

KIN AND KIND

A fight about the genetics of altruism.

BY JONAH LEHRER

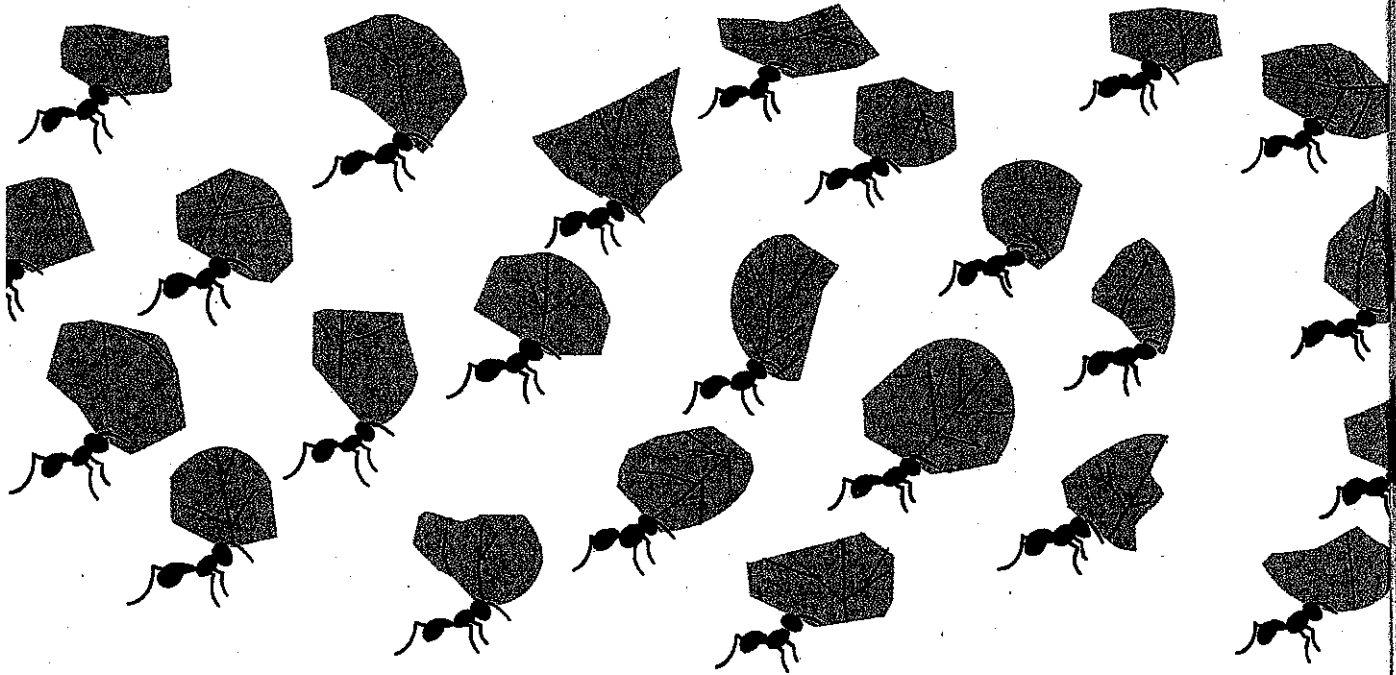
The vampire bat emerges from its cave at the darkest hour of night, after the moon has set. It flies low across the landscape, hunting by smell and sonar. Once the bat finds a victim—it can feed on most warm-blooded animals, from songbirds to cattle—it starts stalking its prey. The bat lands silently a few feet away, then runs on its wings toward the sound

the night, it will begin licking under the wings and on the lips of a chosen colony member. The animals then lock mouths, and the successful hunter starts vomiting warm blood. If such sharing did not take place, scientists estimate that more than eighty per cent of adult vampire bats would die of starvation every year.

Charles Darwin regarded the problem

everywhere, a stubborn anomaly of nature. Bats feed hungry brethren; honeybees commit suicide with a sting to defend the hive; birds raise offspring that aren't their own; humans leap onto subway tracks to save strangers. The ubiquity of such behavior suggests that kindness is not a losing life strategy.

For a century after Darwin, altruism remained a paradox. The first glimmers of a solution arrived in a Bloomsbury pub in the nineteen-fifties. According to legend, the biologist J. B. S. Haldane was several pints into the evening when he was asked how far he would go to save the life of another person. Haldane thought for a moment, and then started scribbling numbers on the back of a napkin. "I would



Darwin saw the existence of altruism as a challenge to his theory of natural selection, yet the biological success of ants is directly related to

of a pulsing vein. A pair of teeth sharper than a scalpel cut into the flesh. Blood leaks from the wound; the bat laps it up. Sometimes the bat consumes its weight in blood during the night.

