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SUPER COOPERATORS



Evolution, Altruism and Human Behaviour
or Why We Need Each Other to Succeed

Martin Nowak
With Roger Highfield



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To Karl and Bob,
relentless cooperators

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The only thing that will redeem mankind is cooperation.

—BERTRAND RUSSELL

PREFACE

The Struggle

From the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows.

—Charles Darwin, *On the Origin of Species*

Biology has a dark side. Charles Darwin referred to this shadowy aspect of nature as the struggle for existence. He realized that competition is at the very heart of evolution. The fittest win this endless “struggle for life most severe” and all others perish. In consequence, every creature that crawls, swims, and flies today has ancestors that once successfully thrived and reproduced more often than their unfortunate competitors. As for the rest, they forfeited any chance to contribute to the next generation. They lost, and now they’re gone.

The struggle was born at least 4 billion years ago, with the first primitive cells. They were simple bacteria, each one little more than a tiny, organized collection of chemicals. If one of these chemical machines had an advantage over its peers, it would reproduce faster. Given better-than-average access to a limited food source, it would prosper and its rivals perish. This struggle continues, and across a spectrum of habitats. Today, Earth is the planet of the cell. Microorganisms now teem in almost every habitat, from poles to deserts to geysers, rocks, and the inky depths of the oceans. Even in our own bodies, bacterial cells outnumber our own. When adding up the total number of cells on Earth today—around 10

to the power of 30, or 1 followed by 30 zeroes—all you have to do is estimate the number of bacterial cells; the rest is pocket change.

The struggle can also be found in those organized collections of cells that we call animals. On the African savannah, a lion crouches in the long grass, muscles tensed and senses tightly focused on a nearby herd. Slowly and silently it stalks the antelope and then suddenly, in a burst of speed, sprints toward an animal, leaps, grabs its neck, and pierces the skin, blood vessels, and windpipe with its long, sharp teeth. It drags the prey to the ground and holds tight until the antelope breathes its last. When the lion finishes with its kill, a shroud of vultures wraps the bloody remains.

In *The Descent of Man*, Darwin remarked that modern man was born of the same struggle on the same continent. “Africa was formerly inhabited by extinct apes closely allied to the gorilla and chimpanzee; and as these two species are now man’s nearest allies, it is more probable that our early progenitors lived on the African continent than elsewhere.” Our ancestors spread out to colonize the Earth during the last 60,000 years or so, outcompeting archaic species such as *Homo erectus* and the big-brained Neanderthals (though if you are European, Asian, or New Guinean, you may have a trace of Neanderthal blood racing through your veins). The struggle for existence continues apace, from competition between supermarkets to drive down prices to cutthroat rivalry between Wall Street firms.

In the game of life we are all driven by the struggle to succeed. We all want to be winners. There is the honest way to achieve this objective. Run faster than the pack. Jump higher. See farther. Think harder. Do better. But, as ever, there is the dark side, the calculating logic of self-interest that dictates that one should never help a competitor. In fact, why not go further and make life harder for your rivals? Why not cheat and deceive them too? There’s the baker who palms you off with a stale loaf, rather than the one fresh out of the oven. There’s the waiter who asks for a tip when the restaurant has already added a service charge. There’s the pharmacist who recommends a well-known brand, when you can get a generic version of the same drug much more cheaply. Nice guys finish last, after all.

Humans are the selfish apes. We're the creatures who shun the needs of others. We're egocentrics, mercenaries, and narcissists. We look after number one. We are motivated by self-interest alone, down to every last bone in our bodies. Even our genes are said to be selfish. Yet competition does not tell the whole story of biology. Something profound is missing.

Creatures of every persuasion and level of complexity cooperate to live. Some of the earliest bacteria formed strings, where certain cells in each living filament die to nourish their neighbors with nitrogen. Some bacteria hunt in groups, much as a pride of lions hunt together to corner an antelope; ants form societies of millions of individuals that can solve complex problems, from farming to architecture to navigation; bees tirelessly harvest pollen for the good of the hive; mole rats generously allow their peers to dine on their droppings, providing a delicious second chance to digest fibrous roots; and meerkats risk their lives to guard a communal nest.

Human society fizzes with cooperation. Even the simplest things that we do involve more cooperation than you might think. Consider, for example, stopping at a coffee shop one morning to have a cappuccino and croissant for breakfast. To enjoy that simple pleasure could draw on the labors of a small army of people from at least half a dozen countries.

Farmers in Colombia grew the beans. Brazil provided the lush green fields of swaying sugar cane that was used to sweeten the beverage. The dash of creamy milk came from cows on a local farm and was heated with the help of electricity generated by a nuclear power station in a neighboring state. The barista, being a pretentious sort of fellow, made the coffee with mineral water from Fiji. As for that flaky croissant, the flour came from Canada, the butter from France, and the eggs from a local cooperative. The pastry was heated and browned in a Chinese-made oven. Many more people worked in supply lines that straddle the planet to bring these staples together.

Delivering that hot coffee and croissant also relied on a vast number of ideas, which have been widely disseminated by the remarkable medium of language. The result is a tightly woven network of coop-

eration stretching across the generations, as great ideas are generated, passed on, used, and embellished, from the first person to drink a beverage based on roasted seeds to the invention of the light bulb that illuminates the coffee shop, to the patenting of the first espresso machine.

