

THE RED QUEEN

*Sex and the Evolution of
Human Nature*

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For Matthew

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Chapter 4

GENETIC MUTINY AND
GENDER

*The turtle lives
'twixt plated decks
Which practically conceal its sex.
I think it clever of the turtle
In such a fix to be so fertile.*

—Ogden Nash

In the Middle Ages, the archetypal British village owned one common field for grazing cattle. Every villager shared the common and was allowed to graze as many cattle on it as he wanted. The result was that the common was often overgrazed until it could support only a few cattle. Had each villager been encouraged to exercise a little restraint, the common could have supported far more cattle than it did.

This "tragedy of the commons"¹ has been repeated again and again throughout the history of human affairs. Every sea fishery that has ever been exploited is soon overfished and its fishermen driven into penury. Whales, forests, and aquifers have been treated in the same way. The tragedy of the commons is, for economists, a matter of ownership. The lack of a single ownership of the commons or the fishery means that everybody shares equally in the cost of overgrazing or overfishing. But the individual who grazes one too many cows or the fisherman who catches one too many netfuls still gets the whole of the reward of that cow or netful. So he reaps the benefits privately and shares the costs publicly. It is a one-way ticket to riches for the individual and a one-way ticket to poverty for the village. Individually rational behavior leads to a collectively irrational outcome. The free-rider wins at the expense of the good citizen.

Exactly the same problem plagues the world of the genes. It is, oddly, the reason that boys are different from girls.

WHY ARE PEOPLE NOT HERMAPHRODITES?

None of the theories discussed so far explains why there are two separate genders.² Why is every creature not a hermaphrodite, mixing its genes with those of others, but avoiding the cost of maleness by being a female, too? For that matter, why are there two genders at all, even in hermaphrodites? Why not just give each other parcels of genes, as equals? "Why sex?" makes no sense without "why sexes?" As it happens, there is an answer. This chapter is about perhaps the strangest of all the Red Queen theories, the one that goes under the unprepossessing name of "intragenomic conflict." Translated, it is about harmony and selfishness, about conflicts of interest between genes inside bodies, about free-rider genes and outlaw genes. And it claims that many of the features of a sexual creature arose as reactions to this conflict, not to be of use to the individual. It "gives an unstable, interactive, and historical character to the evolutionary process."³

The seventy-five thousand pairs of genes that make and run the average human body find themselves in much the same position as seventy-five thousand human beings inhabiting a small town. Just as human society is an uneasy coexistence of free enterprise and social cooperation, so is the activity of genes within a body. Without cooperation, the town would not be a community. Everybody would lie and cheat and steal his way to wealth at the expense of everybody else, and all social activities—commerce, government, education, sport—would grind to a mistrustful halt. Without cooperation between the genes, the body they inhabit could not be used to transmit those genes to future generations because it would never get built.

A generation ago, most biologists would have found that paragraph baffling. Genes are not conscious and do not choose to cooperate; they are inanimate molecules switched on and off by chemical messages. What causes them to work in the right order and create a human body is some mysterious biochemical program, not a democratic decision. But in the last few years the revolution begun by Williams, Hamilton, and others has caused more and

more biologists to think of genes as analogous to active and cunning individuals. Not that genes are conscious or driven by future goals—no serious biologist believes that—but the extraordinary teleological fact is that evolution works by natural selection, and natural selection means the enhanced survival of genes that enhance their own survival. Therefore, a gene is by definition the descendant of a gene that was good at getting into future generations. A gene that does things that enhance its own survival may be said, teleologically, to be doing them *because* they enhance its survival. Cooperating to build a body is as effective a survival “strategy” for genes as cooperating to run a town is a successful social strategy for human beings.

But society is not all cooperation; a measure of competitive free enterprise is inevitable. A gigantic experiment called communism in a laboratory called Russia proved that. The simple, beautiful suggestion that society should be organized on the principle “from each according to his ability, to each according to his need” proved disastrously unrealistic because each did not see why he should share the fruits of his labors with a system that gave him no reward for working harder. Enforced cooperation of the Communist kind is as vulnerable to the selfish ambitions of the individual as a free-for-all would be. Likewise, if a gene has the effect of enhancing the survival of the body it inhabits but prevents that body from breeding or is never itself transmitted through breeding, then that gene will by definition become extinct and its effect will disappear.

Finding the right balance between cooperation and competition has been the goal and bane of Western politics for centuries. Adam Smith recognized that the economic needs of the individual are better met by unleashing the ambitions of all individuals than by planning to meet those needs in advance. But even Adam Smith could not claim that free markets produce Utopia. Even the most libertarian politician today believes in the need to regulate, oversee, and tax the efforts of ambitious individuals so as to ensure that they do not satisfy their ambitions entirely at the expense of others. In the words of Egbert Leigh, a biologist at the Smithsonian Tropical Research Institute, “Human intelligence has yet to design

a society where free competition among the members works for the good of the whole.”⁴ The society of genes faces exactly the same problem. Each gene is descended from a gene that unwittingly jostled to get into the next generation by whatever means was in its power. Cooperation between them is marked, but so is competition. And it is that competition that led to the invention of gender.

As life emerged from the primeval soup several billion years ago, the molecules that caused themselves to be replicated at the expense of others became more numerous. Then some of those molecules discovered the virtues of cooperation and specialization, so they began to assemble in groups called chromosomes to run machines called cells that could replicate these chromosomes efficiently. In just the same way little groups of agriculturalists joined with blacksmiths and carpenters to form cooperative units called villages. The chromosomes then discovered that several kinds of cells could merge to form a supercell, just as villages began to group together as tribes. This was the invention of the modern cell from a team of different bacteria. The cells then grouped together to make animals and plants and fungi, great big conglomerates of conglomerates of genes, just as tribes merged into countries and countries into empires.⁵

None of this would have been possible for society without laws to enforce the social interest over the individual, selfish drive; it was the same with genes. A gene has only one criterion by which posterity judges it: whether it becomes an ancestor of other genes. To a large extent it must achieve that at the expense of other genes, just as a man acquires wealth largely by persuading others to part with it (legally or illegally). If the gene is on its own, all other genes are its enemies—every man for himself. If the gene is part of a coalition, then the coalition shares the same interest in defeating a rival coalition, just as employees of Hertz share the same interest in its thriving at the expense of Avis.

This broadly describes the world of viruses and bacteria. They are disposable vehicles for simple teams of genes, each team highly competitive with other teams but with largely harmonious relations among team members. For reasons that will soon become

apparent, this harmony breaks down when bacteria merge to become cells and cells merge to become organisms. It has to be reasserted by laws and bureaucracies.

And even at the bacterial level it does not entirely hold true. Consider the case of a new, supercharged mutant gene that appears in a bacterium. It is superior to all other genes of its type, but its fate is determined largely by the quality of its team. It is like a brilliant engineer finding himself employed by a doomed, small firm or a brilliant athlete stuck on a second-rate team. Just as the engineer or the athlete seeks a transfer, so we might expect that bacterial genes would have invented a way to transfer themselves from one bacterium to another.

They have. It is called "conjugation," and it is widely agreed to be a form of sex itself. Two bacteria simply connect to each other by a narrow pipe and shunt some copies of genes across. Unlike sex, it has nothing to do with reproduction, and it is a relatively rare event. But in every other respect it is sex. It is genetic trade.

Donal Hickey of the University of Ottawa and Michael Rose of the University of California at Irvine were the first to suggest in the early 1980s that bacterial "sex" was invented not for the bacteria but for the genes—not for the team but for the players.⁶ It was a case of a gene achieving its selfish end at the expense of its teammates, abandoning them for a better team. Their theory is not a full explanation of why sex is so common throughout the animal and plant kingdoms; it is not a rival to the theories discussed heretofore. But it does suggest how the whole process got itself started. It suggests an origin for sex.

From the point of view of an individual gene, then, sex is a way to spread laterally as well as vertically. If a gene were able to make its owner-vehicle have sex, therefore, it would have done something to its own advantage (more properly, it would be more likely to leave descendants if it could), even if it were to the disadvantage of the individual. Just as the rabies virus makes the dog want to bite anything, thus subverting the dog to its own purpose of spreading to another dog, so a gene might make its owner have sex just to get into another lineage.

