THE MATING MIND

How Sexual Choice Shaped the Evolution of Human Nature

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For Rosalind

Runaway is especially good at explaining the evolutionarily unpredictable—why extreme traits can arise in one species but not in closely related species. Many of the human mind's most interesting capacities do not appear in other apes, and those of most hominids are not discernible from the archeological record. Runaway requires polygyny, and almost every human culture throughout history has been overtly polygynous to some extent. Runaway is extremely fast once it gets going. The fossil record reveals a few rapid increases in brain size punctuated by long periods of relative stasis, which could mark a series of runaway events.

The two major problems with the runaway brain theory are the multi-step progressiveness of brain size evolution, and the minimal sex differences in human mental ability. Pure runaway is not biased in any particular direction, yet for the last two million years human brain evolution has shown a consistent trend towards larger size and higher intelligence. Runaway should not be so consistent. Moreover, pure runaway should have produced large-brained, hyper-intelligent males, and small-brained, ape-minded females. That has not happened. I have reviewed some factors that may have minimized sex differences: genetic correlation between the sexes, the overlap of mental capacities for courtship behavior and for sexual choice, and mutual mate choice. But the most compelling of these factors, mutual mate choice, is not consistent with a pure runaway process.

I think that mutual mate choice in humans is so important that the pure runaway brain theory just cannot be right. This chapter started by praising it, but has ended by burying it. I do not think that female creative intelligence is a genetic side-effect of male creative intelligence, or arose simply as a way of assessing male courtship displays. I think that female creative intelligence evolved through male mate choice as much as male creative intelligence evolved through female mate choice. I shall turn next to a model of sexual selection that works better with mutual mate choice. It emphasizes how sexual ornaments advertise each sex's fitness to the other sex—a function of mate choice that may stretch back to the origins of sexual reproduction itself.

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A Mind Fit for Mating

Before sexual reproduction evolved, there were several ways for organisms to accomplish the evolutionary task of spreading their DNA around. There was the divide-and-conquer strategy: wrap DNA in single cells that busily eat nutrients until they grow large enough to split in half, leaving each half to grow and split in turn. Bacteria are the masters of this technique, capable of doubling their populations every few minutes, but vulnerable to mass extermination through perils such as toothbrushes and soap.

There was also the cloning-factory strategy: grow a body with billions of cells, and then assign the task of DNA-spreading to a privileged minority of those cells, which bud off to make new, genetically identical bodies. Many fungi reproduce this way, epitomizing the rustic virtues of simplicity and fecundity. Yet this strategy, though successful in the short term, stores up trouble for the long term. Once a harmful mutation arises, as it sooner or later will, there is no means of expunging it. This propensity to accumulate damaging mutations makes such asexual species quite unsuited to evolving much sophistication. This is because bodily and mental sophistication require a great deal of DNA, and the more DNA one has, the more trouble mutations cause.

In the last few hundred million years, an increasing number of species have turned to a third way of spreading their DNA around—the fashionable new method called sexual reproduction, with improved mutation-cleansing powers. One grows a trillion-celled body to produce packets of DNA, makes sure those DNA packets find complementary DNA packets from suitable others, and permits the DNA to combine with that of another individual to

produce offspring that bear traits from both parents. Of the 1.7 million known species on our planet, most engage in sexual reproduction. Sexual species include almost all plants larger than a buttercup and almost all animals larger than your thumb. It includes most insects, all birds, and all mammals, including all primates.

Copying Errors

At the beginning, this DNA-combining called sex was probably not very selective. It was simply the most convenient way to make sure that not all of your offspring inherited your mutations. In evolution, mutations are generally a bad thing. Since almost all mutations are harmful, organisms evolve sophisticated DNA repair machinery to correct mutations. Of course, in the long term, mutations are necessary for evolutionary progress, because a tiny minority prove helpful when a species faces new challenges. But organisms don't plan for the long term. To the organism, mutations are simply copying errors—mistakes made when trying to spread DNA by producing offspring.