The result, that simple everyday breakfast, is an astonishing cooperative feat that straddles both space and time. That little meal relies on concepts and ideas and inventions that have been passed down and around among vast numbers of people over hundreds, even thousands of years. The modern world is an extraordinary collective enterprise. The knowledge of how to select beans, make flour, build ovens, and froth milk is splintered in hundreds of heads. Today, the extent to which our brains collaborate matters as much as the size of our brains.

This is the bright side of biology. The range and the extent to which we work together make us supreme cooperators, the greatest in the known universe. In this respect, our close relatives don't even come close. Take four hundred chimpanzees and put them in economy class on a seven-hour flight. They would, in all likelihood, stumble off the plane at their destination with bitten ears, missing fur, and bleeding limbs. Yet millions of us tolerate being crammed together this way so we can roam about the planet.

Our breathtaking ability to cooperate is one of the main reasons we have managed to survive in every ecosystem on Earth, from scorched, sun-baked deserts to the frozen wastes of Antarctica to the dark, crushing ocean depths. Our remarkable ability to join forces has enabled us to take the first steps in a grand venture to leave the confines of our atmosphere and voyage toward the moon and the stars beyond.

By *cooperation*, I mean more than simply working toward a common aim. I mean something more specific, that would-be competitors decide to aid each other instead. This does not seem to make sense when viewed from a traditional Darwinian perspective. By helping another, a competitor hurts its own fitness—its rate of reproduction—or simply blunts its competitive edge. Yet it is easy to think of examples: a friend drives you to the dentist though it makes her late for work; you donate fifty dollars to charity rather than spending it on yourself. The cells in your body, rather than reproduce willy nilly to selfishly expand

their own numbers, respect the greater needs of the body and multiply in an orderly fashion to create the kidney, the liver, the heart, and other vital organs.

Many everyday situations can be viewed as choices about whether or not to cooperate. Let's say you want to open a savings account with a British bank (as we discovered in *Mary Poppins*, which appeared long before the credit crunch, "a British bank is run with precision"). Imagine that you are standing at the counter as a smiling clerk patiently explains the various options on offer. Banks like to confuse their customers by offering a large number of accounts that differ in terms of fees, interest rates, access, and conditions. If you ask for the best interest rate, the clerk can interpret this apparently simple question in two ways. From his point of view, the best interest rate is the most meager and restrictive, the one that earns the bank the maximum profit. From the customer's point of view, the best rate is the one that earns the most money. If the clerk offers the former, that is an example of defection. But if he recommends an account that gives you, and not the bank, the maximum return, that is an example of cooperation.

Once cooperation is expressed in this way, it seems amazing. Why weaken your own fitness to increase the fitness of a competitor? Why bother to look after anyone besides number one? Cooperation goes against the grain of self-interest. Cooperation is irrational. From the perspective of Darwin's formulation for the struggle for existence, it makes no sense to aid a potential rival, yet there is evidence that this occurs among even the lowliest creatures. When one bacterium goes to the trouble of making an enzyme to digest its food, it is helping to feed neighboring cells too—rivals in the struggle to survive.

This looks like a fatal anomaly in the great scheme of life. Natural selection should lead animals to behave in ways that increase their own chances of survival and reproduction, not improve the fortunes of others. In the never-ending scrabble for food, territory, and mates in evolution, why would one individual ever bother to go out of its way to help another?

BEYOND COOPERATION

We are all dependent on one another, every soul of us on earth.

—George Bernard Shaw, *Pygmalion*

Scientists from a wide range of disciplines have attempted for more than a century to explain how cooperation, altruism, and self-sacrifice arose in our dog-eat-dog world. Darwin himself was troubled by selfless behavior. Yet in his great works, the problem of cooperation was a sideshow, a detail that had to be explained away. That attitude prevails among many biologists even today.

In stark contrast, I believe that our ability to cooperate goes hand in hand with succeeding in the struggle to survive, as surmised more than a century ago by Peter Kropotkin (1842–1921), the Russian prince and anarchist communist who believed that a society freed from the shackles of government would thrive on communal enterprise. In *Mutual Aid* (1902), Kropotkin wrote: “Besides *the law of Mutual Struggle* there is in Nature *the law of Mutual Aid*, which, for the success of the struggle for life, and especially for the progressive evolution of the species, is far more important than the law of mutual contest. This suggestion . . . was, in reality, nothing but a further development of the ideas expressed by Darwin himself.”

I have spent more than two decades cooperating with many great minds to solve the mystery of how natural selection can lead to mutual aid, so that competition turns into cooperation. I have introduced some new ideas to this well-explored field and refined this mix with my own specialty, which relies on blending mathematics and biology. My studies show that cooperation is entirely compatible with the hard-boiled arithmetic of survival in an unremittingly cold-eyed and competitive environment. Based on mathematical insights, I have created idealized communities in a computer and charted the conditions in which cooperation can take hold and bloom. My confidence in what I have found has been bolstered by research on a wide range of species, from bugs to people. In light of all this work, I have now pinned down

five basic mechanisms of cooperation. The way that we human beings collaborate is as clearly described by mathematics as the descent of the apple that once fell in Newton's garden.