Hickey and Rose are especially intrigued by genes called transposons, or jumping genes, that seem to be able to cut themselves out of chromosomes and stitch themselves back into other chromosomes. In 1980 two teams of scientists simultaneously came to the conclusion that the transposons seemed to be examples of "selfish" or parasitic DNA, which spreads copies of itself at the expense of other genes. Instead of looking for some reason that transposons exist for the benefit of the individual, as scientists had done before, they simply saw it as bad for the individual and good for the transposons.⁷ Muggers and outlaws do not exist for the benefit of society but to its detriment and for the benefit of themselves. Perhaps transposons were, in Richard Dawkins's words, "outlaw genes."⁸ Hickey then noticed that transposons were much more common among outbreeding sexual creatures than among inbreeding or asexual ones. He ran some mathematical models which showed that parasitic genes would do well even if they had a bad effect on the individual they inhabited. He even found some cases of parasitic genes of yeast that spread quickly in sexual species and slowly in asexual ones. Such genes were on "plasmids," or separate little loops of DNA, and it turns out that in bacteria such plasmids actually provoke the very act of conjugation by which they spread. They are like rabies viruses making dogs bite one another. The line between a rogue gene and an infectious virus is a blurred one.⁹

NOBODY IS DESCENDED FROM ABEL

Despite this little rebellion, life is fairly harmonious in the bacterial team. Even in a more complicated organism such as an amoeba, formed by an agglomeration of ancestral bacteria sometime in the distant past,¹⁰ there is little difference between the interests of the team and the individual members. But in more complicated creatures the opportunities for genes to thrive at the expense of their fellows are greater.

The genes of animals and plants turn out to be full of half-

suppressed mutinies against the social harmony. In some female flour beetles there exists a gene called *Medea* that kills those offspring that do *not* inherit it.¹¹ It is as if the gene booby-traps all the female's young and defuses only those that it itself inhabits. Whole selfish chromosomes called B chromosomes exist that do nothing but ensure their transmission to the next generation by invading every egg the insect makes.¹² Another insect, a scale insect, has an even more bizarre genetic parasite. When its eggs are fertilized, sometimes more than one sperm penetrates the egg. If this happens, one of the sperm fuses with the egg's nucleus in the normal way; the spare sperm hang around and begin dividing as the egg divides. When the creature matures, the parasitic sperm cells eat out its gonads and replace them with themselves. So the insect produces sperm or eggs that are barely related to itself, an astonishing piece of genetic cuckoldry.¹³

The greatest opportunity for selfish genes comes during sex. Most animals and plants are diploid: Their genes come in pairs. But diploidy is an uneasy partnership between two sets of genes, and when partnerships end, things often get acrimonious. The partnerships end with sex. During meiosis, the central genetic procedure of sex, the paired genes are separated to make haploid sperm and eggs. Suddenly each gene has an opportunity to be selfish at its partner's expense. If it can monopolize the eggs or sperm, it thrives and its partner does not.¹⁴

This opportunity has been explored in recent years by a group of young biologists, prominent among them Steve Frank of the University of California at Irvine, and Laurence Hurst, Andrew Pomiankowski, David Haig, and Alan Grafen at Oxford University. Their logic goes like this: When a woman conceives, her embryo gets only half of her genes. They are the lucky ones; the unlucky other half languish in obscurity in the hope of another toss of the coin when she next breeds. For, to recapitulate, you have twenty-three pairs of chromosomes, twenty-three from your father and twenty-three from your mother. When you make an egg or a sperm, you pick one from each pair to give a total of twenty-three chromosomes. You could give all the ones you inherited from your mother

or all the ones from your father, or more likely a mixture of the two. Now a selfish gene that loaded the dice so that it stood a better than fifty-fifty chance of getting into the embryo might do rather well. Suppose it simply killed off its opposite number, the one that came from the other grandparent of the embryo.

Such a gene exists. On chromosome two of a certain kind of fruit fly there is a gene called "segregation distorter," which simply kills all sperm containing the other copy of chromosome two. The fly therefore produces half as much sperm as normal. But all of the sperm contains the segregation distorter gene, which has thereby ensured a monopoly of the fly's offspring.¹⁵

Call such a gene Cain. Now it so happens that Cain is Abel's virtually identical twin, so he cannot kill his brother without killing himself. This is because the weapon he uses against Abel is merely a destructive enzyme released into the cell—a chemical weapon, as it were. His only hope is to attach to himself a device that protects him—a gas mask (though it in fact consists of a gene that repels the destructive enzyme). The "mask of Cain" protects him from the gas he uses against Abel. Cain becomes an ancestor, and Abel does not. Thus a gene for chromosomal fratricide will spread as surely as a murderer will inherit the Earth. Segregation distorters and other fratricidal genes go under the general name of "meiotic drive" because they drive the process of meiosis, the division of the partnerships, into a biased outcome.¹⁶

Meiotic-drive genes are known in flies and mice and a few other creatures, but they are rare. Why? For the same reason that murder is rare. The interest of the other genes has been reasserted through laws. Genes, like people, have other things to do than kill each other. Those genes that shared Abel's chromosome and died with him would have survived had they invented some technique to foil Cain. Or, to put it another way, genes that foil meiotic drivers will spread as surely as meiotic drivers will spread. A Red Queen race is the result.

David Haig and Alan Grafen believe that such a response is indeed common and that it consists of a sort of genetic scrambling, the swapping of chunks of chromosomes. If a chunk of chromo-

some lying next to Abel suddenly swapped places with the chunk lying next to Cain, then the mask of Cain would be unceremoniously removed from Cain's chromosome and plonked onto Abel's. The result: Cain would commit suicide, and Abel would live happily ever after.¹⁷

This swapping is called "crossing over." It happens between virtually all pairs of chromosomes in most species of animal and plant. It achieves nothing except a more thorough mixing of the genes—which is what most people thought its purpose was before Haig and Grafen suggested otherwise. But Haig and Grafen are implying that crossing over need not serve any such function; it is merely a piece of intracellular law enforcement. In a perfect world policemen would not exist because people would never commit murder. Policemen were not invented because they adorn society but because they prevent the disruption of society. So, according to the Haig-Grafen theory, crossing over polices the division of chromosomes to keep it fair.

This is not, by its nature, the sort of theory that lends itself to easy confirmation. As Haig remarks, in a dry Australian manner, crossing over is like an elephant repellent. You know it's working because you don't see any elephants.¹⁸

Cain genes survive in mice and flies by hugging their masks close to them so that they are not likely to be parted by crossing over. But there is one pair of chromosomes that is especially plagued by Cain genes, the "sex chromosomes," because these peculiar chromosomes do not engage in crossing over. In people and many other animals, gender is determined by genetic lottery. If you receive a pair of X chromosomes from your parents, you become a female; if you receive an X and a Y, you become a male (unless you are a bird, spider, or butterfly, in which case it is the other way around). Because Y chromosomes contain the genes for determining maleness, they are not compatible with Xs and do not cross over with them. Consequently, a Cain gene on an X chromosome can safely kill the Y chromosome and not risk suicide. It biases the sex ratio of the next generation in favor of females, but that is a cost borne by the whole population equally, whereas the benefit

of monopolizing the offspring is received by the Cain gene itself—just as in the case of free-riders causing the tragedy of the commons.¹⁹

IN PRAISE OF UNILATERAL DISARMAMENT

By and large, however, the common interest of the genes prevails over the ambitions of the outlaws. As Egbert Leigh has put it, “a parliament of genes” asserts its will. Yet the reader may be getting restless. “This little tour of the cellular bureaucracy,” he says, “fun though it was, has brought us no closer to the question asked at the beginning of the chapter—why there are two genders.”²⁰

Have patience. The road we have chosen—to seek conflicts between sets of genes—leads to the answer. For gender itself may prove to be a piece of cellular bureaucracy. A male is defined as the gender that produces sperm or pollen: small, mobile, multitudinous gametes. A female produces few, large, immobile gametes called eggs. But size is not the only difference between male and female gametes. A much more significant difference is that there are a few genes that come only from the mother. In 1981 two scientists at Harvard whose perspicacity we will reencounter throughout the book, Leda Cosmides and John Tooby, pieced together the history of an even more ambitious genetic rebellion against this parliament of genes, one that forced the evolution of animals and plants into strange new directions and resulted in the invention of two genders.²¹

