genes provide a benefit for everyone in the group (including themselves) at a personal cost, as represented by the following single-locus model, where p is the proportion of altruists in the group, b is the group benefit and s is the individual cost:

$$W(AA) = (1 + pb)(1 - 2s) \quad (1)$$

$$W(Aa) = (1 + pb)(1 - s) \quad (2)$$

$$W(aa) = (1 + pb) \quad (3)$$

It is obvious from this model that the A gene has the lowest relative fitness within the group whenever s is a positive number. The A gene can increase its own absolute fitness if b is sufficiently large compared with s , but this fact was irrelevant to Wright. After all, natural selection is based on relative fitness. If $\Delta p < 0$ within groups, then something must be added to the model for the A gene to evolve in the total population. That 'something' is a population of groups that vary in their frequency of A, such that groups with the most altruists differentially contribute to the total population (group-level selection). Defining altruism in terms of relative fitness within groups came naturally for a population geneticist such as Wright – and virtually every other author of an explicit group selection model.

Williams found the relative fitness criterion reasonable enough to use Wright's equations in his own model of group selection in family groups (Williams & Williams,

1957). His more general analysis of group selection in *Adaptation and Natural Selection* was also based on relative fitness, as the following passage shows (Williams, 1966, pp. 92–93):

It is universally conceded by those who have seriously concerned themselves with this problem that...group-related adaptations must be attributed to the natural selection of alternative groups of individuals and that the natural selection of alternative alleles within populations will be opposed to this development. I am in entire agreement with the reasoning behind this conclusion. Only by a theory of between-group selection could we achieve a scientific explanation of group-related adaptations.

While we are reviewing the history of these concepts, it is worth noting when the term 'altruism' actually came into use. Darwin did not use the term, although it was clear that he was talking about behaviours that cause individuals to 'sacrifice themselves for the common good', as he put it in the passage quoted above. Haldane used the term, whereas Wright used equivalent phrases such as 'socially advantageous but individually disadvantageous'. Williams & Williams (1957, pp. 32–33) addressed the use of the term explicitly:

The term 'altruistic' adaptation is convenient and has been used (Haldane, 1932), but we prefer to avoid terms so burdened with value judgments and emotional flavour. In this paper individuals that sacrifice themselves for the good of others are called *social donors*, and those that do not or that do so to a lesser degree, *social nondonors*.

Thus, Williams & Williams (1957) avoided the term 'altruism' in the same way that some evolutionists avoid the term 'rape' to refer to forced copulations. Hamilton (1963) followed Haldane by titling his first paper 'The Evolution of Altruistic Behavior', which he defined as 'any case where an animal behaves in such a way as to promote the advantages of other members of the species not its direct descendants at the expense of its own'. It should be clear from these examples that everyone was talking about the same general class of behaviours, even if not everyone used the term 'altruism'.

I have recounted these facts at some length to illustrate two important points. First, defining altruism in terms of relative fitness within groups is so central to the concept of group selection that the group selection controversy cannot be understood without it. If any definition of altruism is historically entrenched, it is this one. Second, there are excellent *conceptual* reasons for the relative fitness criterion. Traits for which $\Delta p < 0$ within groups are precisely those that require the ingredients of group selection to evolve. If natural selection is based on relative fitness, then why *should not* altruism be defined in terms of relative fitness within and among groups?

Genuine pluralism requires group selection theory and its definition of altruism based on relative fitness to be included in the club of accepted theories, along with

selfish gene theory and the 'old' and 'new' versions of inclusive fitness theory already discussed. West *et al.* take some steps in this direction, but they do not go far enough. To their credit, they acknowledge the existence of a 'new' form of group selection that is equivalent to other legitimate theoretical frameworks. Unfortunately, they also commit a number of errors that contribute to, rather than resolving semantic confusion:

- 1 They portray the 'new' group selection as if it has no historical or conceptual continuity with the 'old' group selection.
- 2 They claim that the rejection of the 'old' group selection in the 1960s remains fully justified, as if nothing needs to be revised.
- 3 They suggest that the 'new' group selection does not provide new insights, compared with inclusive fitness theory, casting doubts upon its basic utility.