These mechanisms tell us much about the way the world works. They reveal, for example, that your big brain evolved to cope with gossip, not the other way around; that your guts have cone-like glands to fend off that potentially deadly breakdown of cellular cooperation that we know as cancer; that you are more generous if you sense that you are being watched (even if you are not); that the fewer friends you have, the more strongly your fate is bound to theirs; genes may not be that selfish, after all; if you are a cooperator, you will find yourself surrounded by other cooperators so that what you reap is what you sow; no matter what we do, empires will always decline and fall; and to succeed in life, you need to work together—pursuing the snuggle for existence, if you like—just as much as you strive to win the struggle for existence. In this way, the quest to understand cooperation has enabled us to capture the essence of all kinds of living, breathing, red-blooded evolving processes.

Cooperation—not competition—underpins innovation. To spur creativity, and to encourage people to come up with original ideas, you need to use the lure of the carrot, not fear of the stick. Cooperation is the architect of creativity throughout evolution, from cells to multicellular creatures to anthills to villages to cities. Without cooperation there can be neither construction nor complexity in evolution.

I can derive everyday insights—as well as many unexpected ones—from mathematical and evolutionary models of cooperation. While the idea that the trajectory of spears, cannonballs, and planets can be traced out by equations is familiar, I find it extraordinary that we can also use mathematics to map out the trajectory of evolution. And, of course, it is one thing to know how to foster cooperation but it is quite another to explain why an action helps us get along with each other and to what extent. The mathematical exploration of these mechanisms enables us to do this with profound understanding and with precision too. This is proof, as if we need it, that math is universal.

In the following chapters I will explain the origins of each mecha-

nism of cooperation and interweave this train of thought with my own intellectual journey, one that began in Vienna and then continued to Oxford, Princeton, and now Harvard. En route, I have had the honor to cooperate with many brilliant scientists and mathematicians. Two of them proved particularly inspirational: Karl Sigmund and Robert May, for reasons that will become clear. I have also had to enlist the help of computer programs, students willing to play games, and various funding bodies, from foundations to philanthropists. It is a lovely and intoxicating thought that a high degree of cooperation is required to understand cooperation. And to further underline this powerful idea, this book is also a feat of cooperation between Roger Highfield and myself.

The implications of this new understanding of cooperation are profound. Previously, there were only two basic principles of evolution—mutation and selection—where the former generates genetic diversity and the latter picks the individuals that are best suited to a given environment. For us to understand the creative aspects of evolution, we must now accept that cooperation is the third principle. For selection you need mutation and, in the same way, for cooperation you need both selection and mutation. From cooperation can emerge the constructive side of evolution, from genes to organisms to language and complex social behaviors. Cooperation is the master architect of evolution.

My work has also shown that cooperation always waxes and wanes. The degree to which individuals are able to cooperate rises and falls, like the great heartbeat of nature. That is why, even though we are extraordinary cooperators, human society has been—and always will be—riven with conflict. Global human cooperation now teeters on a threshold. The accelerating wealth and industry of Earth's increasing inhabitants—itself a triumph of cooperation—is exhausting the ability of our home planet to support us all. There's rising pressure on each of us to compete for the planet's dwindling resources.

Many problems that challenge us today can be traced back to a profound tension between what is good and desirable for society as a whole and what is good and desirable for an individual. That conflict can be found in global problems such as climate change, pollution, resource depletion, poverty, hunger, and overpopulation. The biggest issues of

all—saving the planet and maximizing the collective lifetime of the species *Homo sapiens*—cannot be solved by technology alone. They require novel ways for us to work in harmony. If we are to continue to thrive, we have but one option. We now have to manage the planet as a whole. If we are to win the struggle for existence, and avoid a precipitous fall, there's no choice but to harness this extraordinary creative force. We now have to refine and to extend our ability to cooperate. We must become familiar with the science of cooperation. Now, more than ever, the world needs SuperCooperators.

SuperCooperators

The Prisoner's Dilemma

I believe that mathematical reality lies outside us, that our function is to discover or observe it, and that the theorems which we prove, and which we describe grandiloquently as our "creations," are simply the notes of our observations.

—Godfrey H. Hardy,
A Mathematician's Apology

At first, I did not appreciate the point of mathematics. I played with numbers during lessons in high school. I enjoyed solving problems. Arithmetic lessons were fun. Math was, all in all, quite interesting. But it was unclear to me what it was for. Perhaps it was a kind of mental gymnastics that had been devised—along with Latin—with the express purpose of making the children's lives just that little bit harder.

At university I changed my mind. I had an epiphany, a spine-tingling moment when I realized that the precisely defined terms, equations, and symbols of mathematics are fundamental. I came to realize that mathematics holds the key to formulating the laws that govern the cosmos, from the grandest filaments, voids, and structures that stretch across the heavens to the peculiar behavior of the tiniest and most ubiquitous grains of matter. More important, it could say something profound about everyday life.

Mathematics is characterized by order and internal consistency as well as by numbers, shapes, and abstract relationships. Although you

might feel that these concepts only inhabit the human mind, some of them are so real and absolute that they mean precisely the same thing to us as they would to a clever many-tentacled alien floating on an icy exoplanet on the far side of the universe. In fact, I would go even further than saying the ideas of mathematics are objective and concrete. The cosmos itself is mathematical: everything and anything that happens in it is the consequence of universal logic acting on universal rules.

