Chapter 7: **FAMILIES**

[W]ith the working ant we have an insect differing greatly from its parents, yet absolutely sterile; so that it could never have transmitted successively acquired modifications of structure or instinct to its progeny. It may well be asked how is it possible to reconcile this case with the theory of natural selection?

—*The Origin of Species* (1859)

[Yesterday] Doddy [Darwin's son William] was generous enough to give Anny the last mouthful of his gingerbread & today . . . he again put his last crumb on the sofa for Anny to run to & then cried in rather a vain-glorious tone "oh kind Doddy" "kind Doddy."

—Observations of Darwin's children (1842)[1]

We all like to think of ourselves as selfless. And on occasion we are. But we are pigs compared to the social insects. Bees die for their fellow bees, disemboweling themselves upon stinging an intruder. Some ants, also in defense of the colony, detonate themselves. Other ants spend their lives as doors, keeping out insects that lack security clearance, or as food sacks, hanging bloated from the ceiling in case of scarcity.[2] These pieces of furniture have no offspring.

Darwin spent more than a decade wondering how natural selection could have produced whole castes of ants that create no descendants. Meanwhile, he was creating plenty of descendants himself. The problem of insect sterility had gotten his attention by the time his fourth child, Henrietta, was born in late 1843, and he still had not solved it by the birth of his tenth and last child, Charles, in 1856. For all those years, he kept the theory of natural selection secret, and one reason may be the seemingly blatant contradiction of it by ants. The paradox seemed "insuperable, and actually fatal to my whole theory."[3]

Darwin probably didn't suspect, as he pondered the insect puzzle, that the solution to it could explain, as well, the texture of his growing family's everyday life: why his children showed affection for one another, why they sometimes fought; why he felt compelled to teach them the virtues of kindness, why they sometimes resisted; even why he and Emma grieved more deeply the loss of one of their children than another. Understanding self-sacrifice among insects would unlock the dynamics of family life among mammals, including people.

Though Darwin finally conceived, at least vaguely, the correct explanation of insect sterility, and suspected that it might have relevance to human behavior, he came nowhere near seeing the breadth and diversity of the relevance. Neither did anyone else until a century later.

One reason for this may be that Darwin's explanation, as he phrased it, was hard to grasp. In *The Origin of Species* he wrote that the paradox of evolved sterility "is lessened, or, as I believe, disappears, when it is remembered that selection may be applied to the family, as well as to the individual, and may thus gain the desired end. Thus, a well-flavoured vegetable is cooked, and the individual is destroyed; but the horticulturist sows seeds of the same stock, and confidently expects to get nearly the same variety; breeders of cattle wish the flesh and fat to be well marbled together; the animal has been slaughtered, but the breeder goes with confidence to the same family."[4]

However strange it may seem to bring plant and animal breeders into the picture, this made perfect sense after 1963, when a young British biologist named William D. Hamilton sketched out the theory of kin selection.[5] Hamilton's theory is an articulation and extension of Darwin's insight in the language of genetics, a language that didn't exist in Darwin's day.

The term *kin selection* itself suggests a link with Darwin's assertion that "selection may be applied to the family," and not just to the individual organism. But this suggestion, while true, is misleading. The beauty of Hamilton's theory is that it sees selection as taking place not so much at the level of the individual *or* the family, but, in an important sense, at the level of the gene. Hamilton was the first to clearly sound this central theme of the new Darwinian paradigm: looking at survival from the gene's point of view.

Consider a young ground squirrel that has not yet produced any offspring and that, upon sighting a predator, gets up on its hind legs and delivers a loud alarm call, which may attract the predator's attention and bring sudden death. If you look at natural selection the way almost all biologists looked at it through the mid-twentieth century—a process concerned with the survival and reproduction of animals, and of their offspring—this warning call doesn't make sense. If the ground squirrel giving it has no offspring to save, then the warning call is evolutionary suicide. Right? This is the question that was momentously answered in the negative by Hamilton.

In the Hamiltonian view, attention shifts from the ground squirrel that is sounding the alarm to the gene (or, in real life, the series of genes) responsible for the alarm. After all, ground squirrels don't live forever, and neither do any other animals. The only potentially immortal organic entity is a gene (or, strictly speaking, the pattern of information encoded in the gene, since the physical gene itself will pass away after conveying the pattern through replication). So, in an evolutionary time frame, over hundreds or thousands or millions of generations, the question isn't how individual animals fare; we all know the finally grim answer to that one. The question is how individual *genes* fare. Some will pass away and some will thrive, and which do which is a matter of consequence. How will a "suicidal warning call" gene fare?

The somewhat surprising answer, which lay at the core of Hamilton's theory, is: quite well, under the right circumstances. The reason is that the ground squirrel containing the gene may have some nearby relatives who will be saved by the alarm call, and some of those relatives probably carry the same gene. Half of all brothers and sisters, for example, can be assumed to possess the gene (unless they're half-siblings, in which case the fraction is a still nontrivial one-fourth).

If the warning call saves the lives of four full siblings that would otherwise die, two of which carry the gene responsible for it, then the gene has done well for itself, even if the sentry containing it pays the ultimate sacrifice. This superficially selfless gene will do much better over the ages than a superficially selfish gene that induced its carrier to scurry to safety while four siblings—and two copies of the gene, on average—perished.* The same is true if the gene saves only one full sibling, while giving the sentry a one-in-four chance of dying. Over the long run, there will be two genes saved for every gene lost.

GENES FOR BROTHERLY LOVE

There is nothing mystical going on here. Genes don't magically sense the presence of copies of themselves in other organisms and try to save them. Genes aren't clairvoyant, or even conscious; they don't "try" to do anything. But should a gene appear that *happens* to make its vehicle behave in ways that help the survival or reproductive prospects of other vehicles likely to contain a copy of that gene, then the gene may thrive, even if prospects for *its* vehicle are lowered in the process. This is kin selection.

This logic could apply, as in this case, to a gene that inclines a mammal to produce a warning call when it sees a threat to its home burrow, where relatives reside. The logic could also apply to a gene that leads an insect to be sterile, so long as the insect spends its life helping fertile relatives (who contain the gene in "unexpressed" form) to survive or reproduce. And the logic could apply to genes inclining human beings to sense early on who their siblings are and thereafter share food with them, give guidance to them, defend them, and so on—genes, in other words, leading to sympathy, empathy, compassion: genes for love.

A failure to appreciate familial love had helped keep the principle of kin selection from clear view before Hamilton's day. In 1955, in

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*Actually, a ground squirrel (or a person) shares much more than half of his genes with a sibling—and, indeed, with other members of his species. But fairly *novel* genes, genes that have just appeared within a population, will, on average, reside in half of an organism's full siblings. And novel genes are the ones that matter when we're talking about the evolution of new traits.

a popular article, the British biologist J.B.S. Haldane had noted that a gene inclining you to jump in a river and save a drowning child, taking a one-in-ten chance of dying, could flourish so long as the child were your offspring or your brother or sister; the gene could even spread, at a slower rate, if that child were your first cousin, since first cousins share, on average, one eighth of your genes. But rather than sustain this train of thought, he cut it short by observing that in emergencies people don't have time to make mathematical calculations; and surely, he said, our Paleolithic ancestors hadn't run around calculating their degree of relatedness to each other. So Haldane concluded that genes for heroism would spread only "in rather small populations where most of the children were fairly near relatives of the man who risked his life."[6] In other words: an indiscriminate heroism, reflecting the *average* degree of relatedness to people in the general vicinity, could evolve if that average were fairly high.

For all Haldane's insight in looking at things from the gene's, rather than the individual's, point of view, his failure to follow this logic to its end is odd, to say the least. It's as if he thought natural selection realizes its calculations by having organisms consciously repeat them, rather than by filling organisms with feelings that, in their fine contours, are proxies for calculation. Hadn't Haldane noticed that people tend to have the warmest feelings for the people who share the largest fraction of their genes? And that people are more inclined to risk their lives for the people they feel warmly toward? Why should it matter that Paleolithic men weren't math whizzes? They were animals; they had feelings.

