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Commentary

Dissecting cooperation

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How cooperative behaviour has arisen and why it can persist in a world of selfish individuals has rightly turned out to be a perennial favourite in evolutionary biology and behavioural ecology ever since Darwin. The steady proliferation of new models and of novel interpretations of older concepts every now and then requires to look back and to arrange one's own ideas (and those of others). At present, the time appears to be particularly ripe to do so. This is because a few heretic and not so heretic statements about the basics of kin selection have initiated animated discussions (Fletcher et al., 2006; Foster et al., 2006a,b; Wilson and Hölldobler, 2005; Wilson, 2005), while at the same time several new attempts have been made to unify the various concepts of cooperation (Fletcher and Zwick, 2006; Johnstone, 2000; Lehmann and Keller, 2006; Reeve, 1998). The ongoing debate seems to be kindled in part by an inconsistent usage of terms, such as cooperation, altruism, mutualism, kin selection, and group selection (Foster et al., 2006a), whose originally rather stringent definitions have become more relaxed over time so that some terms are now used interchangeably (for discussions see Foster, 2006; Foster et al., 2006a; Lehmann and Keller, 2006; West et al., 2006, 2007).

In their valuable attempt to integrate cooperative breeding into theoretical concepts of cooperation, Bergmüller et al. (2007) present a concise, hierarchical classification of proximate mechanisms by which cooperation, defined as *interactions between two or more individuals that result in net benefits for all of the individuals involved*, can be maintained in evolution. They explicitly focus 'on the response of individuals to changes in the behaviour of others, not simply the net outcome of the interactions', and suggest investigating cooperative breeding by breaking it down into a series of interactions, which each could be manipulated and whose respective payoff matrices could be determined. We agree that such an approach can yield important new information on the dynamics in long-term associations

and might reveal existing networks of manipulation and counter-manipulation that structure the society. But we wonder whether indeed this approach will strongly transform our understanding of why cooperation has initially evolved and why it still persists in a particular system.

The starting point of Bergmüller et al. (2007) – that general theories of cooperation have rarely been applied to cooperatively breeding animals – reflects a rather narrow definition of "cooperation" as interaction and the common conceptual division between cases in which help is directed towards relatives and cases in which help is directed towards non-kin. However, general theories of cooperation, in which cooperation is a posteriori explained in terms of reproductive success or fitness (e.g., kin selection theory, multilevel selection theory, see also Stephens and Anderson, 1997), encompass both indirect and direct fitness benefits. These theories have repeatedly and with great success been applied also to cooperative breeding systems (Russell, 2004; Koenig and Dickinson, 2004; Solomon and French, 1997). They show that, though the details between species differ widely, in addition to kinship several ecological parameters favour helping at the nest, including the lack of breeding sites, inbreeding avoidance, parental territory quality, the possibility for load lightening, improved chances of inheriting the territory and a mating partner. Cooperation and altruism may be selected in evolution whenever they confer net benefits to both interacting partners. In the case of cooperation, as defined by Hamilton (1964) and Lehmann and Keller (2006), or "mutual benefit" (West et al., 2006, 2007), both partners gain in lifetime direct fitness. In the case of altruism, again as defined by Hamilton (1964) and others, the recipient of help gains in lifetime direct fitness, while the helper suffers a cost in lifetime direct fitness, which usually is more than compensated by gains in indirect lifetime fitness (see also Bourke and Franks, 1995; Lehmann and Keller, 2006). All cases of cooperation, including cooperative breeding, can thus in principle be explained using an inclusive fitness framework. Kin selection and multilevel selection theories are therefore as well applicable to groups consisting of related individuals as when individuals help non-relatives. We

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would like to remind that a recent meta-analysis clearly documents that helpers preferentially aid relatives, though the effects of direct versus indirect fitness still need to be disentangled (Griffin and West, 2003). Cases, where helpers predominantly help non-relatives, appear to be comparatively rare (Cockburn, 1998; Dunn et al., 1995; Reyer, 1984).