Beyond the dimensions of space and time, mathematics inhabits a nonmaterial realm, one that is eternal, unchanging, and ever true. The empire of mathematics extends far beyond what we can see around us, beyond what we are able to perceive, and far beyond what we can imagine. There's an unseen, perfect, and transcendental universe of possibilities out there. Even in the wake of cosmic degradation, collapse, and ruin, the inhabitants of other universes will still be there to gaze on the unending beauty of mathematics, the very syntax of nature. The truth really is out there and it can be expressed in this extraordinary language.

Some would go even further than this. They regard the mathematics that describes our cosmos as a manifestation of the thoughts of a creator. Albert Einstein once remarked: "I believe in Spinoza's God, Who reveals Himself in the lawful harmony of the world." For the seventeenth-century Dutch philosopher who had so impressed Einstein, God and nature were as one (*deus sive natura*), and the practice of doing math was tantamount to a quest for the divine. Whenever I think about this connection, I am always reminded of the last, thrilling lines of Goethe's *Faust*:

*All that is changeable / Is but refraction
The unattainable / Here becomes action
Human discernment / Here is passed by
Woman Eternal / Draws us on high.*

My epiphany at university was that somewhere in this infinite, unimaginable ocean of truth there is a corporeal mathematics, a splash of math that you can feel, smell, and touch. This is the mathematics of the tangible, from the equations that govern the pretty patterns formed

by the red petals of a rose to the laws that rule the sweeping movements of Mars, Venus, and other planets in the heavens. And of all those remarkable insights that it offers, I discovered that mathematics can capture the quintessence of everyday life, the ever-present tension that exists between conflict and cooperation.

This tension is palpable. It tugs at the emotions of participants in an internet purchase, where there is a temptation for buyers not to pay for goods and sellers not to send them. The tension surfaces when weighing whether to contribute to the public good, whether through taxes or licenses, or whether to clear up after a picnic on the beach or sort out items of everyday rubbish that can be recycled. One can feel this strain between the personal and public in transport systems too, which trust that enough people will pay for a ticket to ensure that they can operate sufficient buses, trains, and trams.

This tension between the selfish and selfless can be captured by the Prisoner's Dilemma. Although it is a simple mathematical idea, it turns out to be an enchanted trap that has ensnared some of the brightest minds for decades. I myself became so infatuated with playing this extraordinary mathematical game that I changed my course at university and, at a stroke, changed the course of my life.

My work on the Dilemma gave me the first critical insights into why our traditional understanding of evolution is incomplete. It revealed why, in addition to the fundamental forces of mutation and selection, we need a third evolutionary force, that of cooperation. It provided a way to hone my understanding of the mechanisms that make someone go out of her way to help another. The Dilemma has played a key role in cementing the foundations for an understanding of the future of human cooperation.

PRISONER OF THE DILEMMA

As a schoolboy, I wanted to be a doctor. Then I read *The Eighth Day of Creation: Makers of the Revolution in Biology* (1979) by *Time* magazine journalist Horace Judson. This wonderful chronicle of the birth of

molecular biology put an end to my medical ambitions. I made up my mind there and then to study the very chemical basis of life, the molecules that build our cells, power them, organize them, and run them. I would pursue biochemistry at the University of Vienna. Not everyone was enthusiastic about my decision. My parents were troubled by my move away from a career as a medical doctor, a guaranteed way to become a respected pillar of society. Their only child was now going to study a subject that, as far as they were concerned, had mostly to do with yeast, which was central to fermenting beer and wine.

In October 1983 I walked into my first lecture and encountered “girls”—many more than I had ever seen before and conveniently all in one place. Thanks to the female-dominated intake of a pharmacology course, girls made up nearly two-thirds of the six hundred people now crammed around me in the lecture hall. Having been educated at an all-boys school, I thought I was in paradise. Among the handful of chemistry students was Ursula, who like me was struggling to keep pace with the university’s intensive introduction to mathematics. Six years later, we were married. I still wonder whether I was selected for my ability to solve mathematical problems.

As I became besotted at the University of Vienna, the emphasis of my studies gradually changed. I adored physics in the first year, then physical chemistry in the second year. In the third year, I had the great good fortune to be lectured on theoretical chemistry by the formidable Peter Schuster, who helped to establish the Viennese school of mathematical biology and, later, would become the president of the illustrious Austrian Academy of Sciences and deliver a lecture to Pope Benedict XVI on the science of evolution. I knew immediately that I wanted to work with Peter. In the fourth year, I began to study with him for a diploma thesis. An ebullient character, he was supremely knowledgeable and his interests extended well beyond science. Once, when we went mountain climbing together, he declared: “There’s no such thing as bad weather, only insufficient equipment.”

The moment when I realized that I was well and truly smitten by mathematics came a year later, while on an Alpine jaunt with Peter. It was March 1988, during my early days as a doctoral student, and I

was on a retreat. With me was a fresh crop of talent, including Walter Fontana, who today is a prominent biologist at Harvard Medical School. Our group was staying in a primitive wooden hut in the Austrian mountains to enjoy lots of fresh air, work, and play. We skied, we listened to lectures, we drank beer and wine, and we contemplated the mysteries of life. Best of all, we discussed new problems and theory, whether in the cozy warmth of the little hut or outside, in the chilled Alpine air. As the ideas tumbled out at high altitude, our breath condensed into vapor. I can't remember if they were mathematical dreams or just clouds of hot air. But the experience was exhilarating.