Although the vampire bat has traditionally been seen as a ghoulish predator, it interests biologists for another reason: it is deeply altruistic. The bats live in expansive colonies, with hundreds or thousands sharing the same dark cave. Bats must feed constantly—they starve to death within sixty hours—and this has led to the evolution of an unusual way of sharing food. If a vampire bat fails to find a victim during

of altruism—the act of helping someone else, even if it comes at a steep personal cost—as a potentially fatal challenge to his theory of natural selection. After all, if life were such a cruel “struggle for existence,” then how could a selfless individual ever live long enough to reproduce? Why would natural selection favor a behavior that made us less likely to survive? In “The Descent of Man,” Darwin wrote, “He who was ready to sacrifice his life, as many a savage has been, rather than betray his comrades, would often leave no offspring to inherit his noble nature.” And yet, as Darwin knew, altruism is ev-

jump into a river to save two brothers, but not one,” Haldane said. “Or to save eight cousins but not seven.” His drunken answer summarized a powerful scientific idea. Because individuals share much of their genome with close relatives, a trait will also persist if it leads to the survival of their kin. According to Haldane’s moral arithmetic, making a sacrifice for a family member is just another way of promoting our own DNA.

Haldane never expanded his napkin calculations into a formal mathematical theory. That task fell to William Hamilton, a young graduate student at Univer-

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sity College London. He struggled for years on the project, often working late at night on a bench in Waterloo Station, where the commuting crowds eased his loneliness. In 1964, he submitted a pair of papers to the *Journal of Theoretical Biology*. The papers hinged on one simple equation: $rB > C$. Genes for altruism could evolve if the benefit (B) of an action exceeded the cost (C) to the individual once relatedness (r) was taken into account. The equation confirmed the truth of Haldane's joke: once kinship was part of the calculation, altruism could be easily explained in genetic terms. Hamilton referred to his model as "inclusive fitness theory," since it expanded the Darwinian definition of "fitness"—how many offspring an individual manages to have—to

Boston to Miami. "I had nothing else to do, so I caught up on all my back journals," Wilson told me recently, when I visited him at his office, at Harvard. "When I began reading Hamilton's paper, my first response was that the equation was way too short. I thought, There's no way it can be this easy. But then I reread the paper. And then I read it again. And that's when I got jealous." Wilson wanted to understand the altruism at work in ant colonies, and he became convinced that Hamilton had solved the problem. To further the cause of inclusive fitness, Wilson included the idea in a series of influential articles and books, introducing the startling logic of Hamilton's equation to biologists. "I really became an evangelist for the idea," Wilson says. "And this was not an easy idea to sell. Nobody wanted to believe that one equation could explain altruism. Eventually, though, people saw that we were right. I won that argument decisively."

By the late nineteen-seventies, Hamilton's work was featured prominently in textbooks; his original papers have become some of the most cited in evolutionary biology. As Wilson realized, the equation allowed naturalists to make sense of animal behavior using genetic models, giving the field a new sense of rigor. "Before Hamilton, there were different explanations for every species," Wilson says. "There was no overarching theory, nor was there any way to connect what we saw in the field to what we were learning about genes and cooperation in the lab. Hamilton helped solve both those problems." In fact, inclusive fitness theory solved those problems so well that it was soon applied to biological traits completely unrelated to altruism, such as homosexuality, tribal violence, and alarm calls. In an obituary published after Hamilton's death, in 2000, the Oxford biologist Richard Dawkins referred to Hamilton as "the most distinguished Darwinian since Darwin."

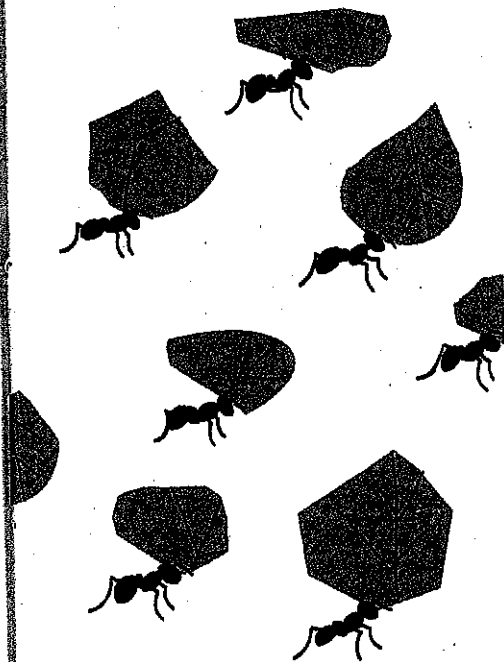
But now, in an abrupt intellectual shift, Wilson says that his embrace of Hamilton's equation was a serious scientific mistake. "I'm going to be blunt: the equation doesn't work," he says. "It's a phantom measure. It can't explain nearly as much as people think it can. Back when I first read Hamilton, inclusive fitness seemed to make sense of so many different mysteries. But now we know more. And I'm not

afraid to admit I was wrong." Wilson's apostasy, which he lays out in a forthcoming book, "The Social Conquest of the Earth," has set off a scientific furor. The vast majority of his academic colleagues are convinced that he was right the first time, and that his recantation has damaged the field. There have been denunciations in the press and signed group letters in prestigious journals; some have hinted that Wilson, who is eighty-two, should retire. The controversy is fuelled by a larger debate about the evolution of altruism. Can true altruism even exist? Is generosity a sustainable trait? Or are living things inherently selfish, our kindness nothing but a mask? This is science with existential stakes.

