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Why kin and group selection models may not be enough to explain human other-regarding behaviour

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Abstract

Models of kin or group selection usually feature only one possible fitness transfer. The phenotypes are either to make this transfer or not to make it and for any given fitness transfer, Hamilton's rule predicts which of the two phenotypes will spread. In this article we allow for the possibility that different individuals or different generations face similar, but not necessarily identical possibilities for fitness transfers. In this setting, phenotypes are preference relations, which concisely specify behaviour for a range of possible fitness transfers (rather than being a specification for only one particular situation an animal or human can be in). For this more general set-up, we find that only preference relations that are linear in fitnesses can be explained using models of kin selection and that the same applies to a large class of group selection models. This provides a new implication of hierarchical selection models that could in principle falsify them, even if relatedness—or a parameter for assortativeness—is unknown. The empirical evidence for humans suggests that hierarchical selection models alone are not enough to explain their other-regarding or altruistic behaviour.

Keywords: Kin selection; Group selection; Altruism; Hamilton's rule; Preference relation

1. Introduction

In models of selection for altruistic behaviour, all individuals in all generations usually face the possibility of one and the same fixed fitness transfer (see for instance Hamilton, 1964, 1975; Charnov, 1977; Michod and Abugov, 1980; Michod and Hamilton, 1980; Grafen, 1984, Nunney, 1985; Queller, 1985, 1992; Taylor, 1989; Wilson and Dugatkin, 1997). Consequently, the two phenotypes are (1) to make this transfer and (2) not to make it. The fitness transfer is characterized by costs c to the acting individual and benefits b to the receiving individual and the best known prediction from kin selection theory is Hamilton's rule, that states that phenotype 1 will win if $c - rb < 0$, where r is relatedness, and phenotype 2 will win if not. In reality, however, different individuals in different generations may face a variety of possible fitness transfers. If we take as a possibility for a fitness transfer, for instance, a situation in which a chimpanzee can assist a brother in a fight, then it is clear that not all fights will be the same; the risk of getting hurt yourself varies, as well as the benefit to the brother. Another example is a situation in which a parent can try to save a child from drowning or being eaten by a predator. Such situations will also come with differences in risk of drowning or getting hurt yourself, as well as differences in the odds of actually saving the child. One may conclude that Hamilton's rule implies that some of these risks will be taken and others will not, and indeed if we treat all of the different fitness transfers *separately*, Hamilton's rule does make a prediction as for which phenotype will be selected for that particular fitness transfer. However, it is not very plausible that every such possible fitness transfer has a pair of possible phenotypes of its own and that selection has operated separately on every pair in this whole continuum of pairs of phenotypes. This being a rather unlikely scenario, one at least expects natural selection to exploit the similarities between varying situations more efficiently, in the sense that successive mutations build one coherent system to control behaviour in similar situations. The suggestion made in this paper is

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therefore to take preference relations for phenotypes, because they allow for the possibility that individual behaviour in a variety of dilemmas can be characterized with only a few parameters. Preference relations also allow for a description of behaviour that more closely matches with how other-regarding behaviour actually seems to be implemented in, for instance, humans.

With selection operating on preference relations, we can prove a result that has two different implications. The first one is positive: when phenotypes are taken to be preference relations, we still find that the end result is that individuals behave *as if* selection would have operated on every possible fitness transfer separately. That is good news, because it solves the unrecognized problem when going from Hamilton's rule—as a prediction in a setting with one fixed fitness transfer—to a prediction of behaviour in a world where individuals may face differing situations. The other implication is less reassuring. It is relatively straightforward to show that all preference relations that result from a process of kin selection must be linear in fitnesses. The same applies to standard group selection models. This new implication of most known hierarchical selection models can therefore in principle also rule them out as the sole explanations of other-regarding, altruistic behaviour. Observed human altruistic preference relations, for instance, are rather hard to interpret as being linear in fitnesses, and therefore we either have to find reasons why payoffs in monetary or food terms translate to fitnesses in rather peculiar ways, or accept that there is more to the evolution of other-regarding behaviour than the standard hierarchical selection models only.

2. What is a preference relation?

In mathematical economics, or microeconomics, the concept of a preference relation is used as a general way to handle human behaviour when faced with choices. There is however nothing uniquely human to being faced with choices and therefore there is also no reason to restrict the use of preference relations to economics. Because not all readers will be familiar with microeconomics, a few central definitions will be repeated (see Mas-Colell et al., 1995).

Assume a set of alternatives X. Elements x and y from this set X are to be compared to each other, and therefore we have a binary relation on X, denoted by $\succsim$. This binary relation is called a preference relation, and we read $x \succsim y$ as "x is weakly preferred to y". Given any preference relation $\succsim$, we can derive two other important relations on X:

1. The strict preference relation, $\succ$, defined by
   $$x \succ y \;\Leftrightarrow\; x \succsim y \;\text{ but not } y \succsim x.$$
2. The indifference relation, $\sim$, defined by
   $$x \sim y \;\Leftrightarrow\; x \succsim y \;\text{ and } y \succsim x.$$

In the examples in this section, X will be the set of two-dimensional vectors in $\mathbb{R}^2_+$, where $x = [x_{self}, x_{other}] \in X$ is a combination of fitnesses of the individual itself and the other. If $x \succ y$ that means that when the status quo is y, an individual with this preference relation does make the fitness transfer that consists of incurring a fitness loss $c = y_{self} - x_{self}$ himself, while the other gains $b = x_{other} - y_{other}$.

Usually we restrict attention to preference relations that have some consistent structure. That can be done by looking at preference relations that can be represented by (continuous) utility functions. A function $u : X \to \mathbb{R}$ is a utility function representing preference relation $\succsim$ if, for all x and y in X, the following holds: $x \succsim y \Leftrightarrow u(x) \geqslant u(y)$. It is important to note that all utility functions represent some preference relation, but not all preference relations have a utility function that represents them. Utility functions also have the practical advantage that they can describe preference relations in a concise and insightful manner, but there is also a conceptual reason why they are useful here. If we can represent choice behaviour by a utility function with one or a few parameters, it seems likely that there are also shortcuts that in one go code for behaviour in all the different dilemmas, rather than a preference relation being merely a list of which alternative would be chosen for each possible fitness transfer separately. The latter case would bring us back in the situation where a preference relation is nothing but a combination of phenotypes for every possible fitness transfer as described in the Introduction. A utility function on the other hand captures the idea that a simple structure can lead to choice behaviour for a variety of dilemmas, and that the parameters of this choice behaviour can evolve.

In the remainder of this section, a few examples of utility functions are given. They stem from the literature in experimental economics, in which the elements of X represent money combinations rather than combinations of fitnesses. The examples will nonetheless help to illustrate the possible shapes that preference relations can have. They will also provide material for the final section, where we will discuss whether money, food or risks can plausibly be linked to fitness such that the preferences we observe can be explained with hierarchical selection models. To visualize the different preference relations, pictures with iso-utility curves will be drawn. An iso-utility curve is a set of points that represent alternatives that yield the same value of the utility function.

2.1. Altruism only (or spite)

The first family of preference relations has members that are determined by a parameter α and are defined by utility functions

$$u_\alpha(x_{self}, x_{other}) = x_{self} + \alpha x_{other}.$$

These utility functions are linear in both x_{self} and x_{other}, where x_{self} has coefficient 1 and x_{other} has coefficient α. An intuitive interpretation of α as the weight that one