Technically speaking, Haldane was right insofar as he went. Within a small, closely related population, an indiscriminate altruism could indeed evolve. And that's true even though some of the altruism would get spent on people who weren't relatives. After all, even if you channel your altruism precisely toward siblings, some of it is wasted, in evolutionary terms, since siblings don't share all your genes, and any given sibling may not carry the gene responsible for the altruism. What matters, in both cases, is that the altruism gene *tends* to improve prospects for vehicles that will *tend* to carry copies of itself; what matters is that the gene does more good than harm, in the long run, to its own proliferation. Behavior always takes place amid uncertainty, and all natural selection can do is play the odds. In the Haldane scenario the way to play the odds is to instill a mild and generalized altruism, the exact strength depending on the average extent of kinship with people regularly in the vicinity. This is conceivable.

But as Hamilton noted in 1964, natural selection will, given the opportunity, improve the odds by minimizing uncertainty. Any genes that sharpen the precision with which altruism is channeled will thrive. A gene that leads a chimpanzee to give two ounces of meat to a sibling will eventually prevail over a gene that leads it to give an ounce to a sibling and an ounce to an unrelated chimp. So unless identifying kin is very hard, evolution should produce a strong and well-targeted strain of benevolence, not a weak and diffuse strain. And that is what has happened. It has happened, at least to some extent, with ground squirrels, which are more likely to deliver warning calls in the presence of close kin.[7] It has happened, to some extent, with chimpanzees and other nonhuman primates, which often have uniquely supportive sibling relationships. And it has happened, to a great extent, with us.

Maybe the world would be a better place if it hadn't. Brotherly love in the literal sense comes at the expense of brotherly love in the biblical sense; the more precisely we bestow unconditional kindness on relatives, the less of it is left over for others. (This, some believe, is what kept Haldane, a Marxist, from facing the truth.) But, for better or worse, the literal kind of brotherly love is the kind we have.

Many social insects recognize their kin with the help of chemical signals called pheromones. It is less clear how humans and other mammals figure out (consciously or unconsciously) who their kin are. Surely seeing our mother feed and care for a child day after day is one conspicuous cue. We may also, by observing our mother's social affiliations, develop a sense for, say, who her sister is, and hence who her sister's offspring are. Besides, since the advent of language, mothers have been able to tell us who's who—instruction it is in their genetic interest to give and in our genetic interest to heed. (That is to say, genes inclining the mother to help children identify kin would thrive, as would genes inclining children to pay attention.) It's hard to say what other kin-recognition mechanisms, if any, are at work, since experiments that might settle the question involve unethical things like removing children from families.[8]

What's clear is that mechanisms exist. Anyone with siblings—anyone in any culture—is familiar with the empathy for a sibling in great need, the sense of fulfillment at giving aid, the guilt at not giving it. Anyone who has endured a sibling's death is familiar with grief. These people know what love is, and they have kin selection to thank for it.

That goes double for males, who, in the absence of kin selection, might never have felt deep love at all. Back before our species became high in male parental investment, there was no reason for males to be intensely altruistic toward offspring. That sort of affection was the exclusive province of females, in part because only they could be sure who their offspring were. But males could be pretty sure who their brothers and sisters were, so love crept into their psyches via kin selection. Had males not thus acquired the capacity for sibling love, they might not have been so readily steered toward high male parental investment, and the even deeper love it brings. Evolution can only work with the raw materials that happen to be lying around; if love for certain kinds of children—siblings—hadn't been part of males' minds several million years ago, the path to loving their own children—the path to high MPI—might have been too tortuous.

THE NEW MATH

With Hamilton's theory in hand, it's easier to appreciate the connection Darwin saw between a cow that has "well marbled" beef, and gets slaughtered and eaten, and an ant that works hard all its life without issue. The cow gene responsible for the good marbling, to be sure, has done nothing for its vehicle, which is now slaughtered, and may do nothing for the direct genetic legacy of its vehicle; dead cows can't have more offspring. But the gene will still do much for the indirect genetic legacy of its vehicle, for by producing the marbling, it prompts a farmer to feed and breed the vehicle's close relatives, some of which contain copies of the gene. So too with the sterile ant. The ant has no direct legacy, but the genes responsible for this fact do just fine, thank you, so long as the time and energy that would have been devoted to reproduction are profitably spent helping close relatives be prolific. Though the gene for sterility lies dormant in these relatives, it is there, and passes to the next generation, where it again produces gobs of sterile altruists devoted to its transmission. This is the exact sense in which worker bees and tasty cattle are alike: some genes, by impeding their transmission through one conduit, lubricate their transmission through others, and the net result is more transmission.

That Darwin, working with no knowledge of genes, with no sound understanding of the nature of heredity, should sense this parallel a century before Hamilton is one of the higher tributes to the care and precision of his thought.

Still, let there be no doubt about the superiority of Hamilton's version of kin selection to Darwin's. It is accurate enough to say, as Darwin did, that sometimes (as with insect sterility) natural selection operates on the family and sometimes on the individual organism. But why not keep things simple? Why not just say that in both of these cases, the ultimate unit of selection is the gene? Why not make a single brief statement that encompasses all forms of natural selection? Namely: those genes that are conducive to the survival and reproduction *of copies of themselves* are the genes that win. They may do this straightforwardly, by prompting their vehicle to survive, beget offspring, and equip the offspring for survival and reproduction. Or they may do this circuitously—by, say, prompting their vehicle to labor tirelessly, sterilely, and "selflessly," so that a queen ant can have lots of offspring containing them. However the genes get the job done, it is selfish from *their* point of view, even if it seems altruistic at the level of the organism. Hence the title of Richard Dawkins's book, *The Selfish Gene*. (The title has caught flack from people who note that genes don't have intentions, and so can't be "selfish." True, of course, but the phrase wasn't meant literally.)

Naturally, the level of the organism is of primary concern to human beings; human beings are organisms. But it's of secondary importance to natural selection. If there is a sense in which natural selection "cares" about anything—and there is, metaphorically—that thing isn't us; it's the information in our sex cells, our eggs and our sperm. Of course, natural selection "wants" us to behave in certain

ways. But, so long as we comply, it doesn't care whether we are made happy or sad in the process, whether we get physically mangled, even whether we die. The only thing natural selection ultimately "wants" to keep in good shape is the information in our genes, and it will countenance any suffering on our part that serves this purpose.

This was the philosophical import of the simple point Hamilton made abstractly, skeletally, in a 1963 letter to the editors of the journal *The American Naturalist*. He imagined a gene G that causes an altruistic behavior and noted: "Despite the principle of 'survival of the fittest' the ultimate criterion which determines whether G will spread is not whether the behavior is to the benefit of the behaver but whether it is to the benefit of the gene G; and this will be the case if the average net result of the behavior is to add to the gene-pool a handful of genes containing G in higher concentration than does the gene-pool itself."[9]

Hamilton gave flesh to this observation the next year with his paper "The Genetical Evolution of Social Behaviour" in *The Journal of Theoretical Biology*. The paper, after going underappreciated for years, has become one of the most widely cited works in the history of Darwinian thought, and has revolutionized the mathematics of evolutionary biology. Before the theory of kin selection, it was common to talk as if the final arbiter in evolution were "fitness," whose ultimate manifestation, it seemed, was the sum total of the organism's direct biological legacy. Genes that made an organism fitter—that maximized the number of offspring, grand-offspring, and so on—would be the genes that flourished. Now the final arbiter of evolution is thought of as "inclusive fitness," which takes into account also the genes' indirect legacy, realized via siblings, cousins, and so on. Hamilton wrote in 1964: "Here then we have discovered a quantity, inclusive fitness, which under the conditions of the model tends to maximize in much the same way that fitness tends to maximize in the simpler classical model."

