

A cognitive approach to the study of animal cooperation

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The study of cooperative behavior in animals has played a central role in the field of behavioral ecology (Dugatkin 1997). Moving away from early views that cooperation either permeated the animal world (Kropotkin 1908) or was completely lacking in nonhumans (Huxley 1888), modern behavioral ecologists are attempting to build a sound theoretical framework for understanding the evolution of cooperation (Hamilton 1964; Wilson 1975; Axelrod and Hamilton 1981; Brown 1983; Dugatkin 1997; Sober and Wilson 1998). Progress in building such models has been good, and this is reflected in the hundreds of controlled studies of cooperation in animals that can be found in the primary literature (Dugatkin 1997).

In the past, one of us (L.A.D.) has argued that there are four paths to cooperation (Dugatkin et al. 1992; Mesterton-Gibbons and Dugatkin 1992; Dugatkin 1997). These paths can go by slightly different names, but are generally referred to as reciprocity, byproduct mutualism, group selection, and kin selection (Mesterton-Gibbons and Dugatkin 1992; Dugatkin et al. 1992). As with any attempt to build an umbrella theory, objections with slicing the cooperation pie into four pieces certainly exist.

Here, our goal is not to settle these arguments, but rather to present the case that splitting up cooperation into the four paths mentioned above (reciprocity, byproduct mutualism, group selection, and kin selection) is quite useful in terms of understanding the different cognitive prerequisites required for various forms of cooperation to take place in animals. To accomplish this goal, we shall outline each of these four paths to cooperation, and at the same time describe what each path requires, and how they differ in terms of individual recognition and memory of specific events (the two cognitive variables we shall focus on).

Before proceeding any further, it might be useful to briefly touch on the relationship between individual recognition and memory of specific events. One important facet of this relationship is that individual recognition can exist in the absence of memory of specific events and vice versa. For example, I may recognize you by some mosaic of facial features, but not necessarily remember anything about what you have done. Conversely, I may be able to remember that someone did X to me, without recalling who it was who actually undertook X.

The notion of individual recognition itself is not without its problems. It could be argued that individual recognition is simply one case of what might be thought of as "category" recognition (Barnard and Burk 1979; Dugatkin and Sih 1995, 1998). A great deal of empirical work in animals has shown that animals can distinguish things based on size (e.g., large v. small), color (e.g., red v. blue), etc. If animals are able to employ enough such categories when applied to other individuals, eventually individual recognition will come about (Barnard and Burk 1979). As we shall soon see, some paths to cooperation require a simple form of category recognition, while others require individual recognition per se.

Reciprocity

Trivers (1971) suggested that one path to cooperative behavior among humans and nonhumans alike is reciprocity. Under Trivers' formulation, reciprocity evolves when the (potentially) minor cost that one individual paid to help another individual in need is made up for when the recipient returns the favor (reciprocated) sometime in the future. Such a system is, however, subject to cheating (=not cooperating = defecting), as the greatest "payoff" attainable in such scenarios goes to the recipient of a cooperative action, who then fails to reciprocate in turn.

To formalize the evolution of reciprocity, behavioral ecologists employ the Prisoner's Dilemma game (Axelrod 1984; Dugatkin and Reeve 1998). Using mathematical formulae and computer simulations, Axelrod and Hamilton (1981) examined the success of an array of strategies (behavioral rules) in the iterated Prisoner's Dilemma game. They found that if the