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Inclusive fitness theory and eusociality

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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 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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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.

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.