COMMENTARY
Balancing synthesis with pluralism in sociobiology

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'One may indeed compare a theory to a particular view of some object. Each view gives only an appearance of the object in some aspect. The whole object is not perceived in any one view but, rather, it is grasped only *implicitly* as that single reality which is shown in all these views' (Bohm, 1980, original emphasis).

The puzzle of why organisms cooperate has led to a great many ingenious explanations that come from all walks of the academic community. Whereas concentration on this problem has lead to great progress in our understanding of cooperation, it has also resulted in a significant problem. With many of the ideas originating in rather different fields with their own methodologies, any newcomer to the field is faced with a confusing world of terminology, techniques and debates. She will be forced to read of kin selection, inclusive fitness, trait-group selection, cultural group selection, population genetics, classical game theory and skew theory to name but a few. Into this arena, any serious attempt at synthesis should be greatly welcomed. And Lehmann and Keller (2006) should be congratulated for demonstrating that many of the explanations for the evolution of cooperation can be brought together in a common language. The point I wish to make here, however, is that no matter how convincing a synthesis this is, one should not come away with the idea that theirs is the only correct or even the best way to analyse cooperation. As evolutionary biologists, we are even further from such a position than the theoretical physicists to whom the above quote was aimed. While synthesis is badly needed, therefore, so too is a pluralism of methodology that recognizes that each approach brings its own strengths to the problem.

A valuable synthesis

Lehmann and Keller present a clear framework for thinking about the evolution of cooperation. [I use *cooperation* here to mean actions that benefit others (Sachs *et al.*, 2004), which is what Lehmann and Keller call *helping*]. Their emphasis follows directly from Hamilton's (1964) original focus upon the question of why an individual will ever act in a way that reduces personal

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reproduction (altruism). As such, the framework clearly separates factors that contribute to the evolution of altruism vs. those factors promote cooperation through personal reproductive benefits (indirect vs. direct fitness effects, Brown, 1987). Furthermore, they demonstrate that the majority of work since Hamilton can be classified in their terms.

This is an admirable achievement as it suggests that the different approaches to social evolution are, in the most, focusing upon different aspects of common processes rather than being distinct or contradictory. Another nice consequence is to give Hamilton rightful credit as one of the key players in sociobiology. Any framework has its limits, however, and although the approach of Lehmann and Keller is perfectly valid, it will not suit all tastes. I make this perhaps obvious point in the hope that it might help to dispel future debates over which methodology is 'the best'. It seems that all too often an apparently objective debate over methodology will spring up which, in reality, is a subjective debate over what is the most interesting. This is particularly obvious in clashes between the humanities and the sciences (e.g. Meaney, 2001) but applies equally to sociobiology. Clearly, we benefit from a diversity of approaches and one must simply choose the technique that is appropriate to the question at hand (Kokko, 2005).

The kin selection partition into direct and indirect fitness effects makes the Lehmann and Keller framework particularly useful when one is interested in the evolution of altruism (Foster *et al.*, 2006). However, altruism is not always of most interest and two brief examples relating to my own work will hopefully illustrate the merits of alternative approaches. In these, partitioning social effects into costs and benefits to the individual, as occurs in Hamilton's rule and the Lehmann and Keller framework, is not necessarily the most intuitive path. The two examples are intended to each illustrate a slightly different point. The first example is well captured by the Lehmann and Keller framework but highlights that a different partitioning of the effects of a social action can be revealing. Meanwhile, the second concerns a process that is only covered in the simplest possible way in Lehmann and Keller. This is intended to illustrate that there are major processes at play in the evolution of cooperation that lie beyond this synthesis.