So far I have treated all genes as similar in their pattern of inheritance. But this is not quite accurate. When a sperm fertilizes an egg, it donates just one thing to that egg: a bagful of genes called a nucleus. The rest of it stays outside the egg. A few of the father’s genes are left behind because they are not in the nucleus at all; they are in little structures called “organelles.” There are two main kinds of organelles, mitochondria, which use oxygen to extract energy from food, and chloroplasts (in plants), which use sunlight to make food from air and water. These organelles are

almost certainly the descendants of bacteria that lived inside cells and were “domesticated” because their biochemical skills were of use to the host cells. Being descendants of free-living bacteria, they came with their own genes, and they still have many of these genes. Human mitochondria, for example, have thirty-seven genes of their own. To ask, “Why are there two genders?” is to ask, “Why are organelle genes inherited through the maternal line?”²² Why not just let the sperm’s organelles into the egg, too? Evolution seems to have gone to extraordinary lengths to keep the father’s organelles out. In plants a narrow constriction prevents the father’s organelles from passing into the pollen tube. In animals the sperm is given a sort of strip search as it enters the egg to remove all the organelles. Why should this be?

The answer lies in the exception to this rule: an alga called *Chlamydomonas* that has two genders called plus and minus rather than male and female. In this species the two parents’ chloroplasts engage in a war of attrition that destroys 95 percent of them. The 5 percent remaining are those of the plus parent, which by force of sheer numbers overwhelm the minus ones.²³ This war impoverishes the whole cell. The nuclear genes take the same dim view of it as the prince takes in *Romeo and Juliet* of the war between two of his subjects:

*Rebellious subjects, enemies to peace,
 Profaners of this neighbour-stained steel, —
 Will they not bear? What, ho! you men, you beasts,
 That quench the fire of your pernicious rage
 With purple fountains issuing from your veins,
 On pain of torture, from those bloody hands
 Throw your mistemper’d weapons to the ground,
 And hear the sentence of your moved prince.
 Three civil brawls, bred of an airy word,
 By thee, Old Capulet, and Montague,
 Have thrice disturb’d the quiet of our streets.
 . . . If ever you disturb our streets again,
 Your lives shall pay the forfeit of the peace.*

As the prince soon discovers, even this severe sentence is insufficient to suppress the quarrel. Had he followed the example of the nuclear genes, he would have killed all the Montagues. The nuclear genes of both father and mother between them arrange that the organelles of the male are slaughtered. It is an advantage (to the male nucleus, not to the male organelles) to be of the type that allows its organelles to be killed, so that a viable offspring results. So owners of docile, suicidal organelles (in the minus gender) would proliferate. Soon any deviation from a ratio of fifty-fifty killers and victims would benefit the rarer type and cause the ratio to correct itself. Two genders have been invented: killer, which provides the organelles, and victim, which does not.

Laurence Hurst of Oxford uses these arguments to predict that two genders are a consequence of sex by fusion. That is, where sex consists of the fusing of two cells, as in *Chlamydomonas* and most animals and plants, you find two genders. Where it consists of "conjugation"—the formation of a pipe between the two cells and the transfer of a nucleus of genes down the pipe—and there is no fusion of cells, then there is no conflict and no need for killer and victim genders. Sure enough, in those species with sex by conjugation, such as ciliated protozoa and mushrooms, there are many different genders. In those species with sex by fusion, there are almost invariably two genders. In one especially satisfying case there is a "hypotrich" ciliate that can have sex in either fashion. When it has fusion sex, it behaves as if it had two genders. When it has conjugation sex, there are many genders.

In 1991, just as he was putting the finishing touches on this tidy story, Hurst came across a case that seemed to contradict it: a form of slime-mold that has thirteen genders and fusion sex. But he delved deeper and discovered that the thirteen genders were arranged in a hierarchy. Gender thirteen always contributes the organelles, whomever it mates with. Gender twelve contributes them only if it mates with gender eleven and downward. And so on. This works just as well as having two genders but is a great deal more complicated.²⁴

SAFE SEX TIPS FOR SPERM

Along with most of the animal and plant kingdoms, we practice fusion sex and we have two genders. But it is a much modified form of fusion sex. Males do not submit their organelles to be slaughtered; they leave them behind at the border. The sperm carries just a nucleus cargo, a mitochondrial engine, and a flagellum propeller. The sperm-making cells go to great lengths to strip off the rest of the cytoplasm before the sperm is complete and redigest it at some expense. Even the propeller and engine are jettisoned when the sperm meets the egg; only the nucleus travels farther.

Hurst explains this by raising once again the matter of disease.²⁵ Organelles are not the only genetic rebels inside cells; bacteria and viruses are there as well. And exactly the same logic applies to them as to organelles. When cells fuse, the rival bacteria in each engage in a struggle to the death. If a bacterium living happily inside an egg suddenly finds its patch invaded by a rival carried by a sperm, it will have to compete, and that might well mean abandoning its latency and manifesting itself as disease. There is ample evidence that diseases are reawakened by other "rival" infections. For example, the virus that causes AIDS, known as HIV, infects human brain cells but lies dormant there. If, however, cytomegalovirus, an entirely different kind of virus, infects a brain cell already infected with HIV, then the effect is to reawaken the HIV virus, which proliferates rapidly. This is one of the reasons HIV seems more likely to go on to cause AIDS if the infected person gets a second, complicating infection. Also, one of the features of AIDS is that all sorts of normally innocuous bacteria and viruses, such as Pneumocystis, or cytomegalovirus or herpes, which live calmly inside many of our bodies, can suddenly become virulent and aggressive during the progression of AIDS. This is partly because AIDS is a disease of the immune system, and immune surveillance of these diseases is therefore lifted, but it also makes evolutionary sense. If your host is going to die, you had better multiply as fast as possible. So-called opportunist infections there-

fore hit you when you are down. Incidentally, one scientist has suggested that the cross-reactivity of the immune system (infection with one strain causes immune resistance to another strain of the same species of parasite) might be the parasite's way of slamming the door on rival members of its species once it is inside.²⁶

If it pays a parasite to go for broke when a rival appears, then it pays a host to prevent cross-infection with two strains of parasite. And nowhere is the risk of cross-infection greater than during sex. A sperm fusing with an egg risks bringing its cargo of bacteria and viruses as well; their arrival would awaken the egg's own parasites and cause a battle for possession that would leave the egg sick or dead. To avoid this, therefore, the sperm tries to avoid bringing into the egg material that might harbor bacteria or viruses. It passes just the nucleus into the egg. Safe sex indeed.

Proof of this theory will be hard to come by, but suggestive support comes from *Paramecium*, a protozoan that mates by conjugation—passing spare nuclei through a narrow tube. The procedure is hygienic in the sense that only the nuclei travel through the tube. Two paramecia stay linked for only two minutes or so; any longer and cytoplasm would also pass through the tube. The tube is too narrow even for the nucleus, which only just squeezes through. And it may be no accident that *Paramecium* and its relatives are the only creatures that possess such tiny nuclei, which are used as stores of genes (“coding vaults” they have been called) and from which larger, working copies are made for everyday use.²⁷

DECISION TIME

Gender, then, was invented as a means of resolving the conflict between the cytoplasmic genes of the two parents. Rather than let such conflict destroy the offspring, a sensible agreement was reached: All the cytoplasmic genes would come from the mother, none from the father. Since this made the father's gametes smaller, they could specialize in being more numerous and mobile, the better to find eggs. Gender is a bureaucratic solution to an antisocial habit.

This explains why there are two genders, one with small gametes, the other with large ones. But it does not explain why every creature cannot have both genders on board. Why are people not hermaphrodites? Were I a plant, the question might not arise: Most plants are hermaphrodites. There is a general pattern for mobile creatures to be "dioecious" (with separate genders) and sessile creatures, such as plants and barnacles, to be hermaphroditic. This makes a sort of ecological sense. Given that pollen is lighter than seed, a flower that produces only seed can have only local offspring. One that also produces pollen can generate plants that spread far and wide. A law of diminishing returns applies to seed but not to pollen.

