Cooperation and communication networks

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Indirect fitness benefits have long been accepted as one of the main explanations for the evolution of cooperative breeding. However, recent studies have shown that helpers can be unrelated to the breeders and may have access to reproduction or to other direct benefits. Understanding the basis for cooperation in the absence of relatedness is therefore a renewed challenge for research on cooperative breeding. In this context, the review by Bergmüller and colleagues represents an important contribution to the field by bringing together for the first time the theories of classic cooperation and cooperative breeding and thereby providing new avenues for research. This paper is likely to be particularly relevant to theoretical studies of cooperation in cooperatively breeding systems given the emphasis on clarifying concepts and the attempt to define which types of “traditional” cooperation fall into the different theories that attempt to account for direct benefits for cooperative breeders. Although the partitioning of different potential direct benefits (pay to stay, prestige and group augmentation) into the proposed categories of cooperation may be debatable to some extent, it does constitute an important first step.

A central issue when dealing with cooperation in cooperatively breeding systems, as acknowledged by the authors, is how to deal with the fact that cooperative breeding typically involves multiple players. As pointed out, situations where several individuals (as opposed to only two) cooperate to perform a certain task are problematic to address from a theoretical point of view because individuals invest into common goods, which should cause cooperation to collapse. Public goods allow societies composed largely of co-operators to outperform societies composed mainly of non-cooperators. However, public goods also provide an incentive for individuals to be selfish by benefiting from the public good. The authors refer to current solutions to this problem. In particular, they mention a study on humans, where being altruist could increase one’s ‘reputation’ (Milinski et al., 2002) and another study on population dynamics in structured populations where reproduction in groups, combined with dispersal between groups, results in variations in group size and high investors having greater fitness than low investors (Killingback et al., 2006). We believe there is another possible solution to this ‘tragedy of the commons’ that deserves attention: considering interactions in the framework of animal communication networks (McGregor, 2005). Two key features of communication networks are that several individuals are involved and information can be gathered from interactions by individuals (“eavesdroppers”) that do not take part in the interactions (McGregor and Dabelsteen, 1996; Naguib and Todt, 1997; Oliveira et al., 1998; Otter et al., 1999; Doutrelant and McGregor, 2000; Doutrelant et al., 2001; Peake et al., 2001). Although not part of the classic cooperation theory, Bshary and d’Souza (2005) pointed out that recent developments in cooperation theory can be linked to the concept of communication networks and the network context has been pivotal in their understanding of a classic example of cooperation: cleaner fish–client interactions.

In communication networks, it has been argued that some behaviour not primarily intended as signals can evolve a signalling function if they contain reliable information used by an audience of eavesdroppers (see also Lotem et al., 1999; Borgia and Colerman, 2000; Johnstone and Bshary, 2004; Bshary and Grutter, 2006). Individuals are expected to eavesdrop when such behaviour increases their fitness; similarly, if individuals gain from being observed they should perform the behaviour relevant to the eavesdroppers more frequently in presence of an audience of eavesdropper(s) (Doutrelant et al., 2001; Bshary and Grutter, 2006; Doutrelant and Covas, 2007).

It has been suggested that helping behaviour in cooperatively breeding species might have evolved a secondary signalling function (Zahavi, 1995; Putland, 2001; Doutrelant and Covas, 2007). Helping can be associated with direct fitness benefits for the helpers such as increased likelihood of reproducing (Reyer, 1986; Whittingham et al., 1997; Richardson et al., 2002; Webster et al., 2004) or being accepted in a coalition (Heinsohn et al.,
suggesting that helping contains information used for fitness-related decisions by others (the individuals helped, the potential mates or the coalition partners). In addition, helping involves costly behaviours such as parental care (Heinsohn and Cockburn, 1994; Heinsohn and Legge, 1999; Russell et al., 2003) or territorial defence (Maklakov, 2002) and thus should contain reliable information on individual quality. Finally, but in our view most significantly, helping behaviour takes place in a network – the breeding group, the colony or the border of the territory – where the help performed by one individual can often be observed by others, and hence the information can be easily transmitted and helping could be a complex behaviour functioning to help and to signal.

There are essentially three different types of signalling hypotheses associated with cooperative behaviour: (1) individuals might be expected to use helping behaviour to signal individual quality or social status (Zahavi, 1995; Putland, 2001); (2) helping might be a way of ‘paying the rent’ (Gaston, 1978) for being accepted in a group or territory (e.g. Stiver 2004); and/or (3) helping behaviour might be used for obtaining direct or indirect reciprocity, as shown in humans (Trivers, 1971; Nowak and Sigmund, 1998, 2005; Wedekind and Milinski, 2000). Hence, potential signalling functions of helping could be directed at individuals of the other sex in order to have future access to mating (Putland, 2001), at parents in order to be kept in the territory (Stiver et al., 2005), at allies in order to form coalitions (Zahavi, 1995; Putland, 2001; Stiver et al., 2005) or at the individuals helped or observing the help in order to receive help later (direct and indirect reciprocity: Trivers, 1971; Nowak and Sigmund, 1998, 2005; Wedekind and Milinski, 2000). The signal contained in helping might be unreliable if the helpers bring prey to the nest but eat it themselves instead of feeding it to the nestlings (e.g. Boland et al., 1997 but see Canestrari et al., 2004; Clutton-Brock et al., 2005). Although the possibility of cheating might advocate against the hypothesis of helping evolving a signalling function, since reliability is a major requirement of many signals (Johnstone, 1998; Maynard-Smith and Harper, 2003), the other individuals in the feeding group should be able to evaluate the nestlings’ satiety or condition. In addition, receivers outside the breeding group might be able to evaluate whether the food was or was not delivered through the vocalisations produced by the nestlings during the visit to the nest and after the helper’s departure, and hence those birds might use helping as a reliable signal. Cheating might also be prevented by parents if they do not tolerate non-working helpers. The importance of such factors in preventing the spread of deceit has been shown in other systems (Johnstone, 1998). If cheating cannot be prevented, then the capacity to find food, bring it back and display it instead of feeding it to the nestlings may be a signal of foraging ability.

A key test of the signalling hypotheses is to determine or, preferably, manipulate the identity of the audience during interactions. The target audience varies under each hypothesis and the behaviour of helpers is expected to change accordingly. In addition, the different types of signal falling under each hypothesis make different assumptions which should be used in tests of hypotheses. When the signal is used to display individual quality with conflicting fitness interests between emitter and receiver, such as in mate attraction or in establishing coalitions, the signal is expected to be costly. However, if a signal is used in a strict cooperation purpose (for example, if a related bird only needs to show it is feeding nestlings to its parents as a form of ‘paying the rent’), the signal does not need to be so costly and the individual only needs to be seen performing a certain task.

Experimental manipulation of the costs of the signal might be feasible using some of the techniques used to manipulate the cost of reproduction (e.g. supplemental feeding of the helper or using small weights to increase energetic expenditure during flight). Manipulating the identity of the audience will be challenging because the audience must be altered without otherwise disrupting the network of known individuals. Removal experiments could alter the audience through temporary removal of an individual. However, we suggest that simulating a change in audience through acoustic or video playback is likely to be more feasible. Playback manipulations investigating songbird extra-pair behaviour have shown females to be particularly sensitive to information acquired by eavesdropping in a network context (Otter et al., 1999; Mennill et al., 2002).

To conclude, Bergmüller et al. (2007) bridged the gap between theories of cooperation and of cooperative breeding. We propose that, in addition, linking these two theories with theories of signal evolution in a communication network would provide fruitful avenues of research.

References