The mix of bright-eyed students was enriched with impressive academics. Among them was Karl Sigmund, a mathematician from the University of Vienna. With his wild shock of hair, bottle-brush mustache, and spectacles, Karl looked aloof and unapproachable. He was cool, more like a student than a professor. Karl would deliver all his lectures from memory with a hypnotic, almost incantatory rhythm. On the last day of that heady Alpine meeting, he gave a talk on a fascinating problem that he himself had only just read about in a newspaper article.

The article described work in a field known as game theory. Despite some earlier glimmerings, most historians give the credit for developing and popularizing this field to the great Hungarian-born mathematician John von Neumann, who published his first paper on the subject in 1928. Von Neumann went on to hone his ideas and apply them to economics with the help of Oskar Morgenstern, an Austrian economist who had fled Nazi persecution to work in the United States. Von Neumann would use his methods to model the cold war interaction between the United States and the Soviet Union. Others seized on this approach too, notably the RAND Corporation, for which von Neumann had been a consultant. The original "think tank," the RAND (*Research and Development*) Corporation was founded as Project RAND in December 1945 by the U.S. Army Air Force and by defense contractors to think the unthinkable.

In his talk, Karl described the latest work that had been done on the Prisoner's Dilemma, an intriguing game that was first devised in 1950

by Merrill Flood and Melvin Dresher, who worked at RAND in Santa Monica, California. Karl was excited about the Dilemma because, as its inventors had come to realize, it is a powerful mathematical cartoon of a struggle that is central to life, one between conflict and cooperation, between the individual and the collective good.

The Dilemma is so named because, in its classic form, it considers the following scenario. Imagine that you and your accomplice are both held prisoner, having been captured by the police and charged with a serious crime. The prosecutor interrogates you separately and offers each of you a deal. This offer lies at the heart of the Dilemma and goes as follows: If one of you, the defector, incriminates the other, while the partner remains silent, then the defector will be convicted of a lesser crime and his sentence cut to one year for providing enough information to jail his partner. Meanwhile, his silent confederate will be convicted of a more serious crime and burdened with a four-year sentence.

If you both remain silent, and thus cooperate with each other, there will be insufficient evidence to convict either of you of the more serious crime, and you will each receive a sentence of two years for a lesser offense. If, on the other hand, you both defect by incriminating each other, you will both be convicted of the more serious crime, but given reduced sentences of three years for at least being willing to provide information.

In the literature, you will find endless variants of the Dilemma in terms of the circumstances, the punishments and temptations, the details of imprisonment, and so on. Whatever the formulation, there is a simple central idea that can be represented by a table of options, known as a payoff matrix. This can sum up all four possible outcomes of the game, written down as two entries on each of the two lines of the matrix. This can sum up the basic tensions of everyday life too.

Let's begin with the top line of the payoff matrix: You both cooperate (that means a sentence of two years each and I will write this as -2 to underline the years of normal life that you lose). You cooperate and your partner defects (-4 years for you, -1 for him). On the second line come the other possible variants: You defect, and your partner cooperates (-1 for you, -4 for him). You both defect (-3 years each). From

a purely selfish point of view, the best outcome for you is the third, then the first, then the fourth, and finally the second option. For your confederate the second is the best option, followed by the first, fourth, and third.

		opponent	
		cooperate	defect
player	cooperate	-2,-2	-4,-1
	defect	-1,-4	-3,-3

What should you do, if you cast yourself as a rational, selfish individual who looks after number one? Your reasoning should go like this. Your partner will either defect or cooperate. If he defects, you should too, to avoid the worst possible outcome for you. If he cooperates, then you should defect, as you will get the smallest possible sentence, your preferred outcome. Thus, no matter what your partner does, it is best for you to defect.

Defecting is called a dominant strategy in a game with this payoff matrix. By this, the theorists mean that the strategy is always the best one to adopt, regardless of what strategy is used by the other player. This is why: If you both cooperate, you get two years in prison but you only get one year in prison if you defect. If the other person defects and you hold your tongue, then you get four years in prison, but you only get three years if you both defect. Thus no matter what the other person does, it is better for you to defect.

But there's a problem with this chain of reasoning. Your confederate is no chump and is chewing over the Dilemma in precisely the same way as you, reaching exactly the same conclusion. As a consequence, you both defect. That means spending three years in jail. The Dilemma

comes because if you both follow the best, most rational dominant strategy it leaves both of you worse off than if you had both remained silent! You both end up with the third best outcome, whereas if you had both cooperated you would have both enjoyed the second best outcome.

That, in a bitter nutshell, is the Prisoner's Dilemma. If only you had trusted each other, by cooperating, you would both be better off than if you had both acted selfishly. With the help of the Dilemma, we can now clearly appreciate what it means to cooperate: one individual pays a cost so that another receives a benefit. In this case, if both cooperate, they forfeit the best outcome—a one-year sentence—and both get second best. This is still a better result than either of you can achieve if you both defect.