But it does not explain why animals took a different route. The answer lies in those muttering organelles left behind at the gate when the sperm entered the egg. In a male any gene in an organelle is in a cul-de-sac because it will be left behind by the sperm. All of the organelles in your body and all of the genes in them came from your mother; none came from your father. This is bad news for the genes, whose life's work, remember, is to pass into the next generation. Every man is a dead end for organelle genes. Not surprisingly, there is a "temptation" for such genes to invent solutions to their difficulty (that is, those that do solve the problem spread at the expense of those that do not). The most attractive solution for an organelle gene in a hermaphrodite is to divert all of the owner's resources into female and away from male reproduction.

This is not pure fantasy. Hermaphrodites are in a state of constant battle against rebellious organelle genes trying to destroy their male parts. Male-killer genes have been found in more than 140 species of plant. They grow flowers, but the male anthers are stunted or withered: Seed but no pollen is produced. Invariably the cause of this sterility is a gene that lies inside an organelle, not a nuclear gene. By killing the anthers, the rebellious gene diverts more of the plant's resources into female seed, through which it can be inherited. The nucleus has no such bias toward females; indeed, if the rebels are achieving their aims in many members of the species, the nucleus would benefit greatly from being the only

plant on the block capable of producing pollen. So wherever they appear, male-sterility genes are soon blocked by nuclear fertility restorers. In maize, for example, there are two male-sterility organelle genes, each suppressed by a separate nuclear restorer. In tobacco there are no less than eight such pairs of genes. By hybridizing different strains of maize, plant breeders can release the male-sterile genes from nuclear suppression because the suppressor from one parent no longer recognizes the rebel from the other. They wish to do this because a field of male-sterile maize cannot fertilize itself. By planting a different, male-fertile strain among it, the breeders can collect hybrid seed. And hybrid seed, benefiting from the mysterious boost known as hybrid vigor, out-yields both its parents. Male-sterile/female-fertile strains of sunflower, sorghum, cabbage, tomato, maize, and other crops are a mainstay of farmers all over the world.²⁸

It is easy to spot when male-sterile genes are at work. The plants have two types: hermaphrodite and female. Such populations of plants are known as gynodioecious; androdioecious plants, with males and hermaphrodites only, are almost unknown. In wild thyme, for example, about half the plants are usually female, the rest hermaphrodites. The only way to explain the fact that they have stopped halfway along the one-way street is to posit a continuing battle between the organelles' male-killer genes and nuclear fertility restorer genes. Under certain conditions the battle will reach a stalemate; any further advance by one side gives the other an advantage and the ability to force it back. The more common male-killers get, the more restorer genes will be favored, and vice-versa.²⁹

The same logic does not apply to animals, many of which are not hermaphrodites. It pays an organelle gene to kill males only if by doing so some energy or resource is diverted to the sisters of the killed males; hence, male-killing is rarer. In hermaphroditic plants, if the male function dies, the female function of the plant grows more vigorously or produces more seed. But a male-killer gene in, say, a mouse, by killing the males in a brood, does not benefit those mice's sisters at all. Killing males because they are evolutionary culs-de-sac for organelles would be pure spite.³⁰

Consequently, the battle is resolved rather differently in

animals. Imagine a population of happy hermaphroditic mice. There arrives in its midst a mutation, which happens to kill male gonads (testes). It spreads because females that have the gene do rather well: They have twice as many babies because they put no effort into making sperm. Soon the population consists of hermaphrodites and females, the latter possessing the male-killing gene. It is possible for the species to escape back to hermaphroditism by suppressing the male-killer gene, as many plants have obviously done, but it is just as likely that something else will happen before a mutation that causes the suppression can appear and take effect.

Maleness is a rather rare commodity at this stage. The few remaining hermaphroditic mice are at a premium because only they can produce the sperm that the all-female mice still need. The rarer they get, the better they do. No longer does it pay to have the male-killing mutation. Rather, the reverse. What would really pay the nuclear genes would be a female-killer gene so that one of the hermaphrodites could give up its female function altogether and concentrate on selling sperm to the rest. But if such a female-killing gene appeared, then the remaining hermaphrodites, which lack both the female-killer and the male-killer genes, are no longer at a premium. They are competing with pure males and pure females. Most of the sperm on offer comes complete with female-killer genes, and most of the eggs available to fertilize come complete with male-killer genes, so their offspring are constantly forced to specialize. The genders are separated.³¹

The answer to the question "Would you not avoid paying the cost of maleness by being a hermaphrodite?" is simple: Yes, but there is no way to get there from here. We are stuck with two genders.

THE CASE OF THE IMMACULATE TURKEYS

By separating their genders, animals ended the first mutiny of the organelles. But it was a temporary victory. The organelle genes renewed their mutiny, this time with the "aim" of driving all males

into extinction and leaving the species all-female. This might seem to be a suicidal ambition because a male-less sexual species would become extinct in one generation, taking all of its genes with it, but there are two reasons this does not faze the organelles. First, they can and do convert the species into a parthenogenetic species, able to give virgin birth without sperm—in effect, they try to abolish sex—and second, they behave like cod fishermen or whale hunters or the grazers of commons. They seek short-term competitive advantage even when it leads to long-term suicide. A rational whale hunter does not spare the last pair of whales so that they can breed; he kills them before his rival does and banks the proceeds. Likewise, an organelle does not spare the last male lest the species become extinct, for it faces extinction anyway if it is in a male.

Consider a ladybird beetle's brood. If the male eggs die, the female eggs in the brood eat them and get a free meal as a result. Not surprisingly, there are male-killing genes at work in ladybirds, flies, butterflies, wasps, and bugs—about thirty species of insects have been studied so far—if and only if the young in a brood are in competition with one another. Those male-killing genes are not in organelles, however, but in bacteria that live inside the insects' cells. Those bacteria, like the organelles, are excluded from sperm but not from eggs.³²

In animals such genes are called sex-ratio distorters. In at least twelve species of small parasitic wasps called *Trichogramma*, a bacterial infection makes the female produce only female young even from unfertilized eggs. Since all wasps have a peculiar system of sex determination in which unfertilized eggs become male, this does not condemn the race to extinction and helps the bacterium get into the next generation via the cytoplasm of the egg. The whole species becomes parthenogenetic for as many generations as the bacterium is there. Treat the wasps with an antibiotic and, lo and behold, two genders reappear among the offspring. Penicillin cures virgin birth.³³

In the 1950s scientists at an agricultural research center in Beltsville, Maryland, noticed that some turkey eggs began to develop without being fertilized. Despite heroic efforts by the scientists,

these virgin-born turkeys rarely progressed beyond the stage of simple embryos. But the scientists did notice that vaccinating the fowl against fowl pox with a live virus increased the proportion of eggs likely to begin developing without sperm, from 1–2 percent to 3–16 percent. By selective breeding and the use of three live viruses they were able to produce a strain of Pozo Gray turkeys nearly half of whose eggs would begin to develop without sperm.³⁴

If turkeys, why not people? Laurence Hurst has pursued an obscure hint of a gender-altering parasite among human beings. In a small French scientific journal there appeared in 1946 an astonishing story. A woman came to the attention of a doctor in Nancy when she was having her second child; her first, a daughter, had died in infancy. She expressed no surprise on learning that the second child was also a daughter. In her family, she said, no sons were ever born.

Her tale was this: She was the ninth daughter of a sixth daughter. Her mother had no brothers, nor did she. Her eight sisters had thirty-seven daughters and no sons. Her five aunts had eighteen daughters and no sons. In all, seventy-two women had been born in two generations of her family and not one man.³⁵

That such a thing should happen by chance is possible but amazingly unlikely: less than one chance in a thousand billion billion. The two French scientists who described the case, R. Lienhart and H. Vermelin, also ruled out selective spontaneous abortion of males on the grounds that there were no signs of it. Indeed, many of the women were unusually fecund. One had twelve daughters, two had nine, and one had eight. Instead, the scientists conjectured that the woman and her relatives contained some kind of cytoplasmic gene that feminized every embryo it infected, regardless of the sex chromosomes present. (There is no evidence, incidentally, that virgin birth was involved. The woman's eldest sister was a celibate nun and childless.)

