THE SELFLESS GENE

Olivia Judson

Olivia Judson (1970-) teaches evolutionary biology at Imperial College London, and writes on science for such publications as The Economist, The New York Times, *and* Nature. *She most recently published a book on the sex lives of animals:* Dr. Tatiana's Sex Advice to All Creation *(Holt, 2003). This article first appeared in* The Atlantic Monthly *(October 2007).*

At 2 a.m. on February 26, 1852, the Royal Navy troopship Birkenhead, which was carrying more than 600 people, including seven women and 13 children, struck a rock near Danger Point, two miles off the coast of South Africa. Almost immediately, the ship began to break up. Just three lifeboats could be launched. The men were ordered to stand on deck, and they did. The women and children (along with a few sailors) were put into the lifeboats and rowed away. Only then were the men told that they could try to save themselves by swimming to shore. Most drowned or were eaten by sharks. The heroism of the troops, standing on deck facing almost certain death while others escaped, became the stuff of legend. But the strange thing is, such heroics are not rare: Humans often risk their lives for strangers — think of the firemen going into the World Trade Center — or for people they know but are not related to.

How does a propensity for self-sacrifice evolve? And what about the myriad lesser acts of daily kindness — helping a little old lady across the street, giving up a seat on the subway, returning a wallet that's been lost? Are these impulses as primal as ferocity, lust, and greed? Or are they just a thin veneer over a savage nature? Answers come from creatures as diverse as amoebas and baboons, but the story starts in the county of Kent, in southern England.

EVOLVING GENEROSITY

Kent has been home to two great evolutionary biologists. In the 19th century, Charles Darwin lived for many years in the village of Downe. In the 20th, William Donald Hamilton grew up catching beetles and chasing butterflies over the rolling hills near Badgers Mount.

Hamilton was a tall man with a craggy face and the tops of a couple of fingers missing from a childhood accident — he blew himself up while making explosives. He died in 2000, at age 63, after an illness contracted while undertaking another risky endeavor: a trip to the Congo to collect chimpanzee feces. When I first met him, in Oxford in 1991, he had a terrific shock of white hair, rode a rickety bicycle at prodigious speed, and was preoccupied with the question of why sex is useful in evolutionary terms. (For my doctorate, I worked with him on this question.) But he began his career studying social behavior, and in the early '60s he published a trio of now-classic papers in which he offered the first rigorous explanation of how generosity can evolve, and under what circumstances it is likely to emerge.

Hamilton didn't call it generosity, though; he called it altruism. And the particular behaviors he sought to explain are acts of extreme self-sacrifice, such as when a bee dies to defend the hive, or when an animal spends its whole life helping others rear their children instead of having some of its own.

To see why these behaviors appear mysterious to biologists, consider how natural selection works. In every generation, some individuals leave more descendants than others. If the reason for their greater "reproductive success" is due to the particular genes they have, then natural selection has been operating.

Here's an example: Suppose you're a mosquito living on the French Mediterranean coast. Tourists don't like mosquitoes, and the French authorities try to keep the tourists happy by spraying insecticide. Which means that on the coast, mosquitoes bearing a gene that confers insecticide resistance tend to leave many more descendants than those lacking it — and so today's coastal mosquitoes are far more resistant to insecticide than those that live inland.

Extreme altruists, by definition, leave no descendants: They're too busy helping others. So at first blush, a gene that promotes extreme altruism should quickly vanish from a population.

Hamilton's solution to this problem was simple and elegant. He realized that a gene promoting extreme altruism could spread if the altruist helped its close relations. The reason is that your close relations have some of the same genes as you do. In humans and other mammals, full brothers and sisters have, on average, half the same genes. First cousins have, on average, an eighth of their genes in common. Among insects such as ants and bees, where the underlying genetics work differently, full sisters (but not brothers) typically have three-quarters of their genes in common.