These claims rely upon misunderstandings of both the 'old' and 'new' group selection, as the following examples show:

On the relation between the 'old' and 'new' group selection. West *et al.* state, 'A third source of confusion is that the new group selection approach has involved the use of several fundamental terms in ways that were different from their established (valuable and clear) meanings... Specifically, it has identified within-group selection as "individual selection" and between-group selection as "group selection"' (p. 425). Later they state that the 'new' group selection has 'redefined' altruism in terms of relative fitness within groups (p. 428). These claims simply do not square with the history of group selection theory, as outlined above (see also Borrello, 2005; Okasha, 2005, 2006). When Price (1970, 1972), Hamilton (1975) and I (Wilson, 1975) built the first models associated with the 'new' group selection, we were expanding the definition of groups but we were not altering the definition of altruism based on relative fitness. That is why we saw the 'new' group selection as a generalization that was fully continuous with previous models. In Hamilton's (1996) autobiographical account of the period, he recalls excitedly telling Price 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' (p. 173). Hamilton was referring to the *old* group selection, as it had been previously conceptualized, not something that he and Price had just invented. Genuine pluralism requires an accurate understanding of both the historical and conceptual development of ideas (Wilson & Wilson, 2007). West *et al.* do not contribute to this goal when they portray the 'new' group selection as if it is disconnected from its own past.

On the theoretical plausibility of the 'old' group selection. West *et al.* cite early critiques of the 'old' group selection (such as Maynard Smith, 1964, 1976) as if they remain fully valid, ignoring the subsequent theoretical literature.

As one example, Maynard Smith (1964) haystack model assumes a worst-case scenario, in which altruism goes extinct in every group colonized by even a single selfish allele before any individuals disperse from the group. Wilson (1987) relaxed this assumption by assuming that altruism is governed by the same *bs* and *cs* as in Hamilton's equation. When this very reasonable assumption is incorporated into the haystack model, altruistic alleles decline in frequency within each group but they are still present after 10 or even 20 generations. In the meantime, the altruistic alleles greatly increase the size of their group, especially given exponential growth. Group selection remains a significant force, even when the groups last for many generations between dispersal phases. The haystack model therefore supports rather than refutes the 'old' group selection (e.g. as envisioned by Maynard Smith). Moreover, the haystack model represents a highly plausible population structure, especially for microbial organisms. As a second example, most evolutionary models of social behaviour assume (for simplicity) that altruism and selfishness are coded by a single gene or multiple genes with additive effects. Peck (2004) relaxed this assumption by modelling altruism and selfishness as suites of traits that must occur in the right combinations to function correctly. In this case, when a selfish individual migrates into an altruistic group, the genes do not spread because they become dissociated by sexual reproduction and no longer occur in the right combination. Many other examples could be cited, leading to the unsurprising conclusion that a subject as complicated as group selection was not theoretically settled 40 years ago.

On empirical evidence for the 'old' group selection. West *et al.* treat Wynne-Edwards' (1962) as the prime example of the 'old' group selection that should still be avoided at all costs. Yet, Wynne-Edwards' hypothesis that organisms can evolve to avoid overexploiting their resources has now received both theoretical (e.g. Werfel & Bar-Yam, 2004) and empirical (e.g. Vulic & Kolter, 2001) support. For example, Kerr *et al.* (2006) created a metapopulation of bacteria (the resource) and phage (the consumer) by culturing them in 96-well microtitre plates. Migration between groups was executed by a high-throughput liquid-handling robot according to a prespecified migration scheme. Biologically plausible migration rates enabled 'prudent' phage strains to out-compete more 'rapacious' strains in the metapopulation, despite their selective disadvantage within each well, exactly as envisioned by Wynne-Edwards. As Kerr *et al.* put it (p. 77), 'spatially restricted migration reduces the probability that phage reach fresh hosts, rendering rapacious subpopulations more prone to extinction through dilution. Consequently, the tragedy of the commons is circumvented at the metapopulation level scale in the restricted treatment'. More generally, the well-established fact that reduced virulence often evolves by group selection in disease organisms provides a

confirmation of Wynne-Edwards' hypothesis – not for all species, but for at least some species.

On crediting the insights of multilevel selection theory. Genuine pluralism requires crediting a given framework for achieving insights that were not forthcoming from other frameworks, even if they can be accounted for in retrospect. The 'new' inclusive fitness theory is credited in this way by West *et al.*, but the 'new' group selection is portrayed primarily as redundant with inclusive fitness theory in a confusing way, leaving it mysterious why anyone would want to use it. Then insights that were originally derived from multilevel selection theory are described without crediting the source. One important insight achieved by multilevel selection theory in the 1990s is that population viscosity does not necessarily promote the evolution of altruism (Wilson *et al.*, 1992). It is true that limited dispersal causes relatives to interact with each other (=increased genetic variation among groups), but it also causes their progeny to compete. Group selection requires not only variation among groups, but also a way for altruistic groups to export their productivity to other regions of the metapopulation. This insight was confirmed by inclusive fitness theory in retrospect (Queller, 1992; Taylor, 1992a,b), but it was not forthcoming from inclusive fitness theory, illustrating the advantage of multiple perspectives. As Queller (1992, p. 322) put it, 'The original insight stems not from inclusive fitness thinking but from the alternative method of partitioning selection into within-group and between-group effects'. West *et al.* cite this finding as an important insight (p. 428) without attributing it to the multilevel perspective. As a second example, a burgeoning literature on the biological and cultural evolution of cooperation in human society is based largely on multilevel selection theory (e.g. Sober & Wilson, 1998; Gintis, 2000; Wilson, 2002, 2006; Fehr & Fischbacher, 2003; Richerson & Boyd, 2005; Bowles, 2006). West *et al.* describe this literature as if it is just plain wrong and confusing to use the relative fitness criterion (e.g. p. 422), which is hardly in the spirit of genuine pluralism.

