10 What We Don't Know about the Evolution of Cooperation in Animals

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The starting point for many studies of the evolution of cooperation is to explain why cooperation ever happens at all. Beginning with the premise that each individual's actions should serve that individual's interests, the question is why would anyone ever act in the interest of someone else? Models in evolutionary biology set up this question as a quantitative problem, in which the interests of the cooperating actor must be measured in the currency of reproductive success. How can we add up the benefits of cooperation so that it turns out that acting cooperatively serves the interests of the actor? The problem is to find an account that gives a net benefit, in reproductive success, to an individual that cooperates.

Recent discussion about the role of genetic relatedness in the evolution of cooperation centers around disagreement about how best to add up the benefits of social life. Some say that the best way is to count the reproductive success of the cooperating actor and add a measure of the reproductive success of relatives affected by those actions (Abbot et al., 2011). Others say this procedure does not necessarily give the best answer (Nowak, Tarnita & Wilson, 2010). Still others say that the argument is moot since all the available ways of counting are instances of the same general procedure (Sober & Wilson, 1998).

In any case, adding up benefits to see how evolution will proceed is a merely theoretical exercise unless we can relate actual behavior to ecological outcomes. To measure the benefits of cooperation, we need to know how particular kinds of cooperative behavior function, and why acting cooperatively matters to the individuals involved: what one animal does for another, and what difference this makes to each animal's livelihood and its relations with the rest of its environment. As Calcott (2008) points out, we need to understand what produces benefits before we can measure how the benefits are distributed.

How cooperative behavior benefits individuals is an empirical question, with unique answers related to the ecology of any particular social system. Any attempt to find out how individuals benefit from participating in a cooperative society leads directly to the conceptual problem of how to integrate the study of organization at

the individual and group levels. Empirical studies of cooperation in animal groups reveal webs of interactions that do not easily come apart to provide a measure of what each individual is getting. Theoretical attempts to demonstrate how cooperation could evolve from self-interest often lead to models that depict cooperation as uncooperative, with cheaters, spiters, defectors, and so on, who adjust their actions according to self-interest. But cooperative group processes are not easily understood this way.

Cooperative social relations, whose evolution we are trying to explain, are by nature resistant to the usual procedures for constructing evolutionary models, because such models require us to consider the individual separately from the group. But to specify the benefits to an individual of its life within a group, we have to grapple with the problem of characterizing how the welfare of the individual and that of the group are related.

Social Insects

Social insects provide a canonical example of cooperation. A colony consists of one or more queens, who lay eggs, and workers, who usually do not. Being a worker and not reproducing is called "altruism," defined as having both some benefit to others in the colony and some cost to the altruist in its loss of reproduction. The assumption is that by not laying eggs, the worker is instead providing some benefits to others through her work. In this way, not laying eggs has come to be considered to be equivalent to cooperation.

Thus the form of cooperation in social insects that kin selection was originally invoked to explain is defined negatively. In eusocial social insect colonies, there are individuals that do not reproduce. The evolutionary question was to explain how not reproducing could possibly be inherited. As originally formulated by Hamilton (1970), the problem is that once genes for not reproducing appear, they should quickly be lost in future generations because they are imprisoned in individuals that do not reproduce. Hamilton's solution was to notice that probably the relatives of workers would have the same genes as the workers do, so the genes could be passed on when the relatives reproduce.

Hamilton's argument about the role of kin selection in the evolution of worker sterility rested on the peculiar haplodiploid genetic system of the ants, bees, and wasps. This system has the consequence that a worker is more closely related to her sisters than she would be to her daughters. However, this is true only if the mother of the workers, the queen, mates only once. Since Hamilton introduced this idea, it has become clear that in many ant species the queens mate many times, so his argument does not apply. Others have argued for using kin selection in different ways to explain the evolution of worker sterility (Queller & Strassman, 1998).

The discussion about kin selection and the evolution of worker sterility sidesteps broader questions about the evolution of cooperation in social insects. Not laying eggs is not equivalent to cooperation. Workers sometimes lay eggs and still work, and they often do not work even when they don't lay eggs. This means that identifying who lays the eggs is not sufficient to produce an accurate count of the benefits of cooperation. To explain how cooperation in social insects evolved, we also have to count up the benefits of a worker's work. So we need to understand what workers do, and then figure out how to measure the extent to which each worker's actions contribute to the colony's ability to thrive and reproduce.

To determine how an ant's work benefits the colony, the first step is to find out how the colony operates and its ecological relations. A worker goes out and gets a seed, and brings it back to the nest. That seed is taken deep into the nest and stored. Months later, it is fed to a larva. We do not know how to calculate the benefit to the other ants of that worker's foraging trip. If it had stayed in the nest instead, how much worse off would the colony be, and how quickly would another ant have replaced it? The answer varies with current conditions: how much food the colony has stored, how many larvae need to be fed, the amount of each nutrient available in that seed, and so on.

