Inclusive fitness theory and eusociality

Nowak *et al.*[1] argue that inclusive fitness theory has been of little value in explaining the natural world, and that it has led to negligible progress in explaining the evolution of eusociality. However, we believe that their arguments are based upon a misunderstanding of evolutionary theory and a misrepresentation of the empirical literature. We will focus our comments on three general issues.

First, Nowak *et al.*[1] are incorrect to suggest a sharp distinction between inclusive fitness theory and "standard natural selection theory". Natural selection explains the appearance of design in the living world, and inclusive fitness theory explains what this design is for. Specifically, natural selection leads organisms to become adapted as if to maximize their inclusive fitness[2–4]. Inclusive fitness theory is based upon population genetics, and is used to make falsifiable predictions about how natural selection shapes phenotypes, and so it is not surprising that it generates identical predictions to those obtained using other methods[2,5–7].

Second, Nowak *et al.*[1] are incorrect to state that inclusive fitness requires a number of "stringent assumptions" such as pairwise interactions, weak selection, linearity, additivity and special population structures. Hamilton's original formulations did not make all these assumptions, and generalizations have shown that none of them is required[3,5,6,8]. Inclusive fitness is as general as the genetical theory of natural selection itself. It simply partitions natural selection into its direct and indirect components.

Nowak *et al.*[1] appear to have confused the completely general theory of inclusive fitness with models of specific cases. Yes, researchers often make limiting assumptions for reasons of analytical tractability when considering specific scenarios[5,7], as with any modelling approach. For example, Nowak *et al.*[1] assume a specific form of genetic control, where dispersal and helping are determined by the same single locus, that mating is monogamous, and so on. However, the inclusive fitness approach has facilitated, not hindered, empirical testing of evolutionary theory[9–11]. Indeed, an advantage of inclusive fitness theory is that it readily generates testable predictions in situations where the precise genetic architecture of a phenotypic trait is unknown.

Third, we dispute the claim of Nowak *et al.*[1] that inclusive fitness theory "does not provide any additional biological insight", delivering only "hypothetical explanations", leading only to routine measurements and "correlative studies", and that the theory has "evolved into an abstract enterprise largely on its own", with a failure to consider multiple competing hypotheses. We cannot explain these claims, which seem to overlook the extensive empirical literature that has accumulated over the past 40 years in the fields of behavioural and evolutionary ecology[9–11] (Table 1). Of course, studies must consider the direct consequences of behaviours, as well as consequences for relatives, but no one claims otherwise, and this does not change the fact that relatedness (and lots of other variables) has been shown to be important in all of the above areas.

We do not have space to detail all the advances that have been made in the areas described in Table 1. However, a challenge to the claims of Nowak *et al.*[1] is demonstrated with a single example, that of sex allocation (the ratio of investment into males versus females). We choose sex allocation because: (1) Nowak *et al.*[1] argue that inclusive fitness theory has provided only "hypothetical explanations" in this field; (2) it is an easily quantified social trait, which inclusive fitness theory predicts can be influenced by interactions between relatives; and (3) the study of sex allocation has been central to evolutionary work on the eusocial insects. In contrast to the claims of Nowak *et al.*[1],

recent reviews of sex allocation show that the theory explains why sex allocation varies with female density, inbreeding rate, dispersal rate, brood size, order of oviposition, sib-mating, asymmetrical larval competition, mortality rate, the presence of helpers, resource availability and nest density in organisms such as protozoan parasites, nematodes, insects, spiders, mites, reptiles, birds, mammals and plants[5,12,13].

The quantitative success of this research is demonstrated by the percentage of the variance explained in the data. Inclusive fitness theory has explained up to 96% of the sex ratio variance in across-species studies and 66% in within-species studies[13]. The average for all evolutionary and ecological studies is 5.4%. As well as explaining adaptive variation in behaviour, inclusive fitness theory has even elucidated when and why individuals make mistakes (maladaptation), in response to factors such as mechanistic constraints[13]. It is not clear how Nowak *et al.*[1] can characterize such quantifiable success as "meagre". Their conclusions are based upon a discussion in the Supplementary Information of just three papers (by authors who disagree with the interpretations of Nowak *et al.*[1]), out of an empirical literature of thousands of research articles. This would seem to indicate a failure to engage seriously with the body of work that they recommend we abandon.

