Clash of the Titans

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Edward O. Wilson is an expert on social insects, but early in his career, he addressed human sociality. His book *Sociobiology* (1975) initiated a field that has become a major research area in the behavioral sciences and included a controversial chapter on human social evolution. In *The Social Conquest of Earth*, E. O. Wilson updates his earlier groundbreaking treatment of *Homo sapiens*. He stakes out a strong position on the levels-of-selection debate, rejects inclusive-fitness theory, and redefines *eusociality* to include *Homo sapiens*. The book is based on several articles published in professional journals, including those of E. O. Wilson and Hölldobler (2005); D. S. Wilson and Wilson (2007); E. O. Wilson (2008); and, most prominently, Nowak, Tarnita, and Wilson (2010).

E. O. Wilson's work has stirred up a vigorous—and sometimes highly intemperate—debate that has shaken the very foundations of population biology. In this review, I address the fundamental issues involved and suggest a resolution that may be acceptable to both sides of this clash of the Titans.

E. O. Wilson's treatment of eusociality in *The Social Conquest of Earth* is a major innovation. A species is customarily defined as *eusocial* if it is composed of colonies in each of which there is a reproductive division of labor, as in the cases of social bees and termites, in whose societies a single or a few individuals (queens and their mates) reproduce and other castes do not. In humans, by contrast, adults are generically reproductives.

E. O. Wilson defends the notion that humans are eusocial by recalling that early hominins adopted collective child rearing in a fixed location defended by some group members while others dispersed to forage, scavenge, or hunt (Burkart et al. 2009, Chapais 2009, Hrdy 2009, Gintis and van Schaik 2012, Pagano 2012). All known eusocial species went through a similar stage of collective brood rearing. With *alloparenting* (the provision of parental care by individuals other than the recipient's biological parent) in a fixed location established, E. O. Wilson argues, there is strong selection on traits that improve cooperative behavior, which would culminate in eusociality.

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E. O. Wilson's theory thus diverges from the widely held view that human sociality can be explained by invoking Hamilton's (1964a, 1964b) inclusive-fitness theory. Inclusive-fitness theory shows that a personally costly behavior can spread if the behavior offers sufficient benefits to genetically related individuals. E. O. Wilson now rejects this theory, writing in *The Social Conquest of Earth* (p. 51) that

> The foundations of the general theory of inclusive fitness based on the assumptions of kin selection have crumbled, while evidence for it has grown equivocal at best.… Inclusive-fitness theory, often called kin selection theory, is both mathematically and biologically incorrect.

E. O. Wilson favors the more traditional individual-fitness-maximization model in understanding *advanced eusociality*, which is defined as occurring if the workers are sterile or if worker reproduction is suppressed by policing (Frank 1995) or queen

manipulation (Reeve and Keller 1997). Therefore, he writes in *Social Conquest* on page 144,

> The origin and evolution of eusocial insects can be viewed as processes driven by individual-level natural selection. It is best tracked from queen to queen from one generation to the next, with the workers of each colony produced as phenotypic extensions of the mother queen.… The defending worker is part of the queen's phenotype, as teeth and fingers are part of your own phenotype.

To supporters of inclusive-fitness theory, these statements are outrageous and strike a blow at population genetics itself. E. O. Wilson and his coauthors simply could not be believed. Because of its visibility in the journal *Nature*, Nowak, Tarnita, and Wilson's (2010) critique of inclusive-fitness theory has drawn the collective ire of a host of prominent population biologists. *Nature* subsequently published several brief communications in which Nowak, Tarnita, and Wilson's (2010) claims were vigorously rejected, one of which had 134 signatures (Abbot et al. 2011, Boomsma et al. 2011, Strassman et al. 2011). Rousset and Lion (2011) accused Nowak, Tarnita, and Wilson (2010) of saying nothing new and of using "rhetorical devices." They then attacked the journal *Nature* itself, arguing (p. 1390) that

> The publication of this article illustrates more general concerns about the publishing process.… *Nature*'s extravagant editorial characterization of the paper as "the first mathematical analysis of inclusive-fitness theory" recklessly tramples on nearly 50 years of accumulated knowledge.

In passing sentence on *The Social Conquest of Earth*, Dawkins (2012) concluded, "To borrow from Dorothy Parker, this is not a book to be tossed lightly aside. It should be thrown with great force."