Hamiltonian math contains a potent symbol—*r*—introduced earlier by the biologist Sewall Wright but now given new consequence; *r* represents the degree of relatedness among organisms. Among full siblings, *r* is ½, among half-siblings, nieces, nephews, aunts, and uncles, it is ¼, and among first cousins it is ⅛. The new math says that genes for sacrificial behavior will thrive so long as the cost to the altruist (in terms of impact on future reproductive success) is less than the benefit to the recipient (ditto) times the degree of relatedness between the two. That is, so long as *c* is less than *br*.

When Hamilton introduced the theory of kin selection, he used as his example the very group of organisms that had perplexed Darwin. Like Darwin, he had been struck by the extraordinary self-sacrifice among many insects of the order Hymenoptera, notably the highly social ants, bees, and wasps. Why is this intensity of altruism, and its attendant social cohesion, found in so few other parts of the insect world? There may be several evolutionary reasons, but Hamilton put his finger on what seems a central one. He noted that, thanks to a bizarre form of reproduction, these species feature an unusually large *r*. Sister ants share ¾ of their genes by common descent, not just ½. So altruism of extraordinary magnitude is justified in the eyes of natural selection.

When *r* is even larger than ¾, the evolutionary argument for altruism, and social solidarity, grows even stronger. Consider the cellular slime mold, which is so tightly interwoven that it has inspired reasoned debate as to whether it is best thought of as a society of cells or a single organism. Because slime-mold cells reproduce asexually, the *r* among them is 1; they are all identical twins. From the point of view of the gene, then, there is *no* difference between the fate of its own cell and the fate of a nearby cell. It's not surprising that many slime-mold cells fail to reproduce, and devote themselves instead to buffering fertile fellow cells from the elements. Their neighbors' welfare, in evolutionary terms, is identical to their own. *That's* altruism.

So too with human beings—not groups of human beings, but the groups of cells that *are* human beings. At some point hundreds of millions of years ago, multicellular life arose. Societies of cells became so highly integrated as to qualify for the title "organism," and these organisms eventually begat us. But as the cellular slime mold attests, the line between society and organism is unclear. It is fair, technically speaking, to consider even so coherent an organism as a human being a tight-knit community of single-celled organisms. These cells exhibit a kind of cooperation and self-sacrifice that makes even the machine-like efficiency of an insect colony look ragged by comparison. Almost all of the cells in the human body are sterile. Only the sex cells—our "queen bees"—get to make copies of themselves for posterity. That the zillions of sterile cells act as if they were perfectly content with this arrangement is doubtless grounded in the fact that the *r* between them and the sex cells is 1; genes in sterile cells are transmitted to future generations as assuredly via sperm or egg as they would be if their particular cellular vehicles were doing the transmitting. Again: when *r* is 1, altruism is ultimate.

THE LIMITS OF LOVE

The reverse side of this coin is that when *r* isn't 1, altruism isn't ultimate. Even pure sibling love—brotherly love—isn't total love. J.B.S. Haldane is said to have remarked once that he would never give his life for a brother—but, rather, for "two brothers or eight cousins." Presumably he was joking—parodying, perhaps, what he wrongly considered the overly fine extension of Darwinian logic. But his joke captures a basic truth. To define the degree of commitment to any relative is to define the degree of indifference and, potentially, antagonism; the cup of common interest between siblings is half-empty as well as half-full. While it makes genetic sense to help a brother or sister, even at great expense, that expense is not unlimited.

Thus, on the one hand, no modern Darwinian would expect a child to monopolize the food supply while a brother or sister grew weak from hunger. But neither should we expect that, given two siblings and one sandwich, the question of its allotment will be amicably resolved. It may not be hard to teach children to share with brothers and sisters (at least in some circumstances), but it is hard to teach them to share *equally*, for this runs against their genetic interest. That, at any rate, is what natural selection implies. We can leave it for veteran parents to say whether the prediction is borne out.

The divergence of genetic interests between siblings creates an exasperating, if sometimes charming, paradox. They fiercely compete for the affection and attention of their parents, with all the resources that can bring, and in the process display jealousy so petty that it's hard to credit them with love; but let one of them become truly needy, or seem genuinely endangered, and love will surface. Darwin saw one such shift in attitude on the part of his son Willy, then nearly five years old, toward younger sister Annie. "Whenever she hurts herself when we are present Willy appears not to mind, & sometimes makes a great noise as if to distract our attention," Darwin wrote. But one day Annie hurt herself with no adults in view, so Willy couldn't assume that any real danger was being addressed. Then his reaction "was quite different. He first attempted to comfort her very nicely & then said he would call Bessy & she not being in sight his fortitude gave way & he began to cry also."[10] Darwin didn't explain this, or any instances of sibling love, in terms of kin, or what he called "family," selection; he seems never to have seen the connection between insect self-sacrifice and mammalian affection.[11]

The biologist who first emphasized the partial emptiness of the cup of common genetic interest is Robert Trivers. He has noted, in particular, that a child's genetic interest diverges not only from a brother's or sister's, but from a parent's. Each child should, in theory, see itself as twice as valuable as its sibling, while the parent, being equally related to the two, values them equally. Hence another Darwinian prediction: not only will siblings have to be taught to share equally; parents will, in fact, try to teach them.

In 1974, Trivers dissected parent-offspring conflict in a paper by that name. By way of illustration, he discussed the contentious mammalian issue of when a suckling should get off the teat. A caribou calf, he observed, will continue to suckle long after milk has ceased to be essential to its survival, even though this prevents the mother from conceiving another calf that will share some of its genes. After all: "the calf is completely related to himself but only partially related to his future siblings. . . ."[12] The time will come when the nutritional rewards from suckling are so marginal that genetic interest favors another calf over milk. But the mother, valuing (implicitly) the two offspring equally, reaches that point sooner. So the theory of natural selection, stated in terms of inclusive fitness, implies that conflict over weaning will be a regular part of mammalian life—as it seems to be. The conflict can last for several weeks and become pretty wild, as infants shriek for milk and even strike their mother. Veteran baboon

watchers know that a good way to find a baboon troop is to listen each morning for the sound of mother-offspring strife.[13]

In the battle over resources, expect children to use any tools at their disposal, including dishonesty. The dishonesty may be crude and directed at other siblings. ("Willy sometimes tries a little ruse to prevent Annie wishing to have his apple. . . .'Yours is larger than mine Annie.' ") But the ruse may be more subtle, and directed to a larger audience, including parents. One good way to short-circuit parental demands for greater sacrifice is to exaggerate—or, shall we say, selectively highlight—sacrifices already made. An example appears at the head of this chapter: Willy, then two years old, and nicknamed Doddy, had given his younger sister his last bit of gingerbread and then exclaimed, for all to hear, "Oh kind Doddy, kind Doddy."[14] Many parents are familiar with this sort of conspicuous nonconsumption.

Another ploy children use to extract resources from parents is to embellish their needs. Emma Darwin recorded three-year-old son Leonard's actions after "he scraped 2 little bits of skin off his wrist": "He thought Papa did not pity him enough & nodded emphatically at him. 'The skin's come off—& its lost—& the bleed's coming out.' " A year later Leonard was heard to say, "Papa, I have coughed awfully—many times awfully—five awfullys—and more, too—so mayn't I have some black stuff [licorice]?"[15]

To further bolster an image of entitlement, youngsters may stress the cruelty and injustice being inflicted by parents. At peak intensity, this emphasis is known as a temper tantrum—part of young life not just in our species, but also among chimpanzees, baboons, and other primates. Many a young outraged chimp has been known, as one primatologist put it half a century ago, to "glance furtively at its mother or the caretaker as if to discover whether its action was attracting attention."[16]

Fortunately for young primates, parents are ripe for exploitation. Attention to a child's crying and complaining is in the interest of the parent's genes, since cries and complaints may signal real needs felt by a vehicle containing copies of them. In other words: parents love their children and can be blinded by that love.

lection, an official bias against them: "One should postulate adaptation at no higher a level than is necessitated by the facts."[25] In other words: first look very hard for a way that genes underlying a trait could be favored in everyday, head-to-head competition. Only after failing should you resort to competition between separate populations, and then with great caution. This has become the unofficial credo of the new paradigm.

