SHORT COMMUNICATION

Social semantics: how useful has group selection been?

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Abstract

In our social semantics review (*J. Evol. Biol.*, 2007, 415–432), we discussed some of the misconceptions and sources of confusion associated with group selection. Wilson (2007, this issue) claims that we made three errors regarding group selection. Here, we aim to expand upon the relevant points from our review in order to refute this claim. The last 45 years of research provide clear evidence of the relative use of the kin and group selection approaches. Kin selection methodologies are more tractable, allowing the construction of models that can be applied more easily to specific biological examples, including those chosen by Wilson to illustrate the utility of the group selection approach. In contrast, the group selection approach is not only less useful, but also appears to frequently have negative consequences by fostering confusion that leads to wasted effort. More generally, kin selection theory allows the construction of a unified conceptual overview that can be applied across all taxa, whereas there is no formal theory of group selection.

Introduction

A greater understanding in evolutionary biology is often obtained by looking at the same problem in different ways (Maynard Smith, 1983). This fact is well established in the field of social evolution, where explanations for behaviours such as cooperation can be carved up in a number of ways, each with their own advantages (Frank, 1998; Sachs *et al.*, 2004; Lehmann & Keller, 2006; West *et al.*, 2007c). Wilson suggests that in our social semantics review (West *et al.*, 2007b), we did not allow for 'genuine pluralism,' because we did not allow for group selection. As fans of pluralism (West *et al.*, 1999), we would like to address this general issue, before turning to the specific criticisms of Wilson's three suggested errors. First, as we emphasized in our original paper, we do not claim that group selection is incorrect. Our point was

that although it can be a potentially useful tool (e.g. Gardner *et al.*, 2007b), it frequently leads to confusion and time wasting (see below; West *et al.*, 2007b, pp. 420–421 and 424–425). Second, Wilson's (2007) paper is not a call for genuine pluralism; it is just a return to the old confusions about group selection, most of which were solved more than 20 years ago (Grafen, 1984; Frank, 1986b). There are some important pluralist issues within the field of social evolution, but Wilson does not address any of these. For example, the different ways in which direct fitness explanations for cooperation can be divided up (Sachs *et al.*, 2004; Bergmüller *et al.*, 2007; West *et al.*, 2007c), distinguishing between the evolution and maintenance of traits (Boomsma & Ratnieks, 1996; West *et al.*, 2007b), and the relationships between the whole range of theoretical methodologies (e.g. neighbour modulated, inclusive fitness, quantitative genetic, population genetic, multi-locus, etc.; Hamilton, 1964; Frank, 1998; Wolf *et al.*, 1999; Gardner *et al.*, 2007b; Taylor *et al.*, 2007b). [Correction added after publication 28 November 2007: in the preceding paragraph, citations have been changed to journal style].

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Error 1: the old and the new

Wilson (2007) claims that our first error is the portrayal of 'the ''new'' group selection as if it had no historical or conceptual continuity with the old ''group'' selection.' In fact, we agree that there are historical and conceptual links between old and new group selection – that is why we discussed them together in the same section of our original review (West *et al.*, 2007b). However, as we emphasized in our original paper, although there are links, there are also important differences that need to be clarified. In particular, 'new' group selection assumes that there are multiple levels of selection, which can vary in their importance. This levels-of-selection view is entirely consistent with the principle that organisms are expected to behave as if they were maximizing their inclusive fitness (Grafen, 2006; Gardner *et al.*, 2007b). In contrast, 'old' group selection assumes that selection at the level of the group is the sole driving force of natural selection. This leads to the expectation that individual organisms will always act for the good of the group. Although the old and new views can coincide, the inclusive fitness approach is more general because it gives the correct prediction irrespective of the degree of within-group selection.

Error 2: the old

Wilson (2007) suggests that our second error is the claim 'that the rejection of the 'old' group selection in the 1960s remains fully justified, as if nothing needs to be revised.' Wilson is correct that we claimed this (West *et al.*, 2007b). There is no theoretical or empirical example of group selection that cannot be explained with kin selection. In no case has it been demonstrated that an additional force of 'old' group selection is required to provide an explanation.

Wilson provides two examples to demonstrate the importance of old group selection. However, both cases can be explained by kin selection theory, and do not require old group selection. Indeed, in none of the original papers did the authors need to invoke or even mention old group selection.

