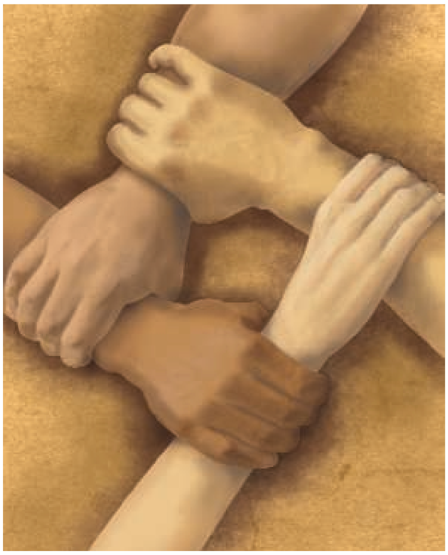
On the Origin of Cooperation



COOPERATION HAS CREATED A CONUNdrum for generations of evolutionary scientists. If natural selection among individuals favors the survival of the fittest, why would one individual help another at a cost to itself? Charles Darwin himself noted the difficulty of explaining why a worker bee would labor for the good of the colony, because its efforts do not lead to its own reproduction. The social insects are "one special difficulty, which first appeared to me insuperable, and actually fatal to my theory," he wrote in *On the Origin of Species*.

And yet cooperation and sacrifice are rampant in nature. Humans working together have transformed the planet to meet the needs of billions of people. Countless examples of cooperation exist between species: Cleaner fish pick parasites off larger fish, and nitrogen-fixing bacteria team up with plants, to name just a few.

In some cases, cooperation has fueled key evolutionary transitions, helping to create integrated systems. Worker ants have no offspring of their own and instead feed their queen's offspring in colonies often considered "superorganisms" many thousands of individuals strong. Cells managed to specialize and stay together, giving rise to multicellular organisms. "At each of those levels, formerly independent reproductive units and targets of selection become integrated into a single reproductive unit and target of selection," notes biologist James Hunt of North Carolina State University (NCSU) in Raleigh.

So pervasive is cooperation that Martin Nowak of Harvard University ranks it as the third pillar of evolution, alongside of mutation and natural selection. "Natural selection and mutation describe how things change at the same level of organization," he explains. "But natural selection and mutation alone wouldn't explain how you get from the world of bacteria 3 billion years ago to what you have now." Cooperation leads to integration, and integration to the complexity we see in modern life.

The challenge of cooperation is to explain how self-interest is overcome given the way natural selection works. Darwin suggested that selection might favor families whose members were cooperative, and researchers today agree that kinship helps explain cooperation. But cheaters—those who benefit without making sacrifices—are likely to evolve because they will have an edge over individuals who spend energy on helping others, thus threatening the stability of any cooperative venture. That puzzle has inspired biologists, mathematicians, even economists to come up with ways to explain how cooperation can arise and thrive. Researchers have spent countless hours observing social organisms from man to microbes, finding that even single-celled organisms have sophisticated means of working together. As genomics has come of age, researchers are getting down to the genetic nuts and bolts of cooperation in a variety of systems for the first time.

All in the family

To help explain the puzzle of how cooperation evolved, Darwin suggested that it might benefit members of a family to help each other. The British biologist William Hamilton took this idea to heart in the 1960s. He formalized modern thinking about cooperation with the proposal that the offspring of relatives counted toward one's individual fitness. Relatives' progeny share some of your genes, so helping them furthers the spread of the shared genes. The more offspring relatives produce, the more those genes will spread. Helpers will therefore evolve if their overall reproductive output rises enough to make up for any loss of direct reproductive output.

Hamilton worked out a formula for predicting "inclusive fitness"—your offspring plus some proportion of your relatives' offspring—and used that as a guide to determining whether cooperation should evolve in various circumstances. He concluded that inclusive fitness could indeed explain the evolution of highly social insects, whose colonies are composed of related individuals, thus solving Darwin's problem.

This concept implies that individuals will behave differently depending on the degree of relatedness. As another Brit, J. B. S. Haldane, was reported to have put it 30 years earlier, "Would I lay down my life to save my brother? No, but I would to save two brothers or eight cousins."