In the same book, Williams put his doctrine to vivid use. Without resort to group selection, he proposed what is now the accepted explanation for the human moral sentiments. Writing in the mid-sixties, just after Hamilton had explained the origin of altruism among kin, Williams suggested a way that evolution could extend altruism beyond the barrier of kinship.

Chapter 9: **FRIENDS**

> *[I]t is not a little remarkable that sympathy with the distresses of others should excite tears more freely than our own distress; and this certainly is the case. Many a man, from whose eyes no suffering of his own could wring a tear, has shed tears at the sufferings of a beloved friend.*
>
> —*The Expression of the Emotions in Man and Animals* (1872)[1]

Darwin, perhaps sensing the weakness of his main theory of the moral sentiments, threw in a second theory for good measure. During human evolution, he wrote in *The Descent of Man,* "as the reasoning powers and foresight . . . became improved, each man would soon learn from experience that if he aided his fellow-men, he would commonly receive aid in return. From this low motive he might acquire the habit of aiding his fellows; and the habit of performing benevolent actions certainly strengthens the feeling of sympathy, which gives the first impulse to benevolent actions. Habits, moreover, followed during many generations probably tend to be inherited."[2]

That last sentence, of course, is wrong. We now know that habits are passed from parent to child by instruction or example, not via the genes. In fact, no life experiences (except, say, exposure to radiation) affect the genes handed down to offspring. The very beauty of Darwin's theory of natural selection, in its strict form, was that it didn't require the inheritance of acquired traits, as had previous evolutionary theories, such as Jean-Baptiste de Lamarck's. Darwin saw this beauty, and stressed mainly the pure version of his theory. But he was willing, especially as he grew older, to invoke more dubious mechanisms to solve especially nettlesome issues, such as the origin of the moral sentiments.

In 1966, George Williams suggested a way to make Darwin's musings about the evolutionary value of mutual assistance more useful: take out not only the last sentence, but also the part about "reasoning" and "foresight" and "learning." In *Adaptation and Natural Selection,* Williams recalled Darwin's reference to the "low motive" of doing favors in hopes of reciprocation and wrote: "I see no reason why a conscious motive need be involved. It is necessary that help provided to others be occasionally reciprocated if it is to be favored by natural selection. It is not necessary that either the giver or the receiver be aware of this." He continued, "Simply stated, an individual who maximizes his friendships and minimizes his antagonisms will have an evolutionary advantage, and selection should favor those characters that promote the optimization of personal relationships."[3]

Williams's basic point (which Darwin certainly understood, and stressed in other contexts)[4] is one we've encountered before. Animals, including people, often execute evolutionary logic not via conscious calculation, but by following their feelings, which were designed as logic executers. In this case, Williams suggested, the feelings might include compassion and gratitude. Gratitude can get people to repay favors without giving much thought to the fact that that's what they're doing. And if compassion is felt more strongly for some kinds of people—people to whom we're grateful, for example—it can lead us, again with scarce consciousness of the fact, to repay kindness.

Williams's terse speculations were transmuted into a full-fledged theory by Robert Trivers. In 1971, exactly one hundred years after Darwin's allusion to reciprocal altruism appeared in *The Descent of Man,* Trivers published a paper titled "The Evolution of Reciprocal Altruism" in *The Quarterly Review of Biology.* In the paper's abstract, he wrote that "friendship, dislike, moralistic aggression, gratitude, sympathy, trust, suspicion, trustworthiness, aspects of guilt, and some forms of dishonesty and hypocrisy can be explained as important adaptations to regulate the altruistic system." Today, more than two decades after this nervy pronouncement, there is a diverse and still-growing body of evidence to support it.

GAME THEORY AND RECIPROCAL ALTRUISM

If Darwin were put on trial for not having conceived and developed the theory of reciprocal altruism, one defense would be that he came from an intellectually disadvantaged culture. Victorian England lacked two tools that together form a uniquely potent analytical medium: game theory and the computer.

Game theory was developed during the 1920s and thirties as a way to study decision making.[5] It has become popular in economics and other social sciences, but it suffers from a reputation for being a bit too, well, cute. Game theorists cleverly manage to make the study of human behavior neat and clean, but they pay a high price in realism. They sometimes assume that what people pursue in life can be tidily summarized in a single psychological currency—pleasure, or happiness, or "utility"; and they assume, further, that it is pursued with unwavering rationality. Any evolutionary psychologist can tell you that these assumptions are faulty. Humans aren't calculating machines; they're animals, guided somewhat by conscious reason but also by various other forces. And long-term happiness, however appealing they may find it, is not really what they're designed to maximize.

On the other hand, humans are designed *by* a calculating machine, a highly rational and coolly detached process. And that machine does design them to maximize a single currency—total genetic proliferation, inclusive fitness.[6]

Of course, the designs don't always work. Individual organisms often fail, for various reasons, to transmit their genes. (Some are bound to fail. That is the reason evolution so assuredly happens.) In the case of human beings, moreover, the design work was done in a social environment quite different from the current environment. We live in cities and suburbs and watch TV and drink beer, all the while being pushed and pulled by feelings designed to propagate our genes in a small hunter-gatherer population. It's no wonder that people often seem not to be pursuing any particular goal—happiness, inclusive fitness, whatever—very successfully.

Game theorists, then, may want to follow a few simple rules when applying their tools to human evolution. First, the object of the game should be to maximize genetic proliferation. Second, the context of the game should mirror reality in the ancestral environment, an environment roughly like a hunter-gatherer society. Third, once the optimal strategy has been found, the experiment isn't over. The final step—the payoff—is to figure out what feelings would lead human beings to pursue that strategy. Those feelings, in theory, should be part of human nature; they should have evolved through generations and generations of the evolutionary game.

Trivers, at the suggestion of William Hamilton, employed a classic game called the prisoner's dilemma. Two partners in crime are being interrogated separately and face a hard decision. The state lacks the evidence to convict them of the grave offense they committed but does have enough evidence to convict both on a lesser charge—with, say, a one-year prison term for each. The prosecutor, wanting a harsher sentence, pressures each man individually to confess and implicate the other. He says to each: If you confess but your partner doesn't, I'll let you off scot-free and use your testimony to put him away for ten years. The flip side of this offer is a threat: If you *don't* confess but your partner does, *you* go to prison for ten years. And if you confess and it turns out your partner confesses too, I'll put you both away, but only for three years.[7]

If you were in the shoes of either prisoner, and weighed your options one-by-one, you would almost certainly decide to confess—to "cheat" on your partner. Suppose, first of all, that your partner cheats on you. Then you're better off cheating: you get three years in prison, as opposed to the ten you'd get if you stayed mum while he confessed. Now, suppose he doesn't cheat on you. You're still better off cheating: by confessing while he stays mum, you go free, whereas you'd get one year if you too kept your silence. Thus, the logic seems irresistible: betray your partner.

Yet if both partners follow this nearly irresistible logic, and cheat on each other, they end up with three years in jail, whereas both could have gotten off with one year had they stayed mutually faithful and kept their mouths shut. If only they were allowed to communicate and reach an agreement—then cooperation could emerge, and both would be better off. But they aren't, so how can cooperation emerge?

The question roughly parallels the question of how dumb animals, which can't make promises of repayment, or, for that matter, grasp the concept of repayment, could evolve to be reciprocally altruistic. Betraying a partner in crime while he stays faithful is like an animal's benefiting from an altruistic act and never returning the favor. Mutual betrayal is like neither animal's extending a favor in the first place: though both might benefit from reciprocal altruism, neither will risk getting burned. Mutual fidelity is like a single successful round of reciprocal altruism—a favor is extended and returned. But again: Why extend the favor if there's no guarantee of return?

