Sociobiology in turmoil again

Raghavendra Gadagkar

Altruism is defined as any behaviour that lowers the Darwinian fitness of the actor while increasing that of the recipient. Such altruism (especially in the form of lifetime sterility exhibited by sterile workers in eusocial insects such as ants, bees, wasps and termites) has long been considered a major difficulty for the theory of natural selection. In the 1960s W. D. Hamilton potentially solved this problem by defining a new measure of fitness that he called inclusive fitness, which also included the effect of an individual's action on the fitness of genetic relatives. This has come to be known as inclusive fitness theory, Hamilton's rule or kin selection. E. O. Wilson almost single-handedly popularized this new approach in the 1970s and thus helped create a large body of new empirical research and a large community of behavioural ecologists and kin selectionists. Adding thrill and drama to our otherwise sombre lives, Wilson is now leading a frontal attack on Hamilton's approach, claiming that the inclusive fitness theory is not as mathematically general as the standard natural selection theory, has led to no additional biological insights and should therefore be abandoned. The world cannot but sit up and take notice.

Keywords: Altruism, eusociality, Hamilton's rule, inclusive fitness theory, kin selection, sociobiology.

THE science of sociobiology is in turmoil again and this time on theoretical grounds. And yes, E. O. Wilson (of Harvard University) is at the epicentre of it; but, believe it or not, this time around he is leading the attack and his followers (erstwhile?) are at the receiving end. In 1975, Wilson wrote *Sociobiology – The New Synthesis*[1] and gave birth to the science of sociobiology making it at once famous and intensely controversial. Sociobiology is the study of the evolution by natural selection, of social behaviour in animals (humans, plants and microbes also included). Last time around the controversy was because Wilson boldly extended to humans the principles of animal sociobiology. This his critics thought (wrongly in my opinion) smacked of biological determinism and would rob people of individual freedom and help perpetuate inequalities along gender, social, political, racial and other dimensions[2–5]. This time around the controversy concerns much more technical and mundane questions, such as which kind of mathematical formulation is best suited to study the evolution of social behaviour, especially altruism. But the current situation is not without interest to the non-specialist and especially to the historian and chronicler of science.

Altruism and eusociality

Among the various kinds of social interactions seen commonly in group-living species, the most paradoxical and hence the most interesting kind is altruism. The term altruism is used to describe any social interaction that lowers the Darwinian fitness (number of offspring produced in one's lifetime) of the actor and increases that of the recipient. The most extreme forms of altruism are shown by the so-called eusocial insects such as ants, bees, wasps and termites that live in colonies with overlapping generations (usually offspring staying back to help their parents raise additional offspring), and divide labour such that one or a small number of individuals reproduce whereas the rest are sterile workers caring for the offspring of the reproductives[6,7]. The evolution of such eusociality is hence the main problem of sociobiology. The evolution of the altruistic worker caste of eusocial insects remained without any satisfactory explanation for a hundred years since Darwin first recognized the problem they posed to his theory of natural selection in 1859 (ref. 8).

Hamilton's inclusive fitness theory

W. D. Hamilton produced an elegant formal theory that provided a potential solution to this problem. Hamilton argued that we should expand the definition of fitness and defined a new quantity he called inclusive fitness. Inclusive fitness is the sum of two components, a direct com-

