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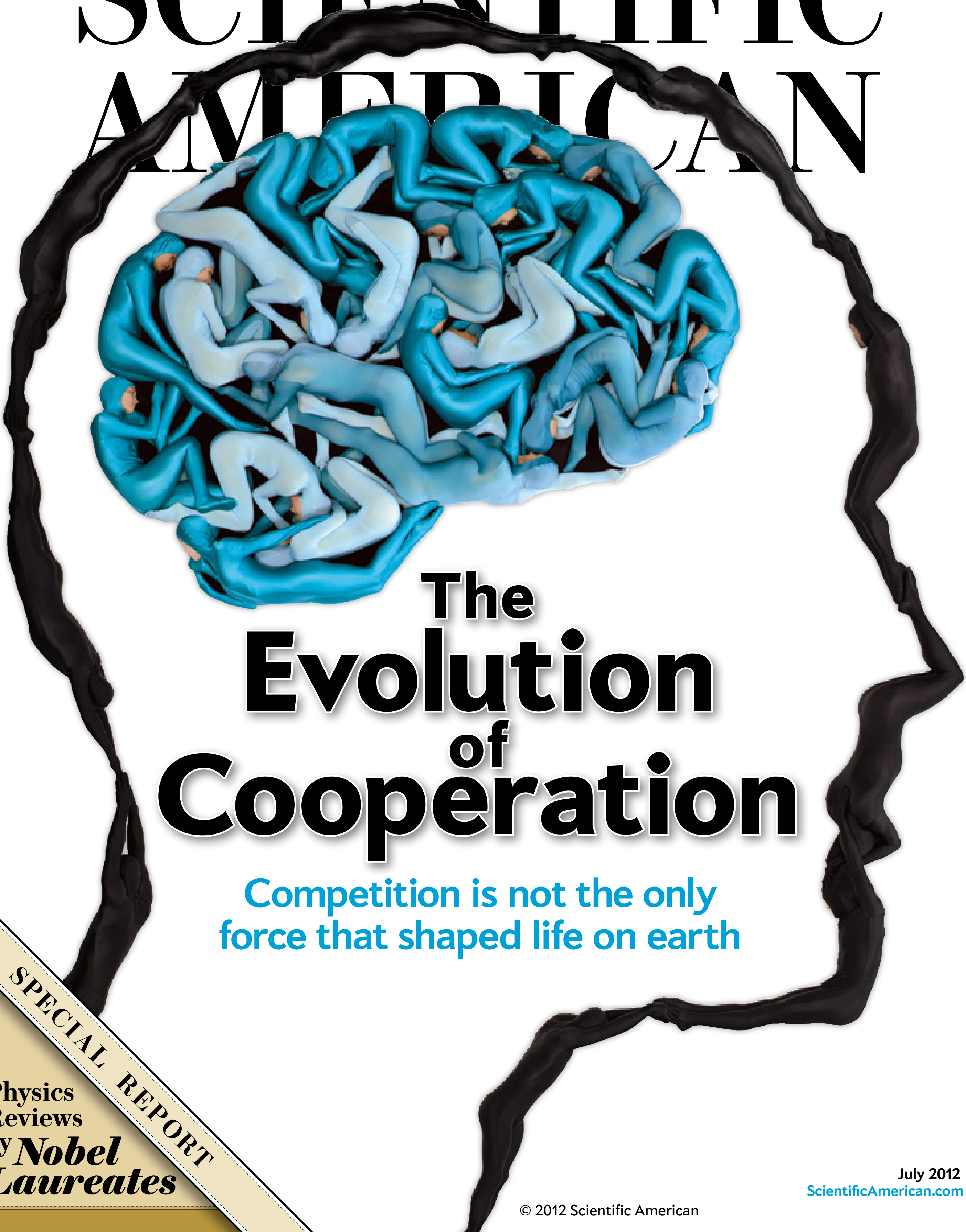