Breaking down cooperation into a long series of interactions and estimating the individual fitness payoff of each decision appears to us to be a very useful approach for better understanding the mechanisms by which cooperative systems work. For example, by experimental removal of reproductive-destined eggs from the combs of cooperatively breeding paper wasp queens, Reeve and Nonacs (1992) demonstrated that subordinate wasps react aggressively to the apparent stealing and eating of eggs by the dominant queen. Their finding suggested the existence of a “social contract” about the partitioning of reproduction, which can be stabilized against reproductive cheating by aggressive retaliation. Though of considerable interest concerning the resolution of conflict in foundress associations through mutual policing and punishment (see also Rissing et al., 1996; Tibbetts and Reeve, 2000), the results of the experimental manipulation have had comparatively little impact on our understanding of which factors in the first place have led to the evolution of cooperative breeding among unrelated insect queens. In cooperatively breeding social insects, observing series of interactions may even lead to counter-intuitive results. For example, unrelated, co-founding queens of the neotropical ant *Pachycondyla inversa* form dominance hierarchies, in which the dominants by antennal boxing and biting consistently force the subordinates to leave the nest and to take over the risky task of foraging for food (Kolmer and Heinze, 2000). Because the dominant eventually also feeds on the eggs laid by the subordinate queen, social dominance is associated with a highly skewed contribution of co-founding queens to the colony's first workers (Kolmer et al., 2002). This raises the question why the subordinate, despite of the consistently negative payoff it receives in its interactions with the dominant, reliably returns to the joint nest instead of deserting and founding solitarily. The answer emerges only from the observations that, once the colony has become mature and produces sexuals, aggressive interactions cease and reproduction is more or less equally partitioned among nestmate queens (Heinze et al., 2001), and that cooperatively initiated ant societies in general appear to have a higher survival rate than solitarily founded societies (Bernasconi and Strassmann, 1999).

The approach suggested by Bergmüller et al. (2007) will be widely applicable to reveal the power play structuring cooperation in vertebrate societies and, as shown above, also in founding associations of ant or wasp queens, but it will quickly come to its limits when many individuals interact over a prolonged period of time. Repeated interactions and reciprocity have first been used to analyse human behaviour in dyadic encounters, such as the repeated prisoner's dilemma (Axelrod and Hamilton, 1981; Trivers, 1971). Similarly, indirect reciprocity through image scoring and similar concepts were first developed to explain human altruism in small and manageable groups (Nowak and Sigmund, 1998). These concepts undoubtedly work best when few individuals interact, and in addition they require rather

restrictive conditions to be stable in evolution. For example, gene flow between groups of interacting individuals counteracts the evolution of image scoring (Leimar and Hammerstein, 2001). Furthermore, individuals need rather complex cognitive abilities to recognize each other in person. Though recent studies suggest that individual recognition may occur even in some insect societies, which traditionally were seen as being composed of anonymous nestmates, (Tibbetts, 2002; D'Ettore and Heinze, 2005), the constrictive premises of reciprocity are often not met and consequently, as yet few clear examples for the evolution of cooperation through reciprocal altruism exist in the animal kingdom (de Waal, 2005; Milinski, 1987; Wilkinson, 1984).

One final point we wonder about is the concept of pseudoreciprocity. By-product mutualism, in which the activities of an organism provide benefits predominantly for it but at the same time can incidentally provide benefits to others, has often been seen as starting point in the evolution of cooperation between species (Leimar and Connor, 2003; Leimar and Hammerstein, 2006). In contrast, the concept of pseudoreciprocity, as originally defined, is currently less well explored (Connor, 1986). The evolutionary stability of cases, in which an individual invests in another in order to obtain or to increase the by-product benefits it can get from this individual, seems to be crucially dependent on the impossibility of cheating. Otherwise, cheaters would easily reap the enhanced by-product benefits without paying the investment costs. Although this needs to be explored in a formal model, the same criticism as to image scoring might also apply to pseudoreciprocity: gene flow between groups of interacting individuals might counteract the evolution of pseudoreciprocity.

To summarize, the application of repeated interaction theory will presumably yield exciting information on the mechanisms maintaining cooperative breeding, but probably not provide so many new insights into the evolution of cooperative breeding. A full understanding of cooperative breeding will require both approaches. We feel that it is critically important to take the net outcome of cooperation into account, i.e., differential fitness, via which selection works. Recently, advances have been made to integrate reciprocity and repeated interactions with kin selection and multilevel selection theory, using a precise definition of ‘cooperation’. In particular, Lehmann and Keller (2006) aimed at integrating benefits from repeated interactions into a general inclusive fitness framework and to thus bridge the gap between models that have previously been applied to either explain cooperative interactions among relatives or among non-relatives (see also Boyd, 2006). By explicitly concentrating on models that are applicable in the absence of indirect fitness benefits, some of the prospects arising from this more integrative approach are missed out.

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