The idea that kinship helps drive cooperative behavior has proved a powerful one, but it cannot explain all of cooperation. Humans, for example, often cooperate with nonrelatives. "No other species seems to have succeeded in establishing large-scale cooperation among genetically unrelated strangers," wrote economist Ernst Fehr of the University of Zurich, Switzerland, in the 25 November 2004 issue of *Nature*.

To help explain our cooperative nature, in the 1970s, Robert Trivers, now at Rutgers University in New Brunswick, New Jersey, came up with the idea of reciprocal altruism—"You scratch my back, and I'll scratch yours," as he put it. Researchers inspired by his work used computer simulations to approximate what might happen in real life over many generations. Programmers created games in which two players had the option to cooperate and found that cooperation could evolve and be maintained between two people if they did "tit for tat," following each other's lead in deciding whether to cooperate.

But this progress can't explain how large cooperative groups—in which the chances of reencountering a helper or a helped person were small—could evolve. Also, researchers had to consider the prospect of cheating: When multiple individuals work together to find food, make a home, or defend their communities, if a few people fail to contribute and became freeloaders, others may follow, destabilizing cooperation altogether.

THE YEAR OF DARWIN

This essay is the ninth in a monthly series. For more on evolutionary topics online, see the Origins blog at **blogs.sciencemag.org/origins**. For more on cooperation, listen to a podcast by author Elizabeth Pennisi at **www.sciencemag.org/multimedia/podcast.**

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Published by AAAS

One for all. Cooperation comes in many forms, among species—as with cleaner shrimp and fish tending a moray eel (*far left*), as well as within species, as in (*left to right*) ants, lions, and wasps.

> "The same core theories that are used to understand cooperation in humans and other animals can also be applied to microbes."
>
> —Kevin Foster, Harvard University

In 1998, Nowak and Karl Sigmund of the University of Vienna proposed a way around these issues, at least in the case of humans. They developed a mathematical model suggesting that people decide what to do based not only on whether others have helped them but also on whether others have helped others. "Reputations were also important," Nowak explains. A person with a reputation for helping gets help, even from someone who has not benefited directly from that person in the past. This could allow cooperative strategies in games to be successful and, by extension, cooperative societies to evolve, Nowak argued.

Other game-playing experiments bore this out. In 2004, Robert Boyd of the University of California, Los Angeles, showed through simulations that this strategy worked particularly well if those who did not help or had a reputation for being slackards were shunned and were refused help.

But Fehr thought even this didn't fully explain humans' extremely cooperative nature. In his labor market studies, he found that people tend to be more cooperative than economic theory would predict: Fairly paid employees voluntarily worked harder than predicted based solely on self-interest, for example. He also noticed that people tended to cooperate with strangers, even though there is little chance these interactions would affect their reputations. He wondered what motivational and social forces might drive and sustain this behavior.

After working with many game-playing experiments, Fehr suggested that punishment also plays a key role in making cooperation successful. In 2002, he reported an experiment in which participants decided whether to keep money they were given or contribute some or all of it to a group project. Participants also had the option to punish noncontributors. Punishment was rampant, and about 75% of the time, it was the above-average contributors—"cooperators"—who penalized freeloaders. When punishment was not part of the game, average contributions dropped. Other work has pointed out that over the long term, the mere threat of punishment—rather than punishment itself—is enough to inhibit cheating. So the cost to punish decreases, but the benefit remains.

Nowak thinks altruistic leanings may in part be instinctive, having evolved because for most of human history, small, related groups were the norm, and reputations were always at stake. But he downplays the importance of punishment, as it may have long-term negative effects such as escalating interpersonal conflicts. When individuals encounter each other repeatedly, "rewards work much better" in perpetuating cooperation, he insists. In the 1 January issue of *Nature*, he and his colleagues concluded, based on modeling experiments, that punishment rarely pays and that refusing to help noncooperators is much more effective. And on page 1272, they report that in repeated games involving 192 subjects interacting in groups of four via a computer, reward led to increased contributions from individuals and a greater payoff for the group. Punishment can work to keep cooperation going, he says, but in those experiments, punitive actions led to a lower payoff and did not change how much people contributed to the group. Given that Fehr's experiments show the opposite, the role of punishment is still a matter of debate.