# The Evolution of Cooperation

**Competition is not the only force that shaped life on earth**

**SPECIAL REPORT**

**Physics Reviews by *Nobel Laureates***

July 2012
ScientificAmerican.com

EVOLUTION

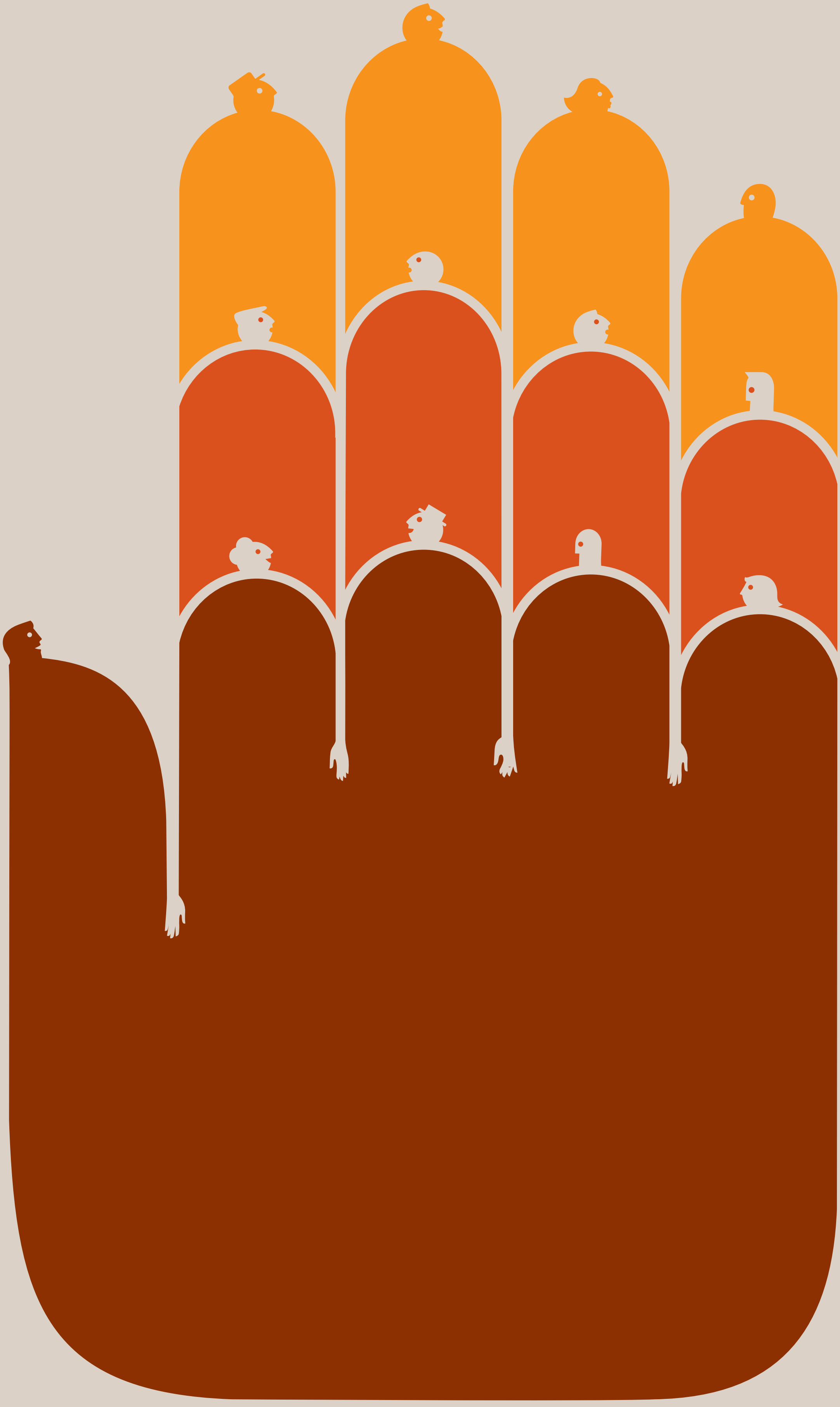
# WHY WE HELP

## Far from being a nagging exception to the rule of evolution, cooperation has been one of its primary architects

*By Martin A. Nowak*



*Illustration by Noma Bar*



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LAST APRIL, AS REACTORS AT JAPAN'S FUKUSHIMA DAIICHI NUCLEAR POWER PLANT WERE MELTING down following a lethal earthquake and tsunami, a maintenance worker in his 20s was among those who volunteered to reenter the plant to try to help bring things back under control. He knew the air was poisoned and expected the choice would keep him from ever marrying or having children for fear of burdening them with health consequences. Yet he still walked back through Fukushima's gates into the plant's radiation-infused air and got to work—for no more compensation than his usual modest wages. "There are only some of us who can do this job," the worker, who wished to remain anonymous, told the *Independent* last July. "I'm single and young, and I feel it's my duty to help settle this problem."