Wilson's (2007) first example is the coordinated movement into stationary phase by *Escherichia coli* bacteria when resources become limiting (Vulić & Kolter, 2001). Stationary phase leads to a reduced use of resources, and hence a greater chance of surviving until resources become plentiful again. The problem is that this strategy could be exploited by a cheat that maintains a higher growth rate, and hence could rise in frequency during stationary phase. However, this cooperative movement to stationary phase can be easily explained by kin selection theory. The clonal nature of bacterial populations means that interacting cells will often be highly related, and so a reduced rate of resource use provides an indirect fitness advantage by freeing up more resources for relatives (Gardner *et al.*, 2007c). Indeed,

indirect fitness benefits to relatives can explain a number of cases where selection has favoured bacteria to use resources more slowly and efficiently (West *et al.*, 2006b, 2007a).

Wilson's (2007) second example was concerned with how local migration can select for lower virulence in phage parasites of bacteria (Kerr *et al.*, 2006). In this case, bacteria can exploit their host resources either slowly (lower virulence) or rapidly (higher virulence). Slower exploitation gives higher productivity in the long run, but this strategy can be out-competed. The selective forces here are analogous to the stationary-phase example, and again can be explained by kin selection theory (see also Gandon & Michalakis, 1999; Roze & Rousset, 2003). A more efficient use of host resources is favoured when there is a higher relatedness between the phage infecting a bacterium – local migration leads to a higher relatedness and hence selects for lower virulence (Hamilton, 1972; Frank, 1996). In contrast, increased migration leads to a lower relatedness (a higher likelihood of low- and high-virulence phage in the same host) and hence selects for higher virulence. Furthermore, lower migration means that if adopting a higher virulence leads to overexploitation and extinction of a patch, it is one's relatives who will pay the cost of this (see also an analogous experiment carried out on a virus–insect system; Boots & Mealor, 2007; Buckling, 2007).

More generally, Wilson (2007) claims that it is a 'well-established fact that reduced virulence often evolves by group selection in disease organisms.' Tellingly, this statement was not backed up with any references. The leading theoretical and empirical papers on parasite virulence have always highlighted the importance of kin selection and relatedness between parasites within a host as a driving force in the evolution of virulence (e.g. Bremermann & Pickering, 1983; Frank, 1992, 1996; Herre, 1993; van Baalen & Sabelis, 1995). There is no theoretical or empirical study on the evolution of virulence that requires old group selection. Indeed, this area provides a clear demonstration of the confusion that can be caused by old group selection thinking – the infamous misconception amongst parasitologists that parasites should evolve reduced virulence over time, so as not to damage the populations of their hosts (Herre, 1993; Bull, 1994; Read, 1994). Reduced virulence is only favoured if the reduced damage to their hosts provides either a direct benefit to the parasites themselves or an indirect benefit to their relatives – there is no theoretical model or empirical example that shows otherwise (Frank, 1996).

The crux of Wilson's (2007) misunderstanding is the assumption that selection for a reduced exploitation of some resource is evidence for old group selection. This is clearly not the case as reduced exploitation could be favoured for a number of reasons, because of direct or indirect fitness benefits. In the earlier cases, we have

emphasized how indirect fitness benefits can favour reduced exploitation, but it is also possible to imagine other cases where direct fitness benefits would be the driving force and so even kin selection would not need to be invoked. Consequently, Wilson is confusing a debate over the level of selection with the issue of whether reduced exploitation of resources can be favoured.

Error 3: the new

Wilson (2007) identifies our third error as the suggestion that 'the ''new'' group selection does not provide new insights, compared with kin selection theory, casting doubts upon its basic utility.' In our original paper, we emphasized that the new group selection methodology is not only correct and a potentially useful tool (it can be useful to look at things from multiple perspectives), but that it often leads to considerable confusion (West *et al.*, 2007b). In contrast, the kin selection approach is easy to both use and apply to real biological cases (West *et al.*, 2007b). Our argument here was not based on philosophical grounds, but upon hard evidence from more than 40 years of research.

There are three central issues here, none of which were disputed by Wilson:

(1) No group selection model has ever been constructed where the same result cannot be found with kin selection theory. Occasionally, theoretical papers appear that claim to describe a situation where group selection can explain cooperation in a case where kin selection is not important (e.g. Wilson, 1975; Colwell, 1981; Sober & Wilson, 1998; Gintis, 2000; Fehr & Fischbacher, 2003; Gintis *et al.*, 2003; Wilson & Hölldobler, 2005; Nowak, 2006; Traulsen & Nowak, 2006; Taylor & Nowak, 2007). However, in all cases, a more thorough analysis has shown that this is as a result of a misunderstanding. Specifically, the assumptions of group selection models lead to either: (a) limited dispersal, and hence interactions between relatives, which provides an indirect (kin-selected) benefit to cooperation, or (b) competition between groups which provides a direct fitness benefit to cooperation within groups (Hamilton, 1975; Grafen, 1984; Harvey *et al.*, 1985; Frank, 1986b; Gardner & West, 2004a; Wenseleers *et al.*, 2004; Foster *et al.*, 2006; Lehmann & Keller, 2006; Helanterä & Bargum, 2007; Lehmann *et al.*, 2007a,b; West *et al.*, 2007b).