The case of Madame B, as she was described, is tantalizing in the extreme. Did her daughters and nieces have only daughters? Did her first cousins? Is there still, in Nancy, an ever-growing dynasty of women, so that the city's sex ratio will soon be unbal-

anced? Was the explanation proffered by the French doctors the right one? If so, what was the gene and wherein did it live? It might have been in a parasite or in an organelle. How did it work? We may never know.

THE ALPHABETICAL BATTLE OF THE LEMMINGS

With the exception of some female inhabitants of the city of Nancy, the gender of a human being is determined by his or her sex chromosomes. When you were conceived, your mother's egg was chased by two kinds of your father's sperm, one containing an X chromosome and one containing a Y chromosome. Whichever got there first decided your gender. Among mammals, birds, most other animals, and many plants, this is the usual way of going about things: Gender is determined genetically, by sex chromosomes. Those with an X and a Y are male, those with two Xs are female.

But even the invention of sex chromosomes and their success in largely suppressing the rebellion of cytoplasmic genes did not succeed in making life harmonious in the society of genes. The sex chromosomes themselves began to have an interest in the gender of their owners' children. In man, for instance, the genes that control gender are on the Y chromosome. Half of a man's sperm are X carriers and half are Y carriers. To father a daughter, the man must fertilize his mate with an X carrier. In doing so he passes none of the Y's genes to her. From the Y's point of view, his daughter is unrelated to him. Therefore, a Y gene that causes the death of all the man's X-bearing sperm and ensures its own monopoly of the man's children will thrive at the expense of all other kinds of Y genes. That all those children are sons and the species will therefore go extinct matters not in the least to the Y; he has no foresight.

This phenomenon of the "driving Y" was first predicted by Bill Hamilton in 1967.³⁶ He saw it as a powerful danger that was liable to drive species extinct suddenly and silently. He wondered what prevented it from happening, if anything did. One solution

was to gag the Y chromosome, removing all but its gender-determining role. Indeed, Y chromosomes are kept in a kind of house arrest most of the time: Only a few of their genes are expressed, and the rest are entirely silent. In many species gender is determined not by the Y chromosome but by the ratio of the number of X chromosomes to the number of ordinary chromosomes. One X fails to masculinize a bird, two succeed; and in most birds, the Y chromosome has withered away altogether.

The Red Queen is at work. Far from settling down to a fair and reasonable way of determining gender, nature has to face an infinite series of rebellions. It suppresses one only to find it has opened the way to another. For this reason gender determination is a mechanism full of, in the words of Cosmides and Tooby, "meaningless complexity manifesting unreliability, aberrations, and (from the individual's point of view) waste."³⁷

But if the Y chromosome can drive, so can the X. The lemming is a fat arctic mouse famous among cartoonists for apocryphally throwing itself off cliffs in hordes. It is famous among biologists for its tendency to explode in numbers and then collapse again when overcrowding has destroyed its food supply. But it is notable for another reason: It has a peculiar way of determining the gender of its babies. It has three sex chromosomes, W, X, and Y. XY is a male; XX, WX, and WY are all females. YY cannot survive at all. What has happened is that a mutant form of driving X chromosome, W, has appeared that overrules the masculinizing power of the Y. The result is an excess of females. Since this puts males at a premium, you might expect that males would soon evolve the ability to produce more Y-bearing than X-bearing sperm, but they have not done so. Why? At first biologists thought it had something to do with population explosions during which an excess of daughters is a good idea, but recently they have determined that this is unnecessary. The female-biased sex ratio is stable for genetic, not ecological, reasons.³⁸

A male that produces only Y sperm can mate with an XX female and produce all sons (XY) or with a WX female and produce half sons and half daughters or with a WY female. In the last

case he has only WY daughters because YY sons die. The net result, therefore, is that if he mates with one of each, he will have as many daughters as sons, and all his daughters will be WY females, who can have only daughters. So, far from restoring the sex ratio to equality by producing only Y sperm, he has kept it unbalanced toward females. The case of the lemming demonstrates that even the invention of sex chromosomes did not prevent mutinous chromosomes from altering the sex ratio.³⁹

LOTTERY OR CHOICE?

Not all animals have sex chromosomes. Indeed, it is hard to see why so many do. They make gender a pure lottery, governed by an arbitrary convention with the sole advantage of (usually) keeping the sex ratio at fifty-fifty. If the first sperm to reach your mother's egg carried a Y chromosome, you are a male; if it carried an X chromosome, you are a female. There are at least three different and better ways to determine your gender.

The first, for sedentary creatures, is to choose the gender appropriate to your sexual opportunities. For example, be a different gender from your neighbor because he or she will probably turn out to be your mate. A slipper limpet, which delights in the Latin name *Crepidula fornicata*, begins life as a male and becomes a female when it ceases peregrinating and settles on a rock; another male lands on it, and gradually it, too, turns female; a third male lands, and so on, until there is a tower of ten or more slipper limpets, the bottom ones being female, the top ones male. A similar method of gender determination is employed by certain reef fish. The shoal consists of lots of females and a single large male. When he dies, the largest female simply changes gender. The blue-headed wrasse changes gender from female to male when it reaches a certain size.⁴⁰

This sex change makes good sense from the fish's point of view because there is a basic difference between the risks and rewards of being male or female. A large female fish can lay only a few more eggs than a small one, but a large male fish, by fighting

for and winning a harem of females, can have a great many more offspring than a small male. Conversely, a small male does worse than a small female because he fails to win a mate at all. Therefore, among polygamists the following strategy often appears: If small, be female; if large, be male.⁴¹

There is a lot to be said for such stratagems. It is profitable to be a female while growing up and get some breeding done, and then change sex and hit the jackpot as a polygamist male once you are big enough to command a harem. Indeed, the surprise is that more mammals and birds do not adopt this system. Half-grown male deer spend years in a state of celibacy awaiting the chance to breed, while their sisters produce a fawn a year.

A second way of determining gender is to leave it to the environment. In some fish, shrimp, and reptiles, gender is determined by the temperature at which the egg is incubated. Among turtles, warm eggs hatch into females; among alligators, warm eggs hatch into males; among crocodiles, warm and cool eggs hatch into females, intermediate ones into males. (Reptiles are the most adventurous sex determiners of all. Many lizards and snakes use genetic means, but whereas XY iguanas become male and XX female, XY snakes become female and XX male.) Atlantic silverside fish are even more unusual. Those in the North Atlantic determine their gender by genes as we do; those farther south use the temperature of the water to set the gender of the embryo.⁴²

This environmental method seems a peculiar way of going about it. It means that unusually warm conditions can lead to too many male alligators and too few females. It leads to "intersexes," animals that are neither one thing nor the other.⁴³ Indeed, no biologist has a watertight explanation for why alligators, crocodiles, and turtles employ this technique. The best one is that it is all size related. The warm eggs hatch as larger babies than the cool ones. If being large is more of an advantage to males than females (true of crocodiles, in which males compete for females) or vice versa (true of turtles, in which large females lay more eggs than small ones, whereas small males are just as capable of fertilizing females as large ones), then it would pay to make warm eggs hatch

as the gender that most benefits from being large.⁴⁴ A clearer example of the same phenomenon is the case of a nematode worm that lives inside an insect larva. Its size is set by the size of the insect; once it has eaten all of its home and host, it grows no more. But whereas a big female worm can lay more eggs, a big male worm cannot fertilize more females. So big worms tend to become female and small ones male.⁴⁵

A third way of determining gender is for the mother to choose the sex of each child. One way of achieving this is peculiar to monogonont rotifers, bees, and wasps. Their eggs become female only if fertilized. Unfertilized eggs hatch into males (which means that males are haploid and have only one set of genes to the females' two). Again, this makes some sort of sense. It means that a female can found a dynasty even if she never meets a male. Since most wasps are parasites that live inside other insects, this may help a single female who happens on an insect host to start a colony without waiting for a male to arrive. But haplodiploidy is vulnerable to certain kinds of genetic mutiny. For example, in a wasp called *Nasonia*, there is a rare supernumerary chromosome called PSR, inherited through the male line, that causes any female egg in which it finds itself to become a male by the simple expedient of getting rid of all the father's chromosomes except itself. Reduced to just the haploid maternal complement of chromosomes, the egg develops into a male. PSR is found where females predominate and has the advantage that it is in the rare, and therefore sought-after, gender.⁴⁶

