THE EVOLUTION OF COOPERATION

Four paths to the evolution and maintenance of cooperative behavior

The ants and termites have renounced the 'Hobbesian war,' and they are the better for it. Their wonderful nests, their buildings, superior in size relative to man; their paved roads and overground vaulted galleries; their spacious halls and granaries; their cornfields, harvesting and 'malting' grain; their rational method of nursing eggs and larvae, and of building special nests for rearing aphids whom Linnaeus so picturesquely describes as 'the cows of the ants' and finally, their courage, pluck and superior intelligence—all these are the normal outcome of the mutual aid which they practice at every stage of their busy and laborious lives. (Kropotkin 1908, p. 37)

Peter Kropotkin, anarchist, Prince of Russia, and natural historian, saw cooperation all around him in his travels, and he documented these observations in his immensely readable book, Mutual Aid (1908). Kropotkin, of course, was not the first to devote time and effort to the study of cooperation. In Leviathan, the great British philosopher and political scientist Thomas Hobbes ([1651] 1977) argued that one critical function of government is to enforce cooperation among its constituents. Without such enforcement, Hobbes believed that man's nature would surely lead to a "war of all against all." Hobbes did not, however, believe that cooperation was unnatural to other species. In fact, he devoted a number of pages in Leviathan to his arguments about why social insects are cooperative, and man is not (at least, not by nature).

Within evolutionary biology, interest in the evolution of cooperation can be traced at least as far back as Darwin (1859), who feared that the self-sacrificial behavior that defines many of the eusocial insects (e.g., ants, bees, and wasps) was a threat to his entire theory of natural selection. In the first half of the twentieth century, the study of cooperation was primarily (but not exclusively) kept alive by W. C. Allee, A. E. Emerson, and their colleagues. Although these biologists amassed a large amount of data that documented cooperation among animals (e.g., Allee 1951), they did not develop a new theory on how cooperation evolved. From 1963 to the present, four paths to cooperation--reciprocity, byproduct mutualism, kin-selected cooperation, and group selection--have been delineated. Each of these paths has a corresponding model that attempts to explain the evolution and maintenance of that particular path to cooperation. Sufficient empirical evidence now exists to test these models. In this article, I outline the four paths to cooperation (including their respective models) and
Reciprocity

Trivers (1971) suggested that both altruistic and cooperative behavior might evolve if individuals exchanged or reciprocated cooperative (or altruistic) acts. Essentially, the minor cost that one individual might pay to help another could be more than made up for if, sometime in the future, the second individual helps the first. As Trivers (1971) noted, such a system is subject to cheating because the greatest payoff attainable goes to the recipient of a cooperative action who fails to reciprocate in turn. How then might reciprocity evolve in such a world?

One way to examine this question is through the use of game theory, an economic tool that has also proven to be a powerful predictive tool for behavioral and evolutionary ecologists (Dugatkin and Reeve in press, Pool 1995). The prisoner's dilemma game (Figure 1) formalizes the question of how reciprocity could arise when cheating often provides such a large payoff. This game takes its name from a scenario in which two suspects are interrogated by police, but the payoffs for the prisoner's dilemma game can be applied to any number of behavioral situations in which animals find themselves. Figure 1 shows that if both players (individuals involved in an interaction) choose to cooperate, then they each receive R (reward). This payoff is relatively high, but it is not as great as T (the temptation to cheat payoff—that is, the payoff obtained by someone who cheats but whose partner cooperates). If both players cheat, then they each receive P (punishment). A player who cooperates but whose partner cheats receives S (sucker's payoff). The prisoner's dilemma game is defined as the scenario in which T > R > P > S. (An additional stipulation, namely that 2R > T + S, is sometimes added to the definition of this game.) The dilemma is that on any single interaction, it is always better to cheat, because T > R and P > S. Therefore, both players should opt to cheat, in which case they both receive P. But had they only opted to cooperate with one another, each would have received R, which is greater than P.
Figure 1. The prisoner's dilemma game. The game is defined by the inequalities $T > R > P > S$ and $2R > T + S$ (see text). Payoffs are shown for Player 1.

