

COMMENTARY

Cooperation and conflict during evolutionary transitions in individuality

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Cooperation received much less attention 30 years ago than other forms of ecological interaction, such as competition and predation. Workers generally viewed cooperation as being of limited interest, of special relevance to certain species (e.g. social insects, birds, humans and our primate relatives) but not of general significance to life on earth. This view has changed, due in large part to the study of evolutionary transitions in individuality (ETIs). What began as the study of animal social behaviour some 40 years ago has now embraced the study of social interactions at all levels in the hierarchy of life. Instead of being seen as a special characteristic clustered in certain lineages of social animals, cooperation is now seen as the primary creative force behind ever greater levels of complexity through the creation of new kinds of individuals. Cooperation plays this central role in ETIs because it exports fitness from the lower level (its costs) to the new higher level (its benefits).

How did this shift in understanding the importance of cooperation come about? Darwin (1859), Wilson (1975) and Hamilton (1963, 1964a,b) all understood the importance of cooperation for social organisms. There was pioneering work done as early as 1902 on the importance of cooperation in the struggle for existence (Kropotkin, 1902), and there was the now widely accepted theory of Margulis (1970, 1981) and others on the endosymbiotic origins of mitochondria and chloroplasts in the eukaryotic cell. However, cooperation was also viewed as a destabilizing force in ecological communities and likely of limited significance because of the positive feedback loops it creates (May, 1973). Sociobiology had defined altruism as its core problem (Wilson, 1975), but the altruism problem was not viewed as general to life on earth until workers began applying cooperation thinking to the evolution of interactions at other levels in the hierarchy of life in addition to social organisms, such as to the level of genes within gene groups (e.g. Eigen & Schuster, 1979) and to the level of cells within cell groups (e.g. Buss, 1987). Concomitant with the generalization of the cooperation problem was the development of multi-level selection theory (Maynard Smith, 1964; Price, 1970, 1972; e.g. Hamilton, 1975; Wade, 1978; Wilson, 1980). The evolutionary transitions problem (Maynard Smith, 1988, 1991; Maynard Smith & Szathm-

áry, 1995) grew out of these two developments which, in effect, extended the sociobiology revolution to all kinds of replicating units in the hierarchy of life.

Lehmann & Keller (2006) propose a four-way classification scheme for population models of the evolution of cooperation, according to the issue of whether the benefits are direct (individual selection) or indirect (kin selection). Within the first category of direct benefits, a distinction is made according to whether the benefits are mediated through the behaviour of another individual (as through learning in reciprocation) or not. Within the second category of kin-selected indirect effects, a distinction is made as to whether there are many genes involved in the traits or a few (as in the 'green-beard' effect).

The distinction between direct and indirect effects is widely used to describe social behaviour and the evolution of fitness effects associated with interactions between individuals. This distinction seems less helpful, however, when one's interest concerns the origin of the individuals themselves, i.e. ETIs. Indeed the direct-indirect distinction presumes that one knows what the individual is. Direct or indirect with regard to what? The individual, of course.

Transforming our understanding of life is the realization that evolution occurs not only through evolution within populations but also during ETIs – when groups become so integrated they evolve into a new higher-level individual. The major landmarks in the diversification of life and the hierarchical organization of the living world are consequences of a series of ETIs: from nonlife to life, from networks of cooperating genes to the first prokaryotic-like cell, from prokaryotic to eukaryotic cells, from unicellular to multicellular organisms, from asexual to sexual populations, and from solitary to social organisms. It is a major challenge to understand why (environmental selective pressures) and how (underlying genetics, physiology and development) the basic features of an evolutionary individual, such as fitness heritability, indivisibility, and evolvability, shift their reference from the old to the new level. Classifying the many factors involved in the evolution of cooperation into a few general categories as Lehmann & Keller (2006) have done will certainly help in meeting this challenge.