This, briefly, is the theory of sex allocation: Animals choose the appropriate gender for their circumstances unless forced to rely on the genetic lottery of sex chromosomes. But in recent years biologists have begun to realize that the genetic lottery of sex chromosomes is not incompatible with sex allocation. If they could distinguish between X and Y sperm, even birds and mammals could bias the sex ratios of their offspring, and they would be selected to do so in exactly the same way as crocodiles and nematodes—to produce more of the gender that most benefits from being bigger when the offspring are likely to be big.⁴⁷

PRIMOGENITURE AND PRIMATOLOGY

In the course of the neo-Darwinian revolution of the 1960s and 1970s, Britain and America each produced a grand old revolutionary whose intellectual dominance remains secure to this day: John Maynard Smith and George Williams, respectively. But each country also produced a brilliant young Turk whose precocious intellect exploded on the world of biology like a flare. Britain's prodigy was Bill Hamilton, whom we have already met. America's was Robert Trivers, who as a Harvard student in the early 1970s conceived a whole raft of new ideas that proved far ahead of his time. Trivers is a legend in biology, as he is the first ingenuously to confirm. Unconventional to the point of eccentricity, he divides his time between watching lizards in Jamaica and thinking in a redwood grove near Santa Cruz, California. One of his most provocative ideas, conceived jointly with fellow student Dan Willard in 1973, may hold the key to understanding one of the most potent and yet simple questions a human being ever asks: "Is it a boy or a girl?"⁴⁸

If you include Chelsea Clinton, daughter of the forty-second president of the United States, it is a curious statistical fact that all the presidents have between them had ninety sons and only sixty-one daughters. A sex ratio of 60 percent male in such a large sample is markedly different from the population at large, though how it came about nobody can guess—probably by pure chance. Yet presidents are not alone. Royalty, aristocrats, and even well-off American settlers have all consistently produced slightly more sons than daughters. So do well-fed opossums, hamsters, coypus, and high-ranking spider monkeys. The Trivers-Willard theory links these diverse facts.⁴⁹

Trivers and Willard realized that the same general principle of sex allocation, which determines the gender of nematodes and fish, applies even to those creatures that cannot change sex but that take care of their young. They predicted that animals would be found to have some systematic control over the sex ratio of their own young. Think of it as a competition to have the most grandchildren. If males are polygamous, a successful son can give you far

more grandchildren than a successful daughter, and an unsuccessful son will do far worse than an unsuccessful daughter because he will fail to win any mates at all. A son is a high-risk, high-reward reproductive option compared with a daughter. A mother in good condition gives her offspring a good start in life, increasing the chances of her sons' winning harems as they mature. A mother in poor condition is likely to produce a feeble son who will fail to mate at all, whereas her daughters can join harems and reproduce even when not in top condition. So you should have sons if you have reason to think they will do well and daughters if you have reason to think they will do poorly—relative to others in the population.⁵⁰

Therefore, said Trivers and Willard, especially in polygamous animals, parents in good condition probably have male-biased litters of young; parents in poor condition probably have female-biased litters. Initially this was scoffed at as farfetched conjecture, but gradually it has received grudging respect and empirical support.

Consider the case of the Venezuelan opossum, a marsupial that looks like a large rat and lives in burrows. Steven Austad and Mel Sunquist of Harvard were intent on disproving the Trivers-Willard theory. They trapped and marked forty virgin female opossums in their burrows in Venezuela. Then they fed 125 grams of sardines to each of twenty opossums every two days by leaving the sardines outside the burrows, no doubt to the delight and astonishment of the opossums. Every month thereafter they trapped the animals again, opened their pouches, and sexed their babies. Among the 256 young belonging to the mothers who had not been fed sardines, the ratio of males to females was exactly one to one. Among the 270 from mothers who had been fed sardines, the sex ratio was nearly 1.4 to 1. Well-fed opossums are significantly more likely to have sons than poorly fed ones.⁵¹

The reason? The well-fed opossums had bigger babies; bigger males were much more likely to win a harem of females in later life than smaller males. Bigger females were not much more likely to have more babies than small females. Hence, the mother opossums were investing in the gender most likely to reward them with many grandchildren.

Opossums are not alone. Hamsters reared in the laboratory can be made to have female-biased litters by keeping them hungry during adolescence or pregnancy. Among coypus (large aquatic rodents), females in good condition give birth to male-biased litters; those in poor condition give birth to female-biased litters. In white-tailed deer, older mothers or yearlings in poor condition have female fawns more often than by chance alone. So do rats kept in conditions of stress. But in many ungulates (hoofed animals), stress or poor habitat has the opposite effect, inducing a male-biased sex ratio.⁵²

Some of these effects can be easily explained by rival theories. Because males are often bigger than females, male embryos generally grow faster and are more of a strain on the mother. Therefore, it pays a hungry hamster or a weak deer to miscarry a male-biased litter and retain a female-biased one. Moreover, proving biased sex ratios at birth is not easy, and there have been so many negative results that some scientists maintain the positive ones are merely statistical flukes. (If you toss a coin long enough, sooner or later you will get twenty heads in a row.) But neither explanation can address the opossum study and others like it. By the late 1980s many biologists were convinced that Trivers and Willard were right at least some of the time.⁵³

The most intriguing results, however, were those that concerned social status. Tim Clutton-Brock of Cambridge University studied red deer on the island of Rhum off the Scottish coast. He found that the mother's condition had little effect on the gender of her calves, but her rank within the social group did have an effect. Dominant females were slightly more likely to have sons than daughters.⁵⁴

Clutton-Brock's result alerted primatologists, who had long suspected biased sex ratios in various species of monkey. In the Peruvian spider monkeys studied by Meg Symington, there was a clear association between rank and gender of offspring. Of twenty-one offspring born to lowest-ranked females, twenty-one were female; of eight born to highest-ranked females, six were male; those in the middle ranks had an equal sex ratio.⁵⁵

But an even greater surprise was in store when other monkeys revealed their gender preferences. Among baboons, howler monkeys, rhesus macaques, and bonnet macaques, the opposite preference prevailed: high-ranking females gave birth to female offspring, and low-ranking females give birth to male offspring. In the eighty births to twenty female Kenyan baboons studied by Jeanne Altmann of the University of Chicago, the effect was so pronounced that high-ranking females were twice as likely to have daughters as low-ranking ones. Subsequent studies have come to less clear conclusions, and a few scientists believe that the monkey results are explained by chance. But one intriguing hint suggests otherwise.⁵⁶

Symington's spider monkeys preferred sons when dominant, whereas the other monkeys preferred daughters. This may be no accident. In most monkeys (including howlers, baboons, and macaques) males leave the troop of their birth and join another at puberty—so-called male-exogamy. In spider monkeys the reverse applies: Females leave home. If a monkey leaves the troop it is born into, it has no chance to inherit its mother's rank. Therefore, high-ranking females will have young of whatever gender stays at home in order to pass on the high rank to them. Low-ranking females will have young of whatever gender leaves the troop in order not to saddle the young with low rank. Thus high-ranking howlers, baboons, and macaques have daughters; high-ranking spider monkeys have sons.⁵⁷

This is a highly modified Trivers-Willard effect, known in the trade as a local-resource competition model.⁵⁸ High rank leads to a sex bias in favor of the gender that does not leave at puberty. Could it possibly apply to human beings?

DOMINANT WOMEN HAVE SONS?