The match between model and reality isn't perfect.[8] With reciprocal altruism there is a time lag between the altruism and its reciprocation, whereas the players in a prisoner's dilemma commit themselves concurrently. But this is a distinction without much of a difference. Because the prisoners can't communicate about their concurrent decisions, each is in the situation faced by prospectively altruistic animals: unsure whether any friendly overture will be matched. Further, if you keep pitting the same players against one another, game after game after game—an "iterated prisoner's dilemma"—each can refer to the other's past behavior in deciding how to act toward him in the future. Thus each player may reap in the future what he has sown in the past—just as with reciprocal altruism.

All in all, the match between model and reality is quite good. The logic that would lead to cooperation in an iterated prisoner's dilemma is fairly precisely the logic that would lead to reciprocal altruism in nature. The essence of that logic, in both cases, is non-zero-sumness.

NON-ZERO-SUMNESS

Suppose you are a chimp that has just killed a young monkey and you give some meat to a fellow chimp that has been short of food lately. Let's say you give him five ounces, and let's call that a five-point loss for you. Now, in an important sense, the other chimp's gain is larger than your loss. He was, after all, in a period of unusual need, so the real value of food to him—in terms of its contribution to his genetic proliferation—was unusually high. Indeed, if he were human, and could think about his plight, and were forced to sign a binding contract, he might rationally agree to repay five ounces of meat with, say, six ounces of meat right after payday next Friday. So he gets six points in this exchange, even though it cost you only five.

This asymmetry is what makes the game non-zero-sum. One player's gain isn't canceled out by the other player's loss. The essential feature of non-zero-sumness is that, through cooperation, or reciprocation, *both* players can be better off.[9] If the other chimp repays you at a time when meat is bountiful for him and scarce for you, then he sacrifices five points and you get six points. Both of you have emerged from the exchange with a net benefit of one point. A series of tennis sets, or of innings, or of golf holes eventually produces only one winner. The prisoner's dilemma, being a non-zero-sum game, is different. Both players can win if they cooperate. If caveman A and caveman B combine to hunt game that one man alone can't kill, both cavemen's families get a big meal; if there's no such cooperation, neither family does.

Division of labor is a common source of non-zero-sumness: you become an expert hide-splicer and give me clothes, I carve wood and give you spears. The key here—and in the chimpanzee example above, as well as in much non-zero-sumness—is that one animal's surplus item can be another animal's rare and precious good. It happens all the time. Darwin, recalling an exchange of goods with the Fuegian Indians, wrote of "both parties laughing, wondering, gaping at each other; we pitying them, for giving us good fish and crabs for rags, &c.; they grasping at the chance of finding people so foolish as to exchange such splendid ornaments for a good supper."[10]

To judge by many hunter-gatherer societies, division of economic labor wasn't dramatic in the ancestral environment. The most common commodity of exchange, almost surely, was information. Knowing where a great stock of food has been found, or where someone encountered a poisonous snake, can be a matter of life or death. And knowing who is sleeping with whom, who is angry at whom, who cheated whom, and so on, can inform social maneuvering for sex and other vital resources. Indeed, the sorts of gossip that people in all cultures have an apparently inherent thirst for—tales of triumph, tragedy, bonanza, misfortune, extraordinary fidelity, wretched betrayal, and so on—match up well with the sorts of information conducive to fitness.[11] Trading gossip (the phrase couldn't be more apt) is one of the main things friends do, and it may be one of the main reasons friendship exists.

Unlike food or spears or hides, information is shared without being actually surrendered, a fact that can make the exchange radically non-zero-sum.[12] Of course, sometimes information is of value only if hoarded. But often that's not the case. One Darwin biographer has written that, after scientific discussions between Darwin and his friend Joseph Hooker, "each vied with the other in claiming that the benefits he had received . . . far outweighted whatever return he might have been able to make."[13]

Non-zero-sumness is, by itself, not enough to explain the evolution of reciprocal altruism. Even in a non-zero-sum game, cooperation doesn't *necessarily* make sense. In the food-sharing example, though you gain one point from a single round of reciprocal altruism, you gain *six* points by cheating—accepting generosity and never returning it. So the lesson seems to be: if you can spend your life exploiting people, by all means do; the value of cooperation pales by comparison. Further, if you can't find people to exploit, cooperation *still* may not be the best strategy. If you're surrounded by people who are always trying to exploit you, then reciprocal exploitation is the way to cut your losses. Whether non-zero-sumness actually fuels the evolution of reciprocal altruism depends heavily on the prevailing social environment. The prisoner's dilemma will have to do more than simply illustrate non-zero-sumness if it is to be of much use here.

Testing theories, of course, is a general problem for evolutionary biologists. Chemists and physicists test a theory with carefully controlled experiments that either work as predicted, corroborating the theory, or don't. Sometimes evolutionary biologists can do that. As we've seen, researchers have nutritionally deprived pack rat mothers to see if they would, as predicted, then favor female offspring. But biologists can't experiment with human beings the way they do with pack rats, and they can't conduct the ultimate experiment: rewind the tape and replay evolution.

Increasingly, though, biologists can replay approximations of evolution. When Trivers laid out the theory of reciprocal altruism in 1971, computers were still exotic machines used by specialists; the personal computer didn't even exist. Though Trivers put the prisoner's dilemma to good analytical use, he didn't talk about actually *animating* it—creating, inside a computer, a species whose members regularly confront the dilemma and may live or die by it, and then letting natural selection take its course.

During the late 1970s, Robert Axelrod, an American political scientist, devised such a computer world and then set about populating it. Without mentioning natural selection—which wasn't, initially, his interest—he invited experts in game theory to submit a computer program embodying a strategy for the iterated prisoner's dilemma: a rule by which the program decides whether to cooperate on each encounter with another program. He then flipped the switch and let these programs mingle. The context for the competition nicely mirrored the social context of human, and prehuman, evolution. There was a fairly small society—several dozen regularly interacting individuals. Each program could "remember" whether each other program had cooperated on previous encounters, and adjust its own behavior accordingly.

After every program had had 200 encounters with every other program, Axelrod added up their scores and declared a winner. Then he held a second generation of competition after a systematic culling: each program was represented in proportion to its first-generation success; the fittest had survived. And so the game proceeded, generation after generation. If the theory of reciprocal altruism is correct, you would expect reciprocal altruism to "evolve" inside Axelrod's computer, to gradually dominate the population.

It did. The winning program, designed by the Canadian game theorist Anatol Rapoport (who had once written a book called *Prisoner's Dilemma*), was named TIT FOR TAT.[14] TIT FOR TAT was guided by the simplest of rules—literally: its computer program was five lines long, the shortest submitted. (So if the strategies had been created by random computer mutation, rather than by design, it probably would have been among the first to appear.) TIT FOR TAT was just what its name implied. On the first encounter with any program, it would cooperate. Thereafter, it would do whatever the other program had done on the previous encounter. One good turn deserves another, as does one bad turn.

The virtues of this strategy are about as simple as the strategy itself. If a program demonstrates a tendency to cooperate, TIT FOR TAT immediately strikes up a friendship, and both enjoy the fruits of cooperation. If a program shows a tendency to cheat, TIT FOR TAT cuts its losses; by withholding cooperation until that program reforms, it avoids the high costs of being a sucker. So TIT FOR TAT never gets repeatedly victimized, as indiscriminately cooperative programs do. Yet TIT FOR TAT also avoids the fate of the indiscriminately *un*cooperative programs that try to exploit their fellow programs: getting locked into mutually costly chains of mutual betrayal with programs that would be perfectly willing to cooperate if only you did. Of course, TIT FOR TAT generally forgoes the large one-time gains that can be had through exploitation. But strategies geared toward exploitation, whether through relentless cheating or repeated "surprise" cheating, tended to lose out as the game wore on. Programs quit being nice to them, so they were denied both the large gains of exploitation and the more moderate gains of mutual cooperation. More than the steadily mean, more than the steadily nice, and more than various "clever" programs whose elaborate rules made them hard for other programs to read, the straightforwardly conditional TIT FOR TAT was, in the long run, self-serving.