The leaf-cutter ant is the best mushroom farmer in the world. Thriving in the tropical forests of the New World, the dark-red ants live in vast, subterranean nests. The workers organize themselves into seven functions, as in an assembly line. Some ants do nothing but cut leaves, harvesting up to seventeen per cent of the total leaf production in a rain forest every year. Others haul the plant shards back to the nest, while others tear the leaves into even smaller pieces. But the ants cannot eat these leaves directly, since they are laced with toxic chemicals. Instead, they must turn the mulching leaves into a fungus, which grows only within their colonies. One group of ants tends these underground mushroom gardens, weeding out competing fungi and keeping the chambers at an ideal temperature and humidity. The leaf-cutter ants have managed their monoculture farms for tens of millions of years.

E. O. Wilson has devoted his career to ants. As he notes, they are perhaps the most successful form of multicellular life in history, with some fourteen thousand known species. They account for roughly the same amount of biomass as human beings. This biological success is especially remarkable because it depends entirely on the ability of ants to cooperate, to form intricate societies structured around hard work and shared sacrifice. As King Solomon declared, in Proverbs, "Go to the ant, thou sluggard; consider her ways and be wise."

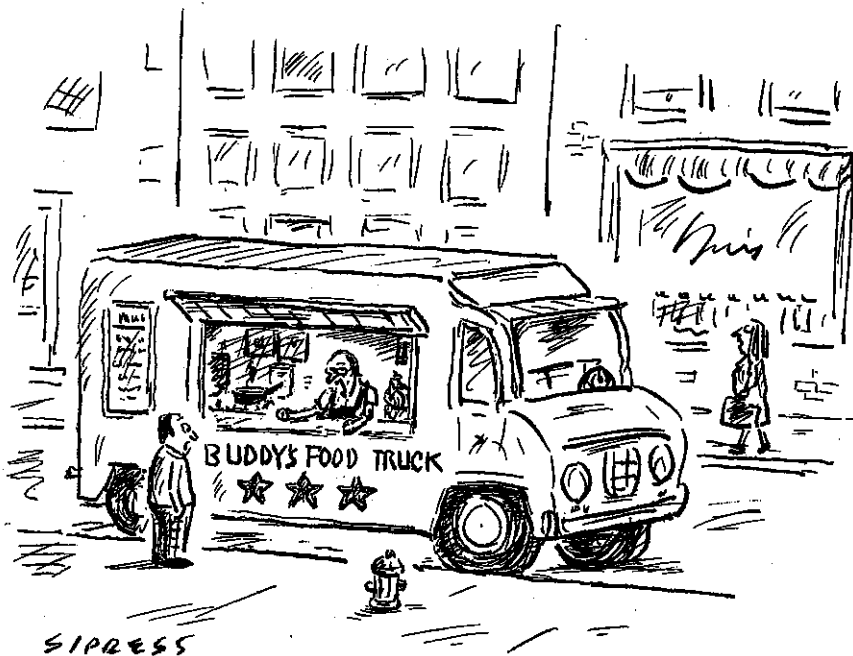
For the past sixty years, Wilson has been studying insects at Harvard University. His office, in the Museum of



their ability to form complex cooperative societies.

include the offspring of surviving relatives. The math seemed to solve the biological problem, but in doing so it opened up a moral problem: altruism, it suggested, isn't really altruistic at all; rather, it is just another means of spreading our genes. Instead of having sex, we're saving kin.

At first, Hamilton's concept of inclusive fitness was entirely ignored. Many biologists were turned off by the math, and few mathematicians were interested in the problems of biology. The following year, however, an ambitious entomologist named E. O. Wilson read the paper while taking an eighteen-hour train ride from



"The Michelin stars are for the tires."

Comparative Zoology, is down a dark hallway cluttered with metal filing cabinets. The room shares a wall with the museum, which means that the shouts of young schoolkids echo through the air. "I don't mind the noise," Wilson says. "It's like the twittering of birds." His hair is gray and cropped close; like the haircut of a little boy, it is mostly defined by those strands which refuse to stay down. He was born in Birmingham, Alabama, and his Southern drawl has been softened by decades in New England, so that his speech is now most notable for a slight lisp and the long pauses of a man who is used to being listened to. The shelves in his office are mostly taken up by his own books—he's published twenty-four, two of which received the Pulitzer Prize—and thick reference works on insects.

The discovery that made Wilson's reputation occurred in 1959, when he was a young professor at Harvard. Wilson was trying to understand how a fire-ant colony coordinated its behavior. He noticed that whenever the ants encountered a piece of food too large to carry they would drag the tip of their abdomen on the ground on their way back to the nest. Wilson assumed that the insects were laying a scent trail. Before long, he was dissecting dozens of ant bellies, searching for the source of the chemical. The work was madden-

ing: because ant organs are microscopic, Wilson was forced to use sewing needles and watchmaker's forceps, carefully plucking out each gland from the creatures. "I wanted to steal the ants' signal and speak with it myself," Wilson says. But nothing worked—the fire ants were uninterested.