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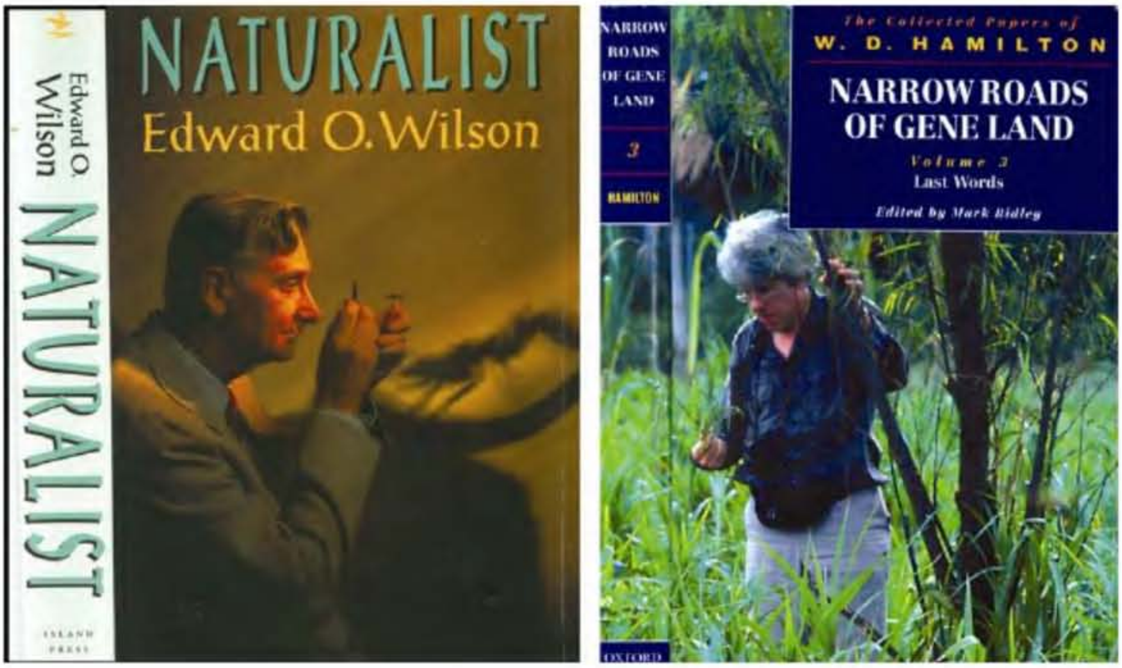

Figure 1.

ponent gained through producing offspring and an indirect component gained through aiding genetic relatives. Hamilton made these two components additive by devaluing each offspring or relative by the genetic relatedness to them. Thus in a diploid, outbred population offspring are multiplied by 0.5, siblings by 0.5, nephews and nieces by 0.25, cousins by 0.125 and so on. Thus the inclusive fitness of 1.0 gained by producing two offspring ($2 \times 0.5 = 1.0$) can also be gained by an altruistic, sterile individual by raising two siblings, four nephews or eight cousins. From this Hamilton predicted that altruism will be favoured by natural selection when the inequality $b \cdot r > c$ is satisfied, where b is the benefit of the act of altruism to the recipient, c the cost of the act to the actor and r the genetic relatedness between the actor and the recipient. This inequality has now come to be known as Hamilton's rule. Hamilton's theory is also frequently referred to as the inclusive fitness theory or kin selection[9–11]. As is often the practice I will use kin selection, inclusive fitness theory and Hamilton's rule, interchangeably. In addition to providing a general theory for the evolution of altruism in all kinds of species and situations, Hamilton realized that his theory had a special application to social Hymenoptera. Insects in the order Hymenoptera (to which ants, bees and wasps but not termites belong), are haplodipoid, i.e. males are produced parthenogenetically from unfertilized eggs and are thus haploid, whereas females are produced from diploid eggs by normal development. Since males are haploid and produce sperms by mitosis, all the sperms of any male are clones of each other making two full sisters to be related to each other by 0.75 instead of the usual 0.5 seen in diplo-diploid species. It follows then that a female hymenopteran would get more inclusive fitness by raising a sister instead of raising an offspring. And that is what sterile workers in eusocial hymenopteran colonies often do. When Hamilton wrote his papers such eusociality had been known to have arisen at least 11 times in the insect order Hymenoptera (accounting for only 2% of animal species), while only once in the rest of the animal kingdom, i.e. in termites. Not surprisingly, this correlation of eusociality with haplodiploidy, which has since come to be known as the haplodiploidy hypothesis, was considered as striking evidence for the inclusive fitness theory[6,11].