In social insects, colonies can be considered the reproductive individuals. Colonies produce reproductive males and females (the queens); the males and females of different colonies mate, and the newly mated queens found new colonies. Each new colony is thus the offspring of the colonies that produced the founding queen and those that produced her mate or mates.

Since the colony reproduces as a single unit, producing more colonies, the benefits to any individual depend on the reproductive success of the colony, which in turn depends on how all the individuals in the colony function together. What we are learning about the organization of social insect colonies suggests new perspectives on what it means for a colony to operate well. A social insect colony regulates its behavior as a result of a network of interactions among workers (Gordon, 2010). For example, in a harvester ant colony, at any time there are many workers doing nothing. In the standard kin-selection story, these inactive workers are viewed as cheaters, serving their own interest at others' expense, who need to be policed. But inactive workers may in fact serve to buffer the interaction rate, keeping response down and dampening positive feedback from interactions (Pacala, Gordon & Godfray, 1996). Thus a worker, by doing nothing, may contribute to the ability of the colony to respond appropriately to changing conditions.

Harvester ants regulate foraging using a simple feedback system. They live in the desert and eat seeds. While a forager is out in the hot sun searching for a seed, it loses water. The ants get water from metabolizing the fats in the seeds they eat. So a colony

must spend water to obtain water, as well as food. A colony also has to deal with its neighbors, with whom it competes for food. If a colony does not use its foraging area for several days, its neighbors will collect seeds there instead (Gordon, 1992). Thus, for a given current food supply and current amount of brood to feed, the colony has to manage the trade-off between loss of water when it forages and loss of foraging area to neighbors where it does not forage.

From moment to moment, the colony adjusts the numbers foraging to the current food supply. Each forager spends most of its trip searching (Beverly et al., 2009), so the more food is available, the more quickly it finds food and the more quickly it returns to the nest. The rate at which foragers return with food is the feedback that regulates how quickly foragers leave the nest on the next trip (Gordon, Holmes & Nacu, 2008). The more food, the faster the foragers come back and the sooner more ants go out.

Colonies differ in how closely they regulate foraging (Gordon et al., 2011). In experiments where we manipulate how many foragers return, some colonies adjust within minutes, while others are less likely to change foraging activity. It seems that what differs among colonies is an outgoing forager's responsiveness to returning foragers. When foragers are less responsive, then foraging activity is steadier. When foragers are more responsive, then foraging activity is fine-tuned to the current level of food availability.

How closely a colony regulates foraging determines how it manages water loss and competition with neighbors for foraging area. The ecological question is: How important is the regulation of foraging for a colony's survival, growth, and reproductive success? If individual responsiveness to returning foragers is inherited from parent to offspring colonies, and it matters to a colony how well it regulates foraging, then natural selection can shape the regulation of foraging.

The regulation of foraging by an ant colony is a facet of its cooperative behavior. Working together, the ants help the colony to manage its food and water supply. Each individual forager's contribution consists of waiting for the right number of foragers with food to touch its antennae, going out to find a seed and bring it back, meeting the outgoing foragers along the way back inside, and then, after enough interactions, going out again. All of this is stochastic; the ant does the right thing, in a certain range of conditions, most of the time.

Suppose that natural selection is shaping this cooperative behavior by favoring the colonies that regulate foraging more closely. If the reactions of foragers are heritable from parent to offspring colonies, such selection could occur when the colonies with foragers who are a little more likely to rush out on a trip when a few foragers come back with food have higher fitness than the colonies whose foragers require more persuasion. The only way to measure the effect of any individual's contribution is to compare the reproductive success of its colony to that of other colonies in the population.

Colonies, and thus the ants in them, differ in the values used in the algorithm that links forager-return rate to the probability of going out on the next foraging trip (Prabhakar, Dektar & Gordon, 2012). The benefits to the colony of an individual's particular version of the forager-response algorithm depend on how that version contributes to the colony's water and food stores and relations with its neighbors. The benefits to the individual arise from how much the resulting ecology allows the colony to reproduce. To understand how benefit is generated requires understanding the colony-level behavior that regulates foraging.

Group Behavior

Many studies of cooperative behavior in animals, like models of its evolution, start from the same kind of question that Hamilton asked about social insects. For Hamilton, the problem was why some individuals do not reproduce. More generally, the problem is usually framed as why animals live or hunt in groups. This is seen as a sacrifice, analogous to worker sterility, of all of the resources or food that the animal could obtain on its own. Living in a group means the animal has to share, and sometimes has to put up with being bossed around by others. What does it get in return, and does it get more, the larger the group?