Group selection

Others have applied a different focus when thinking about the evolution of cooperation. They have become convinced that competition among groups can foster cooperation

All for one. Studies of hunter-gatherers such as the Hadza help clarify how cooperation arose in humans.

CREDITS (TOP TO BOTTOM): JUPITERIMAGES; © BRIAN WOOD within them. In other words, evolutionary forces can act on several levels, with natural selection's push to make individuals less cooperative being countered by competition at the level of the group, because groups with greater cooperation among members tend to survive better. Darwin noted in *The Descent of Man* that this seemed to be true of human groups. If two tribes were competing, and "the one tribe included a great number of courageous, sympathetic and faithful members, who were always ready to warn each other of danger, to aid and defend each other, this tribe would succeed better and conquer the other," he wrote.

That is true for more modern warring groups, says Samuel Bowles, an economist at the Santa Fe Institute in New Mexico. "From military history, it's [known] that groups that are more likely to cooperate are more likely to be successful," he says. Frequent violent encounters with other human groups made such cooperation essential in our past, Bowles and his colleagues have argued.

Helping hands. Rescuers save a swimmer in this drill in China; such cooperative behavior toward nonrelatives is rare outside humans.

Their most recent study backs up that contention. In the 5 June issue of *Science* (p. 1293), Bowles evaluated archaeological evidence from about 50,000 years ago, as well as ethnographic and historical reports on certain hunter-gatherer populations—those whose lifestyles, he argued, came the closest to resembling ancient human societies.

Bowles found that the percent of adult deaths due to warfare ranged from 0% to 46% at the different sites, averaging out to about 14%—significantly higher than the death toll rates in 20th century Europe with its two world wars. Such frequent warfare made altruistic cooperation among group members essential to survival, says Bowles.

Using game theory, he has simulated what happens in war and concluded that humans could have easily evolved what he calls parochial altruism—wherein you help others in the group, independent of familial relationship, and harm outsiders. "It could have promoted a predisposition to cooperate in groups even at considerable cost to the actor," says Bowles.

From man to microbe

A lot of effort has gone into understanding how humans got to the point at which they could get along, and a lot of cooperative theory has been developed with *Homo sapiens* in mind. But it doesn't take a large brain and a winning smile to cooperate. Even bacterial viruses called phages have prospered by working together. In 2005, Joel Sachs and James Bull, both then at the University of Texas, Austin, demonstrated that traits that reduce competing self-interest evolved in two different types of phages. The two phages were introduced into a bacterial strain at the same time. Over many generations, the two began to package their genomes within a single protein coat, ensuring that both would be transmitted to the next host bacterium. One phage eventually lost the genes needed to make its own coat, they reported.

The more researchers look, the more cooperation they find among microbes. Even better, "the same core theories that are used to understand cooperation in humans and other animals can also be applied to microbes," says Kevin Foster of Harvard. By working with yeast, bacteria, and amoebas, several teams have been able to discern fundamental principles about the evolution of cooperation. "Microbes are experimentally tractable, … and evolutionary dynamics occur over laboratory time scales," says Jeffrey Gore of the Massachusetts Institute of Technology in Cambridge. Relatedness, cheaters, and other factors all come into play to determine the success of these microscopic cooperative ventures.

For example, Stuart West, an evolutionary biologist at the University of Edinburgh in the United Kingdom, studies a group phenomenon called quorum sensing in the opportunistic pathogen *Pseudomonas aeruginosa*. Like other bacteria, this pathogen secretes chemical signals that fellow *Pseudomonas* bacteria in turn respond to by releasing a variety of products, including virulence factors, nutrient-scavenging molecules, and compounds that become the scaffolding for aggregates of microbial cells called biofilms. In the lab, West and his colleagues helped to demonstrate that when *Pseudomonas* individuals sense the accumulation of other *Pseudomonas* nearby, thanks to the increasing concentration of certain biochemicals, they increase their secretion of these helpful substances, providing a benefit to all *Pseudomonas* present.