Hamilton derived a formula — now known as Hamilton's rule — for predicting whether the predisposition toward a given altruistic act is likely to evolve: $rB>C$. In plain language, this says that genes that promote the altruistic act will spread if the benefit (B) that the act bestows is high enough, and the genetic relationship (r) between the altruist and the beneficiary is close enough, to outweigh the act's cost (C) to the altruist. Cost and benefit are both measured in nature's currency: children. "Cheap" behaviors — such as when a small bird squawks from the bushes to announce it's seen a cat or a hawk — can, and do, evolve easily, even though they often benefit nonrelatives. "Expensive" behaviors, such as working your whole life to rear someone else's children, evolve only in the context of close kin.

Since Hamilton first proposed the idea, "kin selection" has proved tremendously powerful as a way to understand cooperative and self-sacrificial behavior in a huge menagerie of animals. Look at lions. Lionesses live with their sisters, cousins, and aunts; they hunt together and help each other with child care. Bands of males, meanwhile, are typically brothers and half-brothers. Large bands are better able to keep a pride of lionesses; thus even males who never mate with a female still spread some of their genes by helping their brothers defend the pride. Or take peacocks. Males often stand in groups when they display to females. This is because females are drawn to groups of displaying males; they ogle them, then pick the guy they like best to be their mate. Again, peacocks prefer to display with their brothers rather than with males they are not related to.

Kin selection operates even in mindless creatures such as amoebas. For instance, the soil-dwelling amoeba *Dictyostelium purpureum*. When times are good, members of this species live as single cells, reproducing asexually and feasting on bacteria. But when times get tough — when there's a bacteria shortage — thousands of individuals join together into a single entity known as a slug. This glides off in search of more-suitable conditions. When it finds them, the slug transforms itself into a fruiting body that looks like a tiny mushroom; some of the amoebas become the stalk, others become spores. Those in the stalk will die; only the spores will go on to form the next amoeboid generation. Sure enough, amoebas with the same genes (in other words, clones) tend to join the same slugs: They avoid mixing with genetic strangers and sacrifice themselves only for their clones.

Kin selection also accounts for some of the nastier features of human behavior, such as the tendency stepparents have to favor their own children at the expense of their stepkids. But it's not enough to explain the evolution of all aspects of social behavior, in humans or in other animals.

Living Together

Animals may begin to live together for a variety of reasons — most obviously, safety in numbers. In one of his most engaging papers, Hamilton observed that a tight flock, herd, or shoal will readily appear if every animal tries to make itself safer by moving into the middle of the group — a phenomenon he termed the "selfish herd." But protection from predators isn't the only benefit of bunching together. A bird in a flock spends more time eating and less time looking about for danger than it does when on its own. Indeed, eating well is another common reason for group living. Some predatory animals — chimpanzees, spotted hyenas, and wild dogs, for example — have evolved to hunt together.

Many social animals thus live in huge flocks or herds, and not in family groups — or even if the nexus of social life is the family, the family group is itself part of a larger community. In species such as these, social behavior must extend beyond a simple "Be friendly and helpful to your family and hostile to everybody else" approach to the world. At the least, the evolution of social living requires limiting aggression so that neighbors can tolerate each other. And often, the evolution of larger social groupings is accompanied by an increase in the subtlety and complexity of the ways animals get along together.

Consider baboons. Baboons are monkeys, not apes, and are thus not nearly as closely related to us as chimpanzees are. Nonetheless, baboons have evolved complex social lives. They live in troops that can number from as few as eight to as many as 200. Females live with their sisters, mothers, aunts, and infants; males head off to find a new troop at adolescence (around age 4). Big troops typically contain several female family groups, along with some adult males. The relationships between members of a troop are varied and complex. Sometimes two or more males team up to defeat a dominant male in combat. Females often have a number of male "friends" that they associate with (friends may or may not also be sex partners). If a female is attacked or harassed, her friends will come bounding to the rescue; they will also protect her children, play with them, groom them, carry them, and sometimes share food with them. If the mother dies, they may even look after an infant in her place.

Yet friendliness and the associated small acts of affection and kindness — a bout of grooming here, a shared bite to eat there — seem like evolutionary curiosities. Small gestures like these don't affect how many children you have. Or do they?