(2) The group selection approach has proved to be less useful than the kin selection approach. We have previously discussed the reasons for this in detail (West *et al.*, 2007b), pp. 424–425), and so only give a brief summary of the reasons here. From a theoretical perspective, kin selection methodologies allow: (a) models to be constructed more simply; (b) more general models to be constructed and (c) a greater variety of biologically-useful situations to be modelled (Taylor, 1981; Frank, 1986b, 1997, 1998; Taylor, 1988a, 1996; Taylor & Frank, 1996; Queller, 2004; Rousset, 2004; Taylor *et al.*, 2007b). From an empirical perspective, kin selection theory has proved to be easier to apply to real biological cases (Grafen, 1984). Empirical biologists measure the kin selection coefficient of relatedness, with molecular markers such as microsatellites (Queller & Goodnight, 1989), and not the corresponding group selection parameters. Furthermore, the kin selection approach has proved more useful for making testable predictions (Grafen, 1984; Frank, 1998; Queller, 2004; West *et al.*, 2007b). It is for these reasons that the great success stories and flourishing areas of social evolution have developed from kin selection theory and not group selection (see Table 1).

(3) The application of group selection theory has led to much confusion and time wasting. Specifically: (a) group selection thinking appears to be easy to misapply, leading to incorrect statements about how natural selection operates, as shown by research in many areas such as microbiology (e.g. Shapiro, 1998; Henke & Bassler, 2004), agriculture (reviewed by Denison *et al.*, 2003) and parasitology (see Error 2), where old group selection ideas have been applied; (b) the incorrect conclusion is commonly made that group selection is distinct from kin selection (e.g. Wilson, 1975; Colwell, 1981; Sober & Wilson, 1998; Gintis, 2000; Fehr & Fischbacher, 2003; Gintis *et al.*, 2003; Peck, 2006; Kreft, 2005; Wilson & Hölldobler, 2005; Nowak, 2006; Traulsen & Nowak, 2006; Taylor & Nowak, 2007); (c) as discussed in detail in our original review, the group selection literature often leads to the confusing redefinition of terms and the use of confusing jargon (West *et al.*, 2007b; pp. 420–421 and 425). Imagine the confusion that could have been avoided if it had been accepted over 20 years

Table 1 The great success stories and flourishing areas of kin selection. This table summarizes some of the most productive and successful areas of social evolution theory – in all cases these have developed from kin selection theory and not group selection. The references given are a mixture of pivotal original papers and more recent reviews or comparative studies.

Area	References
Split sex ratios in social insects	Boomsma & Grafen, 1991; Chapuisat & Keller, 1999
Local mate competition theory	Hamilton, 1967; West *et al.*, 2005
Kin discrimination in cooperative breeding vertebrates	Hamilton, 1964; Griffin & West, 2003
Worker policing in social insects	Ratnieks & Visscher, 1989; Wenseleers & Ratnieks, 2006
Parent–offspring conflict	Trivers, 1974
Sibling conflict	Mock & Parker, 1997
Selfish genetic elements	Hamilton, 1967; Burt & Trivers, 2006
Avoidance of cannibalism	Pfennig *et al.*, 1999
Cooperation in microbes	Griffin *et al.*, 2004; Gilbert *et al.*, 2007
Genomic imprinting	Haig, 2002

ago that 'using group selection for describing causal mechanisms is particularly slippery' (Frank, 1986b).

Wilson (2007) provides two biological examples of the insights provided by new group selection – population viscosity and cooperation in humans. We discuss these below in some detail because: (a) the most important thing about different theoretical methodologies is their relative use in explaining real biological cases; (b) they are presumably the best that group selection has to offer (in contrast to the stunning list of kin selection successes given in Table 1); (c) they actually provide strong support for the points made in our original paper (West *et al.*, 2007b).

Population viscosity

Wilson's first example of the insights provided by group selection is the effect of population viscosity (limited dispersal) on the evolution of cooperation or altruism (Wilson *et al.*, 1992). This problem of population viscosity and cooperation was considered by Hamilton from an inclusive fitness perspective. Hamilton (1964, 1972) suggested that population viscosity (limited dispersal) could favour cooperation because it would tend to keep relatives together – in this case, altruism directed indiscriminately at all neighbours could be favoured, because those neighbours tend to be relatives. However, Hamilton (1971, 1975) later realized that things might not be that simple, as population viscosity would also keep relatives together to compete, which would select against cooperation. The question is, what the relative importance of these opposing forces is?