The popularization of inclusive fitness theory

Although Hamilton published his seminal papers in 1964, his ideas remained largely unknown until Wilson made kin selection (including the haplodiploidy hypothesis) the centre piece of his highly influential and non-controversial book, *The Insect Societies* in 1971 (ref. 6) and his equally influential but highly controversial book, *Sociobiology – The New Synthesis* in 1975 (ref. 1). Since then Hamiltons's ideas have inspired and led to many thousands of research papers and dozens of books, and have given birth to many sub-disciplines such as behavioural ecology and evolutionary psychology. Kin selection in one form or another has been applied to all kinds of animals, plants, microbes (including fungi, bacterial and viruses) and even in the domain of cell and molecular biology[12–19]. The most recent paper I have read applies Hamilton's rule to study the emergence of cooperation in a synthetic microbial system, although this study shows that nonlinear growth responses of microorganisms limit the predictive value of the rule[20]. Some of the phenomena being studied profitably in the framework of inclusive fitness theory include, in addition to selfishness, cooperation, altruism and spite, sex allocation, parent–offspring conflict, intra-genomic conflict, host–parasite interactions and so on. Kin selection remains a major explanatory framework in the study of human social behaviour under the rubric of evolutionary psychology[21,22]. A great deal of the credit for the runaway proliferation of these kinds of studies must go without doubt to Hamilton, but also in large measure to Wilson.

The attack on inclusive fitness theory

During the last five years however, Wilson has taken the whole world by surprise by renouncing kin selection and Hamilton's rule and denying even the need for high relatedness for social evolution. In the first salvo in 2005 (in a paper co-authored with Hölldobler)[23] he said 'in this new assessment of the empirical evidence, an alternative to the standard model (kin selection) is proposed . . . and kin selection . . . [is] either a weak binding or weak dissolutive force . . . . Close kinship may be more a consequence of eusociality than a factor promoting its origin'. In the most recent and most decisive attack contained in a paper published in *Nature* and co-authored with Martin Nowak and Corina Tarnita[24] (also of Harvard University), Wilson laments that ' . . . considering its position for four decades as the dominant paradigm in the theoretical study of eusociality, the production of inclusive fitness theory must be considered meagre' and claims that 'There is no paradoxical altruism that needs to be explained. The epicycles of kin selection and inclusive fitness disappear.' It is impossible for the world not to sit up and take notice.

Nowak *et al.*[24] make four major points.

1. The haplodiploidy hypothesis has failed.
2. Excess or exclusive focus on measurement of relatedness is misleading.
3. The inclusive fitness theory has many limitations, does not work in all situations and is therefore not a general theory. Instead, they claim that ' . . . standard natural selection theory in the context of precise models of population structure represents a simpler approach, allows the evaluation of multiple competing hypothesis, and provides an exact framework for interpreting empirical observations'.
4. The inclusive fitness theory provides no additional biological insight. They claim that ' . . . empirical research on eusocial organisms has flourished, revealing the rich details of caste, communication, colony life cycles and other phenomena at both the individual and colony selection levels'. However, 'almost none of this progress has been stimulated or advanced by inclusive fitness theory, which has evolved into an abstract enterprise largely on its own'.

Let us now consider each of these points in some detail. The first two points are admittedly not new; they have been made many times before by different people. The haplodiploidy hypothesis has indeed failed completely for two reasons. One is that the high genetic relatedness between sisters created by haplodiploidy (0.75) is broken down by the presence of multiple patrilines within colonies (as queens can mate with more than one male) and multiple matrilines (as queens can be replaced from time to time). We have demonstrated both these phenomena in the primitively eusocial wasp, *Ropalidia marginata* and find that levels of intra-colony relatedness drop from the theoretically expected 0.75 to values ranging from 0.2 to 0.4 (refs 25 and 26). Second, the correlation between eusociality and haplodiploidy has all but disappeared due to the discovery of eusociality in a variety of diploid taxa (in addition to the termites already known) including beetles, shrimps, spiders and even a mammal (reviewed in Gadagkar[7]). The argument that exclusive focus on genetic relatedness and the consequent neglect of the benefit and cost terms in Hamilton's rule has also been pointed out as a major stumbling block to further progress[7,25–30]. Focussing only on relatedness and neglecting the cost and benefit terms usually takes the form of assuming (implicitly) that $b = c$, and testing the prediction that altruism should be correlated with relatedness. This is dangerous because, not being able to prove that $b = c$, when altruism is indeed correlated with relatedness we do not know why it is so, and when it is not correlated, again we do not know why. Testing the prediction that altruism should be correlated with relatedness, without measuring the cost and benefit of altruism is an inadequate test of Hamilton's rule. Indeed points 1 and 2 of Nowak *et al.*[24] neatly summarize the major contribution of my own research group working with the Indian primitively eusocial paper wasp, *R. marginata* over the past 2–3 decades[7]. In summary, points 1 and 2 of the Nowak *et al.*[24] paper are correct. They are not new, but in my opinion, they are well worth repeating.

