

COMMENTARY

Kinds of kindness: classifying the causes of altruism and cooperation

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As it was realized that natural selection should favour behaviours that benefit the individual rather than the species it belongs to, explaining the occurrence of altruistic behaviours has become one of the central problems in evolutionary biology. The seminal work of William Hamilton (1964) paved the way for a revolutionary approach, focusing on how genes may benefit copies present in other individuals. After some time it was realized; however, that such 'kin selection' (as the mechanism became known) alone could not explain all observations of individuals helping others. Trivers (1971) suggested that by being nice individuals could induce others to return favours. This idea of reciprocal altruism was put on a sound game-theoretical footing by Axelrod's study of the Iterated Prisoners Dilemma Game (Axelrod & Hamilton, 1981). Reciprocal altruism is generally considered to be a fundamentally different form of altruism but the distinction between these two forms has become blurred, in particular as numerous researchers have started exploring spatial variants of the reciprocal altruism games (Doebeli & Hauert, 2005).

In this issue of *JEB* Lehmann & Keller (2006) review the theoretical literature on the evolution of altruism and cooperation. They synthesize and unify the models into a general theoretical framework. Using this framework they classify the causes of evolution of helping (comprising both altruism and cooperation) into four broad categories. We think this is a laudable and useful undertaking and that such a common framework will facilitate communication, avoid duplication of results and will help identifying and understanding novel scenarios for the evolution of helping.

Lehmann and Keller's model is based on the direct fitness approach, which was pioneered by Taylor & Frank (1996) and is essentially a precise bookkeeping scheme for the costs and benefits of interactions to all members of the population. The scheme focuses on a typical individual (the focal individual or FI) and keeps track of all increments and decrements in the payoff it receives

while it is followed through all possible interactions. If the coefficients of relatedness in the population are known this allows one to cast the selective pressures in terms of kin selection theory.

Lehmann and Keller's unified framework is particularly notable for the fact that it incorporates the costs and benefits of a repeated interaction between individuals, in which the costs and benefits can depend on the history of the interaction. This allows a fair comparison between models based on single moves (where strategies are fixed traits) and those based on repeated games (with responsive strategies). A textbook example is the interaction of two players playing the repeated prisoner's dilemma game. If two players play tit-for-tat with each other both will accrue a net benefit after playing many rounds of the game (Maynard Smith, 1989). Lehmann and Keller's scheme tells us that the interaction between two tit-for-tat players should therefore be interpreted as cooperative. Lehmann and Keller's formalism thus helps to overcome the potential confusion resulting from mixing up the cost and benefit per move with the overall costs and benefits through a repeated interaction.

Although we think there is great merit in Lehmann and Keller's attempt at synthesis we see a number of obstacles that might stand in the way of its general acceptance as a common framework. A first important obstacle is that it does not make clear how kin selection relates to kin discrimination. This is unfortunate as Lehmann and Keller's approach will help to perpetuate the common misconception that kin selection requires discrimination or recognition of related individuals. As Hamilton showed in his classic paper (Hamilton, 1964), altruistic behaviour can be selected if one meets, on balance, sufficiently many individuals who carry the same gene, without having to know who is related and who is not. Part of the confusion is probably caused by Hamilton himself when he remarks that kin selection would probably more effective when individuals adjust their behaviour according to their genealogical relationship with the individuals they interact with.

Lehmann and Keller contribute to this confusion because their formalism suggests that discrimination is a necessary condition for kin selection to operate. That is, they model the efficacy of kin selection as the product of r , the standard coefficient of relatedness (indicating the probability of sharing genes identical by descent) and a component x which, they claim, represents kin discrimination. If true, this implies that kin selection cannot work if individuals do not adjust their behaviour with respect to whom they perceive as kin (if $x = 0$ the model reverts to pure individual selection). However, kin selection can also operate when it is 'blind'. For instance, in so-called 'viscous' populations, where individuals do not disperse far from their place of birth, individuals are highly likely to have kin among their neighbours. Altruism can then be favoured in such populations without kin recognition (Hamilton, 1964; van Baalen &

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Rand, 1998). Recognition is not a simple issue of increasing or decreasing the effect of relatedness. Rather, it will differentially affect the costs and benefits resulting from interactions with different players. By discrimination one can avoid being cheated upon (which would affect the cost and benefits) without modifying the rate with which one encounters kin (the relatedness pattern remains unchanged). Recognition can thus reduce the costs, and in this way allows kin selection to operate at levels of relatedness that without recognition would not be able to sustain altruism. The evolutionary dynamics of kin recognition are still largely unexplored but some tantalizing new insights have been obtained in studies that we discuss below.