Among social animals, one potentially important cause of premature death is murder. Infanticide can be a problem for social mammals, from baboons and chimpanzees to lions and even squirrels. During one four-year study of Belding's ground squirrels, for example, the main cause of death for juveniles was other Belding's ground squirrels; at least 8 percent of the young were murdered before being weaned. Similarly, fighting between adults — particularly in species where animals are well armed with horns, tusks, or teeth — can be lethal, and even if it is not, it may result in severe injuries, loss of status, or eviction from the group.

The possibility of death by murder creates natural selection for traits that reduce this risk. For example, any animal that can appease an aggressor, or that knows when to advance and when to retreat, is more likely to leave descendants than an animal that leaps wildly into any fray. Which explains why, in many social-mammal species, you don't see many murders, though you do see males engaging in elaborate rituals to see who's bigger and stronger. Serious physical fights tend to break out only when both animals think they can win (that is, when they are about the same size).

Thus, among animals such as baboons, friendships mean more than a bit of mutual scratching; they play a fundamental role in an animal's ability to survive and reproduce within the group. Friendships between males can be important in overcoming a dominant male — which may in turn lead to an improvement in how attractive the animals are to females. Similarly, females that have a couple of good male friends will be more protected from bullying — and their infants less likely to be killed. Why do the males do it? Males that are friends with a particular female are more likely to become her sex partners later on, if indeed they are not already. In other words, friendship may be as primal an urge as ferocity.

Becoming Human

The lineage that became modern humans split off from the lineage that became chimpanzees around 6 million years ago. Eventually this new lineage produced the most socially versatile animal the planet has ever seen: us. How did we get to be this way?

One clue comes from chimpanzees. Chimpanzee society is the mirror image of baboon society, in that it's the females that leave home at adolescence, and the males that stay where they were born. Chimpanzee communities can also be fairly large, comprising several different subcommunities and family groups. Males prefer to associate with their brothers and half-brothers on their mother's side, but they also have friendships with unrelated males. Friends hang out together and hunt together — and gang up on other males.

However, unlike baboon troops, which roam around the savannah freely intermingling, chimpanzee communities are territorial. Bands of males patrol the edges of their community's territory looking for strangers — and sometimes make deep incursions into neighboring terrain. Males on patrol move together in silence, often stopping to listen. If they run into a neighboring patrol, there may be some sort of skirmish, which may or may not be violent. But woe betide a lone animal that runs into the patrolling males. If they encounter a strange male on his own, they may well kill him. And sometimes, repeated and violent attacks by one community lead to the annihilation of another, usually smaller, one. Indeed, two of the three most-studied groups of chimpanzees have wiped out a neighboring community.

Chimpanzees have two important sources of premature death at the hands of other chimpanzees: They may be murdered by members of their own community, or they may be killed during encounters with organized bands of hostile neighbors.

Just like humans. Except that humans aren't armed with big teeth and strong limbs. Humans carry weapons, and have done so for thousands of years.

On Love and War

Darwin wondered whether lethal warring between neighboring groups might have caused humans to evolve to be more helpful and kind to each other. At first, the idea seems paradoxical. But Darwin thought this could have happened if the more cohesive, unified, caring groups had been better able to triumph over their more disunited rivals. If so, the members of those cohesive, yet warlike, groups would have left more descendants.

For a long time, the idea languished. Why? A couple of reasons. First, it appears to depend on "group selection." This is the idea that some groups evolve characteristics that allow them to outcompete other groups, and it's long been out of favor with evolutionary biologists. In general, natural selection works much more effectively on individuals than it does on groups, unless the groups are composed of close kin. That's because group selection can be effective only when the competing groups are genetically distinct. Members of a kin group tend to be genetically similar to each other, and different from members of other kin groups. In contrast, groups composed of non-kin tend to contain considerable genetic variation, and differences between such groups are generally much smaller. Moreover, contact between the groups — individuals migrating from one to another, say — will reduce any genetic differences that have started to accumulate. So unless natural selection within the groups is different — such that what it takes to survive and reproduce in one group is different from what it takes in another — migration quickly homogenizes the genetics of the whole population.