African wild dogs hunt in groups. Fanshawe and Fitzgibbon (1993) watched hunts and measured the relation between the size of the hunting group and its success in killing the prey. They found that large groups are no more successful than small ones in killing gazelles, because they are usually able to catch only young or sick gazelles, and it doesn't take many dogs to bring down a small gazelle. Larger groups are more successful in killing wildebeest, however, because the wildebeest is large enough that one dog has to hold it down while the others tear it apart. After the kill, hyenas often show up, and the higher the ratio of dogs to hyenas, the more likely are the dogs to keep control of the carcass.

It is not easy to see how to add up the costs and benefits of group hunting in wild dogs. A dog that hunts in a group of five eats more meat, relative to a dog that hunts alone, when the wildebeest are passing through the area, or when it's a good year for hyenas, but not when the most available prey are gazelles.

Any attempt to count up the benefits of group hunting has to make assumptions about the answers to a host of interesting questions, and making those assumptions distracts us from the fact that we don't know the answers. How do the dogs work together? How fluid are the groups and what is the network structure; do the same individuals tend to hunt together over and over? Does group structure change according to conditions, such as the availability of wildebeest and gazelles, and the group behavior of the local hyenas? The dogs' group size influences their interactions with hyenas, and so there is another set of questions about how the relative size of each

kind of group affects the outcome of a conflict, and how the network structure of the hyena group interacts with that of the dogs.

Many species of fish form schools that move and forage together, forming temporary coordinated groups. A school of fish moves through the water, turning, sometimes breaking apart around an obstacle and then fusing again. To decide whether this is cooperation, and to provide an account for how it could evolve, we'd have to describe the costs and benefits for the fish of being with the others instead of swimming around on its own. The larger the group of fish, the less likely is any individual to be the fish captured by a predator—but a large group is more conspicuous than a fish on its own. A fish in a group is likely to find a food source that a neighboring fish found—but it has to share its discoveries with the others. Both predator hunger and the distribution of food must vary in time and space. To specify the benefits added by each additional fish, we would have to know how often the predators appear, and how many fish they eat, and how patchy are the resources that the fish are searching for.

A separate question is how the fish coordinate their movements. There is no leader or central control. Each fish uses a simple algorithm, based on what it sees of neighboring fish, and on how the neighbors' movements alter the flow of the water (Couzin & Krause, 2003). In the aggregate, this produces the movement of the school.

How does evolution shape this algorithm? Natural selection acts on heritable variation and requires that the variation in behavior is associated with variation in reproductive success. If fish vary slightly in how they respond to each other, and these differences are inherited, and the coherence of a fish's school affects that fish's survival and reproductive success, then over time, in certain conditions, particular algorithms would increase in frequency.

To learn about the evolution of fish schooling behavior, we would have to know why, and in what situations, it matters to a fish how well coordinated is its school. The spectacular maneuvers of fish schools may be unusual. How often do the fish travel together, and under what conditions? What evolves is the fishes' capacity to move in and out of schools, to work as a group sometimes and as individuals at other times. To understand the evolution of this behavior, as of any other instance of cooperation, we have to begin by asking how the behavior is organized and how it functions ecologically.

Individuals and Groups

Evolutionary questions about cooperation are framed by contrast with an imaginary alternative in which each individual is out for itself. But for most animal groups, living in groups probably preceded the particular behavior we are studying. Ants evolved from wasps, who form temporary associations in which some females do not reproduce some of the time. Group living in canids is ancestral to the particular hunting

strategies of African wild dogs. Evolution has shaped an enormous diversity of nuanced interactions in groups, each arising through particular histories and conditions. Considering the benefits of cooperation relative to acting alone invites us to ignore all the ecological detail that could explain how particular kinds of behavior evolved.

It is clear that the more we learn about any cooperative system, the more we grapple with trying to evaluate benefits at different levels—what is good for the individual and what is good for the group. The study of cooperation has always ricocheted back and forth between individual and group. Debates about individual, kin, and group selection are one current manifestation of the basic problem of how to reconcile the individual and group levels when thinking about the advantages of cooperation. These debates can't be resolved in principle. Questions about how animals actually interact, and how individuals function within groups, will help to formulate realistic assessments about how individuals benefit from living together and cooperating.

How individual behavior is related to group behavior is the focus of our debates about how best to count the benefits of cooperation. More fundamentally, how individuals construct groups is what cooperation *is*. We need to ask first how the actions of individuals affect others, and how this produces the development, ecology, and history of the group. Evolutionary models of cooperation can be only as sophisticated as their measures of its benefits. The challenge is to understand the group organization and ecological relations that generate those benefits.

Acknowledgments

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