Generality and mathematical equivalence

The third point concerning the generality or otherwise of the inclusive fitness theory and the equivalence or otherwise of it with standard natural selection models, is more contentious. Standard natural or population genetic model here means studying the competition between alternate alleles, one whose bearer is entirely selfish (e.g. all daughters born in a wasp nest leave to found their own solitary nests), and the other whose bearers practice a finite degree of altruism (i.e. a fraction of the daughters stay back in their nest of birth, function as sterile workers and thus assist their mother to produce more offspring). There is no explicit consideration of cost, benefit or relatedness, but the fate of the two alleles is monitored (theoretically, in a system of equations) exactly as one would do for a non-altruistic or non-social trait. Nowak *et al.*[24] claim that '... inclusive fitness theory is a particular mathematical approach that has many limitations. It is not a general theory of evolution'. And that 'if we are in the limited world where inclusive theory works, then the inclusive fitness condition is identical to the condition derived by standard natural selection theory'. Thus they ask '... if we have a theory that works for all cases (standard natural selection theory) and a theory that works only for a small subset of cases (inclusive fitness theory), and if for this subset the two theories lead to identical conditions, then why not stay with the general theory'? This debate is not entirely new either. The potential lack of generality of Hamilton's rule has long been suspected and commented upon[31–33]. Indeed this topic has been a major preoccupation of theoreticians on both sides of the argument. Inclusive fitness enthusiasts have periodically written papers and books demonstrating and asserting the generality of Hamilton's rule and the complete equivalence of inclusive fitness theory and the standard natural selection model[34–39]. All of these arguments are however based on rather sophisticated and nuanced mathematics on which most empiricists are unable to make an independent judgement and have to rely on the verbal translations provided by the authors. After reading most of the papers from both sides, one is left with the impression that if one bends over backwards and does even more complicated mathematics, one might indeed show that Hamilton's rule is general and that Hamilton's inclusive fitness formulation, handled sensitively and modified as may be required, gives the same result as the standard natural selection approach. If we read between the lines (equations), even the strongest proponents of generality and equivalence are not very inspiring. I will quote three examples to make this point.

(1) Grafen[39] begins an influential paper with the words 'The readers for whom this introduction is intended have met the concept of relatedness and Hamilton's rule, and find it so unproblematic that they are surprised that any clarification, defence, or exposition is necessary. A fair sized literature, to which reference will be made later, deals with relatedness and Hamilton's rule and its very existence is a good indication that there are problems with these ideas. However, this literature is mainly mathematical and I am now to persuade the confident reader, using words only, that clarification, defence, and exposition are, after all necessary for Hamilton's rule and the concept of relatedness.' And he ends with the following conclusion: 'In the central case of weak selection in an outbreeding, homogeneous population, later work has abundantly confirmed the validity of the [Hamilton's] rule as a summary of relevant population genetic models'. The same cannot be said of inbred and heterogeneous populations which appear to be problematic. Grafen tells us that 'The fundamental problem is that the relatedness needed to predict the direction of gene frequency changes differs for dominant and recessive alleles... [and] that the same problem arises in the case of heterogeneous populations'. Grafen concludes that while '... it would not be surprising if the solutions proposed by Hamilton... turn out to be close to the truth most or even all of the time... it is also possible that there are biologically significant exceptions'.