A second reason Darwin's idea has been ignored is that it seems to have a distasteful corollary. The idea implies, perhaps, that some unpleasant human characteristics — such as xenophobia or even racism — evolved in tandem with generosity and kindness. Why? Because banding together to fight means that people must be able to tell the difference between friends (who belong in the group) and foes (who must be fought). In the mid-1970s, in a paper that speculated about how humans might have evolved, Hamilton suggested that xenophobia might be innate. He was pilloried.

But times have changed. Last year, the science journal *Nature* published a paper that tested the idea of "parochial altruism" — the notion that people might prefer to help strangers from their own ethnic group over strangers from a different group; the experiment found that indeed they do. In addition, the idea that natural selection might work on groups — at least in particular and narrow circumstances — has become fashionable again. And so Darwin's idea about the evolution of human kindness as a result of war has been dusted off and scrutinized.

Sam Bowles, an economist turned evolutionary biologist who splits his time between the Santa Fe Institute, in New Mexico, and the University of Siena, in Italy, notes that during the last 90,000 years of the Pleistocene Epoch (from about 100,000 years ago until about 10,000 years ago, when agriculture emerged), the human population hardly grew. One reason for this was the extraordinary climactic volatility of the period. But another, Bowles suggests, was that our ancestors were busy killing each other in wars. Working from archaeological records and ethnographic studies, he estimates that wars between different groups could have accounted for a substantial fraction of human deaths — perhaps as much as 15 percent, on average, of those born in any given year — and as such, represented a significant source of natural selection.

Bowles shows that groups of supercooperative, altruistic humans could indeed have wiped out groups of less-united folk. However, his argument works only if the cooperative groups also had practices — such as monogamy and the sharing of food with other group members — that reduced the ability of their selfish members to outreproduce their more generous members. (Monogamy helps the spread of altruism because it reduces the differences in the number of children that different people have. If, instead, one or two males monopolized all the females in the group, any genes involved in altruism would quickly disappear.) In other words, Bowles argues that a genetic predisposition for altruism would have been far more likely to evolve in groups where disparities and discord inside the group — whether over mates or food — would have been relatively low. Cultural differences between groups would then allow genetic differences to accumulate.

'That's Not the Way You Do It'

If Bowles's analysis is right, it suggests that individuals who could not conform, or who were disruptive, would have weakened the whole group; any group that failed to drive out such people, or kill them, would have been more likely to be overwhelmed in battle. Conversely, people who fit in — sharing the food they found, joining in hunting, helping to defend the group, and so on — would have given their group a collective advantage, and thus themselves an individual evolutionary advantage.

This suggests two hypotheses. First, that one of the traits that may have evolved in humans is conformity, an ability to fit in with a group and adopt its norms and customs. Second, that enforcement of those norms and customs could have been essential for group cohesion and harmony, especially as groups got bigger (bigness is important in battles against other groups).

Let's start with conformity. This hasn't been studied much in other animals, but male baboons do appear to conform to the social regimens of the groups they join. For example, in one baboon troop in Kenya in the 1980s, all the aggressive males died of tuberculosis. The aggressives were the ones to snuff it because they'd eaten meat infected with bovine TB that had been thrown into a garbage dump; only the more-aggressive males ate at the dump. After their deaths, the dynamics of the troop shifted to a more laid-back way of life. Ten years later — by which time all the original resident males had either died or moved on — the troop was still notable for its mellow attitude. The new males who'd arrived had adopted the local customs.

What about humans? According to Michael Tomasello — a psychologist at the Max Planck Institute, in Leipzig, Germany, who studies the behavior of human children and of chimpanzees — children as young as 3 will quickly deduce and conform to rules. If an adult demonstrates a game, and then a puppet comes in and plays it differently, the children will clamor to correct the puppet with shouts of "No, that's not the way you do it — you do it this way!" In other words, it's not just that they infer and obey rules; they try to enforce them, too.

Which brings me to the question of punishment.