Is there any escape from the prisoner's dilemma? That is, can cooperation ever evolve in such a scenario? In 1981, Robert Axelrod, a political scientist, and W. D. Hamilton, an evolutionary biologist, teamed up to address these questions. Using both mathematics and computer simulations, Axelrod and Hamilton (1981) examined the success of an array of strategies in an iterated prisoner's dilemma game (i.e., the prisoner's dilemma game played repeatedly between the same two players). Axelrod and Hamilton found that if the probability of meeting a given partner in the future was above some critical threshold, then a strategy called TIT FOR TAT (TFT; first created by Anatol Rapport, a psychologist at the University of Toronto and a founding father of game theoretical applications to humans), was a robust solution to the iterated prisoner's dilemma.

The TFT strategy instructs a player to cooperate on the initial encounter with a partner and, in subsequent encounters, to copy the partner's last move. Axelrod (1984) hypothesized that TFT's success is attributable to its three defining characteristics: "niceness" (someone employing TFT is never the first to cheat), swift "retaliation" (individuals using TFT immediately respond by cheating, if their partner cheats), and "forgiving" (a partner using TFT remembers only one move back in time and therefore forgives prior defection on the part of a currently cooperating partner—that is, a partner using TFT does not hold grudges). Let us now take a look at two well-studied cases of cooperation via reciprocity.

**Reciprocal grooming in impala.** In many species, allogrooming behavior— that is, the grooming of others— appears to involve some sort of reciprocity (Dugatkin 1997). Ben and Lynn Hart and their colleagues have been studying allogrooming (among other behaviors) in herds of impala (Aepyceros melampus; Hart and Hart 1992). Bouts of reciprocal allogrooming are initiated when one impala begins grooming another. Although in some species grooming is solicited by the individual to be groomed, in impala it is the groomer who initiates this activity. Each bout of allogrooming consists of the initiator grooming the recipient 6-12 times and the recipient responding in kind. A typical exchange involves three to four such bouts (Figure 2). Grooming reduces tick infestation, which left untreated can have detrimental effects on impala health (Hart et al. 1992). Yet grooming is not cost free: It appears to increase electrolyte loss through saliva and to decrease vigilance behavior (Mooring and Hart 1995).

Figure 2. Two male impala. The male on the right is grooming the other individual.
The extent of reciprocity within grooming pairs of impala is impressive. Whether pairs are male-male, female-female, female-male, sub-adult male-subadult male, or fawn-fawn, each partner inevitably receives almost the same number of allogrooming bouts that it hands out (Figure 3). The fact that reciprocal allogrooming is seen in neonatal fawns as young as three days old, and that young deprived of allogrooming exchanges with adults still display this behavior, suggests that there has been strong selection pressure for reciprocal allogrooming.

Figure 3. Reciprocal allogrooming among adult impala. A 45-degree line denotes a perfect match between bouts delivered and bouts received. (a) Female-female pairs. (b) Male-male pairs. (Reprinted from Hart and Hart 1992 with permission of Academic Press.)

**TFT and predator inspection behavior in fish.** Although allogrooming behavior in impala provides strong support for cooperation via reciprocity, our lack of knowledge regarding the relative costs and benefits of this behavior, as well as how impala respond when individuals cheat, makes it difficult to place this example in the context of the prisoner's dilemma or the TFT strategy. These issues (costs, benefits, and response to cheating) have, however, been examined in some detail for predator inspection behavior in guppies (Poecilia reticulata) and in sticklebacks (Gasterosteus aculeatus).

In many fish species, one or a few individuals breaks away from a school and approaches a predator to assess the potential danger. Pitcher et al. (1986) coined the term "predator inspection" to describe a fish's slow,
saltatory movements away from a school and toward a potential predator (see Pitcher 1992 for a review). The costs and benefits of predator inspection probably meet the criteria for a prisoner's dilemma. That is, experimental work, in conjunction with indirect evidence, suggests that, for inspectors, T > R > P > S (but see Dugatkin 1997 for more on the long-standing and vociferous debate over the payoffs of predator inspection). In other words, the best option for a fish is to stay back and watch its partner inspect (T > R), but if both fishes fail to inspect (and receive P), then they are likely worse off than had they both approached the predator (and received R).