Hamilton's rule and its limitations

Kin selection theory holds that an allele for helping another will spread if a mathematical inequality known as *Hamilton's rule* holds. The rule says that the allele will spread if the benefit from the help, in terms of fitness to the recipient, multiplied by the recipient's degree of relatedness to the benefactor, is greater than the cost to the benefactor. *Degree of relatedness* is usually understood as the probability that an allele is identical in the benefactor and the recipient by common descent.

In box 1, I derive a generalization of Hamilton's rule that relaxes key, usually unstated (and often implausible) assumptions about the costs and benefits of helping behavior to relatives versus nonrelatives that are essential in the derivation of the standard form of Hamilton's rule. My generalization makes clear that an allele that causes helping can spread even if it reduces the mean fitness of the population. It follows that Hamilton's rule does not explain eusociality and, indeed, is focused on what may be a minor subset of the biological conditions that favor the fitness of a gene and promote cooperation in metazoan cells and social species (Hammerstein and Leimar 2006); the absence of inclusive-fitness-maximizing behavior even when Hamilton's rule is satisfied is widely observed in social species (Queller and Strassmann 1998, Nonacs 2011). The cooperation of genes in metazoan cells (Leigh 1971) and in social groups (Bowles and Gintis 2011) is therefore effected by selection at a higher level than the gene itself. E. O. Wilson's critique of Hamilton's rule is justified.

Genes survive because they cooperate

Genes survive the evolutionary dynamic, then, not because they maximize inclusive fitness but because they cooperate with other genes in promoting the success of the genome as a whole. Of course, the same argument applies to inclusive fitness at the level of the individual in an advanced eusocial colony.

By contrast, some supporters of Hamilton's rule take the notion that genes maximize inclusive fitness as the very core of evolutionary biological theory. For instance, West and colleagues (2011, p. 233) explained that "since Darwin, the only fundamental change in our understanding of adaptation has been Hamilton's development of inclusive-fitness theory.… The idea [is] that organisms can be viewed as maximizing agents."
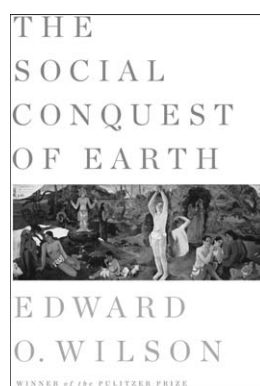
The technical literature says otherwise. The conditions under which evolutionary dynamics lead to inclusive-fitness maximization have been carefully studied by Alan Grafen and his fellow researchers, who have shown that Darwinian population dynamics entail inclusive-fitness maximization at the individual and gene levels, but only assuming that fitness effects are additive (Grafen 1999, 2006, Gardner and Welsh 2011, Gardner et al. 2011). But, of course, the additivity assumption implies that $\alpha = \beta = 0$ in the generalized Hamilton rule, which is expressed in equations 3 and 5 in box 1, in which case Hamilton's rule is fully acceptable.

Core genomes as replicators

In his critique of *The Social Conquest of Earth*, Dawkins (2012) repeated an argument that he first developed in *The Selfish Gene* (1976): Genes are the only *replicators*—the sole entities that are preserved in the evolutionary process. Individuals, in Dawkins's view, are simply *vehicles* that genes build to shuttle themselves successfully from one body to another. Unlike genes, genotypes and groups of genotypes are transitory in sexually reproducing species, he argues; they are broken up and reorganized continually by sexual recombination.

But, in fact, genomes are replicators as much as genes are, and the phenotypes that genomes control include metazoan individuals and social groups, such as E. O. Wilson's eusocial colonies and human societies. This is so because a gene promotes the fitness of its host only if it is complemented by a well-orchestrated configuration of genes with which it interacts (Sober and Lewontin 1982, Hammerstein and Leimar 2006, Noble 2011). Species-defining loci in the genome are therefore necessarily homozygous and identical in both members of a mating pair so that crossing over and meiosis do not destroy the integrity of these complementary loci. Of course, this assertion must be qualified to deal with introns and exons, dominance, maternal–paternal conflicts, autosomal and sex-linked chromosomes, fitness-neutral base replacements, and the like. But these adjustments do not weaken the integrity of the genome. We may call the genes that support this phenotypic commonality the species' *core genome*. The core genome is a replicator and, therefore, subject to the laws of natural selection.