Although they may not always play out on such an epic scale, examples of selfless behavior abound in nature. Cells within an organism coordinate to keep their division in check and avoid causing cancer, worker ants in many species sacrifice their own fecundity to serve their queen and colony, female lions within a pride will suckle one another's young. And humans help other humans to do everything from obtaining food to finding mates to defending territory. Even if the helpers may not necessarily be putting their lives on the line, they are risking lowering their own reproductive success for the benefit of another individual.

For decades biologists have fretted over cooperation, scrambling to make sense of it in light of the dominant view of evolution as "red in tooth and claw," as Alfred, Lord Tennyson so vividly described it. Charles Darwin, in making his case for evolution by natural selection—wherein individuals with desirable traits reproduce more often than their peers and thus contribute more to the next generation—called this competition the "struggle for life most severe." Taken to its logical extreme, the argument quickly leads to the conclusion that one should never ever help a rival and that an individual might in fact do well to lie and cheat to get ahead. Winning the game of life—by hook or by crook—is all that matters.

Why, then, is selfless behavior such a pervasive phenomenon? Over the past two decades I have been using the tools of game theory to study this apparent paradox. My work indicates that instead of opposing competition, cooperation has operated alongside it from the get-go to shape the evolution of life on earth, from the first cells to *Homo sapiens*. Life is therefore not just a struggle for survival—it is also, one might say, a snuggle for survival. And in no case has the evolutionary influence of cooperation been more profoundly felt than in humans. My findings hint at why this should be the case and underscore that just as helping one another was the key to our success in the past, so, too, is it poised to be vital to our future.

## FROM ADVERSARY TO ALLY

I FIRST BECAME INTERESTED in cooperation back in 1987, as a graduate student studying mathematics and biology at the University of Vienna. While on a retreat with some fellow students and professors in the Alps, I learned about a game theory paradox called the Prisoner's Dilemma that elegantly illustrates why cooperation has so flummoxed evolutionary biologists. The dilemma goes like this: Imagine that two people have been arrested and are facing jail sentences for having conspired to commit a crime. The prosecutor questions each one privately and lays out the terms of a deal. If one person rats on the other

### IN BRIEF

**People tend to think** of evolution as a strictly dog-eat-dog struggle for survival. In fact, cooperation has been a driving force in evolution.

**There are five mechanisms** by which cooperation may arise in organisms ranging from bacteria to human beings.

**Humans are especially helpful** because of the mechanism of indirect reciprocity, which is based on reputation and leads us to help those who help others.

and the other remains silent, the incriminator gets just one year of jail time, whereas the silent person gets slammed with a four-year sentence. If both parties cooperate and do not rat on each other, both get reduced sentences of two years. But if both individuals incriminate each other, they both receive three-year sentences.

Because each convict is consulted separately, neither knows whether his or her partner will defect or cooperate. Plotting the possible outcomes on a payoff matrix [*see box below*], one can see that from an individual's standpoint, the best bet is to defect and incriminate one's partner. Yet because both parties will follow that same line of reasoning and choose defection, both will receive the third-best outcome (three-year sentences) instead of the two-year sentences they could get by cooperating with each other.

The Prisoner's Dilemma seduced me immediately with its power to probe the relation between conflict and cooperation. Eventually my Ph.D. adviser, Karl Sigmund, and I developed techniques to run computer simulations of the dilemma using large communities rather than limiting ourselves to two prisoners. Taking these approaches, we could watch as the strategies of the individuals in these communities evolved from defection to cooperation and back to defection through cycles of growth and decline. Through the simulations, we identified a mechanism that could overcome natural selection's predilection for selfish behavior, leading would-be defectors to instead lend helping hands.