Mankind is an ape. Of the five species of ape, three are social, and in two of those, chimpanzees and gorillas, it is the females that leave the home troop. In the chimpanzees of Gombe Stream in Tan-

zania studied by Jane Goodall, young males born to senior females tend to rise to the top faster than males born to junior females. Therefore, female apes of high social status “should”—according to the Trivers-Willard logic—have male young and those of low social status “should” have female young.⁵⁹ Now men are not excessively polygamous, so the rewards of large size to men is not great: big men do not necessarily win more wives, and big boys do not necessarily become big men. But humans are a highly social species whose society is nearly always stratified in some way. One of the prime, indeed, ubiquitous perquisites of high social status in human males, as in male chimpanzees, is high reproductive success. Wherever you look, from tribal aborigines to Victorian Englishmen, high-status males have had—and mostly still do have—more children than low-status ones. And the social status of males is very much inherited, or rather passed on from parent to child, whereas females generally leave home when they marry. I am not implying that the tendency for the female to travel to the male’s home when she marries is instinctive, natural, inevitable, or even desirable, but I am noting that it has been general. Cultures in which the opposite happens are rare. So human society, like ape society but unlike most monkey society, is a female-exogamous patriarchy, and sons inherit their father’s (or mother’s) status more than daughters inherit their parents’ status. Therefore, says Trivers-Willard, it would pay dominant fathers and high-ranking mothers, or both, to have sons and subordinates to have daughters. Do they?

The short answer is that nobody knows. American presidents, European aristocrats, various royals, and a few other elites have been suspected of having male-biased progeny at birth. In racist societies, subject races seem to be slightly more likely to have daughters than sons. But the subject is too fraught with potential complicating factors for any such statistics to be reliable. For example, merely by ceasing to breed once they have a boy—which those interested in dynastic succession might do—people would have male-biased sex ratios at birth. However, there certainly are no studies showing reliably unbiased sex ratios. And there is one tantalizing study from New Zealand that hints at what might be found

if anthropologists and sociologists cared to look into the matter.⁶⁰ As early as 1966, Valerie Grant, a psychiatrist at the University of Auckland in New Zealand, noticed an apparent tendency for women who subsequently gave birth to boys to be more emotionally independent and dominating than those who gave birth to girls. She tested the personalities of eighty-five women in the first trimester of pregnancy using a standard test designed to distinguish "dominant" from "subordinate" personalities—whatever that may mean. Those who later gave birth to daughters averaged 1.35 on the dominance scale (from 0 to 6). Those who later gave birth to sons averaged 2.26, a highly significant difference. The interesting thing about Grant's work is that she began before the Trivers-Willard theory was published, in the 1960s. "I arrived at the idea quite independently of any study in any of the areas in which such a notion might reasonably arise," she told me, "For me the idea arose out of an unwillingness to burden women with the responsibility for the 'wrong' sex child."⁶¹ Her work remains the only hint that maternal social rank affects the gender of children in the way that the Trivers-Willard-Symington theory would predict. If it proves to be more than a chance result, it immediately leads to the question of how people are unconsciously achieving something that they have been consciously striving to achieve for generations unnumbered.

SELLING GENDER

Almost no subject is more steeped in myth and lore than the business of choosing the gender of children. Aristotle and the Talmud both recommended placing the bed on a north-south axis for those wanting boys. Anaxagoras's belief that lying on the right side during sex would produce a boy was so influential that centuries later some French aristocrats had their left testicles amputated. At least posterity had its revenge on Anaxagoras, a Greek philosopher and client of Pericles. He was killed by a stone dropped by a crow, no doubt a retrospective reincarnation of some future French marquis who cut off his left testicle and had six girls in a row.⁶²

It is a subject that has always drawn charlatans like blowflies to a carcass. The old wives' tales that have answered the pleas of fathers for centuries are mostly ineffective. The Japanese Sex Selection Society promotes the use of calcium to increase the chances of having a son—with little effect. A book published in 1991 by two French gynecologists claimed precisely the opposite: that a diet rich in potassium and sodium but poor in calcium and magnesium gives a woman an 80 percent chance of conceiving a son if consumed for six weeks before fertilization. A company offering Americans "gender kits" for \$50 was driven into bankruptcy after the regulators claimed it was deceiving the consumer.⁶³

The more modern and scientific methods are only slightly more reliable. They all rely on trying to separate in the laboratory Y-bearing (male) sperm from X-bearing (female) sperm based on the fact that the latter possess 3.5 percent more DNA. The widely licensed technique invented by an American scientist, Roland Ericsson, which opened its first British clinic in 1993, claims a high success rate but has not published convincing data. It relies on causing the sperm to swim through albumen, which supposedly slows down the heavier X-bearing sperm more than it does the Y-bearing sperm, thus separating them. By contrast, Larry Johnson of the United States Department of Agriculture has developed a technique that works efficiently (about 80 percent male offspring), but it is wholly unsuitable for human beings. It dyes the sperm DNA with a fluorescent dye and then allows the sperm to swim in Indian file past a detector. According to the brightness of the sperm's fluorescence, the detector sorts them into two channels. The Y-bearing sperm, having smaller amounts of DNA, are slightly less brightly fluorescent. The detectors can sort the sperm at 100,000 a second, and the sperm can then be used to fertilize embryos using in-vitro fertilization. But no human being in his right mind would submit his sperm to such dyes or go through expensive in-vitro fertilization just to have a boy.⁶⁴

Curiously, if humans were birds, it would be much easier to alter the chances of having young of one gender or the other because in birds the mother determines the gender of the embryo, not the father. Female birds have X and Y chromosomes (or some-

times just one X), while male birds have two Xs. So a female bird can simply release an egg of the desired gender and let any sperm fertilize it. Birds do make use of this facility. Bald eagles and some other hawks often give birth to females first and males second. This enables the female to get a head start on the male in the nest, which enables it to grow larger (and female hawks are always larger than males). Red-cockaded woodpeckers raise twice as many sons as daughters and use spare sons as nannies for subsequent broods. Among zebra finches, as Nancy Burley of the University of California at Santa Cruz discovered, "attractive" males mated with "unattractive" females usually have more sons than daughters, and vice versa. Attractiveness in this species can be altered by the simple expedient of putting red (attractive) or green (unattractive) bands on the male's legs, and black (attractive) or light blue (unattractive) on the female's legs. This makes them more or less desirable to other zebra finches as mates.⁶⁵

But we are not birds. The only way to be certain of rearing a boy is to kill a girl child at birth and start again, or to use amniocentesis to identify the gender of the fetus and then abort it if it's a girl. These repugnant practices are undoubtedly on offer in various parts of the world. The Chinese, deprived of the chance to have more than one child, killed more than 250,000 girls after birth between 1979 and 1984.⁶⁶ In some age groups in China, there are 122 boys for every 100 girls. In one recent study of clinics in Bombay, of 8,000 abortions, 7,997 were of female fetuses.⁶⁷

It is possible that selective spontaneous abortion also explains much of the animal data. In the case of the coypu, studied by Morris Gosling of the University of East Anglia, females in good condition miscarry whole litters if they are too female-biased, and they start again. Magnus Nordborg of Stanford University, who has studied the implications of sex-selective infanticide in China, believes that such biased miscarriage could explain the baboon data. But it seems a wasteful way to proceed.⁶⁸

There are many well-established natural factors that bias the sex ratio of human offspring, proving that it is at least possible. The most famous is the returning-soldier effect. During and

immediately after major wars, more sons are born than usual in the belligerent countries as if to replace the men that died. (This would make little sense; the men born after wars will mate with their contemporaries, not with those widowed by the war). Older fathers are more likely to have girls, but older mothers are more likely to have boys. Women with infectious hepatitis or schizophrenia have slightly more daughters than sons. So do women who smoke or drink. So did women who gave birth after the thick London smog of 1952. So do the wives of test pilots, abalone divers, clergymen, and anesthetists. In parts of Australia that depend on rainfall for drinking water, there is a clear drop in the proportion of sons born 320 days after a heavy storm fills the dams and churns up the mud. Women with multiple sclerosis have more sons, as do women who consume small amounts of arsenic.⁶⁹

Finding the logic in this plethora of statistics is beyond most scientists at this stage. William James of the Medical Research Council in London has for some years been elaborating a hypothesis that hormones can influence the relative success of X and Y sperm. There is a good deal of circumstantial evidence that high levels of the hormone gonadotrophin in the mother can increase the proportion of daughters and that testosterone in the father can increase the proportion of sons.⁷⁰