Wilson was running out of organs. On one of his last attempts, he removed the Dufour's gland, a tiny structure near the ant's stinger about which little was known. He then used this gland to paint a trail. "The response was explosive," Wilson says, his voice still quickening with excitement. "I got the entire colony chasing me!"

Wilson, along with other researchers, began to identify the specific compounds secreted by the gland. Because each ant contains less than a millionth of a gram of the pheromones, he had to collect tens of thousands of fire ants, dumping entire colonies into a creek and then scooping up the insects once they floated to the surface. The field work wasn't fun—Wilson was stung scores of times—but it allowed him to identify the language of fire ants, a vocabulary of volatile liquids consisting of up to twenty communication signals.

For Wilson, the exquisite logic of this system convinced him that biological behavior could be understood, that even something as complicated as an insect colony could be explained in terms of simple

laws and chemistry. "I was convinced by ants that biology needed to develop a theory of social behavior," he says. "Such a theory was inevitable. It had to exist. And this is why I was so excited by Hamilton's papers."

Hamilton showed that the cooperative nature of many insect societies could be explained by a genetic quirk known as haplodiploidy. In some insect species, females emerge from a fertilized egg, while males develop from unfertilized eggs. (One consequence of this bizarre setup is that males have half the chromosomes of females. They also have a grandfather but no father.) Once haplodiploidy was taken into account, the extreme solidarity among sisters in, say, colonies of leaf-cutter ants ceased to be a mystery. Normally, siblings share fifty per cent of their genes, but female worker ants share three-quarters of theirs—all of their father's genes and half of their mother's. Crucially, sister ants are more closely related to one another than to their own offspring. For Hamilton, female workers were willing to look after the queen because she was essentially a sister-producing machine. Their seemingly selfless service was pure genetic greed.

Ants aren't the only insects to rely on haplodiploidy. As Hamilton noted, the same logic could explain the evolution of sawflies, wasps, and bees. These insects all exhibit an extreme form of altruism known as eusociality, in which individuals live together in vast, cooperative societies. Although eusociality is a relatively rare adaptation, it's incredibly successful: only two per cent of insect species are eusocial, but they account for approximately eighty per cent of all insect biomass. The ability of Hamilton's equation to cut across life forms suggested that it was a general principle of social behavior, and that many of the most important examples of biological cooperation were mere by-products of genetic relatedness.

Wilson was entranced by the haplodiploidy hypothesis and made inclusive fitness an important part of his book "Sociobiology: The New Synthesis" (1975), which explored the role of evolution in shaping social behavior. In the final chapter, Wilson set out to apply biological principles to human beings, attempting to "consider man in the free spirit of natural history, as though we were zoologists from another planet." After all, why

should *Homo sapiens* be exempt from the selfish logic of genes and kin? The equation was a universal truth.

"Sociobiology" sparked a bitter controversy. Wilson was attacked by eminent scientists, many of whom were in his department at Harvard. There was a group letter in *The New York Review of Books* which insisted that the concept of sociobiology provided "a genetic justification of the status quo and of existing privileges for certain groups according to class, race, or sex." Wilson retained his equanimity—"I knew I was right on the science," he says—and now the application of evolutionary theory to humans is no longer controversial. Wilson's idea has produced a colossal scientific-research program, inspiring decades of inquiry in behavioral genetics, neuroscience, and evolutionary psychology. Wilson can barely resist gloating: "That was another argument that I won," he says. "It took a few years, but, boy, did I win."

Still, even as Wilson campaigned for sociobiology, he began to grow dismayed with the scientific framework that made it possible. "I noticed that the foundations of inclusive fitness were crumbling," Wilson says. "The reasoning that had convinced me it was correct no longer held." For instance, after pursuing Hamilton's haplodiploidy hypothesis, scientists discovered that many of the most cooperative insect species, such as termites and ambrosia beetles, weren't actually haplodiploid. Furthermore, tens of thousands of species that did manifest haplodiploidy never evolved eusociality—although these insects were closely related, they didn't share food or serve the queen. By the late nineteen-nineties, the relationship between haplodiploidy and eusociality was no longer statistically significant.

"What happened is that, very quietly, the inclusive fitness theorists stopped talking about haplodiploidy, even though it was their best piece of evidence," Wilson says. At first, Wilson kept his skepticism to himself. He had little interest in dismantling a theory that he'd persuaded so many others to accept. But, after investigating the literature in detail while working on a textbook about ants, he concluded that inclusive fitness was no longer a tenable concept. "The flaws swept in on my consciousness," he says. "I was, quite frankly, surprised by how little progress had been made. I could no longer deny

the possibility that the field had made a wrong turn." It was at this point that Wilson heard from someone outside his field, a mathematician named Martin Nowak, who had reached a similar conclusion.