Finding the factual needles in the haystack of perspectives

Not everything is a matter of perspective. The purpose of science is to evaluate important factual claims. If pluralism does not facilitate this process, then it becomes part of the problem by causing the factual needles to become lost in a haystack of perspectives. Consider some of the early group selection models: Maynard Smith (1964) assumed that groups are colonized by a single fertilized female and persist for a number of generations before the descendants disperse to colonize a new set of groups. Today, many evolutionists would classify this as a kin selection model because members of a group are much more highly related to each other than to members of other groups.

Nevertheless, this was Maynard Smith's conception of *group selection*, which he was *contrasting* with kin selection, as strange as that might seem to those who do not have a thorough historical understanding of the subject. Moreover, he thought that his model was unfavourable for the evolution of altruism, no matter how it is classified. Other early group selection models, such as Boorman & Levitt (1972) and Levin and Kilmer (1974), assumed that groups are geographically isolated except for a trickle of dispersers. These models suggested that a delicate combination of parameter values is required for altruism to evolve, such as groups colonized by a small number of individuals and a low migration rate among groups. Once again, many evolutionists today would classify these as kin selection models because members of a given group are genealogically more related to each other than to members of other groups, but at the time kin selection was associated with interactions among *immediate* genealogical relatives. Moreover, the important factual question is whether altruism *can* evolve in these models, regardless of whether they are classified as group selection or kin selection. The earlier consensus was that altruism cannot evolve because its selective disadvantage within groups invariably outweighs the group-level advantages. This assessment is factually incorrect, based on current knowledge. Altruism is indeed selectively disadvantageous within groups, but nevertheless can evolve in the total population – regardless of whether the model is classified as group selection or kin selection.

Another important factual claim concerns the importance of genealogical relatedness, as opposed to other processes that create nonrandom genetic associations, or even random variation as sufficient for evolving behaviours that are selectively disadvantageous within groups. These other processes can be classified as kin selection or not, depending upon the specific interpretation of the coefficient of relatedness. Nevertheless, all perspectives should converge upon the answer to the factual question of whether altruism can evolve among individuals who are not genealogically related.

For the benefits of pluralism to outweigh the semantic costs, it is necessary to focus on the important factual issues at stake, how these factual issues are conceptualized by various perspectives during the history of a given subject (such as the group selection controversy in the 1960s), and how multiple perspectives can converge on answers based upon current knowledge. I take this to be the spirit of the article by West *et al.* (2007) and the spirit of this article as well.