(2) The purpose of a paper entitled 'how to make a kin selection model' by Taylor and Frank[37] appears to be to 'propose a "direct fitness" formulation of inclusive fitness which often has a more straightforward derivation'.

(3) Gardner *et al.*[35] state that '... derivation of Hamilton's rule using Price's theorem... applies very generally. The cost of this generality is that it hides a lot of detail, and so a naïve application of Hamilton's rule may lead to mistakes. For this reason it is easier to use standard population genetics, game theory, or other methodologies to derive a condition for when the social trait of interest is favoured by selection and then use Hamilton's rule as an aid for conceptualizing this result... '.

Hamilton's rule is thus being periodically challenged and someone keeps coming to its defence. For example, Fletcher and Doebeli[40] challenged Hamilton's rule by producing 'a simple general explanation for the evolution of altruism' to which Grafen[41] responded with a paper entitled 'detecting kin selection at work using inclusive fitness', with the statement '... using a recent reformulation of Hamilton's original arguments... the recent model is analysed and it turns out that kin selection provides a sufficient explanation to considerable quantitative accuracy, contrary to the authors' claims'. Similarly, Lehmann *et al.*[42] have attempted to ward-off another challenge to the inclusive fitness theory, this time from evolutionary graph theory[43,44], with the telling sub-title 'the return of the inclusive fitness effect' and with the claim that 'we show that it is possible to translate evolutionary graph theory into classical kin selection models without disturbing at all the mathematics... '. Curiously, kin selectionists are always at the receiving end and seem to have to take retaliatory action; I do not remember kin selectionists firing any salvo to the other side! Be that as it may, the predicament of the conscientious empiricist who reads all these papers and wishes to be guided by them, is not one of comfort. Besides, the immediate consequences of the generality or otherwise of Hamilton's rule and of the mathematical equivalence or otherwise of the inclusive fitness theory and the standard population genetics theory for the day-to-day work of the empiricist are not so obvious. It is therefore hard to blame the empiricist for concluding that the jury is still out on these matters. It follows then that we should wish these debates continue until all the issues are resolved.

Biological insight

The fourth point of Nowak *et al.*[24] concerning the alleged lack of biological insight from the inclusive fitness theory, is even more contentious. At one level their claim is demonstrably false, given all the inclusive fitness and Hamilton's rule-inspired empirical work listed at the beginning of this article. There is no denying that the inclusive fitness theory has been intuitively appealing and heuristically rich for empiricists and that standard natural selection has a long way to go before it captures the imagination of empiricists in a similar way. But there is a more sober and nuanced interpretation of their criticism. It is that biological insights from standard natural selection models can be different from those derived from the inclusive fitness theory. Constructing a simple standard natural selection model for the evolution of eusociality, Nowak *et al.*[24] convey the following messages to the empiricist. 'Our model has clear implications for productive empirical research. The crucial measurement that needs to be performed is the effect of the size of the colony on the demographic parameters of the queen, such as her oviposition rate and average longevity.' This discordance between the message to empiricists from Hamilton's rule and from the standard natural selection theory may have been true in practice, but need not have been so. As mentioned above, the problem with most empirical studies inspired by Hamilton's rule is that they have neglected the benefit and cost terms and focussed almost exclusively on relatedness. This is partly because relatedness is easy to measure, while benefit and cost are rather difficult. Ironically, that measurement of relatedness is expensive has made it more, not less popular; people are often attracted by the expensiveness of the research! Since my research group cannot hope to compete financially with well-endowed laboratories in developed countries and since use of manpower and a focus on ecology come naturally to us, we have endeavoured to focus equally on all three parameters in Hamilton's rule, viz. benefit, cost and relatedness. And when we have done so, our conclusions have been more consistent with the message from standard natural selection models. Indeed, we have concluded that 'ecological, demographic and physiological factors can be more important in promoting the evolution of eusociality . . . '[7].

How should we react?