Punishment Games

I'll be dictator. Here's how we play: An economist puts some money on the table — let's say $1,000. Since I'm dictator, I get to decide how you and I are going to split the cash; you have no say in the matter. How much do you think I'll give you?

Now, let's play the ultimatum game. We've still got $1,000 to play with, and I still get to make you an offer. But the game has a wrinkle: If you don't like the offer I make, you can refuse it. If you refuse it, we both get nothing. What do you think I'll do here?

As you've probably guessed, people tend to play the two games differently. In the dictator game, the most common offer is nothing, and the average offer is around 20 percent. In the ultimatum game, the most common offer is half the cash, while the average is around 45 percent. Offers of less than 25 percent are routinely refused — so both players go home empty-handed.

Economists scratch their heads at this. In the first place, they are surprised that some people are nice enough to share with someone they don't know, even in the dictator game, where there's nothing to lose by not sharing. Second, economists predict that people will accept any offer in the ultimatum game, no matter how low, because getting something is better than getting nothing. But that's not what happens. Instead, some people forgo getting anything themselves in order to punish someone who made an ungenerous offer. Money, it seems, is not the only currency people are dealing in.

Bring in the neuroscientists, and the other currency gets clearer. If you measure brain activity while such games are being played (and there are many variants, for the fun doesn't stop with dictators and ultimatums), you find that the reward centers of the brain — the bits that give you warm, fuzzy feelings — light up when people are cooperating. But they also light up if you punish someone who wasn't generous, or watch the punishment of someone who wasn't.

Whether these responses are universal isn't clear: The genetic basis is obscure, and the number of people who've had their brain activity measured is tiny. Moreover, most economic-game playing has been done with college students; the extent to which the results hold among people from different cultures and backgrounds is relatively unknown. But the results suggest an intriguing possibility: that humans have evolved both to be good at conforming to the prevailing cultural norms and to enjoy making sure that those norms are enforced. (Perhaps this explains why schemes such as zero-tolerance policing work so well: They play into our desire to conform to the prevailing norms.)

Bringing Out the Best

If the evolutionary scenario I've outlined is even half right, then we should expect to find that there are genes involved in mediating friendly behavior. And there are. Consider Williams syndrome.

People who have Williams syndrome tend to have poor cardiovascular function and a small, pointed, "elfin" face. They are typically terrible with numbers but good with words. And they are weirdly, incautiously friendly and nice — and unafraid of strangers.

They are also missing a small segment of chromosome 7. Chromosomes are long strings of DNA. Most people have 46 chromosomes in 23 pairs; you get one set of 23 from your mother, and the other from your father. In Williams syndrome, one copy of chromosome 7 is normal; the other is missing a small piece. The missing piece contains about 20 genes, some of which make proteins that are important in the workings of the brain. Since one chromosome is intact, the problem isn't a complete absence of the proteins that the genes encode, but an insufficiency. Somehow, this insufficiency results in people who are too nice. What's more, they can't learn not to be nice. Which is to say, someone with Williams syndrome can learn the phrase "Don't talk to strangers" but can't translate it into action.

Much about Williams syndrome remains mysterious. How the missing genes normally influence behavior is unclear; moreover, the environment has a role to play, too. But despite these complexities, Williams syndrome shows that friendliness has a genetic underpinning — that it is indeed as primal as ferocity. Indirectly, it shows something else as well. Most of us are able to apply brakes to friendly behavior, picking and choosing the people we are friendly to; those with Williams syndrome aren't. They cannot modulate their behavior. This is even odder than being too friendly. And it throws into sharp relief one of the chief features of ordinary human nature: its flexibility.

One of the most important, and least remarked upon, consequences of social living is that individual behavior must be highly flexible and tailored to circumstance: An individual who does not know whom to be aggressive toward, or whom to help, is unlikely to survive for long within the group. This is true for baboons and chimpanzees. It is also true for us.

Indeed, the ability to adjust our behavior to fit a given social environment is one of our main characteristics, yet it's so instinctive we don't even notice it, let alone consider it worthy of remark. But its implications are profound — and hopeful. It suggests that we can, in principle, organize society so as to bring out the best facets of our complex, evolved natures.