If you have only one copy of each gene, it is hard to know when certain kinds of copying error have been made. Some errors just won't look right to the DNA repair machinery. They are chemical nonsense, and easily fixed. But other errors look just like ordinary working DNA. These pseudo-normal mutations are the problem. They look like good DNA to the repair machinery, but they do not act like good DNA when you try to grow an organism using them. They undermine the biological efficiency called fitness. Unless there is some way of eliminating them, they will accumulate, generation after generation, gradually eroding the fitness of offspring.

In very recent work, biologists Adam Eyre-Walker and Peter Keightley calculated that the average human has 1.6 harmful new mutations that neither parent had. Our ancestors would have accumulated mutations at the same rate. Geneticist James Crow thinks this estimate too conservative by half, and suggests that we have 3 new harmful mutations per individual every generation.

That doesn't sound too bad, given that we have about 80,000 genes, yet this mutation rate is near the theoretical limit of what selection can cope with. For a species to avoid going extinct as a result of accumulating too many harmful mutations, selection must be able to eliminate mutations at the same average rate that mutations arise, otherwise the species would suffer a "mutational meltdown." For technical reasons, it is very hard to avoid a mutational meltdown when more than one harmful new mutation arises per individual. In fact, it may be impossible without sexual reproduction.

Sexual reproduction probably arose as a way to contain the damage caused by mutations. By mixing up your DNA with that of another individual to make offspring, you make sure that any mutations you have will end up in only half of your offspring. Your sexual partner will have mutations of their own, but they are almost certain to be different mutations on different genes. Because offspring have two copies of each gene, the normal version inherited from one parent often masks the failures of the mutated version inherited from the other parents. Incest is a bad idea because blood relatives often inherit the same mutations, which are not masked by normal genes when close relatives produce offspring. For example, you may need just a little bit of the protein produced by a gene, so one copy of the gene may suffice. The mutated gene's inability to produce a working protein may not matter very much. This masking effect is called genetic dominance. Dominance makes sex very powerful in limiting the damage caused by mutations.

However, dominance is often not perfect, and it is really only a short-term solution. Two normal genes are sometimes still better than one. And hiding the effects of mutations allows them to accumulate over evolutionary time. To keep mutations from accumulating over the longer term, sexual reproduction takes some chances. Consider two parents with average numbers of mutations. Each contributes half of their genes to each offspring. Most of the offspring will inherit nearly the same number of mutations as their parents had. But some may be lucky: they may

inherit a below-average number of mutations from their father, and a below-average number from their mother too. They will have much better genes than average, and should survive and reproduce very well. Their relatively mutation-free genes will spread through future generations. Other offspring may be very unlucky: they may inherit an above-average load of mutations from both parents, and may fail to develop at all, or may die in infancy. When they die, they take a large number of mutations with them into evolutionary oblivion.

This effect is extremely important. By endowing the next generation with unequal numbers of mutations, sexual reproduction ensures that at least some offspring will have very good genes. They will preserve the genetic information that keeps the species working. From a selfish gene's point of view, it does not matter that some offspring have very bad genes full of mutations, because those mutations would have died out sooner or later anyway. Better to concentrate them in as few bodies as possible so they do the least damage over the long term. Investment analysts will recognize that sexual reproduction is a way of implementing a risk-seeking strategy. Since evolution over the long term is a winner-takes-all contest, it is more important to produce a few offspring that have a chance to do very well, than a larger number of mediocre offspring.

Mutations, Fitness, and Sexual Attractiveness

Now, if the goal of sexual reproduction is to keep at least some of your offspring safe from your harmful mutations, it would be foolish to pick your sexual partners at random. Any sex partner will carry his or her own load of mutations. You should pick the partner with the lowest number of harmful mutations: that will give your offspring the highest expected fitness, which means the best chance of surviving and reproducing. If your choice of sexual partner is very good indeed, your genes may hitch a ride to evolutionary stardom on the genetic quality of your mate. Many biologists are coming to the view that mate choice is a strategy for getting the best genes you can for your offspring.