Two years ago, West's team also showed that this system, like those of humans playing evolutionary games, was vulnerable to cheaters, bacteria that secreted no helpful substances but reaped the benefits of those that did. In one experiment, after 48 hours and seven generations, the population of one type of cheater increased from 1% to 45% of the colony, raising the question of how the cooperative wild type could possibly persist. West thinks that relatedness may be the answer: Wild-type bacteria tend to cluster in high densities, crowding out the mutant cheaters, which have a different genetic makeup.

In the 24 February issue of *Current Biology*, West's team extended these findings by exploring cooperation and cheating in *Pseudomonas* when it was growing in high densities on burn wounds in mice. The proportion of cheaters affected the well-being of both microbes and mice, they reported. When more cheaters were present, the mice did better—possibly because fewer virulence factors were being produced—suggesting that one might treat infections of quorum-sensing microbes by introducing cheaters into their midst, says West.

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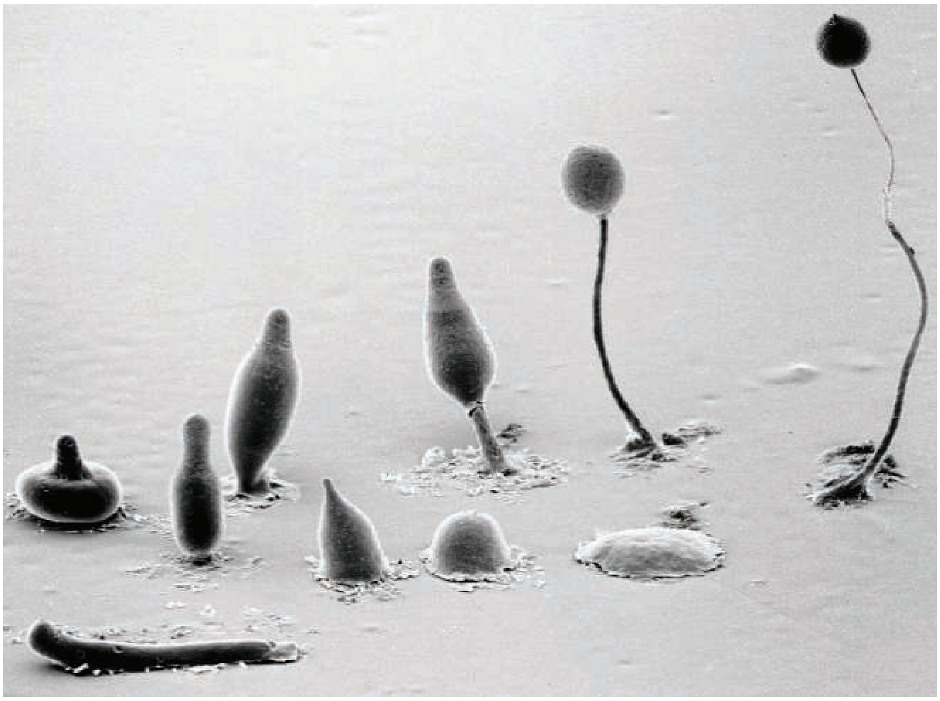