Indeed, Valerie Grant's theory suggests a hormonal explanation for the returning-soldier effect: that during wars women adopt more dominant roles, which affects their hormone levels and their tendency to have sons. Hormones and social status are closely related in many species; and so, as we have seen, are social status and sex ratio of offspring. How the hormones work, nobody knows, but it is possible that they change the consistency of the mucus in the cervix or even that they alter the acidity of the vagina. Putting baking soda in the vagina of a rabbit was proved to affect the sex ratio of its babies as early as 1932.⁷¹

Moreover, a hormone theory would tackle one of the most persistent objections to the Trivers-Willard theory: that there seems to be no genetic control of the sex ratio. The failure of animal breeders to produce a strain that can bias the gender of its off-

spring is glaring. It is not for want of trying. As Richard Dawkins put it: "Cattle breeders have had no trouble in breeding for high milk yield, high beef production, large size, small size, hornlessness, resistance to various diseases, and fearlessness in fighting bulls. It would obviously be of immense interest to the dairy industry if cattle could be bred with a bias toward producing heifer calves rather than bull calves. All attempts to do this have singularly failed."⁷²

The poultry industry is even more desperate to learn how to breed chickens that lay eggs that hatch into chicks of only one gender. At present it employs teams of highly trained Koreans, who guard a close secret that enables them to sex day-old chicks at great speed (though a computer program may soon match them⁷³). They travel all over the world plying their peculiar trade. It is hard to believe that nature is simply unable to do what the Korean experts can do so easily.

Yet this objection is easily answered once the hormonal theory is taken into account. Munching enchiladas in sight of the Pacific Ocean one day, Robert Trivers explained to me why the failure to breed sex-biased animals is entirely understandable. Suppose you find a cow that produces only heifer calves. With whom do you mate those heifers to perpetuate the strain? With ordinary bulls—diluting the genes in half at once.

Another way of putting it is that the very fact that one segment of the population is having sons makes it rewarding for the other segment to have daughters. Every animal is the child of one male and one female. So if dominant animals are having sons, then it will pay subordinate ones to have daughters. The sex ratio of the population as a whole will always revert to 1:1, however biased it becomes in one part of the population, because if it strays from that, it will pay somebody to have more of the rare gender. This insight occurred first to Sir Ronald Fisher, a Cambridge mathematician and biologist, in the 1920s, and Trivers believes it lies at the heart of why the ability to manipulate the sex ratio is never in the genes.

Besides, if social rank is a principal determinant of sex ratio, it would be crazy to put it in the genes, for social rank is

almost by definition something that cannot be in the genes. Breeding for high social rank is a futile exercise in Red Queen running. Rank is relative. "You can't breed for subordinate cows," said Trivers as he munched. "You just create a new hierarchy and reset the thermostat. If all your cows are more subordinate, then the least subordinate will be the most dominant and have appropriate levels of hormones." Instead, rank determines hormones, which determine sex ratio of offspring.⁷⁴

REASON'S CONVERGENT CONCLUSION

Trivers and Willard predict that evolution will build in an unconscious mechanism for altering the sex ratio of an individual's progeny. But we like to think we are rational, conscious decision makers, and a reasoning person can arrive at the same conclusions as evolution. Some of the strongest data to support Trivers and Willard comes not from animals but from the human cultural rediscovery of the same logic.

Many cultures bias their legacies, parental care, sustenance, and favoritism toward sons at the expense of daughters. Until recently this was seen as just another example of irrational sexism or the cruel fact that sons have more economic value than daughters. But by explicitly using the logic of Trivers-Willard, anthropologists have now begun to notice that male favoritism is far from universal and that female favoritism occurs exactly where you would most expect it.

Contrary to popular belief a preference for boys over girls is not universal. Indeed, there is a close relationship between social status and the degree to which sons are preferred. Laura Betzig of the University of Michigan noticed that, in feudal times, lords favored their sons, but peasants were more likely to leave possessions to daughters. While their feudal superiors killed or neglected daughters or banished them to convents, peasants left them more possessions. Sexism was more a feature of elites than of the unchronicled masses.⁷⁵

As Sarah Blaffer Hrdy of the University of California at

Davis has concluded, wherever you look in the historical record, the elites favored sons more than other classes: farmers in eighteenth-century Germany, castes in nineteenth-century India, genealogies in medieval Portugal, wills in modern Canada, and pastoralists in modern Africa. This favoritism took the form of inheritance of land and wealth, but it also took the form of simple care. In India even today, girls are often given less milk and less medical attention than boys.⁷⁶

Lower down the social scale, daughters are preferred even today. A poor son is often forced to remain single, but a poor daughter can marry a rich man. In modern Kenya, Mukogodo people are more likely to take daughters than sons to clinics for treatment when they are sick, and therefore more daughters than sons survive to the age of four. This is rational of the Mukogodo parents because their daughters can marry into the harems of rich Samburu and Maasai men and thrive, whereas their sons inherit Mukogodo poverty. In the calculus of Trivers-Willard, daughters are better grandchildren-production devices than sons.⁷⁷

Of course, this assumes that societies are stratified. As Mildred Dickemann of California State University has postulated, the channeling of resources to sons represents the best investment rich people can make when society is class-ridden. The clearest patterns come from Dickemann's own studies of traditional Indian marriage practices. She found that extreme habits of female infanticide, which the British tried and failed to stamp out, coincided with relatively high social rank in the distinctly stratified society of nineteenth-century India. High-caste Indians killed daughters more than low-caste ones. One clan of wealthy Sikhs used to kill all daughters and live off their wives' dowries.⁷⁸

There are rival theories to explain these patterns, of which the strongest is that economic, not reproductive, currency determines a sexual preference. Boys can earn a living and marry without a dowry. But this fails to explain the correlation with rank. It predicts, instead, that lower social classes would favor sons, not higher ones, for they can least afford daughters. If instead grandchildren production was the currency that mattered, Indian marriage prac-

tices make more sense. Throughout India it has always been the case that women more than men can "marry up," into a higher social and economic caste, so daughters of poor people are more likely to do well than sons. In Dickemann's analysis, dowries are merely a distorted echo of the Trivers-Willard effect in a female-exogamous species: Sons inherit the status necessary for successful breeding; daughters have to buy it. If you have no wealth to pass on, use what you have to buy your daughter a good husband.⁷⁹

Trivers and Willard predict that male favoritism in one part of society will be balanced by female favoritism elsewhere if only because it takes one of each to have a baby—the Fisher logic again. In rodents the division seems to be based on maternal condition. In primates it seems to be based on social rank. But baboons and spider monkeys take for granted the fact that their societies are strictly stratified. Human beings do not. What happens in a modern, relatively egalitarian society?

In that uniform middle-class Eden known as California, Hrdy and her colleague Debra Judge have so far been unable to detect any wealth-related sex bias in the wills people leave when they die. Perhaps the old elite habit of preferring boys to girls has at last been vanquished by the rhetoric of equality.⁸⁰

But there is another, more sinister consequence of modern egalitarianism. In some societies the boy-preferring habit seems to have spread from elites to the society at large. China and India are the best examples of this. In China a one-child policy may have led to the deaths of 17 percent of girls. In one Indian hospital 96 percent of women who were told they were carrying daughters aborted them, while nearly 100 percent of women carrying sons carried them to term.⁸¹ This implies that a cheap technology allowing people to choose the gender of their children would indeed unbalance the population sex ratio.

Choosing the gender of your baby is an individual decision of no consequence to anybody else. Why, then, is the idea inherently unpopular? It is a tragedy of the commons—a collective harm that results from the rational pursuit of self-interest by individuals. One person choosing to have only sons does nobody else any harm,

but if everybody does it, everybody suffers. The dire predictions range from a male-dominated society in which rape, lawlessness, and a general frontier mentality would hold sway to further increases in male domination of positions of power and influence. At the very least, sexual frustration would be the lot of many men.

Laws are passed to enforce the collective interest at the expense of the individual, just as crossing over was invented to foil outlaw genes. If gender selection were cheap, a fifty-fifty sex ratio would be imposed by parliaments of people as surely as equitable meiosis was imposed by the parliament of the genes.