Individuals often associate in groups, and under certain conditions these groups evolve into a new kind of individual. Cooperation is fundamental to this process because it transfers fitness from the lower-level individuals (in terms of its costs) up to the level of the group (the benefits of cooperation), thereby serving to create a new level of fitness and possibly, under certain conditions, a new higher-level individual (Michod, 1999). Indeed, as already mentioned, the major levels in the hierarchy of life (genes, gene networks, cells, eukaryotic cells, multicellular organisms) are thought to have evolved from this process of individuation of groups (Maynard Smith & Szathmáry, 1995; Michod, 1999).

We find the framework employed by Lehmann & Keller (2006) useful in some cases of individuation of groups and less illuminating in others. During the origin of early gene networks (hypercycles) or the origin of the eukaryotic cell, indirect effects were less important as a general organizing factor as the interactions involved different species. And to say that the effects must have involved direct benefits to the players does little to help understand the factors involved. The study of cooperation is often divided by the issue of whether the interactions occur within or between species, because kin selection is possible in the former but not the latter. However, both within and between species cooperation require spatial and or temporal correlations in the behaviour of cooperating individuals. That is to say, there must be behavioural structure—structure in the distribution of behaviours (Michod & Sanderson, 1985).

A basic issue in understanding the evolution of altruism both within and between species is to understand how the benefits of cooperation may be differentially bestowed on the cooperators, so as to make up for the costs of cooperating. This requires structure in the distribution of behavioural interactions, so that the interactions are nonrandom in such a way that cooperating behaviours tend to be positively associated with like behaviours (and similarly for the noncooperating selfish behaviours). Behavioural structure – defined as the population distribution of behaviours conditional on cooperation [after Jacquard's (1974) 'genetic structure'] – was used as a unifying concept in a simple model to relate the various mechanisms by which this nonrandom association may be achieved (Michod & Sanderson, 1985). In this way, it was possible to show how kin selection, group selection, assortment, learning and reciprocation may be related in the same model and understood as different ways to get the requisite level of behavioural structure for altruism to evolve.

Different kinds of models are used when the existing individuals are genetically related (as in the origin of multicellularity), or are from separate species (as in the symbiotic origin of the eukaryotic cell), even though behavioural structure is required in both situations (Michod & Sanderson, 1985; Law, 1991; Frank, 1995, 1997; Michod & Roze, 2001; Michod & Nedelcu, 2003). Because of the need for behavioural structure, competition may also occur among members of cooperative groups, and this may reduce the advantages of cooperation and/or lead to the loss of cooperative types. The hypercycle is a cooperative group of interacting replicators in which cooperation dynamically stabilizes the densities of the different replicators, thereby resisting competitive exclusion of any of the members (Eigen, 1971; Eigen & Schuster, 1977, 1978a,b, 1979).

In the case of within-species interactions, genetic structure may facilitate behavioural structure, and this is the basis of kin selection. In practice it is often difficult to determine the relative contributions of direct and

indirect effects when studying within-species cooperation in a multi-level selection context. Indeed, as Lehmann & Keller (2006) point out, selection in a multilevel setting must involve both direct and indirect effects. So, for example, in the transitions from unicellular to multicellular organization in the volvocine algae, the earliest stages involve both direct and indirect effects. By remaining attached to each other following cytokinesis, the offspring of a parent cell formed a group and the member cells likely benefited directly by avoiding predation by filter feeders, increasing motility, etc. However, kin selection must have also played a role at this stage, as the group members are genetic clones (ignoring mutation). Direct benefits to the cell may also be involved in early forms of division of labour, such as rotation of basal bodies and size gradient of eyespots, because the benefits (motility and phototaxis) of these specializations to the actors in a group context probably exceed their relatively low costs to the cells. However, the evolution of further cooperation was likely facilitated by the high genetic relatedness of the cells in the groups. For example, cellular specialization at motility and building extracellular matrix require individual cells to expend resources to the benefit of all cells in the group at significant cost to the cell. In a similar group of unrelated individuals, there would be nothing to prevent defection in the form of investing all of these resources into reproduction.