To create the Dilemma, it is important to arrange the relative size of each of the payoffs for cooperation and defection in the matrix in the correct way. The Dilemma is defined by the exact ranking of the payoff values, where R is the reward for mutual cooperation; S is the sucker's payoff for cooperating when your fellow player defects; T is the temptation to renege when your fellow player cooperates, and P is the punishment if both players defect. Let's spell this out. When the players both cooperate, the payoff (R) is greater than the punishment (P) if they both defect. But when one cooperates and one defects, the person who is tempted to renege gets the highest payoff (T) while the hapless cooperator ends up with the lowest of all, the sucker's payoff (S). Overall, we can create the Dilemma if T is greater than R which is greater than P which is greater than S. We can rank the payoffs in the basic game in other, different ways and still end up with cooperative dilemmas. But of all of them, the Prisoner's Dilemma is by far the hardest to solve. You can think of it as the ultimate dilemma of cooperation.

We all encounter the Dilemma in one form or another all the time in everyday life. Do I want to help a competitor in the office—for instance, offer to do his work during his holiday—when this person is competing with me for a promotion? When two rival firms set prices, should they both go for as much as they can, colluding in some way, or should one company try to undercut its competitor? Arms races

between superpowers, local rival nations, or even different species offer other examples of the Dilemma at work. Rival countries are better off when they cooperate to avoid an arms race. Yet the dominant strategy for each nation is to arm itself heavily. And so on and so forth.

INCARCERATION

On my first encounter with the Prisoner's Dilemma in that Alpine hut, I was transfixed. By that time, Karl had actually become my prisoner. He didn't have any transport and I offered him a ride back to Vienna. We discussed the Dilemma as we drove back the next day in the same VW that my father still uses today to putter around Austria. Even after I dropped Karl off, I kept him in my sights. Before long, I was doing a PhD with him at the Institute for Mathematics in Vienna. Students who had studied there before me include the great physicist Ludwig Boltzmann, the logician Kurt Gödel, and the father of genetics, Gregor Mendel.

As I pursued my doctorate, Karl and I would often meet in local coffeehouses, the genius loci of past glory. In these inspiring surroundings Gödel had announced his incompleteness theorem, Boltzmann had worked on entropy, and Wittgenstein had challenged the Vienna Circle, a group of intellectuals who would gather to discuss mathematics and philosophy. One day we sat in the Café Central, an imposing building with arched ceilings and marble columns, where Trotsky had planned the Russian revolution.

As we sipped thick, strong coffee and chatted about how to solve the Prisoner's Dilemma, Karl and I rediscovered the subtleties of a problem that had transfixed bright minds for generations. Little did we realize that in the decades that followed, we would devise new mathematics to explore the Dilemma. We would create communities of agents in a computer, study how they evolved, and conduct analyses to reveal the mechanisms able to solve the Dilemma. I would establish teams at Oxford, Princeton, and Harvard as well as collaborations with mathematicians, biologists, chemists, doctors, and economists around the

world to understand how these mechanisms worked and what their wider implications were.

Some scientists regard the Prisoner's Dilemma as a remarkably revealing metaphor of biological behavior, evolution, and life. Others regard it as far too simple to take into account all the subtle forces at play in real societies and in biology. I agree with both camps. The Dilemma is not itself the key to understanding life. For the Dilemma to tell us something useful about the biological world, we need to place it in the context of evolution.

Evolution can only take place in populations of reproducing individuals. In these populations, mistakes in reproduction lead to mutation. The resulting mutants might reproduce at different rates, as one mutant does better in one environment than another. And reproduction at different rates leads to selection—the faster-reproducing individuals are selected and thrive. In this context we can think about the payouts of the Prisoner's Dilemma in terms of what evolutionary scientists call “fitness” (think of it as the rate of reproduction). Now we can express what cooperation in the Prisoner's Dilemma means when placed in an evolutionary context: if I help you then I lower my fitness and increase your fitness.

Here's where the story gets fascinating. Now that we have put the Dilemma in an evolutionary form, we discover that there is a fundamental problem. Natural selection actually opposes cooperation in a basic Prisoner's Dilemma. At its heart, natural selection undermines our ability to work together. Why is this? Because in what mathematicians call a well-mixed population, where any two individuals meet equally often, cooperators always have a lower fitness than defectors—they're always less likely to survive. As they die off, natural selection will slowly increase the number of defectors until all the cooperators have been exterminated. This is striking because a population consisting entirely of cooperators has a higher average fitness than a population made entirely of defectors. Natural selection actually destroys what would be best for the entire population. Natural selection undermines the greater good.

To favor cooperation, natural selection needs help in the form of

mechanisms for the evolution of cooperation. We know such mechanisms exist because all around us is abundant evidence that it does pay to cooperate, from the towering termite mound to the stadium rock concert to the surge of commuters in and out of a city during a working day. In reality, evolution has used these various mechanisms to overcome the limitations of natural selection. Over the millennia they have shaped genetic evolution, in cells or microbes or animals. Nature smiles on cooperation.

These mechanisms of cooperation shape cultural evolution too, the patterns of change in how we behave, the things we wear, what we say, the art we produce, and so on. This aspect of evolution is more familiar: when we learn from each other and alter the way we act accordingly. It also takes place over much shorter timescales. Think about a population of humans in which people learn different strategies to cope with the world around them, whether religion or boat building or hammering a nail into a piece of wood. The impact of cooperation on culture is huge and, for me, the central reason why life is so beguiling and beautiful.

