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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.

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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