The same points can be made with regard to the evolution of the eusocial insects, which Nowak *et al.*[1] suggest cannot be explained by inclusive fitness theory. It was already known that haplodiploidy itself may have only a relatively minor bearing on the origin of eusociality, and so Nowak *et al.*[1] have added nothing new here. Inclusive fitness theory has explained why eusociality has evolved only in monogamous lineages, and why it is correlated with certain ecological conditions, such as extended parental care and defence of a shared resource[14,15]. Furthermore, inclusive fitness theory has made very successful predictions about behaviour in eusocial insects, explaining a wide range of phenomena (Table 2).

Ultimately, any body of biological theory must be judged on its ability to make novel predictions and explain biological phenomena; we believe that Nowak *et al.*[1] do neither. The only prediction made by their model (that offspring are favoured to help their monogamously

Table 1 | Inclusive fitness theory has been important in understanding a range of behavioural phenomena

Research area	Correlational?	Experimental?	Theory–data interplay
Sex allocation	Yes	Yes	Yes
Policing	Yes	Yes	Yes
Conflict resolution	Yes	Yes	Yes
Cooperation	Yes	Yes	Yes
Altruism	Yes	Yes	Yes
Spite	Yes	Yes	Yes
Kin discrimination	Yes	Yes	Yes
Parasite virulence	Yes	Yes	Yes
Parent–offspring conflict	Yes	Yes	Yes
Sibling conflict	Yes	Yes	Yes
Selfish genetic elements	Yes	Yes	Yes
Cannibalism	Yes	Yes	Yes
Dispersal	Yes	Yes	Yes
Alarm calls	Yes	Yes	Yes
Eusociality	Yes	Yes	Yes
Genomic imprinting	Yes	Yes	Yes

Data are taken from refs 9–11. Correlational studies test predictions using natural variation in key variables, whereas experimental studies involve their experimental manipulation. Interplay between theory and data means that theory has informed empirical study, and vice versa. Inclusive fitness is not the only way to model evolution, but it has already proven to be an immensely productive and useful approach for studying eusociality and other social behaviours.

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Table 2 | Areas in which inclusive fitness theory has made successful predictions about behaviour in eusocial insects

Trait examined	Explanatory variables	Correlational studies?	Experimental studies?	Interplay between theory and data?
Altruistic helping	Haplodiploidy versus diploidy	Yes	No	Yes
Worker egg laying	Worker policing	Yes	Yes	Yes
Policing	Relatedness	Yes	Yes	Yes
Level of cooperation	Costs, benefits and relatedness	Yes	Yes	Yes
Intensity of work	Need for work and probability of becoming queen	Yes	Yes	Yes
Sex allocation	Relatedness asymmetries due to variation in queen survival, queen number and mating frequency	Yes	Yes	Yes
Sex allocation	Resource availability	Yes	Yes	Yes
Sex allocation	Competition for mates between related males	Yes	Yes	Yes
Number of individuals trying to become reproductive	Presence of old queens	Yes	Yes	Yes
Workers killing queens	Presence of workers, reproductives or other queens	Yes	No	No
Exclusion of non-kin	Colony membership	Yes	Yes	Yes

Data are taken from refs 12–16.

mated mother if this provides a sufficient benefit) merely confirms, in a less general way, Hamilton's original point: if the fitness benefits are great enough, then altruism is favoured between relatives.

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Only full–sibling families evolved eusociality

The paper by Nowak *et al.*[1] has the evolution of eusociality as its title, but it is mostly about something else. It argues against inclusive fitness theory and offers an alternative modelling approach that is claimed to be more fundamental and general, but which, we believe, has no practical biological meaning for the evolution of eusociality. Nowak *et al.*[1] overlook the robust empirical observation that eusociality has only arisen in clades where mothers are associated with their full-sibling offspring; that is, in families where the average relatedness of offspring to siblings is as high as to their own offspring, independent of population structure or ploidy. We believe that this omission makes the paper largely irrelevant for understanding the evolution of eusociality.