We started with a random distribution of defectors and cooperators, and after each round of the game the winners would go on to produce offspring who would participate in the next round. The offspring mostly followed their parents' strategy, although random mutations could shift their strategy. As the simulation ran, we found that within just a few generations all the individuals in the population were defecting in every round of the game. Then, after some time, a new strategy suddenly emerged: players would start by cooperating and then mirror their opponents' moves, tit for tat. The change quickly led to communities dominated by cooperators.

This mechanism for the evolution of cooperation among individuals who encounter one another repeatedly is known as direct reciprocity. Vampire bats offer a striking example. If a bat misses a chance to feed directly on prey one day, it will beg from its sated peers back at the roost. If it is lucky, one of its roost mates will share its blood meal by regurgitating it into the hungry bat's mouth. The vampires live in stable groups and return to the roost every day after hunting, so group members routinely encounter one another. Studies have shown that the bats remember which bats have helped them in times of need, and when the day comes that the generous bat finds itself in need of food, the bat it helped earlier is likely to return the favor.

What made our early computer simulations even more interesting was the revelation that there are different kinds of direct reciprocity. Within 20 generations the initial tit-for-tat strategy had given way to a more generous strategy in which players might still cooperate even if their rival defected. We had, in essence, witnessed the evolution of forgiveness—a direct-reciprocity strategy that allows players to overlook the occasional mistake.

In addition to direct reciprocity, I later identified four more mechanisms for the evolution of cooperation. In the several thousand papers scientists have published on how cooperators could prevail in evolution, all the scenarios they describe fall into one or more of these five categories.

A second means by which cooperation may find a foothold in a population is if cooperators and defectors are not uniformly distributed in a population—a mechanism termed spatial selection. Neighbors (or friends in a social network) tend to help one another, so in a population with patches of cooperators, these helpful individuals can form clusters that can then grow and thus prevail in competition with defectors. Spatial selection also operates among simpler organisms. Among yeast cells, cooperators make an enzyme used to digest sugar. They do this at a cost to themselves. Defector yeast, meanwhile, mooch off the cooperators' enzymes instead of making their own. Studies conducted by Jeff Gore of the Massachusetts Institute of Technology and, independently, by Andrew Murray of Harvard University have found that among yeast grown in well-mixed populations, the defectors prevailed. In populations with clumps of cooperators and defectors, in contrast, the cooperators won out.

Perhaps one of the most immediately intuitive mechanisms for the evolution of selflessness concerns cooperation among genetically related individuals, or kin selection. In this situation, individuals make sacrifices for their relatives because those relatives share their genes. Thus, although one may be reducing one's own direct reproductive fitness by assisting a relative in need, one is still fostering the spread of those genes the helper shares with recipients. As 20th-century biologist J.B.S. Haldane, who first men-

BASICS

## Natural Defection

**A game theory paradox** called the Prisoner's Dilemma illustrates why the existence of cooperation in nature is unexpected. Two people face jail sentences for conspiring to commit a crime. Their sentences depend on whether they elect to cooperate and remain silent or defect and confess to the crime [*see payoff table below*]. Because neither knows what the other will do, the rational choice—the one that always offers the better payoff—is to defect.

| INDIVIDUAL 1 \ INDIVIDUAL 2 | COOPERATE (remain silent) | DEFECT (confess) |
|---|---|---|
| COOPERATE (remain silent) | 2 years in jail<br>2 years in jail | 4 years in jail<br>1 year in jail |
| DEFECT (confess) | 1 year in jail<br>4 years in jail | 3 years in jail<br>3 years in jail |

tioned the idea of kin selection, put it: "I will jump into the river to save two brothers or eight cousins," referring to the fact that our siblings share 50 percent of our DNA, whereas our first cousins share 12.5 percent. (It turns out that calculating the fitness effects of kin selection is a rather complicated task that has misled many researchers. My colleagues and I are now engaged in an intense debate about the underlying mathematics of kin selection theory.)