In summary I think that we should welcome the publication of the paper by Nowak *et al.*[24]. I am aware that many working in the inclusive fitness/Hamilton's rule framework will attack it for containing some errors and for potentially spreading confusion, etc. But for the healthy growth of science it is useful to periodically rock the boat and when a body of knowledge grows into a large ship we need giants like Wilson to rock it. Let us hope that the inclusive fitness theory and the standard natural selection theory flourish side-by-side in the service of empiricists. This will require that theoreticians espousing standard natural selection models work hard to make their models appealing to empiricists and that empiricists sold on Hamilton's rule make their tests robust by paying attention to all parameters of the model.

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On multiple choice tests and negative marking

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We critically examine the impact of marking schemes in multiple choice tests on the outcomes. We postulate reasonable models for the distribution of marks as well as of the guessing behaviour of the candidates when they do not know the correct answer. Through simulation, we show that the impact is significant. We suggest an alternative for improving the outcome.

Keywords: Gatecrasher, multiple choice test, negative marks, random guess.

Multiple choice tests have been used for screening candidates for a specific objective. Increasingly they are being used as a single test for final selection for admission to a course, award of fellowship, or for a job.

By a multiple choice test we mean a traditional test where each question has exactly one correct answer (among several choices, typically four or five) and to get credit the candidate needs to tick the correct answer (under the assumption that there is exactly one correct answer).

In a multiple choice test, when an answer is incorrect we can be sure that the candidate does not know the answer and in case the answer is correct, we are not sure if the candidate actually knows the answer or the outcome is due to a random guess. That is why whenever we talk of multiple choice tests, the issue of negative marks for an incorrect answer always crops up. Are there negative marks? If so what is the negative marking scheme? The discussion on negative marks often throws up differing views among experts. While some feel that there should be no negative marks as one should not take away credit that has been earned, some others argue that there should be nominal negative marks. Yet others argue that it does not matter: it is the same rule for everyone.

Even among those who feel that there should be negative marks, there is confusion as to the quantum of negative marks for an incorrect answer. Some argue that if every question has n alternatives, the correct negative mark for an incorrect answer should be $1/n$. The common interpretation of correct seems to be that a candidate choosing an answer randomly should not get any advantage on the average. In other words, if a candidate ticks all answers in a test randomly, the expected score of such a candidate should be 0. Simple calculation[1] shows that for this to happen the correct negative mark for an incorrect answer should be $1/(n-1)$. It is easy to show that if the negative score for an incorrect answer is $1/(n-1)$, the expected score of a candidate remains the same as the score based on his knowledge. The expected advantage from random guessing being zero does not guarantee that it has no impact on selection.

An important question that needs to be answered is: how many candidates who should not have been selected get selected because of random guessing. In other words, we need to examine how many candidates gatecrashed into the list of selected candidates. We will discuss this in the next section.

Another factor that has a big impact on the outcome is the difficulties that arise when there are incorrect or ambiguous questions. Often the solution of such a problem is to award marks to all candidates. This has an impact on the final selection. However, we have not factored this here. After all, this can be avoided if the administrators of the test are careful.

Is the impact of random guessing marginal?

Let us analyse the impact of random guessing on the ranks of the candidates and the subsequent selection of the candidates. Let us consider a situation where there are 200,000 candidates and the test is to select up to 1000 candidates (for admission to a course or selection for a job). It is common in India to have selections of such magnitudes, such as in the admission in engineering colleges or in the recruitment of large technology companies. The test consists of 200 questions. The candidate with serial number i knows answers to X_i questions. We will call X_i as the true score of the ith candidate, as it is the score based on his/her knowledge (X_i lies between 0 and 200).

The candidate may guess the answers to the questions for which he/she does not know the answers, getting credit for the ones he/she got right by chance, and possibly getting negative marks for the ones where he/she got the wrong answer. Let Z_i denote the observed score of the ith candidate.

Ideally we should have selected the top 1000 students based on their true scores, i.e. X_is; but true scores are not observable, only Z_is are observable and hence we would select the top 1000 students based on their observed scores.

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