Eusociality is not just any form of condition-dependent reproductive altruism as found in cooperative breeders, but the permanent division of reproductive labour. Clades where helpers became irreversibly eusocial (ants, some bees, some wasps, and termites[2]) are old, radiated into many subclades over evolutionary time, and achieved considerable ecological footprints. A recent comparative study[3] showed that all hymenopteran clades that fit the standard definition of eusociality[4] evolved from life-time monogamous ancestors[5–8]. This implies that high relatedness always preceded or coincided with eusociality, and contrasts with the contention of Nowak *et al.*[1] that eusociality can evolve in any group with parental care, or that high relatedness arises after eusociality.

Given that promiscuity is the most common mating system in animals, strict ancestral monogamy throughout eusocial clades implies that high relatedness was necessary for eusociality to evolve. Nonetheless, necessity does not imply sufficiency. Monogamous lineages may have remained solitary because the benefits of helping at the nest were insufficient to surpass independent breeding. This is elegantly captured by the ratio of the parameters *b* and *c* in Hamilton's rule. In a number of ant, bee and wasp genera the high relatedness condition for eusociality has become secondarily relaxed via evolutionary elaborations such as multiple queen mating, but this has only occurred after worker phenotypes had specialized so that opting out to independent breeding had become selectively disadvantageous or

developmentally impossible[3]. Claiming (in their Supplementary Information, Part B) that it is far simpler to consider that advanced eusocial species just need more sperm[1] muddles proximate and ultimate explanations[9,10]; many multiply-mating queens discard most of the sperm they receive[11,12], indicating that sperm limitation cannot explain polyandry.

We now also know that departures from high relatedness would almost certainly have prevented the evolution of eusociality if they had happened before sterile castes had become permanent[8], that is, before reaching the point of no return to breeding independently[13]. A recent comparative study on birds[14] showed that cooperative breeding is an unstable state that predominantly occurs in monogamous clades and is likely to be lost when parents become more promiscuous. This evidence is not merely correlative: differences in ancestral promiscuity between cooperative and non-cooperative species were found even before cooperation arose, illustrating that monogamy preceded the evolution of helping and that helpers leave when relatedness incentives are reduced. This shows that high relatedness among siblings is critical along with the Hamiltonian *b*/*c* ratio but, as in the insects, relatedness is not sufficient because many monogamous birds are not cooperative breeders.

In light of these reconstructions of the ancestral life histories of numerous social clades, it is surprising that the argument of Nowak *et al.*[1] about eusocial evolution starts by assuming that family structure can be replaced by any form of population structure. This assumption is puzzling given the lack of empirical evidence that this hypothetical 'parasocial' route to eusociality[1,4] (where same-generation individuals associate independent of relatedness) has produced a single extant clade with obligately eusocial workers. We believe that this renders Part A of the Supplementary Information of Nowak *et al.*[1], and the arguments throughout the first two-thirds of the paper, largely irrelevant to the origin of eusociality. Part C of the Supplementary Information addresses the evolution of sterile workers within monogamous or clonal families, meaning that relatedness in these models is invariant. As a consequence, we believe that these models have nothing to say about the importance of relatedness in the evolution of eusociality beyond showing that costs and benefits are also important. This was already clear from Hamilton's rule nearly half a century ago.

It should give pause for thought that none of the long-recognized approximations of inclusive fitness theory raised in the paper was important enough to preclude kin selection theory from developing into a well-integrated network of complementary hypotheses with high predictive power for reproductive decision-making in real-world social organisms. In contrast, the abstractions of Nowak *et al.*[1] fail to provide any new predictions or questions; all they apparently have to offer is the truism that helpers are associated with longer-lived, fecund breeders.