HOW TIT FOR TAT FEELS

TIT FOR TAT's strategy—do unto others as they've done unto you—gives it much in common with the average human being. Yet it has no human foresight. It doesn't *understand* the value of reciprocation. It just reciprocates. In that sense it is perhaps more like *Australopithecus*, our small-brained forebears.

What feelings would natural selection have instilled in an australopithecine to make it employ the clever strategy of reciprocal survive and reproduce, but to follow it more effectively, if more pliably; that as we evolve from a species whose males forcibly abduct females into a species whose males whisper sweet nothings, the whispering will be governed by the same logic as the abduction—it is a means of manipulating females to male ends, and its form serves this function. The basic emanations of natural selection are refracted from the older, inner parts of our brain all the way out to its freshest tissue. Indeed, the freshest tissue would never have appeared if it didn't toe natural selection's bottom line.

Of course, a lot *has* happened since our ancestors parted ways with the great apes' ancestors, and one can imagine a change in evolutionary context that would have removed our lineage from the logic that so imbalances the romantic interests of male and female in most species. Don't forget about the seahorses, sea snipes, Panamanian poison-arrow frogs, and Mormon crickets, with their reversed sex roles. And, less dramatically, but a bit closer to home, there are the gibbons, another of our primate cousins, whose ancestors waved good-bye to ours about twenty million years ago. At some point in gibbon evolution, circumstances began to encourage much male parental investment. The males regularly stick around and help provide for the kids. In one gibbon species the males actually carry the infants, something male apes aren't exactly known for. And talk about marital harmony: gibbon couples sing a loud duet in the morning, pointedly advertising their familial stability for the information of would-be home-wreckers.[42]

Well, human males too have been known to carry around infants, and to stay with their families. Is it possible that at some time over the last few million years something happened to us rather like what happened to the gibbons? Have male and female sexual appetites converged at least enough to make monogamous marriage a reasonable goal?

Chapter 3: **MEN AND WOMEN**

Judging from the social habits of man as he now exists, and from most savages being polygamists, the most probable view is that primeval man aboriginally lived in small communities, each with as many wives as he could support and obtain, whom he would have jealously guarded against all other men. Or he may have lived with several wives by himself, like the Gorilla. . . .

—*The Descent of Man* (1871)[1]

One of the more upbeat ideas to have emerged from an evolutionary view of sex is that human beings are a "pair-bonding" species. In its most extreme form, the claim is that men and women are designed for a lifetime of deep, monogamous love. This claim has not emerged from close scrutiny in pristine condition.

The pair-bond hypothesis was popularized by Desmond Morris in his 1967 book *The Naked Ape*. This book, along with a few other 1960s books (Robert Ardrey's *The Territorial Imperative*, for example), represent a would-be watershed in the history of evolutionary thought. That they found large readerships signaled a new openness to Darwinism, an encouraging dissipation of the fallout from its past political misuses. But there was no way, in the end, that these books could start a Darwinian renaissance within academia. The problem was simple: they didn't make sense.

One example surfaced early in Morris's pair-bonding argument. He was trying to explain why human females are generally faithful to their mates. This is indeed a good question (if you believe they are, that is). For high fidelity would place women in a distinct minority within the animal kingdom. Though female animals are generally less licentious than males, the females of many species are far from prudes, and this is particularly true of our nearest ape relatives. Female chimpanzees and bonobos are, at times, veritable sex machines. In explaining how women came to be so virtuous, Morris referred to the sexual division of labor in an early hunter-gatherer economy. "To begin with," he wrote, "the males had to be sure that their females were going to be faithful to them when they left them alone to go hunting. So the females had to develop a pairing tendency."[2]

Stop right there. It was in the reproductive interests of the *males* for the *females* to develop a tendency toward fidelity? So natural selection obliged the males by making the necessary changes in the females? Morris never got around to explaining how, exactly, natural selection would perform this generous feat.

Maybe it's unfair to single Morris out for blame. He was a victim of his times. The trouble was an atmosphere of loose, hyperteleological thinking. One gets the impression, reading Morris's book, and Ardrey's books, of a natural selection that peers into the future, decides what needs to be done to make things generally better for the species, and takes the necessary steps. But natural selection doesn't work that way. It doesn't peer ahead, and it doesn't try to make things generally better. Every single, tiny, blindly taken step either happens to make sense in immediate terms of genetic self-interest or it doesn't. And if it doesn't, you won't be reading about it a million years later. This was an essential message of George Williams's 1966 book, a message that had barely begun to take hold when Morris's book appeared.

One key to good evolutionary analysis, Williams stressed, is to focus on the fate of the gene in question. If a woman's "fidelity gene" (or her "infidelity gene") shapes her behavior in a way that helps get copies of *itself* into future generations in large numbers, then that gene will by definition flourish. Whether the gene, in the process, gets mixed in with her husband's genes or with the mailman's genes is by itself irrelevant. As far as natural selection is concerned, one vehicle is as good as the next. (Of course, when we talk about "a gene" for anything—fidelity, infidelity, altruism, cruelty—we are usefully oversimplifying; complex traits result from the interaction of numerous genes, each of which, typically, was selected for its incremental addition to fitness.)

A new wave of evolutionists has used this stricter view of natural selection to think with greater care about the question that rightly interested Morris: Are human males and females born to form enduring bonds with one another? The answer is hardly an unqualified yes for either sex. Still, it is closer to a yes for both sexes than it is in the case of, say, chimpanzees. In every human culture on the anthropological record, marriage—whether monogamous or polygamous, permanent or temporary—is the norm, and the family is the atom of social organization. Fathers everywhere feel love for their children, and that's a lot more than you can say for chimp fathers and bonobo fathers, who don't seem to have much of a clue as to which youngsters are theirs. This love leads fathers to help feed and defend their children, and teach them useful things.[3]

At some point, in other words, extensive *male parental investment* entered our evolutionary lineage. We are, as they say in the zoology literature, high in MPI. We're not so high that male parental investment typically rivals female parental investment, but we're a lot higher than the average primate. We indeed have something important in common with the gibbons.

High MPI has in some ways made the everyday goals of male and female humans dovetail, and, as any two parents know, it can give them a periodic source of common and profound joy. But high MPI has also created whole new ways for male and female aims to diverge, during both courtship and marriage. In Robert Trivers's 1972 paper on parental investment, he remarked, "One can, in effect, treat the sexes as if they were different species, the opposite sex being a resource relevant to producing maximum surviving offspring."[4] Trivers was making a specific analytical point, not a sweeping rhetorical one. But to a distressing extent—and an extent that was unclear before his paper—this metaphor does capture the overall situation; even with high MPI, and in some ways because of it, a basic underlying dynamic between men and women is mutual exploitation. They seem, at times, designed to make each other miserable.

WHY WE'RE HIGH IN MPI

There is no shortage of clues as to why men are inclined to help rear their young. In our recent evolutionary past lie several factors that can make parental investment worthwhile from the point of view of the male's genes.[5] In other words, because of these factors, genes inclining a male to love his offspring—to worry about them, defend them, provide for them, educate them—could flourish at the expense of genes that counseled continued remoteness.

One factor is the vulnerability of offspring. Following the generic male sexual strategy—roaming around, seducing and abandoning everything in sight—won't do a male's genes much good if the resulting offspring get eaten. That seems to be one reason so many bird species are monogamous, or at least relatively monogamous. Eggs left alone while the mother went out and hunted worms wouldn't last long. When our ancestors moved from the forests out onto the savanna, they had to cope with fleet predators. And this was hardly the only new danger to the young. As the species got smarter and its posture more upright, female anatomy faced a paradox: walking upright implied a narrow pelvis, and thus a narrow birth canal, but the heads of babies were larger than ever. This is presumably why human infants are born prematurely in comparison to other primates. From early on, baby chimps can cling to their mother while she walks around, her hands unencumbered. Human babies, though, seriously compromise a mother's food gathering. For many months, they're mounds of helpless flesh: tiger bait.