QUEST FOR THE EVOLUTION OF COOPERATION

Mathematics, rightly viewed, possesses not only truth, but supreme beauty—a beauty cold and austere, like that of sculpture, without appeal to any part of our weaker nature, without the gorgeous trappings of painting or music, yet sublimely pure, and capable of a stern perfection such as only the greatest art can show.

—Bertrand Russell, *Study of Mathematics*

My overall approach to reveal and understand the mechanisms of cooperation is easy to explain, even if my detailed workings might appear mysterious. I like to take informal ideas, instincts, even impressions of life and render them into a mathematical form. Mathematics allows me to chisel down into messy, complicated issues

and—with judgment and a little luck—reveal simplicity and grandeur beneath. At the heart of a successful mathematical model is a law of nature, an expression of truth that is capable of generating awe in the same way as Michelangelo's extraordinary sculptures, whose power to amaze comes from the truth they capture about physical beauty.

Legend has it that when asked how he had created David, his masterpiece, Michelangelo explained that he simply took away everything from the block of marble that was not David. A mathematician, when confronted by the awesome complexity of nature, also has to hack away at a wealth of observations and ideas until the very essence of the problem becomes clear, along with a mathematical idea of unparalleled beauty. Just as Michelangelo wanted his figures to break free from the stone that imprisoned them, so I want mathematical models to take on a life beyond my expectations, and work in circumstances other than those in which they were conceived.

Michelangelo sought inspiration from the human form, notably the male nude, and also from ideas such as Neoplatonism, a philosophy that regards the body as a vessel for a soul that longs to return to God. Over the few centuries that science has been trying to make sense of nature, the inspiration for mathematical representations of the world has changed. At first, the focus was more on understanding the physical world. Think of how Sir Isaac Newton used mathematics to make sense of motion, from the movement of the planets around the sun to the paths of arrows on their way to a target. To the amazement of many, Newton showed that bodies on Earth and in the majestic heavens were governed by one and the same force—gravity—even though planets are gripped in an orbit while objects like arrows and apples drop to the ground.

Today, the models of our cosmos are also concerned with biology and society. Among the eddies and ripples of that great river of ideas that has flowed down the generations to shape the ways in which scientists model these living aspects of the world are the powerful currents generated by Charles Darwin (1809–1882), who devised a unifying view of life's origins, a revolutionary insight that is still sending out shock waves today.

Darwin worked slowly and methodically, using his remarkable ability to make sense of painstaking studies he had conducted over decades, to conclude that all contemporary species have a common ancestry. He showed that the process of natural selection was the major mechanism of change in living things. Because reproduction is not a perfect form of replication, there is variation and with this diversity comes the potential to evolve. But equally, as the game of Chinese Whispers (also known as Gossip or Telephone) illustrates, without a way of selecting changes that are meaningful—a sentence that makes sense—the result is at best misleading and at worst a chaotic babble. Darwin came up with the idea that a trait will persist over many generations only if it confers an evolutionary advantage, and that powerful idea is now a basic tenet of science.

Darwin's message is simple and yet it helps to generate boundless complexity. There exists, within each and every creature, some information that can be passed from one generation to the next. Across a population, there is variation in this information. Because when there are limited resources and more individuals are born than can live or breed, there develops a struggle to stay alive and, just as important, to find a mate. In that struggle to survive, those individuals who bear certain traits (kinds of information) fail and are overtaken by others who are better suited to their environs. Such inherited differences in the ability to pass genes down the generations—natural selection—mean that advantageous forms become more common as the generations succeed. Only one thing counts: survival long enough to reproduce.

Darwin's theory to explain the diverse and ever-changing nature of life has been buttressed by an ever-increasing wealth of data accumulated by biologists. As time goes by, the action of selection in a given environment means that important differences can emerge during the course of evolution. As new variations accumulate, a lineage may become so different that it can no longer exchange genes with others that were once its kin. In this way, a new species is born. Intriguingly, although we now call this mechanism “evolution,” the word itself does not appear in *The Origin of Species*.

Darwin himself was convinced that selection was ruled by conflict.

He wrote endlessly about the “struggle for existence” all around us in nature. His theme took on a life of its own as it was taken up and embellished with gusto by many others. Nature is “red in tooth and claw,” as Tennyson famously put it when recalling the death of a friend. The catchy term “survival of the fittest” was coined in 1864 by the philosopher Herbert Spencer, a champion of the free market, and this signaled the introduction of Darwinian thinking into the political arena too.

Natural selection is after all about competition, dog-eat-dog and winner takes all. But Darwin was of course talking about the species that was the best adapted to an environment, not necessarily the strongest. Still, one newspaper concluded that Darwin’s work showed that “might is right & therefore that Napoleon is right & every cheating tradesman is also right.” Darwin’s thinking was increasingly abused to justify the likes of racism and genocide, to explain why white colonialists triumphed over “inferior” native races, to breed “superior” humans and so on. These abuses are, in a twisted and depressing way, a testament to the power of his ideas.

But, as I have already stressed, competition is far from being the whole story. We help each other. Sometimes we help strangers too. We do it on a global scale with charities such as Oxfam, which helps people in more than seventy countries, and the Bill & Melinda Gates Foundation, which supports work in more than one hundred nations. We do it elaborately, with expensive celebrity-laden fund-raising dinners in smart venues. We are also charitable to animals. Why? This may look like an evolutionary loose end. In fact it is absolutely central to the story of life.