The young males of the Australian gray-crowned babbler, a small woodland bird with a curved black beak, have long perplexed biologists. Instead of acting like randy juveniles, seeking out mates and getting into territorial fights, they are content to remain at home, in the nest of their parents. Stranger still, they spend much of their time helping to raise their younger siblings, incubating the eggs and gathering food for the extended family. This behavior, known as cooperative breeding, makes little Darwinian sense. Why are the males squandering their most fertile years at home rather than competing to reproduce? It wasn't until the rise of inclusive fitness theory that biologists could explain this altruistic behavior. In 1976, in one of the first experimental tests of Hamilton's hypothesis, the researchers Jerry and Esther Brown began manipulating the number of helper birds in the babbler nests. When they removed the male helpers, the survival rate of their young siblings plummeted. In fact, the Browns found that each helper generated 1.6 additional offspring, a fitness benefit that helped compensate for its own reproductive loss.

It was stories like this—vivid anecdotes of animal behavior, encapsulated by simple equations—that first got Martin Nowak interested in biology as an undergraduate at the University of Vienna, in the nineteen-eighties. But he didn't want to be a naturalist; observation struck him as too inefficient. Instead, Nowak wanted to understand the details of life through its underlying mathematics. Nowak is now forty-six years old, with a shiny bald head and thick black eyebrows. He speaks with an Austrian accent so perfect it feels like a put-on, his dense sentences lightened by the lilt of his voice. Nowak is widely regarded as one of the most important mathematical biologists in the world, with more than forty publications in *Nature* and fifteen in *Science*. In 2003, he became the director of the Program for Evolutionary Dynamics,

at Harvard, a think tank of theoreticians working on biological problems.

Nowak's interest in inclusive fitness theory began in the early nineteen-nineties, when, as a graduate student at Oxford, he caught an offhand remark by his mentor, the theoretical biologist Robert May. "He referred to inclusive fitness as a cult, not a science," Nowak remembers. "I thought that was interesting, but I didn't really know what he meant." It wasn't until 2006, more than a decade later, that Nowak started looking closely at Hamilton's equation. He soon grew frustrated with its fuzziness. "Everyone talked about this rule, but in very imprecise ways," he said. "It seemed like a kind of pretend math." At the time, he was too immersed in other projects to pursue his skepticism. But then, in October of 2007, he received an e-mail from a young Harvard mathematician named Corina Tarnita, asking for a meeting.

Tarnita, who had grown up on a farm in rural Romania, was a math prodigy—she'd won nearly every major award from the Harvard math department as an undergraduate. But she'd become disenchanted with her graduate research, in an esoteric branch of algebraic geometry. "There were maybe five other people in the world who cared about my work," she says. And so she told her adviser she needed a break and began browsing the shelves of the math library, looking for another subject. That's when she discovered a textbook that Nowak had written on the mathematics of evolution. "I

opened the book up and I realized that this math wasn't so abstract," she told me. "This was math about life." At the time she e-mailed Nowak, Tarnita had a dilemma. She'd recently received a job offer from a large hedge fund, for a lucrative position as a quantitative analyst. She was tempted by the money. "I like fancy clothes and fast cars," she says. "I told myself that if Martin didn't e-mail me back then maybe I would leave Harvard."

Fortunately, Nowak responded and soon invited Tarnita to join his working group. One of her early assignments was to learn about inclusive fitness. She spent a year reading papers and poring over hun-



dreds of studies on the application of Hamilton's equation. "I wanted to figure out how it was actually used by biologists," Tarnita says. "What I discovered is that no one actually uses the equation to make calculations, because then it isn't very helpful."

As Tarnita describes it, the problem with Hamilton's equation—and with the concept of inclusive fitness more generally—is that it attempts to analyze each action in isolation, as a discrete deed with benefits and costs. "Now, that's a very admirable goal," Tarnita says. "But how do you actually calculate those benefits and costs?" To illustrate the challenge, Tarnita imagines a scenario straight out of a soap opera. "Let's say your cousin is drowning, and so you risk your life to save him. That's good, right? You've improved your inclusive fitness. But what you don't realize is that your cousin is actually competing with your brother for a wife. They both love the same woman, but she chooses your cousin. So now your brother doesn't get married, and he doesn't have three kids. Was it still a good idea to save your cousin from drowning?"

Tarnita's point is that the elegance of Hamilton's equation is a façade. When applied to the real world, the math quickly becomes exceedingly convoluted, as it attempts to encompass the extended consequences of every decision. This is why, according to her mathematical tests, inclusive fitness can be applied only under very specific biological circumstances, which almost never exist.

While Tarnita was grinding out the mathematical models, Nowak was searching for allies within biology. The search soon led him to Wilson, who had started publicly criticizing Hamilton and inclusive fitness, pointing out the limitations of the insect data and suggesting alternative hypotheses. "During our first conversation, Wilson told me that he always assumed the math of inclusive fitness must be very strong, because the biology was quite weak," Nowak remembers. "And I told him the opposite. I said I always assumed the biology was solid, because the math was very obscure."

