

COMMENTARY

Cooperating for direct fitness benefits

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Among the great variety of highly stylized models for the evolution of cooperation, some are actually sharpening our eyes. The Prisoner's Dilemma, for example, helps us understand 'free riding' and the difference between one-shot and repeated interactions; Hamilton's basic kin selection model for the evolution of altruism highlights the role of genetic correlations among interacting individuals, etc. What fruitful models of this kind create is a sensitivity to factors that might be crucial to understanding real cases of cooperation. Lehmann & Keller (2006, L&K) rightly emphasize that the identification of selective forces for cooperation can be obscured if one fails to sharply distinguish between these factors. L&K classify the factors into four categories, the first being direct fitness benefits to a cooperator. We wish to extend their argument by focusing on this first category, drawing attention to important further distinctions that arise from taking biological facts and a broader theoretical background into account.

Our commentary emphasizes the scope of direct fitness benefits in cooperation and discusses ways of unfolding the richness of phenomena captured by this category. If one accepts, as seems likely to be true, that the great range of mutualistic species interactions and the mind-boggling integrated complexity of cells and organisms are largely products of direct fitness benefits, it is rather surprising how little effort has gone into modelling these forms of cooperation, compared with the arguably much smaller categories of reciprocity or interactions among relatives, not to mention green-beard genes. We wish to point to important ideas and mention some open questions about the role of direct fitness benefits in the evolution of cooperation.

The market dimension

Consider a cleaner fish 'serving' another fish who acts as its 'customer'. This is a 'trade' in which both partners have a direct benefit. The cleaner receives food and the customer gains by losing ectoparasites. There is thus a direct advantage to both individuals. Similarly, when we get our hair cut in a barbershop, there is a direct benefit

to us and to the barber. The category 'direct benefit' makes these examples look like there is little more to say in order to understand why the cooperative interaction takes place. In real life, however, we tend to compare different barbers for their price and quality. It depends on the state and structure of the barber market, whether we engage in a transaction with a particular partner, and how much of a net benefit we can achieve.

In biology, we are frequently confronted with markets, most notably when studying mating behaviour. But if there are biological markets, their structure should shape cooperation like genetic relatedness or other relevant factors. And indeed, the asymmetry of a typical mating market with its oversupply of male 'fertilization services' is a key to understand many of the observed differences between males and females and their unequal contributions to the cooperative endeavour of producing joint offspring.

Mobility is another important aspect of markets. When the customers' mobility is restricted or expensive, barbers can increase the price or decrease service quality. The reason is that customers then have little to choose from. In the extreme, the barber can act as if he were a monopolist. Economists use the term 'monopolistic competition' for this kind of restriction of market forces. Bshary & Noë (2003) summarize empirical results from cleaner fish studies, indicating that cleaner fish treat those customers for which long-distance moves are costly less well than others – as if the fish had understood the theory of monopolistic competition.

Yet another property of markets is whether they have a tendency to clear or not. To say that a market clears means that its dynamics drive it to a state in which the quantity supplied and the quantity demanded are equal. The consequences of market clearing for cooperation can be dramatic. A number of factors, such as the lack of commitment power in a trade among animals, or strongly restricted information about possible trades, can severely limit the clearing of biological markets (Hammerstein & Hagen, 2005). The functioning of biological markets instead depends heavily on special behavioural and other mechanisms that determine which exchanges will take place.

Common interest

Perhaps the most extreme form of cooperation is that of the genes operating in an organism. Even the most comprehensive survey on selfish genetic elements (Burt & Trivers, 2006) expresses the view that most genes act most of the time to the benefit of the organism. But why is there cooperation among tens of thousands of genes in a given cell?

Although we tend to interpret behavioural cooperation in superorganisms with the help of kin selection theory, this theory is of little use for understanding intragenomic cooperation. The reason is that different genes in an

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organism are usually not identical by descent (unless we focus attention on a single one of them and look at its copies in different cells). The evolution of cooperation among genes of an organism, therefore, seems to differ fundamentally from that of social behaviour in insect societies. Intragenomic cooperation is certainly based on the genes' shared interest to 'keep the organism running' that carries them into the next generation and treats its passengers in a rather fair way. The eukaryotic organism's fair transmission of genes relates in particular to the organization of mitotic and meiotic cell divisions, where molecular devices such as the 'spindle check point' supervise 'passenger movements'. Many selfish B-chromosomes have managed to escape the rules of transmission during meiosis (e.g. in rye, Jones & Puertas, 1993). According to Burt & Trivers (2006), however, B-chromosomes are rare compared with other selfish genetic elements. This indirectly supports the view that policing mechanisms act in eukaryotic cells.