Because of genetic dominance, many mutations are hidden from view. They do not affect body or behavior, so they cannot be used in mate choice. However, dominance is often incomplete, and a lot of genetic variation between individuals does show up in body and behavior. Some traits reveal more genetic information than others. Complex traits such as peacock tails that vary conspicuously between individuals may be especially informative. Their complexity means that their development depends on many genes interacting efficiently. They summarize more genetic information by being more complicated. And their variation at the visible level of body and behavior means that genetic variation can be perceived during mate choice. With sexual selection there is a big incentive to pay very close attention to traits like these.

Such traits are called "fitness indicators." A fitness indicator is a biological trait that evolved specifically to advertise an animal's fitness. Fitness means the propensity to survive and reproduce successfully. It is determined mainly by an individual's genetic quality, which boils down to their mutation load.

There is a close connection between mutations and fitness. If a species has been living in its present environment for many generations, its average genes are probably very well adapted to that environment. Because they have already been tested again and again by natural selection, the average genes in the species are already optimal. If they weren't, they would already have been replaced by different genes. This suggests that any deviation from the genetic norm is a deviation from optimality. Mutations are deviations from the genetic norm. If a set of mutations makes an individual unable to grow an optimal body and unable to produce optimal behavior, then they impair that individual's ability to survive and reproduce. Since fitness means the ability to survive and reproduce, mutations almost always lower fitness; conversely, high fitness implies freedom from harmful mutations. If fitness indicators advertise high fitness, they are also advertising freedom from mutations, which is what mate choice wants. Normal genes are tried and tested, whereas mutations are shots in the dark.

Sexual selection needs some way to connect the sensory abilities

of animals to the mutation levels of the potential mates they are choosing between. Fitness indicators are the connection, for they are the traits that make fitness visible. What they make visible can be favored by mate choice, and what is favored by mate choice can evolve through sexual selection. Fitness indicators are the genetic sieve that lets sexual selection sift out harmful mutations. In this mutation-centered view of sex, sexual ornaments and courtship behaviors evolve as fitness indicators.

The Human Mind as a Set of Fitness Indicators

In the previous chapter we met the runaway brain theory. It has problems: it does not explain the trend of hominid brain evolution toward the big and the bright, and it does not work very well with mutual mate choice. However, there is another possible solution. Perhaps the human mind's most distinctive capacities evolved through sexual selection as fitness indicators.

We could call this the "healthy brain theory," in contrast to the runaway brain theory. The healthy brain theory suggests that our brains are different from those of other apes not because extravagantly large brains helped us to survive or to raise offspring, but because such brains are simply better advertisements of how good our genes are. The more complicated the brain, the easier it is to mess up. The human brain's great complexity makes it vulnerable to impairment through mutations, and its great size makes it physiologically costly. By producing behaviors such as language and art that only a costly, complex brain could produce, we may be advertising our fitness to potential mates. If sexual selection favored the minds that seemed fit for mating, our creative intelligence could have evolved not because it gives us any survival advantage, but because it makes us especially vulnerable to revealing our mutations in our behavior.

Extreme vulnerability to mutation sounds like something that natural selection could not possibly favor. Precisely. It is what sexual selection through mate choice favors. Once sexual choice seized upon the brain as a possible fitness indicator, the brain was helpless to resist. Any individuals who did not reveal their fitness through their courtship behavior were not chosen as sexual partners. Their small, efficient, ironclad, risk-averse, mutation-proof brains died out with them. In their place evolved our sort of brain: huge, costly, vulnerable, revealing.