Following the early work of Manfred Milinski (1987), I have examined the behavior of pairs of inspectors to see whether they behave cooperatively and, specifically, whether they use something akin to the TFT strategy. Although still the subject of much discussion and some controversy, the data gathered so far support the notion that inspectors do use the TFT strategy when inspecting potential predators (Connor 1996, Dugatkin 1991a, b, Lazarus and Metcalfe 1990, Masters and Waite 1990, Milinski 1990a, b, 1992, 1996, Turner and Robinson 1992). That is, consistent with TFT, inspectors appear to be nice (each starts inspecting at approximately the same time), retaliatory (inspectors cease inspecting if their partner stops), and forgiving (if inspector A's partner has cheated it in the past but resumes inspection, then A resumes inspection as well; Dugatkin 1991 b). In addition to this direct support for TFT, evidence exists that inspectors remember the identity and behavior of their co-inspectors and prefer to associate with cooperators rather than cheaters (Dugatkin and Alfieri 1991a, b, Milinski et al. 1990).

**Byproduct mutualism**

A second path to the evolution and maintenance of cooperative behavior is byproduct mutualism (Brown 1983, Connor 1995, West-Eberhard 1975). According to models of by-product mutualism, animals incur an immediate cost or penalty for not acting cooperatively. That is, in byproduct mutualism, the immediate net benefit of cooperating outweighs that of cheating. In some senses, byproduct mutualism is a paradox in the world of cooperation. On the one hand, it is the easiest path to cooperation to understand, because one need not worry about many of the complexities inherent in reciprocity, kinship, or group structure (the other three paths; see below). Furthermore, after all is said and done, byproduct mutualism may be the most common path to cooperation. On the other hand, some behavioral ecologists argue that byproduct mutualism should not even be considered cooperation; cheaters receive a lower payoff than cooperators in byproduct mutualism scenarios, they point out, so there is no temptation to cheat and cooperation is a misnomer. I find this argument unconvincing. Because byproduct mutualism requires coordinated action on the part of the players, and because high payoffs cannot be obtained without the presence of other cooperating individuals, I believe that it is, in fact, a type of cooperation (Dugatkin 1997).

One last caveat about byproduct mutualism: just because the costs and benefits underlying byproduct mutualism clearly favor cooperation, making byproduct mutualism the least paradoxical of the paths to cooperation, it does not follow that this type of cooperation may not involve complex strategies. In fact, arguing that a matrix is simple to understand says nothing about the specific behavioral strategies that an animal might use when its payoffs correspond to such a matrix.

**Hunting behavior, territoriality, and byproduct mutualism in lions.** Until recently, many behavioral ecologists believed that group hunting behavior in lions (Panthera leo) was a classic case of unconditional cooperation (i.e., that lions always cooperate when hunting). Craig Packer and his colleagues have recently shown that such a view of lion hunting behavior is misleading. When stalking large predators that could not be taken by a single hunter, lions hunt in groups, but when hunting smaller prey items, they hunt alone. In other words, they cooperate only when it provides immediate benefits, as byproduct mutualism models predict.

Some aspects of lion cooperative hunting, however, cannot be explained by simple models of byproduct mutualism. For example, hundreds of hours of observing lions hunting show that some pridemates clearly exploit their cooperating compatriots (Grinnell et al. 1995, Scheel and Packer 1991). Using data gathered in the Serengeti National Park, Scheel and Packer (1991) used "finite-mixture models," a statistical tool, to uncover three strategies associated with group hunting in lions: refraining (not hunting), conforming (all hunters behave similarly—they hunt if others hunt), and pursuing (actively hunt, even if others do not). Whether refraining equals cheating, conforming equates with TFT, and pursuing equals pure cooperation remains to be seen, although Packer and Rutton (1988) found no evidence for TFT in the context of cooperative hunting.

**Owners, satellites, and territory defense in pied wagtails.** Pied wagtail birds (Motacilla alba) defend riverside winter territories, foraging on insects that wash onto the banks and searching their territory systematically for new items of food. Intruder wagtails often land on such territories and pose a threat to territory owners.
Sometimes such intruders are tolerated, in which case they are termed "satellites"; at other times they are aggressively chased off a territory. In light of the fact that a territory is worth more to a pied wagtail owner than to an intruder, because owners know which areas have recently been cropped for food whereas intruders do not, then why do owners sometimes tolerate intruders and sometimes chase them off? If an owner permits an intruder to stay, then the owner loses some foraging-related benefits, but it gains assistance in territory defense (Davies and Houston 1981). Davies and Houston (1981) found that owners allowed satellites on their territories on days of high food abundance (when intruder pressure is at its peak) and that this association benefited owners. On days of low food abundance, however, owners actively evicted any intruders attempting to feed on their territory.