Division of Labour

Although policing is one of the factors stabilizing the common interest among genes, and also among workers in colonies of social insects, it may not be as important as one might think. As soon as there is a strong division of labour, this can contribute largely to the overlap of interest among evolving agents and often makes it highly unprofitable to cease cooperation. Consider, for example a clock gene involved in the negative feedback loop that generates the oscillator of the circadian clock (Rensing *et al.*, 2001). Such a gene can do a lot for its own propagation by servicing well the circadian clock. Outside the functional context of the clock it may not have any other functionality. It acts like a cog in a machine and a small number of mutational steps may not enable it to act as a selfish element. Stepping out of its cooperative functional context would make it look like a broken cog. The same may be true for many aspects of the physiology and behaviour of social insects. Why is there no solitary ant, given that genetic relatedness is often relatively low in ant colonies? The answer may also lie in the division of labour.

An objection to this idea might be that individual ants can take different roles instead of being stuck with a single role, whereas the clock gene cannot play the role of many other genes. This objection is not as strong as it seems at first glance. Even when roles in division of labour can be switched within a given organism, this does not imply that different roles can be played simultaneously. Therefore, the individual agent would be in need for others to perform the complementary task. A small amount of policing may suffice to keep such systems operating.

Unfolding the structure of direct benefits

We have argued that direct fitness benefits seem to play a very important role in the evolution of cooperation and

that the analysis of selective forces relating to these benefits requires a number of analytical concepts such as that of markets, common interest and division of labour. The understanding of markets alone requires distinctions about how they are structured, their asymmetries, degree of monopolistic competition, tendency to clear, and what characterizes the biological 'terms of contract'. Common interest needs to be understood in terms of what generates it. Policing obviously plays a role in generating common interest, but how important is this role in relation to other factors, such as the division of labour that makes individuals look like cogs in a machine? Did α -proteobacteria evolve into cell organelles because they were forced through policing to cooperate with the cell in which they ended up as endosymbionts? Current attempts to understand the origin of mitochondria, such as the hydrogen hypothesis (Martin & Müller, 1998), do not lend support to this idea of forced cooperation and try to convince us instead that there has been division of labour from the beginning of this evolutionary interaction.

It is, of course, worth considering the contrasting view that mitochondria may have started as endoparasites that were 'enslaved'. A small hint in this direction would be their current involvement in the organization of programmed cell death that might reflect an ancestral evolutionary state in which mitochondria actively killed cells as parasites. Blackstone & Kirkwood (2003) argue, however, that this idea receives little support if one examines the details of mitochondrial pathways in apoptosis. It seems even more far fetched to ask whether evolution forced genes by policing mechanisms to integrate into chromosomes. Yet the origin of chromosomes is perhaps one of the most important steps towards cooperation as the basis of life. Maynard Smith & Szathmáry (1995) recognized this importance and made a suggestion relating this origin to the efficiency of how division of labour is maintained among the genes. If, at early stages of life, genes were passed to daughter cells in a random fashion, daughter cells would receive biased samples of the genetic material that operated in the original cell. As a result, a major fraction of daughter cells would fail to receive the correct combination of specialized genetic agents and suffer from improper division of labour. In a figurative sense such daughter cells would, for example, have a job for a carpenter but no carpenter. If a 'team of genetic specialists' comes as a 'package', however, each daughter cell will receive the correct mix of 'experts' that causes the cell to function well. The important point is that the team members themselves have an interest in being linked. If a carpenter is needed, it is in the interest of others to associate with the carpenter.

Maynard Smith & Szathmáry admit that some major steps in evolution may depend on events so unlikely that they can hardly be identified. It is equally possible, though, that our fascination with kin selection, repeated

games and green beards has prevented us from unraveling relevant direct fitness benefits that would explain major steps. The recognition of evolutionary conflicts certainly has led us to reveal many of nature's mysteries, but a very strong emphasis on the idea may have blinded us to some of the essentials of cooperation.

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