Our species was not the first to stumble upon the fact that complex behaviors make good fitness indicators. Songbirds reveal their fitness by repeating complicated, melodious songs. Fruitflies do little dances in front of one another to reveal their genetic quality. Bowerbirds construct large mating huts ornamented with flowers, fruits, shells, and butterfly wings, presumably to reveal their quality. In fact, many species appear to use their courtship behaviors as fitness indicators. The distinctive thing about humans is that our courtship behavior reveals so much more of our minds. Art reveals our visual aesthetics. Conversation reveals our personality and intelligence. By opening up our brains as advertisements for our fitness, we discovered whole new classes of fitness indicators, like generosity and creativity.

To suggest that a mental capacity like human creative intelligence evolved as a fitness indicator is not just to throw another possible function into the arena of human evolution theories. This is not a function like hunting, toolmaking, or socializing that contributes directly to fitness by promoting survival and reproduction. Instead, fitness indicators serve a sort of meta-function. They sit on top of other adaptations, proclaiming their virtues. Fitness indicators are to ordinary adaptations what literary agents are to authors, or what advertisements are to products. Of course, they are adaptations in their own right, just as literary agents are people too, and just as advertisements are also products—the products of advertising firms. But fitness indicators work differently. They take long vacations. They are social and sales-oriented. They live in the semiotic space of symbolism and strategic deal-making, not in the gritty world of factory production. The healthy brain theory proposes that our minds are clusters of fitness indicators: persuasive salesmen like art, music, and humor, that do their best work in courtship, where the most important deals are made.

We should not expect sexually selected fitness indicators to look very useful if they are evaluated by traditional survival-of-the-fittest criteria. They do not help animals find food or avoid predators. They do not remove parasites or feed offspring. They look costly and useless. They appear luxuriously superfluous, often resembling a pathological side-effect of something more useful and sensible. But these are precisely the features of many human mental abilities that have puzzled scientists. Art and morality look like evolutionary luxuries. Creative intelligence and language seem useful in moderation, but humans do not have them in moderation—we have them in luxuriant excess.

The idea of mental fitness indicators fills an important gap in evolutionary psychology. Physical fitness indicators form a standard part of sexual selection theory, and are covered in every good evolutionary textbook. Researchers such as Randy Thornhill, Steven Gangestad, David Perrett, Anders Moller, and Karl Grammer have analyzed many aspects of the human face and body as fitness indicators that reveal health, fertility, and youth. Most evolutionary psychologists agree that human mate choice is even more focused on mind than on body, concerned as it is with assessing a person's social status, intelligence, kindness, reliability, and other psychological traits. Yet evolutionary psychology has paid very little attention to the possibility that many of our psychological traits may have evolved as fitness indicators too. The idea is not assessed in Steven Pinker's *How the Mind Works*, David Buss's textbook *Evolutionary Psychology*, or any other major work on evolutionary psychology. In most such works natural selection is used to explain most of the mind's adaptations. Where sexual selection is invoked, it is almost always to explain how our mechanisms for mate choice evolved, or how some basic sex differences in sexual strategies evolved. The idea of sexual selection for mental fitness indicators has yet to be adequately explored.

To understand how these parts of the mind may have evolved as fitness indicators, we have to understand a bit more about what fitness means, why fitness varies enough to be worth worrying about in mate choice, and what makes a good fitness indicator. After we have these principles under our belts, we can have another look at the healthy brain theory.

Evolutionary Fitness and Physical Fitness

Fitness indicators are supposed to reveal fitness—but what does "fitness" really mean? For biologists, fitness means an organism's propensity to survive and reproduce in a particular environment. Fitness in this evolutionary sense has three important features: it is relative to competitors in a species, it is relative to an environment, and it is a statistical propensity rather than an achieved outcome.

Evolutionary fitness is always relative to a population of competitors within a species. "High fitness" for a barnacle, a mayfly, an oak tree, and a human depend on very different traits, and suggest very different numbers of offspring. What ties together fitness across species is the link between fitness and evolutionary change. Genes underlying high fitness will tend to spread through a population, replacing genes for low fitness. Evolution increases fitness, by definition. In this sense, evolution is progressive: when sexual selection favors fitness indicators, it necessarily increases fitness and contributes to evolutionary progress.