The fourth mechanism that fosters the emergence of cooperation is indirect reciprocity, which is quite distinct from the direct variety that Sigmund and I studied initially. In indirect reciprocity, one individual decides to aid another based on the needy individual's reputation. Those who have a reputation for assisting others who fall on hard times might even find themselves on the receiving end of goodwill from strangers when their own luck takes a turn for the worse. Thus, instead of the "I'll scratch your back if you scratch my mine" mentality, the cooperator in this situation might be thinking, "I'll scratch your back, and someone will scratch mine." Among Japanese macaques, for example, low-ranking monkeys that groom high-ranking ones (which have good reputations) may better their own reputations—and hence receive more grooming—simply by being seen with the top brass.

Last, individuals may perform selfless acts for the greater good, as opposed to abetting a single peer. This fifth means by which cooperation may take root is known as group selection. Recognition of this mechanism dates back to Darwin himself, who observed in his 1871 book *The Descent of Man* that "a tribe including many members who ... were always ready to aid one another, and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection." Biologists have since argued fiercely over this idea that natural selection can favor cooperation to improve the reproductive potential of the group. Mathematical modeling by researchers, including me, however, has helped show that selection can operate at multiple levels, from individual genes to groups of related individuals to entire species. Thus, the employees of a company compete with one another to move up the corporate ladder, but they also cooperate to ensure that the business succeeds in its competition with other companies.

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**HELPING OUT: Leaf-cutter ants work together to carry foliage back to their nest (*1*). Cells regulate their own division to avoid causing cancer (*2*). Lionesses cooperatively rear their young (*3*). Japanese macaques groom each other and thus burnish their reputations in their social group (*4*).**

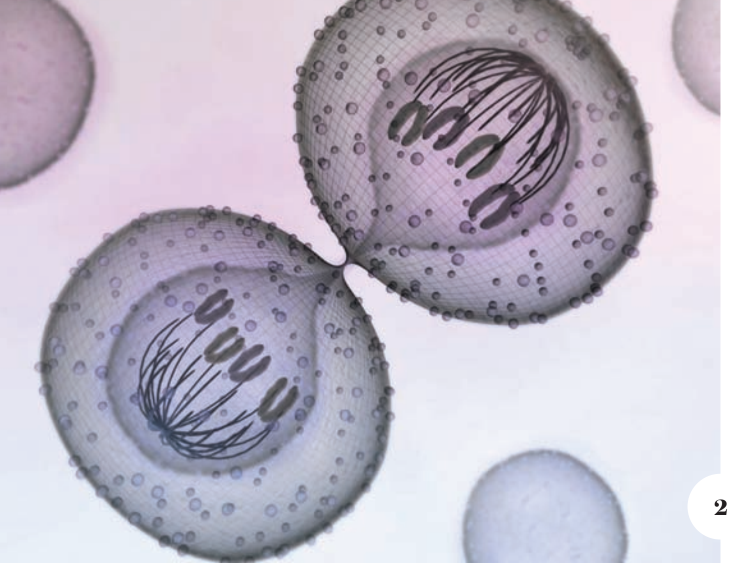
TIM FLACH *Getty Images (ants)*; REBECCA YALE *Getty Images (lions)*

## ONE FOR ALL

THE FIVE MECHANISMS governing the emergence of cooperation apply to all manner of organisms, from amoebas to zebras (and even, in some cases, to genes and other components of cells). This universality suggests that cooperation has been a driving force in the evolution of life on earth from the beginning. Moreover, there is one group in which the effects of cooperation have proved especially profound: humans. Millions of years of evolution transformed a slow, defenseless ape into the most influential creature on the planet, a species capable of inventing a mind-boggling array of technologies that have allowed our kind to plumb the depths of the ocean, explore outer space and broadcast our achievements to the world in an instant. We have accomplished these monumental feats by working together. Indeed, humans are the most cooperative species—supercooperators, if you will.