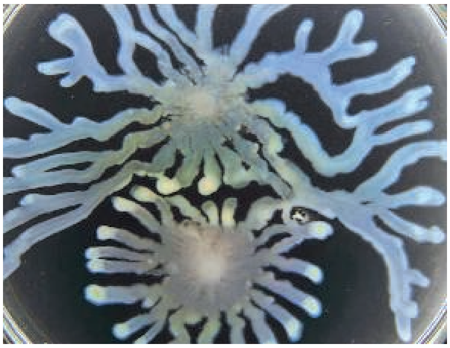

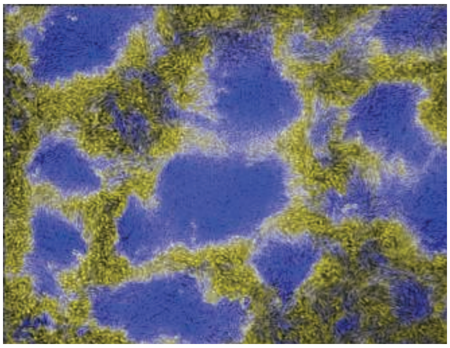

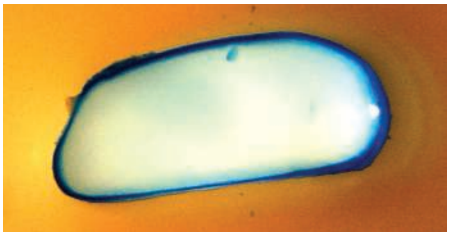

Cooperating microbes. A composite scanning electron micrograph (*above*) shows individual slime mold amoebae forming a fruiting body. *Pseudomonas aeruginosa* strains can swarm (*top right*) to create a biofilm (*middle right*) to make better use of resources. And in a group of yeast cells exposed to ethanol, the outer cells died (blue), but they protected inner cells from harm.

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Perhaps the most celebrated social microbe is the slime mold, *Dictyostelium*, an organism long studied by developmental and cell biologists as a model. More than a century ago, researchers showed that these single-cell amoebae sometimes merge to form stalked fruiting bodies, which produce spores that disperse to more food-rich environments. In the 1980s, researchers recognized that the amoebae forming the stalks were altruistic, giving up their chance at reproduction to help position other amoebae to produce spores. Studies by David Queller and Joan Strassmann of Rice University in Houston, Texas, show that, as with other organisms, cooperation among slime mold amoebae involves tradeoffs and that relatedness matters.

Cheaters are a constant threat: In 2000, Richard Kessin of Columbia University screened for and found such cheating cells, mutants that manage to avoid becoming part of the nonreproductive stalk and instead infiltrate only the fruiting body. If cheaters make up half the population of aggregating amoebae, they can make up about two-thirds the spores in the fruiting body. Working with Baylor College of Medicine and Rice colleagues Gad Shaulsky and Adam Kuspa, Queller and Strassmann have now found more than 100 slime mold genes that confer the ability to cheat. These genes cover the gamut of functions and are involved at different points in the development of the fruiting stalk. "The large number of genes and pathways involved suggest that it may be easy to evolve cheating and difficult to control it fully," the authors wrote in the 28 February 2008 issue of *Nature*.

But their work has also shown that amoebae can keep cheating in check, in large part because the mutations that make cheating possible also tend to keep cheaters from getting into the aggregations at all. In laboratory tests, where it's easier to move about, amoebae lacking the cell-adhesion gene called *csaA* tend to bypass the stalk and settle in as part of the fruiting body, acting as cheaters. But on soil in the wild, the lack of this adhesion protein keeps them from getting into the fruiting-body formation in the first place, says Queller.

The *csaA* gene is an example of a so-called green-beard gene, a gene that enables an individual to recognize—as one could recognize a green beard—and cooperate with others who carry that same gene. Those with green-beard genes help perpetuate copies of the gene in others, regardless of the degree of relatedness among individuals. In the case of slime mold amoebae, the csaA proteins bind to each other, preferentially linking cells that share this green beard, so that they can produce a stalk and fruiting body.

Few real-world green-beard genes are known. But yeast have one, too—another cell-adhesion protein called FLO1 that leads to clumps, or "flocs," of individual yeast cells, as shown in 2008 by Harvard's Foster, Kevin J. Verstrepen of the Catholic University of Leuven in Belgium, and colleagues. As in the slime mold amoebae, only yeast with the gene can come together. When the yeast are in a floc, outer cells inadvertently become altruistic, as they shield inner cells from toxins and other environmental stresses, often at a cost to their own well-being.

That yeast and slime molds have been shown to possess green-beard genes speaks to the power of microbial systems to help pin down how cooperation works: Hamilton had predicted the existence of such genes long before they were discovered. Countless other organisms, from termites to meerkats, provide additional opportunities for the study of cooperation. "The origin of sociality is unlikely to be encompassed by a single explanation," says NCSU's Hunt. "Sociality, like multicellularity, has appeared numerous times, in diverse taxa, and reached many different levels of integration."

–ELIZABETH PENNISI

Published by AAAS

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Science **325** (5945), 1196-1199.
DOI: 10.1126/science.325_1196