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Kin selection and eusociality

ARISING FROM M. A. Nowak, C. E. Tarnita & E. O. Wilson *Nature* **466,** 1057–1062 (2010)

Hamilton[1] described a selective process in which individuals affect kin (kin selection), developed a novel modelling strategy for it (inclusive fitness), and derived a rule to describe it (Hamilton's rule). Nowak *et al.*[2] assert that inclusive fitness is not the best modelling strategy, and also that its production has been "meagre". The former may be debated by theoreticians, but the latter is simply incorrect. There is abundant evidence to demonstrate that inclusive fitness, kin selection and Hamilton's rule have been extraordinarily productive for understanding the evolution of sociality.

Below we list a few examples of what has been learned from applying kin selection theory—there are thousands of others. (1) Organisms overwhelmingly direct costly assistance, and all true altruism, towards kin[3]. (2) Eusociality in insects originated in organisms with parental care and single mating, which means that relatedness among helpers and brood is generally at the level of siblings[4]. (3) Benefits that can make helping more profitable than reproducing independently often take the forms of either fortress defence (termites, naked mole rats, social shrimp, social thrips and aphids, and some ants) or life insurance

(wasps, bees, other ants)[5,6]. (4) Sex ratios, worker egg laying, worker policing, caste conflict and other social interactions in eusocial insects are explained by kin selection theory[5,7].

Kin selection evidence is not merely correlative. Numerous kin selection experiments manipulate relatedness in animals, plants and microbes. Other experiments manipulate costs and benefits and show that kin selection is predictive[8].

Nowak et al.[2] say that the haplodiploid hypothesis is not the only explanation for eusociality, but that has not been in dispute for some time. Haplodiploidy is not necessary for the evolution of eusociality, and is not the same as kin selection[5,7].

Kin selection does not explain all social behaviour, but the claim that it does has never been widely accepted. There are cooperative acts that benefit the actor directly, and between-species mutualisms that must have direct benefits to evolve[9]. But only kin selection can explain true altruism[10].

Kin selection theory is still inspiring new research. Application of kin selection theory to microbes, including those causing human diseases, is expanding[11]. Kin selection is changing our views of imprinting[12] and maternal–fetus diseases in humans[12].

Clearly kin selection is a strong, vibrant theory that is the basis for understanding how social behaviour has evolved. Perhaps the best examples come from kin recognition, a field that did not exist before Hamilton's insights[7]. We are puzzled why Nowak et al.[2] would attack a body of research that has been exemplary as "a domain of empirical knowledge [that has] followed so closely and fruitfully upon an abstract theoretical idea."[13]

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Inclusive fitness in evolution

For over fifty years, the evolution of social behaviour has been guided by the concept of inclusive fitness as a measure of evolutionary success. Nowak et al.[1] argue that inclusive fitness should be abandoned. In so doing, however, they misrepresent the role that inclusive fitness has played in the theory of social evolution by which understanding social behaviour in a variety of disciplines has developed and flourished. By discarding inclusive fitness on the basis of its limitations, they create a conceptual tension which, we argue, is unnecessary, and potentially dangerous for evolutionary biology.

The core argument of Nowak et al[1]. for abandoning inclusive fitness is its limited capacity to predict dynamics in evolutionary models. This is an old point, and one that was hotly debated in the early years of kin selection theory[2]. Inclusive fitness was developed by Hamilton to summarize a difficult frequency-dependent selection problem by using a simple maximization principle. Early work[3] proved that the average inclusive fitness effect is maximized by behavioural evolution in family structured populations and that it provides the surface for the Wright's adaptive topography (arguably one of the most useful tools that has ever been developed for understanding evolution).

Hamilton's great insight was that individual fitness is not maximized by social evolution when relatives are present, inclusive fitness is. The idea that something other than the individual organism could be the fitness-maximizing unit was completely revolutionary at the time and opened new research areas that are still being developed, such as the study of transitions in units of evolution and individuality[4].

Today, inclusive fitness and evolutionary dynamics models are bridged and linked by the unifying concept of invasion fitness[5–11] (Fig. 1). Invasion fitness captures feedbacks between the evolution of social traits and the ecological structure of the evolving population[7–11] (Fig. 2). Invasion fitness embraces average fitness and inclusive fitness maximization at evolutionary steady states[5,7,9–11], and further reveals the difficulty of reducing evolution to a simple maximization process[5,12] (Fig. 1a).