When cast in an evolutionary form, the Prisoner’s Dilemma shows us that competition and hence conflict are always present, just as yin always comes with yang. Darwin and most of those who have followed in his giant footsteps have talked about mutation and selection. But we need a third ingredient, cooperation, to create complex entities, from cells to societies. I have accumulated a wide range of evidence to show that competition can sometimes lead to cooperation. By understanding this, we can explain how cells, and multicellular organisms such as

people, evolved, and why they act in the complicated ways that they do in societies. Cooperation is the architect of living complexity.

To appreciate this, we first need to put evolution itself on a firmer foundation. Concepts such as mutation, selection, and fitness only become precise when bolted down in a mathematical form. Darwin himself did not do this, a shortcoming that he was only too aware of. In his autobiography, he confessed his own inability to do sums: "I have deeply regretted that I did not proceed far enough at least to understand something of the great leading principles of mathematics; for men thus endowed seem to have an extra sense." He seemed aware that more rigor was required to flesh out the implications of his radical ideas about life. He regarded his mind "as a machine for grinding general laws out of large collections of facts." But even Darwin yearned for a more "top down" approach, so he could conjure up more precise laws to explain a great mass of data. He needed a mathematical model.

The modern understanding of the process of inheritance is now called "Mendelian," in honor of Gregor Mendel, who had settled for being a monk after failing his botany exams at the University of Vienna. By sorting out the results of crossing round and wrinkly peas, Mendel revealed that inheritance is "particulate" rather than "blending." Offspring inherit individual instructions (genes) from their parents such that round and wrinkly parents produce either round or wrinkly offspring and not something in between. What is often overlooked in his story is that Mendel was a good student of mathematics. The great geneticist and statistician Sir Ronald Fisher went so far as to call him "a mathematician with an interest in biology." Mendel uncovered these rules of inheritance because he was motivated by a clear mathematical hypothesis, even to the extent of ignoring ambiguous results that did not fit. Had Mendel conducted an open-minded statistical analysis of his results, he might not have been successful.

A simple equation to show the effect of passing genes down the generations was found in 1908 by G. H. Hardy, a cricket-loving Cambridge mathematician who celebrated the artistry of his subject in his timeless book *A Mathematician's Apology*. In an unusual reversal of the usual roles, the work of this pure mathematician was generalized by the

German doctor Wilhelm Weinberg to show the incidence of genes in a population. Robert May (now Lord May of Oxford) once went so far as to call the Hardy-Weinberg law biology's equivalent of Newton's first law. Thanks to Hardy and Weinberg we now had a mathematical law that applied across a spectrum of living things.

This attempt to model how inheritance works in nature was extended in seminal investigations conducted in the 1920s and 1930s by a remarkable trio. First, Sir Ronald Fisher, whose extraordinary ability to visualize problems came from having to be tutored in mathematics as a child without the aid of paper and pen, due to his poor eyesight. There was also the mighty figure of J. B. S. Haldane, an aristocrat and Marxist who once edited the *Daily Worker*. I will return to Haldane in chapter 5. The last of this remarkable trio was Sewall Wright, an American geneticist who was fond of philosophy, that relative of mathematicians (forgive me for cracking the old joke about the difference: while mathematicians need paper, pencil, and a wastepaper basket, philosophers need only paper and pencil).

Together, this threesome put the fundamental concepts of evolution, selection, and mutation in a mathematical framework for the first time: they blended Darwin's emphasis on individual animals competing to sire the next generation with Mendel's studies of how distinct genetic traits are passed down from parent to offspring, a combination now generally referred to as the synthetic view of evolution, the modern synthesis, or neo-Darwinian. With many others, I have also extended these ideas by looking at the Prisoner's Dilemma in evolving populations to come up with the basic mechanisms that explain how cooperation can thrive in a Darwinian dog-eat-dog world.

Over the years I have explored the Dilemma, using computer models, mathematics, and experiments to reveal how cooperation can evolve and how it is woven into the very fabric of the cosmos. In all there are five mechanisms that lead to cooperation. I will discuss each one of them in the next five chapters and then, in the remainder of the book, show how they offer novel insights into a diverse range of issues, stretching from straightforward feats of molecular cooperation to the many and intricate forms of human cooperation.

I will examine the processes that paved the way to the emergence of the first living things and the extraordinary feats of cooperation that led to multicellular organisms, along with how cellular cooperation can go awry and lead to cancer. I will outline a new theory to account for the tremendous amount of cooperation seen in the advanced social behavior of insects. I will move on to discuss language and how it evolved to be the glue that binds much of human cooperation; the “public goods” game, the biggest challenge to cooperation today; the role of punishment; and then networks, whether of friends or acquaintances, and the extraordinary insights into cooperation that come from studying them. Humans are SuperCooperators. We can draw on all the mechanisms of cooperation that I will discuss in the following pages, thanks in large part to our dazzling powers of language and communication. I also hope to explain why I have come to the conclusion that although human beings are the dominant cooperators on Earth, man has no alternative but to evolve further, with the help of the extraordinary degree of control that we now exert over the modern environment. This next step in our evolution is necessary because we face serious global issues, many of which boil down to a fundamental question of survival. We are now so powerful that we could destroy ourselves. We need to harness the creative power of cooperation in novel ways.