Because intruders are typically better off as satellites (as opposed to nonterritorial "floaters"), it pays for the intruder to be involved in cooperative territorial defense and, in return, to get some food when owners allow entrance onto territories. Owners, however, cooperate only when doing so provides immediate benefits—that is, when sufficient food is present. As such, cooperation in both intruding and territory-holding wagtails is best understood as an example of byproduct mutualism.

Kin-selected cooperation

Perhaps the best-known and most well studied path to cooperation is kin selection. Both Darwin (1859) and Haldane (1932) recognized that individuals are more prone to cooperate with relatives. This idea was formalized by W. D. Hamilton in what has become known as inclusive fitness or kin-selection models (Hamilton 1964). The beauty of Hamilton's concept is that it can be distilled to an intuitive form. The core of inclusive fitness models is that they modify prior models by considering the effect of a gene, not only on the individual that bears it, but also on other individuals as well, most importantly those sharing genes that are identical by descent—that is, kin. "Hamilton's rule" states that a gene coding for cooperation (or, for that matter, a gene coding for any trait) evolves when

\[ r_{bc} > 0 \]

where \( b \) is equal to the benefit associated with cooperation, \( c \) is equal to the cost accrued by cooperating, and \( r \) is equal to the coefficient of relatedness—that is, the probability that two individuals share genes that are identical by descendant (i.e., that they share a common ancestor). This equation predicts that as \( r \) increases, the cost-to-benefit ratio needed to favor cooperation decreases. Thus, cooperation should be more common among kin.

Kinship and helping in naked mole-rats. Few animals have received more attention from the news media than the naked mole-rat (Hetercephalus glaber), the first eusocial vertebrate ever discovered (Jarvis 1981, Sherman et al. 1991). Naked mole-rats live in large groups in which a single queen and from one to three reproductive males possess exclusive breeding rights for the colony. Although intracolony aggression (manifested in queen-worker conflict) certainly exists (Reeve and Sherman 1991), cooperation is the order of the day. Nonreproductive males and females, whose average lifetimes are shorter than those of reproductive individuals, are involved in various cooperative behaviors: digging new tunnels for the colony (which is critical for colony survival), sweeping debris from tunnels, grooming, and defending the colony from predator attacks (see Lacey et al. 1991).

Why do nonreproductive individuals not only undertake such cooperative actions, but also yield exclusive reproduction to a single queen and a few males? This question may itself be misleading, because nonreproductive individuals do not so much give up their reproductive function voluntarily, as they are coerced into doing so as a result of aggression on the part of the queen (Faulkes et al. 1991). But this answer simply raises another question: why have nonreproductive individuals not developed better mechanisms for overcoming queen coercion? The answer, at least in part, appears to be related to kinship. Although naked mole-rats are diploid, average relatedness, \( r \), in a colony is 0.81—the highest \( r \) recorded for a nondomesticated species of mammal (Reeve et al. 1990; see Jarvis et al. 1994 for more on factors besides kinship that may have selected for cooperation in naked mole-rats).

Kinship and alarm calls in squirrels. One of the most well-known and oft-cited examples of kinship-based cooperation is Sherman's (1977,1981,1985) work on alarm calls in Belding's ground squirrels (Spermophilus beldingi). In this species, individuals often give alarm calls when a predator is sighted; such calls alert all those in the vicinity (Figure 4). Sherman (1977) proposed numerous alternative hypotheses for this phenomenon. One is that alarm calls serve either to warn relatives or to solicit aid from relatives, depending on the situation. Sherman predicted that if this hypothesis is correct, alarm calling must be associated with the presence of relatives.
Strong support for Sherman's hypothesis came from the finding (Sherman 1977) that female squirrels give alarm calls when a predator is in the vicinity more often than expected by chance, whereas the converse is true for males. Females are generally sedentary and mature and breed near their natal sites, whereas males always emigrate from their birthplace and do not aggregate with siblings after emigration (Sherman 1977). Therefore, females' calls warn close kin (often offspring), whereas males' calls do not. Further support for the kinship hypothesis includes evidence that invading (non-native) females give alarm calls less frequently than native females, and that females with living relatives are more likely to call than are females without any living kin (Sherman 1977).