The three scientists began meeting every week, exchanging stories about insects and game theory. They quickly zeroed in on the paradox they wanted to explain: if cooperation is such a successful strategy—eusocial species dominate their

selfish cousins—then why is it so rare? Why haven't more creatures imitated the altruistic life styles of honeybees and ants?

Wilson convinced the mathematicians that they needed to delve into the details of living things. "What I'd learned from the failure of inclusive fitness is that you can't build a theory out of thin air," Wilson says. "Our theories need to begin with boots on the ground, with a really close look at the species in question."

This emphasis on the empirical marked a shift for Wilson. "I've always been an ambitious synthesizer," he told me. "But I'm now wise enough to know the limitations of that approach." These days, he regards the books that made him famous—"Sociobiology" and "On Human Nature" (1979)—as flawed accounts of evolution, marred by their uncritical embrace of inclusive fitness. He's prouder of an eight-hundred-page textbook that he wrote on *Pheidole*, the most abundant genus of ants. At one point during my conversation with him, he walked over to his bookshelf, gingerly heaved down the enormous volume, and began flipping through the pages and admiring the art work. "There are six hundred and twenty-four species in this book, and I drew every one by hand," he said. "It took me twenty years. I know that sounds obsessive, but that's what it takes. If you want to explain ants, then you have to *know* ants."

Wilson's deep knowledge of insects led him to propose a new model for the evolution of altruism, which he decided was rooted in the contingencies of natural history. The reason eusociality is so rare, he believes, is simply that it requires a long list of preadaptations—traits that must be in place before a further trait can evolve. The most important of these is the formation of a cohesive group, which most often comes about because the daughters don't leave the nest. If the group persists for an extended period, the female insects might then construct a defensible nest. It's only at this point that the species can begin developing the genetic adaptations that enable eusociality, such as the feeding of larvae and the division of labor. Once that happens, the logic of natural selection takes over, as the intensely altruistic life style of the insects allows them to reproduce at an accelerated pace. The key point is that the relatedness of the ant colony—all those kin working together—is a *consequence*

of eusociality, not the cause. The sisters don't get along because they're sisters. Rather, clumps of females just happen to be the most likely to evolve the necessary preadaptations. They work together because they can't leave; they have become slaves to the queen.

This idea was attractive, but it lacked evidence. To test Wilson's theory, Nowak and Tarnita developed a mathematical model for the effect of a eusocial mutation—one that would prevent some daughters of a queen from leaving the nest. They ran computer simulations in which eusocial queens competed against solitary ones, and found that eusociality increases a queen's birth rate eightfold and reduces the probability of her death tenfold. A competitive advantage of this magnitude would explain why, once eusociality emerges, it leads to such striking success. And yet the model also documents the barriers to the evolution of eusociality, since it typically requires a set of unusual mutations and very particular ecological conditions.

In 2010, Tarnita, Nowak, and Wilson published these ideas in *Nature*, in a seven-page paper titled "The Evolution of Eusociality." (The math was contained in a thirty-nine-page online supplement, full of abstruse equations.) The scientists knew that their paper might be controversial, but assumed that the debate would center on the technical details of their model. Instead, the article unleashed a tempest of criticism, much of it aired in public. (Such arguments are a regular occurrence in evolutionary biology, a field that seems to lapse into discord every decade or so.) Andy Gardner, an evolutionary biologist at Oxford University, told the *New York Times* that it was "a really terrible article." Jerry Coyne, a biologist at the University of Chicago, wrote on his blog that "the only reason this paper was published was because it has two big-name authors, Nowak and Wilson, hailing from Mother Harvard. . . . The lesson: if you're a famous biologist you can get away with publishing *dreck*."

The critiques were even harsher in private. Robert Trivers, an eminent biologist at Rutgers and a former collaborator with Wilson, wrote a strongly worded personal e-mail to Nowak. Here's how the letter ends:

Martin, do you really think a quick and cheap paper like this is going to displace

W. D. Hamilton and kinship theory? Do you think anybody actually expert in these matters is going to swallow this tripe? Do you think this is a worthy use of your time? I hope you do not.

Before long, a group of biologists began drafting a response to send to *Nature*. The letter was signed by a hundred and thirty-seven scientists, and insisted that Wilson and the mathematicians misunderstood evolutionary theory and misrepresented the scientific literature. In particular, they were upset by the claim that inclusive fitness theory has produced "meagre" results. The scientists cite a long list of insights that stem directly from Hamilton's equation, such as why animals act spitefully and why some species have such uneven sex ratios. "The case for inclusive fitness is overwhelming," Dawkins says. "To insist otherwise is simply wrong."

Tarnita and Nowak replied in *Nature*, and then again on their Web site, making it clear that they were not trying to discredit Hamilton or disregard the importance of relatedness. Nowak, in a forthcoming edition of his book "Supercooperators," expresses an eagerness to learn from his detractors, but maintains that inclusive fitness is a useless "gyration," characterized by a tendency to "theorize without precision."