Wilson *et al.*'s (1992) key contribution was to show that, in a simple-case scenario, these two opposing forces seem to cancel out, and so population viscosity has negligible influence on the evolution of cooperation. However, group selection methodology could not provide an analytical account of this phenomenon (see also Wright, 1945). Consequently, Wilson *et al.* were forced to use a simulation approach, that had to rely on specific parameter values and was less useful for general interpretation. This problem was solved by Taylor with the use of kin selection methodology – in just a few lines of algebra, he was able to analytically show how and why the effect of increased competition between relatives exactly cancelled the effect of increased relatedness (Taylor, 1992). This provides a clear demonstration of how the kin selection approach is easier to use (it allowed an analytical solution), while also providing a more general solution (that did not assume specific parameter values), and could be easily applied to a range of biological examples (see West *et al.*, 2002a).

More recent theoretical developments in this field provide clear examples of the power and breadth of kin selection theory. Kin selection theory has allowed Taylor's model to be extended in a number of directions to provide a conceptual overview of how population viscosity can favour cooperation under different life-history assump-

tion (Taylor & Irwin, 2000; West *et al.*, 2002a; Lehmann *et al.*, 2006b). A particularly illuminating issue within this field is whether the effect of local competition can be overcome if individuals disperse in groups or 'buds' (Gardner & West, 2006a; Lehmann *et al.*, 2006b). Several attempts were made to examine the effect of budding with a group selection approach with limited success and conflicting confusions. Haldane (1932) first considered the effect of budding dispersal, but found that a group selection approach was intractable, and was not able to solve it. Decades later, Pollock (1983) used group selection to argue that budding does not work. Then, Goodnight (1992) ran some simulations and showed that it did work, but lamented that the problem was too complicated to yield an analytical solution. In contrast, when Gardner & West (2006a) took a kin selection approach, they solved the model with a few lines of algebra (see also Lehmann *et al.*, 2006b). This illustrates how an issue that could not be solved with a group selection approach (even by Haldane!), was easily solved with a kin selection approach (even by Gardner & West!). Other extensions to theory in this area, which have been possible with kin selection, but not group selection, include more complicated population demographies such as fluctuations in group size, finite population sizes, inbreeding depression and clarifying the links with graph theory (Rousset & Billiard, 2000; Roze & Rousset, 2003, 2004; Rousset, 2004; Rousset & Ronce, 2004; Taylor *et al.*, 2007a; Grafen, in press; Lehmann *et al.*, in press).

Research on how limited dispersal influences the evolution of cooperation also illustrates how kin selection theory is easier to apply to real biological cases. The empirical tests of how population viscosity and competition between relatives influence the evolution of cooperation have been stimulated by the kin selection approach (e.g. West *et al.*, 2001a, 2006a; Giron *et al.*, 2004; Griffin *et al.*, 2004). Furthermore, the application of kin selection theory in this case has been able to illuminate how the same issue can apply to other areas of social evolution. One example of this is that population viscosity and competition between relatives not only selects against cooperative and altruistic behaviours, but also selects for harming and spiteful behaviours such as chemical warfare in bacteria and sterile soldiers in polyembryonic wasps (Gardner & West, 2004b,c, 2006b; Gardner *et al.*, 2004, 2007a; Giron *et al.*, 2004; Lehmann *et al.*, 2006a). Another example is that costly dispersal can be favoured as a means to reduce competition between relatives (Hamilton & May, 1977). The huge literature on this has been stimulated by and carried out solely with the kin selection approach, using models that are practically identical to those used to examine the evolution of cooperation through population viscosity (Taylor, 1988b; Taylor & Frank, 1996; Frank, 1998; Gandon & Michalakis, 1999; Gandon & Rousset, 1999; Perrin & Lehmann, 2001; Rousset, 2004).

Cooperation in humans

Wilson's (2007) second example of the insights provided by new group selection is how cooperation in humans can be favoured by punishment or 'strong reciprocity.' Strong reciprocity is defined as a predisposition to help others and to punish those that are not helping, as discussed in further detail in our original review (see pp. 421–422 and 426–427 of West *et al.*, 2007b). It is hard to think of a better example of a field where the group selection approach has failed to clarify the underlying selective forces, and has led to confusion. In the original theoretical papers on the evolution of strong reciprocity, a simulation approach was generally used (as group selection did not allow an analytical solution), but the results were interpreted in terms of group selection (e.g. Gintis, 2000; Fehr & Fischbacher, 2003; Gintis *et al.*, 2003; Bowles & Gintis, 2004). It is unclear how these models work, although a lot of new jargon was introduced and it was claimed that kin selection was not in operation (reviewed by Gardner & West, 2004a; Lehmann *et al.*, 2007b; West *et al.*, 2007b).