Meanwhile, as the genetic payoff of male investment was growing, the cost of investment was dropping. Hunting seems to have figured heavily in our evolution. With men securing handy, dense packages of protein, feeding a family was practical. It is probably no coincidence that monogamy is more common among carnivorous mammals than among vegetarians.

On top of all of this, as the human brain got bigger, it probably depended more on early cultural programming. Children with two

parents may have had an educational edge over children with only one.

Characteristically, natural selection appears to have taken this cost-benefit calculus and transmuted it into feeling—in particular, the sensation of love. And not just love for the *child;* the first step toward becoming a solid parental unit is for the man and woman to develop a strong mutual attraction. The genetic payoff of having two parents devoted to a child's welfare is the reason men and women can fall into swoons over one another, including swoons of great duration.

Until recently, this claim was heresy. "Romantic love" was thought to be an invention of Western culture; there were reports of cultures in which choice of mate had nothing to do with affection, and sex carried no emotional weight. But lately anthropologists mindful of the Darwinian logic behind attachment have taken a second look, and such reports are falling into doubt.[6] Love between man and woman appears to have an innate basis. In this sense, the "pair-bonding" hypothesis stands supported, though not for all the reasons Desmond Morris imagined.

At the same time, the term *pair bonding*—and for that matter, the term *love*—conveys a sense of permanence and symmetry that, as any casual observer of our species can see, is not always warranted. To fully appreciate how large is the gap between idealized love and the version of love natural to people, we need to do what Trivers did in his 1972 paper: focus not on the emotion itself, but on the abstract evolutionary logic it embodies. What are the respective genetic interests of males and females in a species with internal fertilization, an extended period of gestation, prolonged infant dependence on mother's milk, and fairly high male parental investment? Seeing these interests clearly is the only way to appreciate how evolution not only invented romantic love, but, from the beginning, corrupted it.

WHAT DO WOMEN WANT?

For a species low in male parental investment, the basic dynamic of courtship, as we've seen, is pretty simple: the male really wants sex; the female isn't so sure.[7] She may want time to (unconsciously) assess

Chapter 12: SOCIAL STATUS

Seeing how ancient these expressions are, it is no wonder that they are so difficult to conceal.—a man insulted may forgive his enemy & not wish to strike him, but he will find it far more difficult to look tranquil.—He may despise a man & say nothing, but without a most distinct will, he will find it hard to keep his lip from stiffening over his canine teeth.—He may feel satisfied with himself, & though dreading to say so, his step will grow erect & stiff like that of turkey.

—M Notebook (1838)[1]

Among the things Charles Darwin found troubling about the Fuegian Indians was their apparent lack of social inequality. "At present," he wrote in 1839, "even a piece of cloth is torn into shreds and distributed; and no one individual becomes richer than another." Such "perfect equality," he feared, would "for a long time retard their civilization." Darwin noted, by way of example, that "the inhabitants of Otaheite, who, when first discovered, were governed by hereditary kings, had arrived at a far higher grade than another branch of the same people, the New Zealanders—who although benefited by being compelled to turn their attention to agriculture, were republicans in the most absolute sense." The upshot: "In tierra del Fuego, until some chief shall arise with power sufficient to secure any acquired advantages, such as the domesticated animals or other valuable presents, it seems scarcely possible that the political state of the country can be improved."

Then Darwin added, "On the other hand, it is difficult to understand how a chief can arise till there is property of some sort by which he might manifest and still increase his authority."[2]

Had Darwin mulled this afterthought a little longer, he might have begun to wonder whether the Fuegians were, in fact, a people of "perfect equality." Naturally, to an affluent Englishman, reared amid servants, a society never far from starvation will seem starkly egalitarian. There will be no opulent displays of status, no gross disparities. But social hierarchy can assume many forms, and in every human society it seems to find one.

This pattern has been slow to come to light. One reason is that lots of twentieth-century anthropologists have, like Darwin, come from highly stratified societies, and been struck, sometimes charmed, by the relative classlessness of hunter-gatherer peoples. Anthropologists have been burdened, also, by a hopeful belief in the almost infinite malleability of the human mind, a belief fostered especially by Franz Boas and his famous students, Ruth Benedict and Margaret Mead. The Boasian bias against human nature was in some ways laudable—a well-meant reaction against crude political extensions of Darwinism that had countenanced poverty and various other social ills as "natural." But a well-meant bias is still a bias. Boas, Benedict, and Mead left out large parts of the story of humanity.[3] And among those parts are the deeply human hunger for status and the seemingly universal presence of hierarchy.

More recently, anthropologists of a Darwinian bent have started looking closely for social hierarchy. They have found it in even the least likely places.

The Ache, a hunter-gatherer people in South America, seem at first to possess an idyllic equality. Their meat goes into a communal pool, so the best hunters routinely aid their less fortunate neighbors. But during the 1980s, anthropologists took a closer look and found that the best hunters, though generous with meat, hoard a resource more fundamental. They have more extramarital affairs and more illegitimate children than lesser hunters. And their offspring have a better chance of surviving, apparently because they get special treatment.[4] Being known as a good hunter, in other words, is an informal rank that carries clout with men and women alike.

The Aka pygmies of central Africa also appear at first glance to be lacking in hierarchy, as they have no "headman," no ultimate political leader. But they do have a man called a *kombeti* who subtly but powerfully influences big group decisions (and who often earns that rank through his hunting prowess). And it turns out that the *kombeti* gets the lion's share of the food, the wives, and the offspring.[5]

And so it goes. As more and more societies are reevaluated in the unflattering light of Darwinian anthropology, it becomes doubtful that any truly egalitarian human society has ever existed. Some societies don't have sociologists, and thus may not have the *concept* of status, but they do have status. They have people of high status and low status, and everyone knows who is who. In 1945 the anthropologist George Peter Murdock, swimming against the prevailing Boasian current, published an essay called "The Common Denominator of Cultures," in which he ventured that "status differentiation" (along with gift giving, property rights, marriage, and dozens of other things) was a human universal.[6] The closer we look, the righter he seems.

In one sense, the ubiquity of hierarchy is a Darwinian puzzle. Why do the losers keep playing the game? Why is it in the genetic interest of the low men on the totem pole to treat their betters with deference? Why lend your energy to a system that leaves you with less than your neighbors?

One can imagine reasons. Maybe hierarchy makes the whole group so cohesive that most or all members benefit, even if they benefit unequally—exactly the fate that Darwin hoped would someday befall the Fuegians. In other words, maybe hierarchies serve "the good of the group" and are thus favored by "group selection." This theory was embraced by the popular writer Robert Ardrey, a prominent member of the generation of group selectionists whose decline marked the rise of the new Darwinian paradigm. If people weren't inherently capable of submission, Ardrey wrote, then "organized society would be impossible and we should have only anarchy."[7]

Well, maybe so. But judging by the large number of essentially asocial species, natural selection doesn't seem to share Ardrey's concern for social order. It is perfectly willing to let organisms pursue inclusive fitness amid anarchy. Besides, if you start thinking carefully about this group-selectionist scenario, problems arise. Granted, when two tribes meet in combat, or compete for the same resource, the more hierarchical and cohesive may win. But how did it get hierarchical and cohesive in the first place? How would genes counseling submission, and thus lowering fitness, manage to gain a foothold amid the everyday competition among genes within the society? Wouldn't they tend to be banished from the gene pool before they had a chance to demonstrate their goodness for the group? These are the questions group selection theories—such as Darwin's theory of the moral sentiments—often face and often fail to surmount.

The most widely accepted Darwinian explanation for hierarchy is simple, straightforward, and nicely compatible with observed reality. It is only with this theory in hand—only after taking a clear look at human social status, uncolored by morality and politics—that we can get back to the moral and political questions. In exactly what senses *is* social inequality inherent in human nature? Is inequality indeed, as Darwin suggested, a prerequisite for economic or political advancement? Are some people "born to serve" and others "born to lead"?