Still, the debate has not reached a satisfying conclusion. The mathematicians insist that their critics don't understand the math, and the biologists insist that the mathematicians don't understand the biology. Wilson, meanwhile, admits that he can't follow much of his colleagues' math, but says that he knows insects. One of the few scientists able to speak the language of both sides is the man who helped to coordinate the letter to *Nature*, David Queller, of Washington University in St. Louis. He argues that, while the pages of equations employed by Nowak and Tarnita might be technically correct, they don't support their grand conclusions. "Martin is always going on about how inclusive fitness doesn't work in the real world," Queller told me. "But his model is certainly no better. The fact is, inclusive fitness has been tested in a number of ways. It's made predictions, and those predictions are correct."

For their part, the mathematicians seem to regret some of the language

used in the *Nature* paper. "If I could write it again, I would make it more clear that Hamilton's equation inspired lots of good research," Tarnita says. "He got people thinking about relatedness, and that was very important." Nevertheless, Tarnita and Nowak continue to insist that Hamilton's equation is not a precise expression of a biological phenomenon. Rather, it's little more than a rule of thumb, a truism masquerading as a truth.

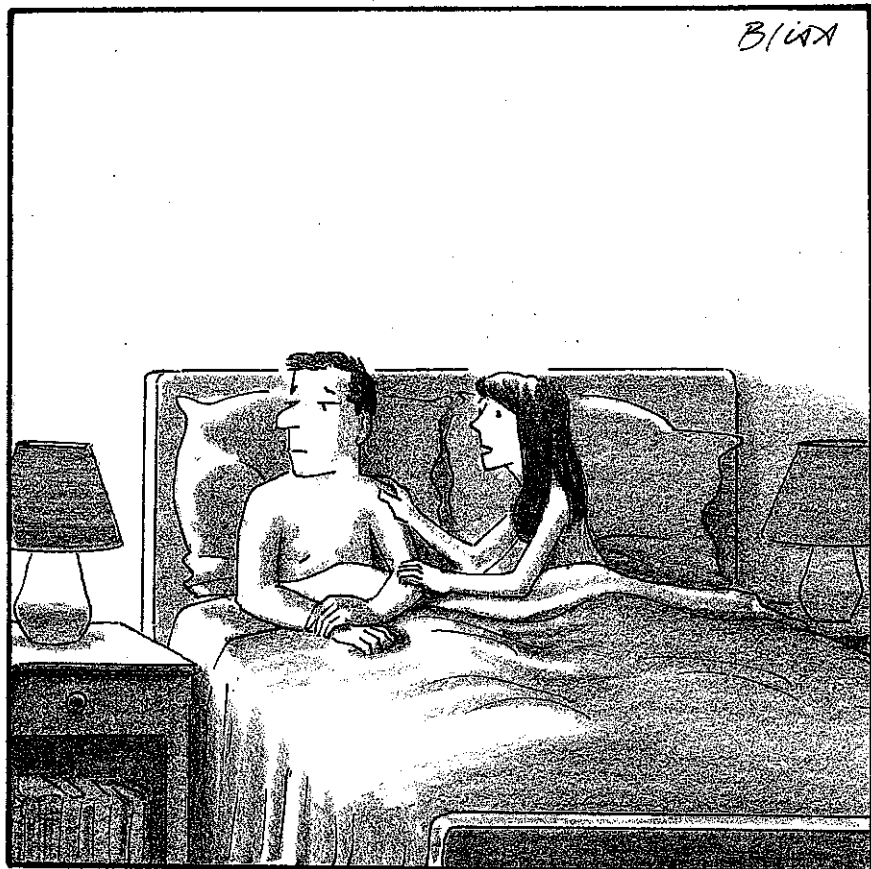
The scientific disagreement is particularly hard to resolve because it's rooted in the distinct perspectives of mathematicians and biologists. Tarnita and Nowak want the equations of altruism to be literal; when they talk about inclusive fitness, they are talking about the mathematical details of $rB > C$. Such computations, of course, are extremely difficult—how does one measure the fitness of an action?—which is why they find Hamilton's work so unsatisfying. "I get that his equation is simple, and that's nice," Tarnita says. "Everyone likes simple equations. But it's too simple. Our model is messier than Hamilton's, but you get a lot more out of it."

Nowak is even blunter. "If the theory works, then it has to work at a mathematical level," he says.

The biologists, on the other hand, don't mind that inclusive fitness often can't be calculated. Instead, they see it as a framework for making sense of the world, an important principle that helps us understand the varied behavior of bats, ants, and other species. The equation, in other words, isn't really an equation. It's just a short summary of a big idea, much like Darwin's description of natural selection.

Wilson is the only one who seems to be enjoying the controversy. His appetite for scientific brawls seems, if anything, to be increasing with age. Wilson likes to quote Schopenhauer on how all new ideas go through three phases. "First, the truth is ridiculed," he says. "Then it meets outrage. Then it is said to have been obvious all along. We're currently in the outrage stage, but we'll be obvious before long."