Under Hamilton's rule, the condition for invasion of an altruistic allele involves a linear function of genetic relatedness. With eco-evolutionary feedbacks, Hamilton's rule becomes part of a more complex and dynamic framework[7,10,11] in which relatedness between interacting individuals is a dynamic property of the population and an outcome of the models, rather than a pre-defined feature (which relatedness was in earlier models of inclusive fitness). Yet in this new framework the assumption of weak selection alone is often sufficient for Hamilton's rule to predict accurately endpoints of altruism

evolution[11] (Fig. 1b). This framework has also begun to provide the testable predictions under competing hypotheses about relatedness and sociality that Nowak *et al.*[1] call for[8–11] (Fig. 2).

Both inclusive fitness and average fitness maximization are general insights about the evolutionary process with great heuristic value, even though they rely on special conditions to predict evolutionary dynamics. Considerable progress in extending evolutionary dynamics models to more general ecological, behavioural and genetic scenarios has been guided by the inclusive fitness concept[4,6–11,13–15]. By opposing 'standard selection theory' and 'inclusive fitness theory', we believe that Nowak *et al.*[1] give the incorrect (and potentially dangerous) impression that evolutionary thinking has branched out into conflicting and apparently incompatible directions. In fact, there is only one paradigm: natural selection driven by interactions, interactions of all kinds and at all levels. Inclusive fitness has been a powerful force in the development of this paradigm and is likely to have a continued role in the evolutionary theory of behaviour interactions.
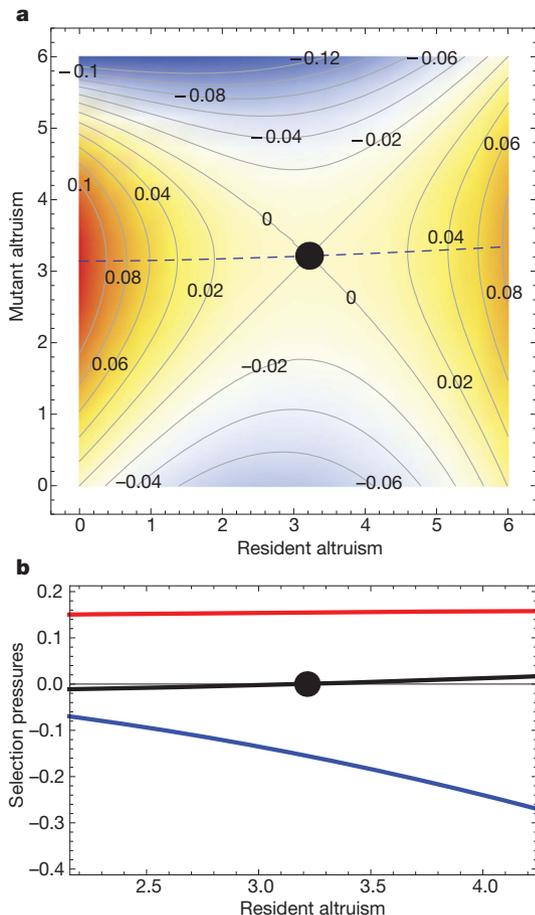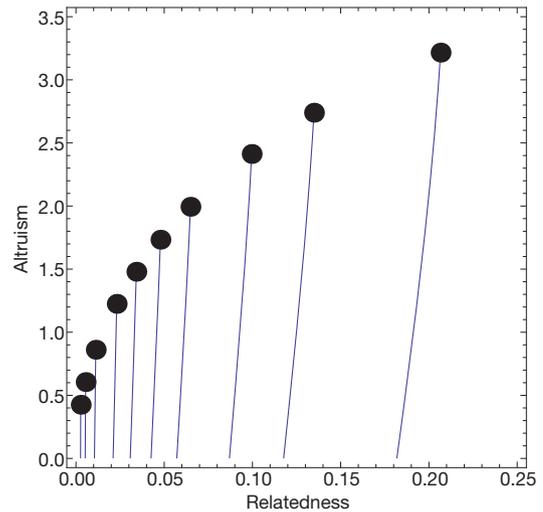