A second limitation of Lehmann and Keller's approach is that focusing on the individual gives a rather static view of a process that may in reality be highly dynamic and interdependent. In Lehmann and Keller's model the costs and benefits of the interaction are assumed to depend only on the rules of the game that partners are involved in, without taking for instance competition for resources into account. Moreover, the coefficient of relatedness (r) is treated as a fixed constant, depending only on the genealogical relationship between individuals and the reproductive genetics of the species (haplodiploid, haploid and so forth). Under these assumptions it suffices to know with whom the FI interacts and what the probabilities are for finding genes identical by descent in those individuals (Rousset & Billiard, 2000). However, this creates the impression that the costs, benefits and the relatedness structure are static properties of a population that are, by assumption, constant and known. Although these assumptions allow Lehmann and Keller to combine kin selection and repeated interaction in a common framework, it relegates the role of feedback and the importance of population dynamical processes to the background.

It is important to realize that relatedness is typically not a given constant but arises as a natural consequence of the spatio-temporal dynamics of the population, that is, the ecology of the species. Unfortunately in most cases it is a difficult exercise to derive relatedness from the governing demographic principles. At best this calculation is tedious but straightforward, sometimes it can only be solved using advanced approximation methods such as population genetics or moment closure techniques, often the calculation is just plainly undable. To consider these quantities as constants, as Lehmann and Keller do, is a potential obstacle to the general application of their unified framework. In spatially extended populations, for example, altruism is selected if a version of Hamilton's Rule is satisfied in which r is the probability that the neighbour of a mutant individual also carries the mutation, a quantity that depends on the local population dynamics (van Baalen & Rand, 1998).

How the obstacles that we discuss stand in the way of general acceptance of Lehmann and Keller's framework becomes evident when one realizes that the evolutionary consequences of kin recognition mechanisms and unstable dynamics lie at the heart of an series of recent publications. Hamilton (1964) already conjectured that with a recognition system (Dawkins evoked the now classic image of green bearded altruists) altruists should be able to direct their help towards related individuals more easily (and thus avoid being exploited by the nonaltruists). As Lehmann and Keller note at several places in their review, this form of altruism, once selected, is inherently unstable. Indeed (and in contrast to what Lehmann and Keller assert), for a long time such instability was thought to imply that the green beard mechanism does *not* favour altruism, because green-bearded nonaltruists will eventually evolve and take over. Recently, however, a number of studies have shown that the green beard mechanism *can* promote altruism, even if the resulting system need not be dynamically stable. Riolo *et al.* (2001) found that altruistic individuals could resist exploitation by nonaltruists if they limit help only to individuals having a 'tag' (a continuously varying arbitrary but observable character) that is sufficiently similar to their own. Lehmann and Keller's conjecture that the green beard mechanism is inherently unstable, and by implication, cannot sustain altruism in the long run has been shown to be incorrect by a number of recent studies (van Baalen & Jansen, 2003; Traulsen & Schuster, 2003; Axelrod *et al.*, 2004; Hammond & Axelrod, 2006; Burtsev & Turchin, 2006; Jansen & van Baalen, 2006). In these studies the dynamics are locally unstable but nevertheless permit global maintenance of altruism.

The study of evolution of altruism and cooperation is a large and active field in which a large number of techniques and models are used. The framework proposed by Lehmann and Keller allows to consider simultaneously kin selection, and repeated interactions which is a big step forward. However, such a model, or a modified form thereof, can only serve as a common framework if it is clear how other models can be brought into this framework. For many of the highly diverse collection of models that have been used (and will continue to be used) it will not be obvious where to place them in Lehmann and Keller's framework. Even if many of the surprising scenarios which foster altruism and cooperation can, in principle, be captured by Lehmann and Keller's model, it can only be done retrospectively and at the expense of insight in other important aspects. Despite this, we see the development of a unifying approach as a major step forward with the potential to facilitate communication and bring together workers that otherwise would not easily be able to compare their results.

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