He seems similarly unconcerned by the reaction of his colleagues. "After Einstein published his theory of relativ-



"Larry, you can't blame everything on the media."

ity, a hundred physicists wrote a paper condemning it," Wilson says. "Einstein's response was marvellous. He said, 'If the theory is wrong, why wouldn't one author suffice?' I feel the same way. When you read their responses, they never say what we've got wrong. And that's because we didn't get anything wrong. I don't want to sound too boastful, but I think this is a big paper. It's a game changer."

And so the argument continues, with both sides promising new papers that will prove the other side wrong. The problem is, of course, that it's hard to imagine what such proof might look like. Despite the impressive tool kit of modern biology, this is still a debate about distant history, shot through with ambiguous facts and contested first principles. Meanwhile, nobody seems to have noticed the irony of the situation: they are fighting over the origins of kindness.

A few years ago, Wilson became obsessed with the red-cockaded woodpecker, an endangered species that inhabits the pine forests of the southeastern United States. Like the Australian gray-crowned babbler, these birds engage in cooperative breeding, as most young males spend several years raising their relatives. But Wilson wasn't just entranced by their altruism. He also marvelled at another peculiar habit of the red-cockaded: it drills into living trees. While most woodpeckers construct nests in dead and dying tree trunks—the rotting wood makes it easier to excavate—the red-cockaded woodpecker spends up to three years hacking away at the healthy wood of a pine tree. This labor is not as thankless as it appears, though. It turns out that drilling into a live pine has ancillary benefits. When the woodpecker bores its holes, resin seeps out, coating the tree trunk in a sticky glue, which prevents the woodpecker's chief predators, such as rat snakes, from gaining access to its nest. The bird has built a trap.

Although it's not uncommon for Wilson to delve into the natural history of a particular species, his interest in this bird has been unusually intense. "I thought it was incredible that these little guys drill into living trees," he says. "And I began wondering if that might play a role in why the young males stick around."

Before long, Wilson was travelling down to the Gulf Coast and looking at the nest sites for himself. He consulted woodpecker experts and spent time wandering around the vanishing pine forests of Florida, searching for small boreholes and slicks of resin and trying to understand what led to cooperative breeding. "And that's when I realized one could come up with a much better explanation than inclusive fitness," he says. According to Wilson, the driving force is the scarcity of suitable nesting sites. Species that engage in cooperative breeding, he notes, "all have very limited territories and are very picky about where they live." This suggests that the young males hang around because they can't find a suitable tree for themselves, and are hoping to inherit the nest of their parents. Babysitting the siblings, then, is just a way of paying rent, a chore performed in exchange for shelter. "My point is that I can explain these helpers without talking about relatedness or inclusive fitness," Wilson says. "These birds are just dealing with the challenges of real estate."

In his more expansive moods, Wilson goes beyond the habits of woodpeckers to speculate on the larger forces at work in the evolution of altruism. He isn't content to tear inclusive fitness down—he wants to replace it with something better. As usual, Wilson's latest proposal is driven by his faith in the power of close observation, as well as by a kind of intuitive empathy with fauna, which seems to be the product of a life spent observing the natural world. While he clearly enjoys having the math back him up, one gets the sense that he wouldn't change his mind if it didn't. At this late stage of his career, Wilson is less interested in equations than in narratives. Indeed, a few years ago he published a novel, albeit one about ants.

Wilson's current explanation for al-

truism has returned to a hypothesis first proposed by Darwin in "The Descent of Man"—that human generosity might have evolved as an emergent property not of the individual but of the group. "There can be no doubt that a tribe including many members who . . . were always ready to give aid to each other and to sacrifice themselves for the common good, would be victorious over most other tribes," Darwin wrote. While acts of altruism can be costly for the individual, Darwin argued that they helped sustain the colony, which made individuals within the colony more likely to survive.

This idea is known as group selection, and it's an explanation that most evolutionary biologists now dismiss, because the advantages of generosity are much less tangible than the benefits of selfishness. (A tribe full of nice guys would be easy prey for a cheater, who would quickly spread his genes through the population.) But Wilson believes that it may hold the key to understanding altruism. To make his case, he cites recent studies of "cooperating" microbes, plants, and even female lions. In all these studies, many of which have been conducted in the controlled conditions of the lab, clumps of cooperators thrive and replicate, while selfish groups wither and die. In a 2007 paper that he co-authored, he summarizes his new view in three terse sentences: "Selfishness beats altruism within groups. Altruistic groups beat selfish groups. Everything else is commentary."

Wilson's larger point is that, to the extent that altruism exists, it isn't an illusion. Instead, goodness might actually be an adaptive trait, allowing more cooperative groups to outcompete their conniving cousins. In a field defined by the cruel logic of natural selection, group selection appears to be the rare hint of virtue, the one biological force pushing back against the obvious advantages of greed and deceit. "I see human nature as hung in the balance between these two extremes," Wilson says. "If our behavior was driven entirely by group selection, then we'd be robotic cooperators, like ants. But, if individual-level selection was the only thing that mattered, then we'd be entirely selfish. What makes us human is that our history has been shaped by both forces. We're stuck in between." ♦