Figure 2 | Co-evolution of altruism and relatedness. Evolutionary trajectories (thin curves) start with zero altruism and converge to evolutionarily stable phenotypes (black circles). Relatedness is dynamic and co-evolves with altruism. Eco-evolutionary models can predict how environmental factors (for example, habitat viscosity) affect altruism evolution. Here, viscosity decreases across trajectories from right to left, and the string of black circles shows how evolved altruism and relatedness should co-vary along an environmental gradient of habitat viscosity.

METHODS

See ref. 10 for details on the model underlying Figs 1 and 2 (and others[7,8,11] for further development). Altruism is a continuous character (with haploid inheritance) evolving in a spatial population network. Invasion fitness is the growth rate of a self-structured mutant cluster. Figure 1a, b is based, respectively, on figures 6E and 4E in ref. 10 with mobility rate = 1 and habitat viscosity = 1/4. Figure 1a makes no special assumption on selection, interactions or population structure. Figure 2 is based on figures 5F and 7F in ref. 10 with mobility rate = 1 and habitat viscosity from 1/4 (right) to 1/256 (left). Figures 1b and 2 only assume weak selection.

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Figure 1 | Fitness landscape and Hamilton's rule. a, Fitness landscape in resident–mutant phenotypic space. Mutant invasion (inclusive) fitness is maximized along the dashed curve and the black circle is an evolutionarily stable phenotype. However, the asymmetrical sign structure implies that evolutionary dynamics do not obey an optimizing principle[12]. **b,** Selection pressures arise from relatedness (red curve), physiological cost of altruism (blue) and change in space occupancy (black). Under weak selection, the latter is negligible (black curve close to zero) and the benefit is proportional to relatedness (see for example, equation (3) in ref. 10), which makes Hamilton's rule a good approximation of selection[10,11]. The black circle indicates the evolutionarily stable phenotype found in **a.**

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In defence of inclusive fitness theory

ARISING FROM M. A. Nowak, C. E. Tarnita & E. O. Wilson *Nature* **466**, 1057–1062 (2010)

Arguably the defining characteristic of the scientific process is its capacity for self-criticism and correction[1]. Nowak *et al.*[2] challenge proposed connections between relatedness and the evolution of eusociality[3], suggest instead that defensible nests and "spring-loaded" traits are key, and present alternative modelling approaches. They then dismiss the utility of Hamilton's insight that relatedness has a profound evolutionary effect[3], formalized in his widely accepted inclusive fitness theory as Hamilton's rule ("Rise and fall of inclusive fitness theory"). However, we believe that Nowak *et al.*[2] fail to make their case for logical, theoretical and empirical reasons.

Logically, both in attacking inclusive fitness and in attempting to reinforce their own positions, Nowak *et al.*[2] cherry-pick examples and fail to distinguish necessary from sufficient causes[1]. Yes, there are hundreds of haplodiploid species that are not eusocial[2]. Yet, there are also hundreds of nest-making (diploid) birds, mammals and reptiles that are not eusocial. Moreover, if the non-eusocial, haplodiploid species pose a problem for inclusive fitness, then the fact that hundreds of them also make nests (including many living in communal or sub-social groups) does not support the proposed alternative.

Theoretically, in promoting their modelling approach, Nowak *et al.*[2] pose a false dichotomy between inclusive fitness theory and "standard natural selection theory". They assert, we believe incorrectly, that inclusive fitness theory suffers from numerous ills (for example, "stringent assumptions"), yet their own models require stringent assumptions, without the benefit of any generality. Indeed, although asserting that "relatedness does not drive the evolution of eusociality", the authors do not present the critical test of removing the effects of relatedness in their model (for example, by randomly assigning daughters to nests). Thus, Nowak *et al.*[2] do not provide any basis for their core assertion, and available data on real biological systems[4–6] directly contradict it.