Luckily, the kin selection approach has been able to clear up the confusion generated by group selection models on how punishment or 'strong reciprocity' favours cooperation in humans. Kin selection models have shown that punishment or cooperation are only favoured if they provide a direct fitness benefit to the actor, or if limited dispersal leads to an indirect fitness benefit to relatives (Gardner & West, 2004a; Gardner *et al.*, 2007b; Lehmann *et al.*, 2007b). This clarified that punishment or strong reciprocity are not alternative evolutionary explanations for cooperation, as had been implied, but merely specific mechanisms for providing direct or indirect fitness benefits to cooperation (Lehmann *et al.*, 2007b). Furthermore, the kin selection approach has highlighted unreasonable assumptions such as when cooperation and punishment were not allowed to evolve independently, and shown that in some cases the models were analysing the opposite of what the authors had thought they were – spite not altruism (Lehmann *et al.*, 2007b).

A historical analysis

In an ideal world, we would assess the relative use of group selection with a historical analysis. We would take an area where the group selection debate had occurred, and examine what had happened as that field matured over a number of years. In such an analysis, the most important factor when considering the utility of group selection would be its application to real biological examples (Trivers, 1998a; b). What has it helped us understand? What do we understand now that we would not without group selection? Luckily, such an analysis is possible within another field highlighted by Wilson (2007) – sex-ratio evolution.

Hamilton (1967) showed that when mating takes place between the offspring of a small number of mothers, before the daughters disperse, then a female-biased sex ratio is favoured by a process that he termed local mate competition (LMC). Taylor (1981) showed that, from an inclusive fitness perspective, this bias is favoured in diploids because it: (a) leads to reduced competition for mates between related males (brothers), and (b) provides more mates for sons. In contrast, Wilson and Colwell (Colwell, 1981; Wilson & Colwell, 1981) argued that the bias was in fact because of group selection and could not be explained by the forces discussed by Taylor. Subsequently, it was shown that this debate was purely semantic and that the two methods were mathematically equivalent and just different ways of looking at the same thing (Frank, 1986b). It was also shown that a female bias could be favoured even in the absence of group structures (Bulmer & Taylor, 1980a).

Since then, the field of LMC has developed into one of the most productive and successful areas of evolutionary biology, with support for LMC theory from a huge range of taxa (Hamilton, 1996; West *et al.*, 2005). A particularly impressive feature of work on LMC, and a key contribution to its success, is that Hamilton's original model has been extended in numerous directions to match the biology of particular organisms, allowing more specific tests of theory (Frank, 1998; West *et al.*, 2005). This allows us to quantify the relative use of the group selection and kin selection approaches, by examining the relative frequency with which these methods led to new areas of theory that could be empirically tested. We have performed this, and found that in 15 of 15 cases, it was kin selection theory that was used (Table 2; $P = 0.00006$, two-tailed sign test). Sex-ratio theory therefore provides clear statistical support for the usefulness of kin selection over group selection.

This short history of LMC theory provides a clear demonstration of the general issues that we have stressed throughout this paper:

(1) Analysis of Hamilton's (1967) basic LMC model showed that kin selection and (new) group selection are mathematically equivalent ways of looking at the same thing. We cannot emphasize strongly enough that it is not the case that one is correct and the other wrong, nor that group selection predicts things that cannot also be predicted with kin selection theory.

(2) The kin selection vs. group selection debate took place over the simplest possible case – Hamilton's (1967) original model. As soon as more specific models were required for more complex life histories, it becomes hard or even impossible to construct these with the group selection approach (Frank, 1998; Queller, 2004). In contrast, the kin selection approach has allowed numerous analytical extensions of Hamilton's theory, to fit the biology of specific organisms (Table 2).

Table 2 Extensions of LMC theory. This table summarizes the ways in which LMC theory has been extended to match the biology of specific organisms. We have only included areas which have led to novel predictions that have then been tested empirically (the empirical evidence for many of these is summarized in West *et al.*, 2005). This excludes other possibilities such as haystacks (Bulmer & Taylor, 1980b; Avilés, 1993; Nagelkerke & Sabelis, 1996), inbreeding depression (Denver & Taylor, 1995), fertility insurance in parasites (Paul *et al.*, 2000; West *et al.*, 2002b; Gardner *et al.*, 2003) and a variety of other population/mating structures (Charnov, 1982; Werren, 1983; Frank, 1986b; Stubblefield & Seger, 1990; Courteau & Lessard, 2000).