During origins of multicellularity, kinship and genetic and behavioural structure depend upon the mode of group formation (for example, do cells aggregate or do they remain together after repeated cell divisions), and, if groups are formed from a propagule, on the size of that propagule. Deriving the group from a single cell, as is common in most major multicellular lineages, is an evolved trait. Presumably, the selective force behind multicellularity involves benefits of increased size, and, if increasing group size is so important, why return to a single cell at the start of each generation? The selective answer depends on the direct costs of reducing propagule size along with the indirect benefits of kinship and selection against selfish mutants (Michod & Roze, 2000; Roze & Michod, 2001). In addition, the evolution of propagule size may involve issues of a fresh epigenetic start (Jablonka, 1994; Jablonka & Lamb, 1995) or the need for sexual fusion.

What framework for understanding cooperation is most helpful when one's interest transcends populations of individuals and seeks to understand the very creation of individuals via multilevel population processes? The basic problem in an ETI is to understand how a group becomes an individual. As already mentioned, cooperation is fundamental to this process, as it exports fitness from the lower to higher levels. However, cooperation by itself does not create a new individual. What is needed for individuation is some kind of specialization of the lower-level units in the fitness components of the new

higher-level unit. As a result of specialization of lower-level units in essential components of fitness of the higher-level unit, the higher-level unit becomes indivisible and hence a true individual. Cooperation may play a role here, as it sets the stage for defection and conflict. The resolution of this conflict may, under certain conditions, involve the specialization of lower-level units and emergence of the higher-level individual. This cooperation, conflict, conflict mediation framework has been applied to the origin of cooperative gene networks (Michod, 1983, 1999), to the origin of the eukaryotic cell (Maynard Smith, 1991; Michod & Nedelcu, 2003) and to the transition to multicellular life (Buss, 1987; Maynard Smith, 1988; Michod, 1996, 1997; Michod & Roze, 1999, 2001; Michod *et al.*, 2003).

An issue not addressed by these models is how altruism originates. By this, we are not referring to the population dynamics question of whether altruism can increase from rarity in a population of defectors, but, rather, where do the fitness effects (costs and benefits) inherent in altruistic behaviours come from. One view is that existing life history variation (fitness trade-offs) is remoulded in the group setting, and this creates the costs and benefits of the altruistic behaviour (Michod, 2006; Michod, *et al.* 2006; Nedelcu & Michod, 2006). For example, traits with positive effects on one component of fitness, say viability, and with negative effects on another component, say fecundity, may become altruistic in a group if the individual expends more effort on the viability component than would be optimal for its own fitness (assuming that increased viability of lower-level individuals also benefits the group). For example, in volvocine green algae, flagellar motility interferes with cell division. In the unicellular members of this lineage, such as *Chlamydomonas*, we may expect evolution to have optimized the time spent in the two states (motile or reproductive) according to environmental conditions. However, in a cell group, those cells expending more time on flagellar activity than would be optimal for their cell fitness are behaving altruistically (assuming that flagellar motility benefits the group, as is known to be the case).

All models have assumptions and limitations, even 'general' ones, and we should not expect any one model to cover everything. The framework proposed by Lehmann & Keller (2006) goes a long way towards clarifying the relationships among a profusion of models addressing the fundamental problem of the evolution of cooperation among established individuals. It is particularly valuable to realize that several classes of models presumed to propose novel mechanisms for the evolution of cooperation are actually special cases assignable to a small number of general classes. In this regard, we found the discussion of the spatial structuring models and tag-recognition/grouping models especially illuminating. Furthermore, we agree that group selection involves both indirect and direct benefits and look forward to

more studies that '...delineate more clearly the role of factors promoting or repressing cooperation and altruism' in a group, as these factors underlie conflict mediation and resolution in a multilevel setting. Understanding these factors is an ongoing problem, and this framework is a step in the right direction.

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