Empirically, Nowak *et al.*[2], in our eyes, misinterpret relevant literature. Emphasizing progressive provisioning of food to immatures as a critical pre-adaptation (that is, a "spring-loaded" trait), they overlook taxa (for example, sweat bees) in which eusociality evolved repeatedly without progressive provisioning[7,8]. It has been suggested that eusociality might rapidly evolve[9], but the statement by Nowak *et al.*[2] that studies of forced sociality in *Lasioglossum* bees show that solitary bees will divide labour "in foraging, tunnelling, and guarding" is incorrect. *Lasioglossum hemichalceum* is social (communal), not solitary[10], and the solitary *Lasioglossum figueresi* was studied in artificial arenas, not nests, so it was impossible for bees to forage, tunnel or guard[11]. Moreover, the small carpenter bees that Nowak *et al.*[2] cite are in a genus (*Ceratina*) that contains no known obligately eusocial species, and only one species in which facultative eusociality occurs at high frequency[12], indicating that even if "spring-loaded" traits exist, Nowak *et al.*[2] have misidentified them.

What is clear is that neither haplodiploidy, nests, nor "spring-loaded" traits is sufficient for the evolution of eusociality. However, the most recent comparative evidence supports the basic prediction of inclusive fitness theory that, regardless of ploidy or the presence of nests or "spring-loaded" traits, high relatedness is key to the evolution of cooperative breeding and/or eusociality[4–6]. Any serious attempt to dismiss inclusive fitness theory must address the results of these important comparative studies[4–6] directly.

Beyond its being completely integrated with "standard natural selection theory"[13], beyond extensive theoretical work showing that it is both flexible and robust[13], beyond the fact that available evidence supports its fundamental prediction that high relatedness is key for the evolution of eusociality[4–6], inclusive fitness theory has the virtue of making general, non-obvious predictions well beyond the issue of eusociality[4–6]. Kin recognition and policing[14,15], mother–fetus conflicts, and patterns of sex allocation (particularly in eusocial insects) stand out[3,14,15]. Collectively, those predictions have again and again been borne out in a vast comparative and experimental empirical literature (for example, refs 3–6, 14, 15) that Nowak *et al.*[2] nonetheless dismiss as "meagre" and "superficial". Nowak *et al.*[2] present a provocative essay, but in their apparent rush to discard inclusive fitness theory, they present an alternative that we believe to be deeply flawed. Although the continued scrutiny of accepted paradigms is an essential part of the scientific process, the reports[2] of the fall of inclusive fitness theory have been greatly exaggerated. If anything, Nowak *et al.*[2] succeed in reminding us of the elegance and power of Hamilton's numerous insights and contributions[3].

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Nowak *et al.* reply

Our paper challenges the dominant role of inclusive fitness theory in the study of social evolution[1]. We show that inclusive fitness theory is not a constructive theory that allows a useful mathematical analysis of evolutionary processes. For studying the evolution of cooperation or eusociality we must instead rely on evolutionary game theory or population genetics. The authors of the five comments[2–6] offer the usual defence of inclusive fitness theory, but do not take into account our new results.

The definition of inclusive fitness given by Hamilton[7] is as follows:

> "Inclusive fitness may be imagined as the personal fitness which an individual actually expresses in its production of adult offspring as it becomes after it has been first stripped and then augmented in a certain way. It is stripped of all components which can be considered as due to the individual's social environment, leaving the fitness which he would express if not exposed to any of the harms or benefits of that environment. This quantity is then augmented by certain fractions of the quantities of harm and benefit which the individual himself causes to the fitnesses of his neighbours. The fractions in question are simply the coefficients of relationship appropriate to the neighbours whom he affects: unity for clonal individuals, one-half for sibs, one-quarter for half-sibs, one-eighth for cousins,...and finally zero for all neighbours whose relationship can be considered negligibly small."

The concept of inclusive fitness assumes that the fitness of individuals can be split into additive components caused by individual actions. This approach rests on specific assumptions, which need not hold for any particular evolutionary process. Therefore inclusive fitness theory is not a general description of natural selection. In Part A of our Supplementary Information[1] we provide a mathematical analysis to prove this point. If there are non-zero selection intensities, or if there are synergistic interactions, or if there is complex population structure, then it is easy to find situations where personal fitness cannot be partitioned into additive components as needed by inclusive fitness theory. Essentially, inclusive fitness theory requires fitness to be a linear function of individual actions, but a full understanding of social evolution must take into account the nonlinearity inherent in biological systems.