Levels of selection

In urging a harmonious resolution to the clash of the Titans, Okasha (2012) suggested that the level of selection is a matter of personal choice or ease of analysis, because mathematical models show that the result is not affected by this choice: All frameworks give the same answer. Many biologists agree with this assessment (Queller 1992, Dugatkin and Reeve 1994, Wilson DS and Sober 1994, Kerr and Godfrey-Smith 2002, Lehmann et al. 2007, Wilson DS and Wilson 2007).

Box 1. A generalized Hamilton's rule.

The derivation of Hamilton's rule is clean, intuitive, and simple. Suppose there is an allele at a locus of a haploid organism that leads individual A to incur a fitness cost c that bestows a fitness gain b on individual B. Suppose the frequency of this allele in the population is q, and the probability that B has a copy of the allele is p. Then, if the size of the population is n, there are qn individuals with the helping allele, and they increase the number of members of the population from n to $n + qn(b - c)$, but they increase the number of helping alleles from qn to $qn + qn(pb - c)$. Therefore, the frequency of the allele from one period to the next will increase if

$$\Delta q = \frac{qn + qn(pb - c)}{n + qn(b - c)} - q = \frac{b(p - q)}{1 - q} - c > 0. \tag{1}$$

Now suppose that B has a degree of relatedness r to A, meaning that B has a copy of the helping allele with probability r by common descent from an ancestor. Then we can write

$$p = r + (1 - r)q,$$

where the second term comes from the fact that if B does not have the helping allele by descent from a common parent, B may still have the allele with the populationwide probability q. Substituting the above expression for p in equation 1, we arrive at Hamilton's rule for the allele to spread:

$$br > c. \tag{2}$$

We can improve the realism of this equation by adding diploidy, inbreeding, dominance, mutual helping, and the like. Uyenoyama and Feldman (1980), Michod and Hamilton (1980), Queller (1992), Rousset and Billard (2000), and many others have shown that something resembling equation 2 will still hold, although in general the frequency q will also appear in the revised equation 2.

Suppose, however, that in performing the helping act, A induces a fitness cost α on nonrelatives and a fitness cost β on the colony as a whole. For example, $\alpha > 0$ can occur if A redirects brooding care from nonrelative to relative larvae, and $\beta > 0$ if A's help reduces its contribution to colonywide tasks. If the population size is n in the current period, population size n' in the next period will include $n + qn(b - c)$ because of the helping behavior but will be reduced by $n\beta q$ and, because the number of nonrelatives is $n(1 - q)$, will be additionally reduced by $n(1 - q)\alpha$. The number of relatives of the helping allele in the current period is qn, which is increased by the helping behavior by $qn(pr - c)$ and decreased through lower colony efficiency by $qn\beta q$. Therefore, the new population size is

$$n' = n(1 - \alpha(1 - q) - \beta q) + qn(b - c), \tag{3}$$

and equation 1 becomes

$$\Delta q = \frac{qn(1 - \beta bq) + qn(pb - c)}{n(1 - \alpha q(1 - q) - \beta q) + qn(b - c)} - q > 0, \tag{4}$$

which simplifies to

$$b(p - q) + (1 - q)q\alpha > c(1 - q).$$

Substituting $p = r + (1 - p)q$, we get what I will call the generalized Hamilton's rule:

$$br + q\alpha > c. \tag{5}$$

Equation 5 shows that the cost to the colony of the helping behavior (β) is ignored in the equation for the fitness of the helping allele and that transferring resources from nonrelatives to relatives ($\alpha > 0$) can lead to an increase in the frequency of the helping allele even if it in no other way benefits relatives ($b = 0$). The effect on population fitness of an increase in the helping allele is then given by equation 6, which is derived from equation 3:

$$\frac{dn'}{dq} = n(b - c - \alpha(1 - 2q) - \beta). \tag{6}$$

There is, of course, nothing to prevent this effect from being negative even when the Hamilton condition $br > c$ is satisfied or from being positive if even if Hamilton's rule is violated.

However, this is true only for accounting purposes; consideration of causal processes tells a different story.