**Group-selected cooperation**

The trait-group selection path to the evolution of cooperation, although controversial (Wilson and Sober 1994), is quite straightforward. In such models, cooperation can evolve even when it has a relative cost to the individual performing it, so long as the within-group cost is offset by some between-group benefit, such that cooperative groups are more productive than selfish groups (Wilson 1980, Wilson and Sober 1994). For such group-level benefits to be manifest, groups must differ in the frequency of cooperators within them, and groups must be able to "export" the productivity associated with cooperation. For example, following Wilson (1990), consider a field of many ant colonies. Further imagine that through most of evolutionary time, ant colonies lacked a specialized forager who would take the often high risk associated with foraging but would share food with nestmates. How could such a cooperative "specialized forager" evolve?

Wilson's thought argument (1990) imagines two types of foragers: unspecialized foragers (u) and specialized foragers (s). In our hypothetical colonies with unspecialized foragers, all queens forage, but in nests with a specialized forager(s), U types forage disproportionately more often but share food equally among all their nestmates. Now suppose that foraging is a costly endeavor because foragers are exposed to predators and risk desiccation. Specialized foragers would therefore bear more costs than their nestmates. Further suppose that experience in foraging makes a queen more efficient, and thus nests with a specialized forager bring in more food than nests lacking such an individual.
Could group selection ever favor the evolution of specialized (altruistic) foragers? The answer is a definitive yes (Wilson 1990). If we let $x$ represent U's costs of foraging (hence $x < 1$) and let $y$ (> 1) represent U's effect on colony survival, then U can evolve if $xy > 1$. In other words, within-group selection against U can be arbitrarily strong (i.e., low $x$ values), as long as between-group selection (represented by $y$) is correspondingly high. It turns out that this thought experiment has been played out in nature in a number of different species and at various levels of complexity.

**Group selection and cooperation in Messor pergandei.** Colonies of the seed harvester ant, Messor pergandei, are usually initiated by multiple unrelated queens (Rissing and Pollock 1986). Adult colonies are very territorial, and brood raiding is seen among young starting colonies in the laboratory. Brood captured by nearby colonies are raised within the victorious nests, and colonies that lose their brood in such interactions die out. All queens produce workers, and there exists a positive relationship between the number of queen foundresses in a colony and the number of initial workers (which can act as brood raiders) produced by that colony. That is, between-queen cooperation increases group productivity, which translates into greater success at brood raiding (Rissing and Pollock 1991).

This example provides all of the elements needed for group selection to operate. Group selection requires the differential productivity of groups based on some trait. In the case of M. pergandei, the trait of interest is queen-queen cooperation, which, although selected against within groups (a queen that did not cooperate might reap some benefits from her cooperative cofoundresses without paying any costs), may be selected for because groups with many cooperators survive brood raiding (i.e., differential productivity of groups; but see Pfennig 1995 for field data suggesting that differential productivity based on foundress associations is weak).

**Group selection and foraging in Acromyrmex versicolor.** The ant Acromyrmex versicolor nests in shady areas and shares many characteristics with M. pergandei: many nests are founded by multiple queens, no dominance hierarchy exists among queens, queens are unrelated, all queens produce workers, and brood raiding among starting nests appears common. However, in A. versicolor, queens forage after colony foundation, whereas M. pergandei queens do not forage outside during the claustral (underground) stage of early colony foundation. As a result of increased predation pressure and parasitization, foraging is dangerous for a queen, but once a queen takes on the role of forager, she remains in that role. What determines which queen eventually emerges as the group's sole forager is still not well understood. However, this decision appears not to be a coercive one--that is, it is not forced on a particular queen by other group mates (Rissing et al. 1989).