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References

- Boorman, S.A. & Levitt, P.R. 1972. Group selection at the boundary of a stable population. *Proc. Natl Acad. Sci.* **69**: 2711–2713.
- Borrello, M.E. 2005. The rise, fall and resurrection of group selection. *Endeavor* **29**: 43–47.
- Bowles, S. 2006. Group competition, reproductive leveling, and the evolution of human altruism. *Science* **314**: 1569–1572.
- Darwin, C. 1871. *The Descent of Man and Selection in Relation to Sex*. Appleton, New York.
- Dawkins, R. 1976. *The Selfish Gene*. Oxford University Press, Oxford.
- Dawkins, R. 1982. *The Extended Phenotype*. Oxford University Press, Oxford.
- Fehr, E. & Fischbacher, U. 2003. The nature of human altruism. *Nature* **425**: 785–791.
- Foster, K.R. 2006. Balancing synthesis with pluralism in sociobiology. *J. Evol. Biol.* **19**: 1394–1396.
- Gintis, H. 2000. *Game Theory Evolving*. Princeton University Press, Princeton, NJ.
- Haldane, J.B.S. 1932. *The Causes of Evolution*. Longmans, Green & Co., London.
- Hamilton, W.D. 1963. The evolution of altruistic behavior. *Am. Nat.* **97**: 354–356.
- Hamilton, W.D. 1964. The genetical evolution of social behavior: I and II. *J. Theor. Biol.* **7**: 1–52.
- Hamilton, W.D. 1975. Innate social aptitudes in man, an approach from evolutionary genetics. In: *Biosocial Anthropology* (R. Fox, ed.), pp. 133–155. Malaby Press, London.
- Hamilton, W.D. 1996. *The Narrow Roads of Gene Land*, v. 1. W.H. Freeman/Spektrum, Oxford.
- Kerr, B., Neuhauser, C., Bohannan, B.J.M. & Dean, A.M. 2006. Local migration promotes competitive restraint in a host–pathogen ‘tragedy of the commons’. *Nature* **442**: 75–78.
- Levin, B.R. & Kilmer, W.L. 1974. Interdermic selection and the evolution of altruism: a computer simulation study. *Evolution* **28**: 527–545.
- Maynard Smith, J. 1964. Group selection and kin selection. *Nature* **201**: 1145–1146.
- Maynard Smith, J. 1976. Group selection. *Q. Rev. Biol.* **51**: 277–283.
- Okasha, S. 2005. Maynard Smith on the levels of selection question. *Biol. Philos.* **20**: 989–1010.
- Okasha, S. 2006. *Evolution and the Levels of Selection*. Oxford University Press, Oxford.
- Peck, J. 2004. Sex causes altruism. Altruism causes sex. Maybe. *Proc. R. Soc. Biol. Sci.* **271**: 993–1000.
- Price, G.R. 1970. Selection and covariance. *Nature* **227**: 520–521.
- Price, G.R. 1972. Extension of covariance selection mathematics. *Ann. Hum. Genet.* **35**: 485–490.
- Queller, D.C. 1992. Does population viscosity promote kin selection? *Trends Ecol. Evol.* **7**: 322–324.
- Richerson, P.J. & Boyd, R. 2005. *Not by Genes Alone: How Culture Transformed Human Evolution*. University of Chicago Press, Chicago, IL.
- Sober, E. & Wilson, D.S. 1998. *Unto Others: The Evolution and Psychology of Unselfish Behavior*. Harvard University Press, Cambridge, MA.

- Taylor, P.D. 1992a. Inclusive fitness in a homogeneous environment. *Proc. R. Soc. Biol. Sci.* **249**: 299–302.
- Taylor, P.D. 1992b. Altruism in viscous populations – an inclusive fitness model. *Evol. Ecol.* **6**: 352–356.
- Taylor, P.D. & Frank, S.A. 1996. How to make a kin selection model. *J. Theor. Biol.* **180**: 27–37.
- Taylor, P.D., Wild, G. & Gardner, A. 2007. Direct fitness or inclusive fitness: how shall we model kin selection? *J. Evol. Biol.* **20**: 301–309.
- Vulic, M. & Kolter, R. 2001. Evolutionary cheating in *Escherichia coli* stationary phase cultures. *Genetics* **158**: 519–526.
- Werfel, J. & Bar-Yam, Y. 2004. The evolution of reproductive constraint through social communication. *Proc. Natl Acad. Sci.* **101**: 11019–11024.
- West, S.A., Griffin, A.S. & Gardner, A. 2007. Social semantics: altruism, cooperation, mutualism, strong reciprocity, and group selection. *J. Evol. Biol.* **20**: 415–432.
- Williams, G.C. 1966. *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*. Princeton University Press, Princeton, NJ.
- Williams, G.C. & Williams, D.C. 1957. Natural selection of individually harmful social adaptations among sibs with special reference to social insects. *Evolution* **11**: 32–39.
- Wilson, D.S. 1975. A theory of group selection. *Proc. Natl Acad. Sci.* **72**: 143–146.
- Wilson, D.S. 1987. Altruism in Mendelian populations derived from sibgroups: the haystack model revisited. *Evolution* **41**: 1059–1070.
- Wilson, D.S. 2002. *Darwin's Cathedral: Evolution, Religion and the Nature of Society*. University of Chicago Press, Chicago, IL.
- Wilson, D.S. 2006. Human groups as adaptive units: toward a permanent consensus. In: *The Innate Mind: Culture and Cognition* (P. Carruthers, S. Laurence & S. Stich, eds), pp. 78–90. Oxford University Press, Oxford.
- Wilson, D.S. & Wilson, E.O. 2007. Rethinking the theoretical foundation of sociobiology. *Q. Rev. Biol.*, in press.
- Wilson, D.S., Pollock, G. & Dugatkin, L.A. 1992. Can altruism evolve in purely viscous populations? *Evol. Ecol.* **6**: 331–341.
- Wright, S. 1945. Tempo and mode in evolution: a critical review. *Ecology* **26**: 415–419.
- Wynne-Edwards, V.C. 1962. *Animal Dispersion in Relation to Social Behavior*. Oliver & Boyd, Edinburgh.

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