Extensions of basic LMC theory	Approach used – kin selection (KS) or group selection (GS)	Authors
Inbreeding in haplodiploids	KS	Frank, 1985; Herre, 1985
Superparasitism	KS	Suzuki & Iwasa, 1980; Werren, 1980
Variable fecundity	KS	Frank, 1985, 1987; Yamaguchi, 1985; Stubblefield & Seger, 1990
Sibmating and split sex ratios	KS	Greeff, 1996; Reece *et al.*, 2004
Partial LMC	KS	Frank, 1986b; Nunney & Luck, 1988; Taylor, 1993
Inbreeding depression in simultaneous hermaphrodies	KS	Charnov, 1987
Limited dispersal by females	KS	Frank, 1986a; Taylor & Crespi, 1994
Asymmetric larval competition	KS	Godfray, 1986; Sykes *et al.*, 2007
Constraint of small clutch size	KS	Green *et al.*, 1982; Nagelkerke & Hardy, 1994; West & Herre, 1998
Inbreeding in protozoan parasites	KS	Read *et al.*, 1992; West *et al.*, 2001b; Nee *et al.*, 2002
Syzygy	KS	West *et al.*, 2000
Soldiers in polyembryonic wasps	KS	Godfray, 1992; Giron *et al.*, 2004; Gardner *et al.*, 2007a
Variance and precision	KS	Green *et al.*, 1982; West & Herre, 1998
Lethal male combat	KS	Abe *et al.*, 2003a,b, 2005
Asymmetric LMC	KS	Shuker et al., 2005

Theoretical unification

We have emphasized how inclusive fitness and kin selection theory are more useful for understanding specific biological cases, but they are also more useful for constructing a general theoretical overview. Considering cooperation, inclusive fitness has provided a unifying framework for all possible explanations of cooperation, allowing very general overviews or classifications (e.g. Sachs *et al.*, 2004; West *et al.*, 2007c, or the recent Target Review by Lehmann & Keller (2006) and associated Commentaries). In contrast, from a group selection perspective: 'Current socio-biology is in theoretical disarray, with a diversity of frameworks that are poorly related to each other' (Wilson & Wilson, 2007). Group selection is not useful for a conceptual overview because whereas some forms of cooperation can be conceptualized with group selection, others cannot (e.g. reciprocity or byproduct benefits; Wilson & Wilson, 2007). Part of this problem may stem from the fact that group selection is not a formal theory, as we discuss below.

The kin selection approach has also proved more useful for making broad generalizations on the relative importance of different mechanisms in explaining cooperation across taxa (Sachs *et al.*, 2004; West *et al.*, 2007c). For example, consider the relative importance of different factors across microbes, insects and vertebrates. In the eusocial insects, the indirect fitness benefits of helping relatives is likely to have been key in the initial origin of cooperation, and is the only possible explanation for the existence of the sterile worker cast (Hamilton, 1964, 1972; Bourke & Franks, 1995; Queller & Strassmann, 1998). Although it is also clear that enforcement strategies such as policing can play an important role in determining the relative advantage of helping relatives (Ratnieks *et al.*, 2006), and that in some species there can even be direct fitness benefits from cooperation (Bernasconi & Strassman, 1999; Queller *et al.*, 2000). The clonal reproduction and limited dispersal of bacteria and other microbes mean that the indirect fitness benefits of helping relatives are also likely to be very important in explaining the many cooperative behaviours that they perform (West *et al.*, 2006b). A different picture emerges from cooperatively breeding vertebrates, where both direct and indirect fitness benefits of helping can be important (Clutton-Brock, 2002; Griffin & West, 2002), with the importance of indirect fitness benefits varying across species, as predicted by Hamilton's rule (Griffin & West, 2003). In contrast, the group selection approach has not led to any broad understanding of the relative importance of different selective forces across taxa. Indeed, if anything, it just seems to lead to confusion, through incorrect statements that have no theoretical or empirical basis, such as 'extra-high relatedness within colonies may be better explained as a consequence rather than a cause of eusociality' (Wilson & Hölldobler, 2005; Wilson & Wilson, 2007).

