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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 correction¹. Nowak *et al.*² challenge proposed connections between relatedness and the evolution of eusociality³, 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 effect³, 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 causes¹. Yes, there are hundreds of haplodiploid species that are not eusocial². 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 evolve⁹, 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 solitary¹⁰, and the solitary *Lasioglossum figueresi* was studied in artificial arenas, not nests, so it was impossible for bees to forage, tunnel or guard¹¹. 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 frequency¹², 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 robust¹³, 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 reports² 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 contributions³.

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Nowak *et al.* reply

REPLYING TO: P. Abbot *et al.* *Nature* **471**, doi:10.1038/nature09831 (2011); J. J. Boomsma *et al.* *Nature* **471**, doi:10.1038/nature09832 (2011); J. E. Strassmann *et al.* *Nature* **471**, doi:10.1038/nature09833 (2011); R. Ferriere & R. E. Michod *Nature* **471**, doi:10.1038/nature09834 (2011); E. A. Herre & W. T. Wcislo *Nature* **471**, doi:10.1038/nature09835 (2011)

Our paper challenges the dominant role of inclusive fitness theory in the study of social evolution¹. 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 Hamilton⁷ 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 Information¹ 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 parameters¹⁰, 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 experiment¹¹.

Neither inclusive fitness theory nor any formulation of Hamilton’s rule can deal with evolutionary dynamics¹². 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 evolution¹³. 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 cooperation¹⁴. Three, Part A of our Supplementary Information¹ 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 Information¹ 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 Wcislo⁶ 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 bees¹⁷. Herre and Wcislo⁶ point out that the experiments of Wcislo¹⁸ 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 Wcislo⁶ 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 Wcislo⁶ 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.