Because there are replicators at various levels of biological organization and because replicators are subject to an evolutionary dynamic, selection must also occur at various levels. A segregation distorter, for instance,

operates at the level of the gene, because selective forces operative at higher levels need not be invoked in its explanation (Sober and Lewontin 1982, Burt and Trivers 2006). Where the core genome specifies structured interactions among related individuals, kin selection occurs and is therefore a form of group selection.

Where the causal relations inscribed in the core genome occur between or among metazoan individuals, analysis in terms of group selection at a level higher than the individual is appropriate. The group could merely affect fitness payoffs to its members, but generally, this will entail that group structure be inscribed in the core genome. Social groups, then, are subject to exactly the same evolutionary forces—replication with mutation, selection, and heredity—as are individual genes and metazoan individuals. Whatever the level at which selection operates, the resulting dynamic can, of course, at least in principle, be translated into changes in gene frequencies.

No altruism in advanced eusocial species

Biological altruism is defined as a behavior that lowers the personal fitness of the focal individual but raises the fitness of other individuals (Foster 2008). In the case of advanced eusociality, worker fitness is zero (i.e., $c = 0$ in equations 2 and 5 in box 1). Altruism in advanced eusocial species is therefore precluded in principle. Even the generalized Hamilton's rule cannot explain altruism in advanced eusocial species, because it does not exist.

In an advanced eusocial colony, E. O. Wilson maintains, the workers "are extensions of the queen's phenotype… robots she has created in her image that allow her to generate more queens and males than would be possible if she were solitary" (p. 143). This is correct. Workers have no active evolutionary role in an advanced eusocial species. They are therefore analogous to robots, just as cells in the metazoan body are—however complex they may be—basically analogous to robots. Of course, mutations in the

parental reproductives can lead workers to behave in ways that reduce the mean fitness of the colony, but such behavior is not an expression of the workers' inclusive fitness but, rather, a transcription error. Such "outlaw" workers are not "policed" but are, rather, eliminated or controlled through an error correction process within the colony. Like cogs in a machine, a worker in such a colony cannot "defect," although it can "fail" as a part in a machine (Hammerstein and Leimar 2006). Richard Dawkins could have explained all this in his famous book *The Extended Phenotype* (1989); he might have saved a lot of futile debate.

Homo sapiens is not a eusocial species

Humans evolved in cohesive groups involving many unrelated families (Boyd and Silk 2002) and lack a reproductive division of labor (but see Foster and Ratnieks 2005). Moreover, human society sustains a high level of cooperation among genealogically distant individuals (Gintis 2000, Richerson and Boyd 2004, Bowles and Gintis 2011). By contrast, the reproductive division of labor is central to sustaining cooperation in eusocial species, just as sequestration of the germline is key to the emergence of complex metazoans (Buss 1987). Thus I argue, *contra* E. O. Wilson, that it is prudent to exclude humans from the eusocial fold.

Much of E. O. Wilson's critique of the inclusive-fitness model of eusociality does not apply directly to humans or to primitively social species. In our work, my colleagues and I routinely deploy inclusive-fitness models, along with higher-level competition among groups, to explain the emergence of altruism in humans (Fehr and Gintis 2008, Bowles and Gintis 2011). In human society, individuals who attempt to maximize their inclusive fitness at the expense of the group are generally penalized not by the "parliament of genes" but by social sanctions, which are parliaments on yet a higher level.

Conclusions

E. O. Wilson's assertion that the inclusive-fitness approach is "both mathematically and biologically incorrect" should be revised. A more accurate assessment is that Hamilton's rule is incomplete, and with a few changes, it can maintain its exalted position in sociobiology. These changes lead us to the generalized Hamilton's rule, which points beyond itself to the need for many additional tools in the biologist's repertoire to explain complex social behavior.

The evolutionary forces that determine the nonlinear interactions among loci in metazoans and among individuals in sociobiological species must be studied using tools such as the phenotypic gambit (Grafen 1984), game theory (DS Wilson 1977, 1980, Taylor 1992, 1996), agent-based modeling (Gintis 2009), and the physiology of suppressor genes (Leigh 1977). E. O. Wilson and the coauthors of his recent publications are to be lauded for expanding our horizons, not scorned for their small mistakes and tendency to overstate their position. So *The Social Conquest of Earth* is, despite some weaknesses, a book that I recommend. It is an inspiring account of a significant advance in our understanding. Contemporary inclusive-fitness theory is a very big boat, and it can only be rocked by giants (Gadagkar 2010).

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