Inclusive fitness theory and eusociality

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Inclusive fitness theory and eusociality

Nowak et al. (hereafter "NTW") argue that inclusive fitness (IF) 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, their arguments are based on a misunderstanding of evolutionary theory and a misrepresentation of the empirical literature. We do not have space to go into all their specific errors, and so we will focus upon three general issues.

First, is there a sharp distinction between IF theory and "standard natural selection theory"? No. Natural selection explains the appearance of design in the living world, and IF theory explains what this design is for. Specifically, natural selection leads organisms to become adapted as if to maximize their IF[1-3]. IF theory is based on 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[1,4-6].

Second, does IF require a number of "stringent assumptions" such as pairwise interactions, weak selection, linearity, additivity and special population structures? No. Hamilton's original formulations did not make all these assumptions, and generalisations have shown that none of them are required[2,4,5,7]. IF is as general as the genetical theory of natural selection itself. It is simply a partition of natural selection into its direct and indirect components.

NTW's error is to have confused the completely general theory of IF with models of specific cases. Yes, researchers often make limiting assumptions for reasons of analytical tractability when considering specific scenarios[4,6], as with any modelling approach. For example, NTW 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 general IF approach has facilitated, not hindered, empirical testing of IF theory[8-10]. Indeed, an advantage of IF theory is that it readily generates testable predictions in situations where the precise genetic architecture of a phenotypic trait is unknown.

Third, NTW claim that IF theory "does not provide any additional biological insight". They argue that it has delivered only "hypothetical explanations", leading only to "routine" measurements and "correlative studies", and that the theory has "evolved into an abstract enterprise on its own", with a "failure to consider multiple competing hypotheses". We cannot explain these puzzling claims, which completely neglect the extensive empirical literature that has accumulated over the past 40 years in the fields of behavioural and evolutionary ecology[8-10] (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 a load of other variables) has been shown to be important in all 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, the falseness of NTW's claims is easily demonstrated with a single example, that of sex allocation (the ratio of investment into males versus females). We choose sex allocation because: (a) NTW argue that IF theory has provided only "hypothetical explanations" in this field; and (b) it is an easily

quantified social trait, which IF theory predicts can be influenced by interactions between relatives; (3) the study of sex allocation has been central to evolutionary work on the eusocial insects. In undeniable contrast to NTW's claims, recent reviews of sex allocation show that the theory has provided strong explanation for why sex allocation varies with variables such as female density, inbreeding rate, dispersal rate, brood size, order of oviposition, sibmating, asymmetrical larval competition, mortality rate, the presence of helpers, resource availability and nest density in organisms such as protozoan parasites, worms, insects, spiders, mites, reptiles, birds, mammals and plants[4,11,12].

The quantitative success of this research can be summarized in one statistic: the percentage of the variance explained in the data. IF theory has explained up to 96% of the sex ratio variance in across-species studies and 66% in within-species studies[12]. The average for evolutionary and ecological studies is 5.4%. In addition, as well as explaining adaptive variation in behaviour, IF theory has even elucidated when and why individuals make mistakes (maladaptation), in response to factors such as mechanistic constraints[12]. It is not clear how NTW can characterize such quantifiable ringing success as "meagre". Their conclusions are based upon a selection of just three papers (by authors who all strongly disagree with NTW's interpretations), out of an empirical literature of thousands of research articles. This betrays a failure to seriously engage with the body of work that they would have us abandon.

The same points can be made with regard to the evolution of the eusocial insects, which NTW suggest cannot be explained by IF theory. Haplodiploidy itself may have only a relatively minor bearing on the origin of eusociality, but by impugning the value of IF theory as well, Nowak et al. discard the baby with the bathwater. IF 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[13,14]. Furthermore, IF 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. The most striking fact about NTW's offering is that it does neither. The only prediction made by their model (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 and immensely important point: if the fitness benefits are great enough, then altruism can be favoured between relatives.

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Research Area	Correlational studies?	Experimental studies?	Interplay between theory and data?
Sex allocation	√	√	√
Policing	√	√	√
Conflict resolution	√	√	√
Cooperation	√	√	√
Altruism	√	√	√
Spite	√	√	√
Kin discrimination	√	√	√
Parasite virulence	√	√	√
Parent-offspring conflict	√	√	√
Sibling conflict	√	√	√
Selfish genetic elements	√	√	√
Cannibalism	√	√	√
Dispersal	√	√	√
Alarm calls	√	√	√
Eusociality	√	√	√
Genomic imprinting	√	√	√

Table 1. Some example areas (non-exhaustive) in which IF theory has been vitally important in understanding a range of behavioural phenomena[8-10]. We are not suggesting that IF is the only way to model evolution, just that it has already proven an immensely productive and useful approach for studying eusociality and other social behaviours.

Trait examined	Explanatory variables	Correlational studies?	Experimental studies?	Interplay between theory and data?
Altruistic helping	Haploidiploidy vs diploidy	√		√
Worker egg laying	Worker policing	√	√	√
Policing	Relatedness	√	√	√
Level of cooperation	Costs, benefits and relatedness	√	√	√
Intensity of work	Need for work and probability of becoming queen	√	√	√
Sex allocation	Relatedness asymmetries due to variation in queen survival, queen number, and mating frequency	√	√	√
Sex allocation	Resource availability	√	√	√
Sex allocation	Competition for mates between related males	√	√	√
Number of individuals trying to become reproductive	Presence of old queens	√	√	√
Workers killing queens	Presence of workers, reproductives or other queens	√		
Exclusion of non-kin	Colony membership	√	√	√

Table 2. Example areas (non-exhaustive) in which IF theory has made very successful predictions about behaviour in eusocial insects[11-15].

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