Given that the five mechanisms of cooperation occur throughout nature, the question is: What makes humans, in particular, the most helpful of all? As I see it, humans, more than any other creature, offer assistance based on indirect reciprocity, or reputation. Why? Because only humans have full-blown language—and, by extension, names for one another—which allows us to share information about everyone from our immediate family members to complete strangers on the other side of the globe. We are obsessed with who does what to whom and why—we have to be to best position ourselves in the social network around us. Studies have shown that people decide on everything from which charities to sponsor to which corporate start-ups to fund based in part on reputation. My Harvard colleague Rebecca Henderson, an expert on competitive strategy in the business world, notes that Toyota gained a competitive edge over other car manufacturers in the 1980s in part because of its reputation for treating suppliers fairly.

The interplay between language and indirect reciprocity leads to rapid cultural evolution, which is central to our adaptability as a species. As the human population expands and the climate



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GETTY IMAGES (*cells*); OSCAR TARNEBERG *Getty Images* (*monkeys*)

changes, we will need to harness that adaptability and figure out ways to work together to save the planet and its inhabitants. Given our current environmental track record, our odds of meeting that goal do not look great. Here, too, game theory offers insights. Certain cooperative dilemmas that involve more than two players are called public goods games. In this setting, everyone in the group benefits from my cooperation, but all else being equal, I increase my payoff by switching from cooperation to defection. Thus, although I want others to cooperate, my "smart" choice is to defect. The problem is that everyone in the group thinks the same way, and so what begins as cooperation ends in defection.

In the classic public goods scenario known as the Tragedy of the Commons, described in 1968 by the late ecologist Garrett Hardin, a group of livestock farmers who share grazing land allow their animals to overgraze on the communal turf, despite knowing that they are ultimately destroying everyone's resource, including their own. The analogies to real-world concerns about natural resources—from oil to clean drinking water—are obvious. If cooperators tend to defect when it comes to custodianship of communal assets, how can we ever hope to preserve the planet's ecological capital for future generations?

## ALL FOR ONE

THANKFULLY, not all hope is lost. A series of computerized experiments conducted by Manfred Milinski of the Max Planck Institute for Evolutionary Biology in Plön, Germany, and his colleagues have revealed several factors that motivate people to be good stewards of the commons in public goods games. The researchers gave each subject €40 and had them play a game via computer in which the object was to use the money to keep the earth's climate under control. Participants were told that for each round of the game, they had to donate some of their money into a common pool. If at the end of 10 rounds there was €120 or more in the common pool, then the climate was safe and the players would go home with the money they had left over. If they raised less than €120, then the climate would break down and everyone would lose all their money.

Although the players often failed to save the climate, missing the mark by a few euros, the investigators observed differences in their behavior from round to round that hint at what inspires generosity. The researchers found that players were more altruistic when they received authoritative information about climate research, indicating that people need to be convinced that there really is a problem to make sacrifices for the greater good. They also acted more generously when they were allowed to make their contributions publicly rather than anonymously—that is, when their reputation was on the line. Another study by researchers at Newcastle University in England underscored the importance of reputation by finding that people are more generous when they feel they are being watched.

These factors come into play every month when I receive my home's gas bill. The bill compares my household's consumption with both the average household gas consumption in my neighborhood outside Boston and that of the most efficient homes. Seeing how our usage stacks up against our neighbors' motivates my family to use less gas: every winter we try to lower the temperature in the house by one degree Fahrenheit.

Evolutionary simulations indicate that cooperation is intrinsically unstable; periods of cooperative prosperity inevitably give way to defective doom. And yet the altruistic spirit always seems to rebuild itself; our moral compasses somehow realign. Cycles of cooperation and defection are visible in the ups and downs of human history, the oscillations of political and financial systems. Where we humans are in this cycle right now is uncertain, but clearly we could be doing a better job of working together to solve the world's most pressing problems. Game theory suggests a way. Policy makers should take note of indirect reciprocity and the importance of information and reputation in keeping defectors in check. And they should exploit the capacity of these factors to make better cooperators of us all in the mother of all public goods games: the seven-billion-person mission to conserve the rapidly dwindling resources of planet Earth. SA

MORE TO EXPLORE


**Five Rules for the Evolution of Cooperation.** Martin A. Nowak in *Science,* Vol. 314, pages 1560–1563; December 8, 2006.

**Super Cooperators: Altruism, Evolution, and Why We Need Each Other to Succeed.** Martin A. Nowak, with Roger Highfield. Free Press, 2012.


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