THE MODERN THEORY OF STATUS HIERARCHIES

Throw a bunch of hens together, and, after a time of turmoil, including much combat, things will settle down. Disputes (over food, say) will now be brief and decisive, as one hen simply pecks the other, bringing quick deferral. The deferrals form a pattern. There is a simple, linear hierarchy, and every hen knows its place. A pecks B with impunity, B pecks C, and so on. The Norwegian biologist Thorleif Schjelderup-Ebbe noticed this pattern in the 1920s and gave it the name "pecking order." (Schjelderup-Ebbe also observed, in a frenzy of politically loaded overextrapolation: "Despotism is the basic idea of the world, indissolubly bound up with all life and existence. . . . There is nothing that does not have a despot."[8] No wonder anthropologists shied away from evolutionary accounts of social hierarchy for so long.)

The order of the pecking is not arbitrary. B had a marked tendency to defeat C in early conflicts, and A tended to prevail over B. So it isn't, after all, such a great challenge to explain the emerging social hierarchy as merely the sum of individual self-interest. Each hen is deferring to hens that will probably win anyway, saving itself the costs of battle.

If you've spent much time with chickens, you may doubt their ability to process a thought as complex as "Chicken A will beat me anyway, so why bother to fight?" Your doubt is well placed. Pecking orders are yet another case where the "thinking" has been done by natural selection, and so needn't be done by the organism. The organism must be able to tell its neighbors apart, and to feel a healthy fear of the ones that have brutalized it, but it needn't grasp the logic behind the fear. Any genes endowing a chicken with this selective fear, reducing the time spent in futile and costly combat, should flourish.

Once such genes pervade the population, hierarchy is part of the social architecture. The society may look, indeed, as if designed by someone who valued order over liberty. But that doesn't mean it was. As George Williams put it in *Adaptation and Natural Selection*, "The dominance-subordination hierarchy shown by wolves and a wide variety of vertebrates and arthropods is not a functional organization. It is the statistical consequence of a compromise made by each individual in its competition for food, mates, and other resources. Each compromise is adaptive, but not the statistical summation."[9]

This isn't the only conceivable explanation of hierarchy that skirts the pitfalls of group selectionism. Another is based on John Maynard Smith's concept of an evolutionarily stable state—more specifically, on his "hawk-dove" analysis of a hypothetical bird species. Imagine dominance and submission as two genetically based strategies, the success of each depending on their relative frequency. Being a dominant (for example, walking around intimidating submissives into giving you half their food) is fine so long as there are lots of submissives around. But as the strategy spreads, it grows less fruitful: there are fewer and fewer submissives to exploit, and meanwhile dominants encounter one another more and more, engaging in costly combat. That's why the submissive strategy can thrive; a submissive animal must often surrender some of its food, but it avoids the fighting that takes an increasingly large toll on dominants. The population should in theory equilibrate, with a fixed ratio of dominants to submissives. And, as with all evolutionarily stable states (recall the bluegill sunfish from chapter three), this equilibrium ratio is the point at which each strategy enjoys the same reproductive success.[10]

There are species that this explanation seems to fit. Among Harris sparrows, darker birds are aggressive and dominant, and lighter ones more passive and submissive. Maynard Smith has found indirect evidence that the two strategies are equally conducive to fitness—the hallmark of an evolutionarily stable state.[11] But when we move to the human species—and, indeed, when we move to other hierarchical species—this explanation for social hierarchy encounters problems. Prominent among them is the number of findings—in the Ache, the Aka, many other human societies, and many other species—that low status brings low reproductive success.[12] This is not the hallmark of an evolutionarily stable mix of strategies. It is the hallmark of low-status animals trying to make the best of a bad situation.

For decades, while many anthropologists have downplayed social hierarchy, psychologists and sociologists have studied its dynamics, watching the facility with which members of our species sort themselves out. Put a group of children together, and before long they fall into distinct grades. The ones at the top are best liked, most frequently imitated, and, when they try to wield influence, best obeyed.[13] The rudiments of this tendency are seen among children only a year old.[14] At first, status equals toughness—high-ranking children are the ones that don't back down—and indeed, for males, toughness matters well through adolescence. But as early as kindergarten, some children ascend the hierarchy via skill in cooperation.[15] Other talents—intellectual, artistic—also carry weight, especially as we grow older.

Many scholars have studied these patterns without bringing a Darwinian slant to their work, but it's hard not to suspect an innate underpinning for such robotic patterns of learning. Besides, status hierarchies run in our family. They emerge with great clarity and complexity in our nearest relatives, the chimps and bonobos, and are found also, if in simpler form, in gorillas, our next closest kin, and in many other primates.[16] If you took a zoologist from another planet, showed him our family tree, and pointed out that the three species nearest our limb were inherently hierarchical, he would probably guess that we are too. If you then told him that hierarchy is indeed found in every human society where people have looked closely for it, and among children too young to talk, he might well consider the case closed.

There is more evidence. Some of the ways people signify their status, and the status of others, seem to hold steady across cultures. Darwin himself, after widely questioning missionaries and other world travelers, concluded that "scorn, disdain, contempt, and disgust are expressed in many different ways, by movements of the features, and by various gestures; and that these are the same throughout the world." He also noted that "a proud man exhibits his sense of superiority over others by holding his head and body erect."[17] A century later, studies would show that posture becomes straighter immediately after social triumph—as, say, when a student gets a high test score.[18] And the ethologist Irenaüs Eibl-Eibesfeldt would find that children in diverse cultures, after losing a fight, lower their heads in self-abasement.[19] These universals of expression have reflections within. People in all cultures feel pride upon social success, embarrassment, even shame, upon failure, and, at times, anxiety pending these outcomes.[20]

Nonhuman primates send some of the same status signals as people. Dominant male chimps—and dominant primates generally—strut proudly and expansively. And after two chimpanzees fight over status, the loser crouches abjectly. This sort of bowing is thereafter repeated to peacefully express submission.

STATUS, SELF-ESTEEM, AND BIOCHEMISTRY

Beneath the behavioral parallels between human and nonhuman primates lie biochemical parallels. In vervet monkey societies, dominant males have more of the neurotransmitter serotonin than do their subordinates. And one study found that in college fraternities, officers, on average, have more serotonin than do their less powerful fraternity brothers.[21]

This is a good opportunity to extinguish a once-flourishing misconception that, though in decline, has yet to die its richly deserved death. It is *not* the case that all behavior under "hormonal control," or some other "biological control," is "genetically determined." Yes, there is a correlation between serotonin (a hormone, like all neurotransmitters) and social status. But no, that doesn't mean that a given person's social status was "in the genes," preordained at birth. If you check the serotonin levels of a fraternity president well before his political ascent, or of an alpha vervet monkey well before his, you may find them unexceptional.[22] Serotonin level, though a "biological" thing, is largely a product of the social environment. It isn't nature's way of destining people at birth for leadership; it's nature's way of equipping them for leadership once they've gotten there (and, some evidence suggests, of encouraging them to make a bid for leadership at a politically opportune moment).[23] You too can have a high serotonin level, if you can get elected president of a college fraternity.

Certainly genetic differences matter. Some people's genes dispose them to be unusually ambitious, or clever, or athletic, or artistic, or various other things—including unusually rich in serotonin. But these traits depend, for their flowering, on the environment (and sometimes on each other), and their eventual translation into status can rest heavily on chance. No one is born to lead, and no one is born to follow. And to the extent that some people are born with a leg up in the race (as they surely are), that birthright probably lies at least as much in cultural as in genetic advantage. In any event, there are good Darwinian reasons to believe that *everyone* is born with the capacity for high serotonin—with the equipment to function as a high-status primate given a social setting conducive to their ascent. The whole point of the human brain is behavioral flexibility, and it would be very unlike natural selection, given that flexibility, to deny anyone a chance at the genetic payoffs of high status, should the opportunity arise.

What does serotonin do? The effect of neurotransmitters is so subtle, and so dependent on chemical context, that simple generalizations are risky. But often, at least, serotonin seems to relax people,