The kin selection approach has also proved extremely useful for conceptually linking different areas of social evolution, such as cooperation, parasite virulence, offspring sex ratios and dispersal (Frank, 1994, 1998;

Hamilton, 1996). For example, the models used to examine the evolution of dispersal and the evolution of cooperation through population viscosity are incredibly similar with the direction of selection given by the same Hamilton's rule [and Price (1970) equation], with practically the same terms (e.g. Perrin & Lehmann, 2001). Another example is the equivalence of fitness through sons under LMC with parasite virulence and the tragedy of the commons (Frank, 1998, p. 130). In contrast, the group selection approach has not made these links clear, and has even failed to stimulate any research in some of these areas, such as the evolution of dispersal. Furthermore, the kin selection approach has also allowed theory to be taken to the next level, by examining how these related traits will co-evolve, such as cooperation and dispersal (Perrin & Lehmann, 2001) or dispersal and sex ratios (Leturque & Rousset, 2003, 2004; Wild & Taylor, 2004; Wild *et al.*, 2006).

There is no formal theory of group selection

A huge problem in settling the kin selection vs. group selection debate is that group selection is not properly defined as a concept. A consequence of this is that there is no formal theory of group selection. Instead, group selection theory comprises a number of illustrative models, each of limited generality, with obscure or nonexistent links between approaches and formalisms, and some models of group selection contradicting others (Okasha, 2006; Gardner & Foster, in press; Wilson & Wilson, 2007).

Perhaps, the most elegant mathematical approach to group selection is the levels-of-selection formalism provided by Price's theorem (Price, 1972; Hamilton, 1975; Frank, 1986b). This neatly partitions total evolutionary change into within- and between-group components, and it could be argued that 'group selection' is described and defined by the between-group component. Price's theorem also provides the formal foundations for kin selection theory (Hamilton, 1970; Grafen, 1985; Frank, 1998), and so this approach has the added benefit of allowing ready translation between these two views of the evolutionary process. However, it has been argued that this is not a formalism of group selection, because it can diagnose group selection at work in situations where it is not needed as an evolutionary explanation. In particular, if we consider a nonsocial trait that gives a straightforward individual advantage, such as good eye-sight, some groups of individuals will be fitter than others simply because they, by chance, contain more of the fitter individuals. Here, selection will operate to favour some groups over others, but the consensus view is that this is not group selection (Heisler & Damuth, 1987; Sober & Wilson, 1998; Okasha, 2006; Wilson & Wilson, 2007).

An alternative formalism, specifically devised to avoid this problem, is provided by the 'contextual-analysis'

approach (Heisler & Damuth, 1987). Here, individual fitness is decomposed into components as a result of individual-genotype and group-genotype, with the former being identified as the target of individual selection and the latter as the target of group selection. Under this view, contextual analysis diagnoses pure individual selection in the earlier eye-sight example. However, now consider that, because of localized resource competition, all groups have a fixed productivity (soft selection; Wallace, 1968) and all competition for reproductive success occurs within the group. This means that an individual who finds herself in a group where the eyesight of her neighbours is better than average will suffer a reduced fitness. Contextual analysis therefore identifies both an impact of individual-genotype and also an impact of group-genotype on the individual's fitness, and hence diagnoses the operation of both individual and group selection. Again, this is undesirable, as group selection should not be in operation when all groups have the same fitness (Okasha, 2006).

We suggest that these problems do not reflect a failure of the levels-of-selection or contextual-analysis approaches, but rather a failure of the concept of group selection itself. If there is an idea of group selection, it does not seem possible to capture it mathematically, which would put it beyond the reach of scientific inquiry. If a theory cannot be formally defined, then it is not scientific, and we are entering the realms of faith. Wilson & Wilson (2007) acknowledge that 'there is no single statistical method that captures all aspects of multilevel selection theory (Okasha, 2006)' but, rather scarily, seem to think that this is an advantage to group selection: 'In fact, the reason that we can spot errors in statistical methods such as the Price equation is because we have such a strong sense of what multilevel selection means before we attempt to devise formal statistical methods.'

Lack of a formal theory of group selection means that, although it is possible to translate all group selection models into corresponding kin selection models, the reverse may not be true. Indeed, kin selection theory has successfully integrated fundamental issues that have not been tackled in the group selection literature. For example, kin selection theory has incorporated the theory of reproductive value and gene-frequency change in class-structured populations (Taylor, 1990, 1996), and this is easily handled by standard methodology (Taylor & Frank, 1996; Frank, 1997, 1998; Taylor *et al.*, 2007b), whereas group selection theory has failed to address these important issues.

This leaves us with the question, of what is group selection? The earlier paragraph suggests that group selection is a potentially useful, albeit informal, way of conceptualizing some issues of kin selection, rather than a general evolutionary approach in its own right. This point was made by Maynard Smith (1976), who placed group selection as a subset of kin selection models which

involved specific group structure. However, some more recent models, which invoke group selection, could potentially be driven by direct fitness benefits. For example, in some of the models for cooperation and punishment in humans, cooperation can provide a benefit to all individuals in the group, through mechanisms such as increased productivity or reducing the rate of group extinction (Gardner & West, 2004a; Lehmann *et al.*, 2007b; West *et al.*, 2007b, pp. 421–422). This emphasizes how the lack of a formal theory means that different authors can use group selection to conceptualize very different things.