Once a queen becomes the sole forager for her nest, she shares with her cofounders all the food she brings into the nest. The forager, then, assumes the risks of foraging and obtains the benefits, whereas the other queens simply obtain the benefits without risks. Within-group cooperation on the part of the forager appears to lead to more workers, which in turn increases the probability that a given nest will be the one to survive the period of brood raiding. Thus, between-group selection for a cooperative specialized forager overwhelms any within-group costs associated with this behavior (Rissing et al. 1989, Seger 1989; see Wilson 1990 for a more extended discussion).

**To the future**

The study of cooperation has evolved from a collection of interesting anecdotes (Kropotkin 1908) to an area of research based on a sound theoretical framework. Controlled studies of cooperation appear frequently in the literature on evolution and social behavior, and there is no reason to believe that the pace at which these studies appear will slow down in the immediate future. Conceptual and theoretical advances leading to models of kin selection, reciprocity, byproduct mutualism, and group selection fueled the boom in empirical studies, but empirical work is now beginning to catch up with theory. There is still much to be done, however, and I will close with a few thoughts on what major issues in the study of cooperative behavior are prime for the picking.

Finer discrimination among the paths to cooperation. The most recent theoretical development attempting to unify work on the evolution of cooperation is called the cooperator's dilemma game (Dugatkin et al. 1992, Mesterton-Gibbons and Dugatkin 1992). The cooperator's dilemma is based on a very general payoff matrix, such that with slight changes this general matrix can be transformed into a model of any of the four paths to cooperation, and hence represents a significant step forward in developing what might be called an "all purpose" model for the evolution of cooperation. Of course, although some cases of cooperation clearly follow a single path, others may contain elements of more than one (e.g., both kinship and reciprocity), and future elaboration of the cooperator's dilemma game needs to handle such cases.

Comparative approaches toward the study of cooperation. With the advent of modern comparative techniques
(e.g., Harvey and Pagel 1991), it is now possible, at least in theory, to examine correlates of cooperation across animal taxa. When comparing taxonomic entities, techniques could be employed to look for cognitive, group size, and medium (e.g., water, air) effects that correlate with cooperation. For example, one could ask whether certain cognitive abilities are commonly associated with reciprocity, byproduct mutualism, kin selection, and group selection, and whether these cognitive abilities are clustered in various taxa. One question might be the following: Is reciprocity more likely in large-brained animals, such as mammals? Although reciprocity is certainly common in this taxon, it is also found in fishes, birds, insects, and many other taxa, and so the answer to this question is not evident beforehand.

The skew toward reciprocity. Theoretical work on the evolution of cooperation is heavily skewed toward models of reciprocity. But is the skew truly representative of cooperation in nature? Part of the bias in the literature could be due to the fact that reciprocity may be the most perplexing and difficult sort of cooperation to explain. After all, in byproduct mutualism, it pays for the individuals involved to cooperate; kinship is so ingrained in the field of behavioral ecology as to need no explanation; and group selection is controversial but easy to grasp intuitively. None of these characteristics, however, holds true for reciprocity, and the prisoner's dilemma game shows just how hard it is for cooperation to evolve under certain conditions.

If this portrait is correct, then the skew toward reciprocity may simply represent the perspective of theoreticians. After all, hard problems require more work, and there is nothing that a theoretician likes more than a challenge. In any event, I believe that in the long run, the skew will not turn out to represent what is happening in nature. Although most empirical studies have been constructed to examine reciprocity, this is in all likelihood simply a case of empiricists following the lead of theoreticians. The more controlled studies we do, the more we see that reciprocity explains only some of the cooperation found in nature. Indeed, I believe that the more empirical work we do, the quicker the bias toward cooperation via reciprocity will disappear.

The problem of cooperation among animals is at the heart of evolutionary and behavioral biology (Wilson 1975). From a general scientific perspective, a more detailed understanding of cooperation will considerably advance our knowledge of animal behavior. From a more utilitarian perspective, the world's human population is now exerting extreme pressures on limited natural resources, making it more important than ever before that cooperation be achieved in conserving these resources. Although I have focused in this article on nonhuman animals, the underlying themes may also help to solve the urgent problem of the commons (Hardin 1968) that is, the problem of designing cooperative social structures for sustainable management of common-property resources Hardin 1994).

**References cited**


ILLUSTRATION

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