The tragedy of the commons

Hardin's tragedy of the commons concerns the notion that selfish herders will tend to overexploit and ruin a shared pasture, resulting in tragedy for all (Hardin, 1968). This analogy has been taken up by sociobiologists to make the point that cheating will tend to disrupt and collapse group adaptations (Leigh, 1977; Frank, 1998). This presents a problem: how do cooperative adaptations arise in the face of selection for selfishness? Although still about cooperation, this is a subtly different problem to

the typical focus upon individual investment in a cooperative trait (Foster, 2004). Instead, the focal currency is the success of the resulting group adaptation. This makes a multi-level or group selection model an intuitive way to tackle the question, which partitions the fitness of an individual (*w*) into its individual and group components (Price, 1970; Hamilton, 1975; Wilson, 1975). For example:

$$w = \frac{f(y)}{f(z)}g(z) \qquad (1)$$

where *y* is investment in reproductive competition of the focal individual and *z* is average competition in the group (Frank, 1998; Foster, 2004). The function *f(z)* defines the positive relationship between investment in selfish competition and reproductive success (within-group selection, Wilson, 1975, 1977) whereas *g(z)* defines the negative relationship between competition and group performance that can cause the tragedy of the commons (between-group selection).

The advantage of partitioning of social effects is this way is that one can investigate what maximizes *g(z)* and thereby identify factors that promote successful group adaptations. Doing this will show that high relatedness is important (Frank, 1998; Foster, 2004), which reflects the overlap between the questions of what promotes investment into cooperation and altruism, and what promotes group adaptations. However, there are other less intuitive factors that promote group adaptations, such as whenever investment into competition or the group adaptation provide diminishing returns [$f''(z) < 0$, $g''(z) < 0$; Foster, 2004]. This latter result is relatively simple to show in this framework, but is much less obvious in a model that partitions fitness purely in terms of effects on the individual.

This all said, it should also be emphasized that identical processes are at play in both this model and that of Lehmann and Keller, and they (eqn 6 in supplementary material of Lehmann and Keller, 2006) and others (Hamilton, 1975; Wilson, 1977; Queller, 1992; Dugatkin & Reeve, 1994; Frank, 1998; Wenseleers et al., 2003) have shown that kin selection and group selection perspectives are entirely compatible (Foster et al., 2006). The distinction is only one of emphasis and choosing the best way to partition effects for the question at hand. In the case of eqn 1, one can simply differentiate and rearrange to obtain a form comparable to Hamilton's rule (Frank, 1998; West & Buckling, 2003).

Species-level selection

The fact that species or social adaptations that are overrun by cheaters are unlikely to persist (Haldane, 1985) is an obvious but oft overlooked factor in the evolution of cooperation. The importance of this process is, at present, hard to assess but theory suggests that it

can have a powerful effect (Nunney, 1999) and I suspect it may prove important for our understanding of cooperation. Like the previous example, species-level selection speaks to a different aspect of the evolution of cooperation than is perhaps typical. Here, we gain insight into why cooperative species often possess properties that limit cheating. One answer is the *post hoc* evolution of policing and enforcement systems (Frank, 2003). But the other is that species-level selection removes those species and social traits that are not pre-adapted for persistence.

How would the effects of species-level selection manifest themselves in the Lehmann and Keller framework? Like policing and enforcement, species-level selection raises the benefit to cost ratio for investment into cooperation across social species, because species with this property will tend to persist. However, it should also be abundantly clear that saying that it will affect costs and benefits does not capture the processes of species-level selection, or indeed policing, in any real depth (identical criticisms can be made for a recent model of mutualisms, Foster & Wenseleers, 2006). As with the tragedy of the commons, therefore, modelling species-level selection will benefit from a multi-level selection perspective that considers processes above the level of the individual. In particular, for species-level selection, factors such as species interactions and community ecology will come into play (D.J. Rankin et al., submitted).

Conclusion

The Lehmann and Keller framework provides a clear way of thinking about the evolution of cooperation and altruism, which stems directly from Hamilton's own emphasis on individual costs and benefits. In doing so, it shows that many explanations for cooperation, which might at first pass appear distinct, can be grouped and classified according to key common principles. We must hope that this spirit of unification will continue with better efforts made to describe results in terms of multiple methodologies (e.g. Wenseleers et al., 2003). This will promote fruitful crosstalk and, most importantly, limit needless debates that derive from terminological confusion and emphasis rather than real differences (Foster et al., 2006). However, it is important not to take this one step further and infer that the Lehmann and Keller framework with its kin selection focus is somehow superior. Rather we should continue to welcome the diversity of approaches to social evolution. So long as we can translate between them, applying multiple methodologies can only deepen our understanding of how and why cooperation evolves.

Acknowledgments

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