Group selection and altruism

Wilson (2007) uses group selection theory to justify the assertion that we can use altruism pluralistically, to mean whatever we want. As Wilson notes, altruism is a 'loaded,' intentional term, and was historically eschewed by researchers who wished to avoid anthropomorphism. However, the action of natural selection does lead to the appearance of intentionality: from the dynamics of gene-frequency change emerge inclusive-fitness-maximizing agents (Grafen, 2006). The formal justification for this view is founded upon an analysis of direct and indirect fitness effects (Fisher, 1930; Hamilton, 1964; Grafen, 2002, 2006), and hence the 'licence for regulated anthropomorphism' (Grafen, 2003) applies only within this particular framework. Thus, it is possible to describe behaviours that reduce the direct fitness of the individual while increasing the fitness of its social partners as 'altruistic,' but using the word in other ways, such as in terms of within- and between-group effects, is informal at best, and has considerable potential for causing confusion (West *et al.*, 2007b; pp. 419–423). For example, defining terms such as altruism relative to the local group clouds the fundamental point that the spread of a gene is determined by its fitness relative to others in the breeding population, and not to others with which it happens to interact (Grafen, 1984, 2002, 2006; Harvey *et al.*, 1985).

Wilson (2007) provides a number of quotations to support his redefinition of terms such as altruism, and support for group selection theory. This raises two issues. First, a large number of his quotations come from before Hamilton (1964) had even provided the formal definition of such terms and devised inclusive fitness theory. Second, selective quotation can give a misleading impression. To give some examples:

- Wilson quotes Williams (1966) as saying: 'It is universally conceded by those who have seriously concerned themselves with this problem that…group-related (*sic*) adaptations must be attributed to the natural selection of alternative (*sic*) groups of individuals and that the natural selection of alternatives 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.' However, Wilson (2007) fails to point out that Williams' next sentence is: 'However, I would question one of the premises on which the reasoning is based,' or that Williams spends the next four chapters describing why he does not think that group-related adaptations exist.

- Wilson (2007) quotes Hamilton's (1996) autobiographical account of how Hamilton excitedly told 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.' However, Wilson (2007) fails to point out that Hamilton (2001, p. 134) also stated in one of his autobiographical sketches that Wilson's view of nonkin group selection 'remains little changed, still without convincing example.'

- Wilson (2007) quotes from Queller's (1992) commentary on population viscosity and cooperation: 'The original insight stems not from inclusive fitness thinking but from the alternative method of partitioning selection into within-group and between-group effects.' However, Wilson (2007) fails to point out that in a later commentary on the same topic, Queller (2004) says 'Does all this mean that we should discard kin selection in favour of the simpler group selection approach? Hardly. Kin selection has yielded far more insights into the complex behaviours of animals such as social insects. For example, elegant theories of sex-ratio conflict in social insects emerge naturally from kin selection models, whereas the corresponding group selection models are so complex that they have not been developed.'

We stress that our aim here is not to win by quotation – instead, we are stressing that the important thing is to determine the relative use of kin selection and group selection in explaining specific biological cases, not whose authority can be invoked by quotation. As Trivers (1998b) put it, 'I do not care whether at their annual convention 900 howling group selectionists endorse *Unto Others* in its entirety or whether the only true believers are a deeply repentant W.D. Hamilton and a devout monk lost somewhere in the Himalayas. I want to understand the matter for myself.'

Conclusions

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. This is because kin selection methodologies are usually easier to use, allow the construction of models that can be better linked to

specific biological examples, lend themselves to empirical testing and allow the construction of a general conceptual overview. In addition, the group selection approach is not only less useful, but also appears to frequently have negative consequences by fostering confusion that leads to wasted effort (see Errors 2 and 3 and West *et al.*, 2007b; pp. 420–421 and 424–425). It is for these reasons that: (a) the arguments about group selection are only continued by a limited number of theoreticians, on the basis of simplified models that can be difficult to apply to real organisms (see Error 3); (b) theoretical models which make testable predictions tend to be made with kin selection theory (Tables 1 and 2); (c) empirical biologists interested in social evolution measure the kin selection coefficient of relatedness rather than the corresponding group selection parameters (Queller & Goodnight, 1989). It is best to think of group selection as a potentially useful, albeit informal, way of conceptualizing some issues, rather than a general evolutionary approach in its own right.

Acknowledgments

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