A brief statement about inclusive fitness and eusociality

Our paper, The evolution of eusociality, has led to considerable controversy. Some of the criticism distorts our arguments, which should remain clear. We therefore provide a brief summary of our main points, all of which stand unrefuted.

1. Inclusive fitness theory is a mathematical framework that can only be applied to a subset of problems, which arise in evolutionary theory. Instead of inclusive fitness we advocate a straightforward methodology that applies in general.

2. The concept of inclusive fitness assumes that personal fitness can be split into additive components caused by individual actions[1]. This assumption requires particular conditions to hold. Inclusive fitness is therefore not a general concept for studying evolution.

3. For those evolutionary processes, where inclusive fitness can be defined, the calculation of inclusive fitness provides no results that are different from a standard calculation of fitness and natural selection.

4. We do not say that relatedness is unimportant. Relatedness is an aspect of population structure, which can affect evolution. Measuring genetic relatedness can provide useful information about population structure and mating behavior. But relatedness data alone are insufficient to characterize an evolutionary process.

5. For a correct interpretation of relatedness, we cannot rely on inclusive fitness theory, because most evolutionary processes do not fall under the scope of inclusive fitness analysis.

6. In an evolutionary model, once fitness is calculated every effect of relatedness is included.

7. We have proposed a specific model for the evolution of eusociality, which makes simple and testable predictions.

8. Our model shows that inclusive fitness theory is not needed to explain the evolution of eusociality.

9. Hamilton's rule has encouraged empiricists to consider costs, benefits and relatedness. It has also led to important studies of kin recognition. However, Hamilton's rule is at best a heuristic. Precise measurements of Hamilton's rule are rarely (if ever) performed[2,3].

10. In most theoretical models Hamilton's rule does not hold, if benefit and cost are properties of individual phenotypes (a problem which was also noted experimentally[4]).

11. There exist generalized versions of Hamilton's rule that are designed to be 'always true', but they are empty statements, which provide no insight for theory[5] or experiment[4].

12. Our paper does not study group selection, and it does not compare group selection and inclusive fitness. But given the limitations of inclusive fitness it is clear that many models of group selection cannot be analyzed in terms of inclusive fitness[6]. Also note that our model for the evolution of eusociality is not a group selection model; instead it describes selection operating at the level of genes.

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June 2011

Further reading:

The evolution of eusociality: main paper, online supplement, reply.

Notes:

1. The definition of inclusive fitness, given by Hamilton 1964, 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 neighbors. The fractions in question are simply the coefficients of relationship appropriate to the neighbors whom he affects; unit for clonal individuals, one-half for sibs, one-quarter for half-sibs, one-eighth for cousins,....and finally zero for all neighbors whose relationship can be considered negligibly small."

The breaking point of the theory is that personal fitness has to be *stripped* and *augmented*. This requirement makes inclusive fitness an imaginary quantity that is typically undefined in theoretical models and impossible to measure in practice.

2. For the lack of precise measurements of Hamilton's rule see Gadagkar (Current Science 99, 1036, 2010).

3. Waibel, Floreano and Keller (PLOS Biol, e1000615, 2011) claim to test Hamilton's rule with robots, but their study is based on computer simulations and is not an empirical test. No actual robots were used to generate the results concerning Hamilton's rule. Moreover, the computer simulation is arranged such that altruistic behavior spreads if br>c. No other outcome would have been possible. It is not surprising that Hamilton's rule holds in a computer simulation that is specifically designed to validate it.

4. Chuang, Rivoire and Leibler (Mol Syst Biol 6:398, 2010) test Hamilton's rule in a synthetic microbial system and conclude that it does not hold in any meaningful way.

5. A recent example is Gardner, West and Wild (JEB 24, 1020, 2011). In this approach cost and benefit are nebulous parameters that depend on population structure.

6. van Veelen (JTB 259, 589, 2009) discusses when inclusive fitness can be used to study group selection.