We distinguish between inclusive fitness theory and standard natural selection theory, because the latter does not require fitness to be split into additive components. We have shown that inclusive fitness theory is a proper subset of the standard theory and makes no independent predictions. Any effect of relatedness is fully captured by the standard approach.

Hamilton's rule states that cooperation can evolve if relatedness exceeds the cost to benefit ratio. If cost and benefit are parameters of individual actions then this rule almost never holds[1,8,9]. There are attempts to make Hamilton's rule work by choosing generalized cost and benefit parameters[10], but these parameters are no longer properties of individual phenotypes. They depend on the entire system including population structure. These extended versions of Hamilton's rule have no explanatory power for theory or experiment[11].

Neither inclusive fitness theory nor any formulation of Hamilton's rule can deal with evolutionary dynamics[12]. This fact alone invalidates the claim that inclusive fitness theory "is as general as the genetical theory of natural selection"[2].

Several aspects of our paper are misrepresented in the comments[2–6]. One, we do not argue that relatedness is unimportant. Relatedness is an aspect of population structure, which affects evolution[13]. Two, we do not dispute the importance of kin recognition. Conditional behaviour based on kin recognition can be seen as a mechanism for the evolution of cooperation[14]. Three, Part A of our Supplementary Information[1] is not a model for evolution of eusociality, but a mathematical framework that demonstrates the limitations of inclusive fitness theory. Four, Part C of our Supplementary Information[1] provides a mathematical model for the evolution of eusociality, which makes simple and testable predictions and explains the rarity of the phenomenon. Five, monogamy and sex ratio manipulation may be important for the evolution of eusociality; such ideas are best tested in the context of the explicit model that we propose.

Abbot *et al.*[2] claim that inclusive fitness theory has been tested in a large number of biological contexts, but in our opinion this is not the case. We do not know of a single study where an exact inclusive fitness calculation was performed for an animal population and where the results of this calculation were empirically evaluated. Fitting data to generalized versions of Hamilton's rule is not a test of inclusive fitness theory, which is not even needed to derive such rules.

The limitations of inclusive fitness theory are also demonstrated by its inability to provide useful calculations for microbial evolution[15,16].

Herre and Wcislo[6] have presented a one-sided account of cases in halictid eusociality, the details of which do not detract in the least from our argument. Halictid bees were not ignored as stated; we cited them three times. Furthermore, communal halictid bees are 'social' only in a primitive sense. They occupy a commons-like tunnel but build and defend their own personal cells as solitary bees[17]. Herre and Wcislo[6] point out that the experiments of Wcislo[18] were designed not to allow foraging, tunnelling, or guarding, but do not mention that these behaviours were tested in other experiments[19,20]. Bees are mass provisioners, as Herre and Wcislo[6] say, and we should have used the phrase 'defence and care of young with mass provisioning (bees) or progressive provisioning (others)'. We thank Herre and Wcislo[6] for pointing out this oversight. Primitively eusocial halictids nevertheless devote considerable care to the cells, guarding them and in many cases opening them to clean out waste.

Various authors mention sex ratio theory, which we do not study in our paper. Nevertheless a precise understanding of sex ratio evolution is based on population genetics and does not require inclusive fitness theory.

BRIEF COMMUNICATIONS ARISING

There is no support for the claim that evolution maximizes inclusive fitness. Nobody has offered a mathematical statement explaining what should be maximized and for which process.

Hamilton's work has stimulated much empirical research and has led to many measurements of relatedness. But we have shown that we cannot rely on inclusive fitness theory to describe how interactions among related individuals affect evolution. Inclusive fitness theory is neither useful nor necessary to explain the evolution of eusociality or other phenomena. It is time for the field of social evolution to move beyond the limitations of inclusive fitness theory.

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