Evolutionary fitness is also relative to environment. It depends on the fit between an organism's traits and an environment's features, which is why it is called "fitness" rather than "quality" or "perfection." The *Alien* films notwithstanding, there is no such thing as a super-organism that could survive and reproduce in every possible environment. When biologists talk about an organism's fitness, they usually assume that the organism's performance is being measured in an environment similar to that in which the species has been evolving for many generations. An organism that shows high fitness in an ancestrally normal environment will not necessarily show high fitness in a novel environment.

Fitness as a propensity is the most slippery concept to grasp. Fitness as I use the term is a statistical propensity, an expectation

that allows us to predict how an individual will probably fare. We attribute propensities all the time to other people: intelligence, kindness, irritability. Like fitness, these traits must be inferred rather than directly perceived. Like fitness, they allow us to make predictions that work on average over the long term, but those predictions are sometimes overridden by situational factors. Fitness is something we attribute to organisms to explain why they survive and reproduce better than their competitors. It is not just a measure of whether they do in fact survive and reproduce, because accidents can happen. A highly fit organism that we expect to thrive may be hit by lightning, or rejected as a sexual partner through some kind of situation-comedy mix-up. These failures to live up to one's fitness do not imply that the concept of fitness is vacuous. Intelligent people sometimes make errors in mental calculations, but that does not invalidate the concept of intelligence. Not all philosophers of biology agree on this propensity idea of fitness, but most do, and so do I.

In other contexts, fitness means something different. "Fitness centers" do not usually contain biologists scribbling down evolutionary equations. Instead, they are frequented by people trying to get fit, to improve their physical fitness. Fitness in the physical sense implies health, youth, athletic ability, and physical attractiveness. When George Bush appointed Arnold Schwarzenegger to head the President's Council on Physical Fitness in the early 1990s, he did not expect Schwarzenegger to improve the quality of the American gene pool. He expected him to get Americans in better shape.

Physical fitness is not relative to a population or an environment, but is relative to a norm of optimal efficiency for a body of a particular species. When we say a man is physically fit, we do not mean he is merely less fat, weak, stiff, and breathless than his peers. A whole population might be physically unfit. To be physically fit is to have a body near the peak of its potential performance, objectively efficient at turning oxygen and food into muscle power and speed. Physical fitness in this sense could even be compared across species. One could say "She is as fit as a champion greyhound." That may be faint praise, but it is not meaningless.

Physical fitness is still environment-relative in the sense that a fit human could not thrive on a neutron star with gravity a billion times stronger than the Earth's. Yet, within the normal operating parameters of a species, physical fitness is useful across a range of situations. An athlete who is fit enough to climb Mount Everest is probably fit enough to scuba-dive, or to fly a rocket to Mars. Physical fitness manifest in one situation usually transfers fairly well to other situations. This is why triathlons and decathlons exist—there are some tradeoffs between the optimal body for distance running and the optimal body for swimming, but some individuals can be better at both than almost anyone else is at either.

Another contrast to evolutionary fitness is that physical fitness is closer to a measurable achievement than a statistical propensity. It is less abstract, and closer to real behavioral outcomes. We expect strength to be manifest in the consistent ability to lift heavy things. We expect aerobic fitness to be manifest in the ability to climb stairs without losing one's breath. Accidents can still keep the fittest athlete from winning a gold medal, but the correlation between physical fitness and physical performance is usually rather high. This is why manifest physical performance is such a good indicator of physical fitness.

Apart from physical fitness, one might also speak of "mental fitness," implying sanity, intelligence, rationality, and communication ability—as when a witness is fit to testify in court. Mental fitness shares most of the important features of physical fitness: it is relative to a norm of optimal psychological efficiency in a particular species, it is fairly general across psychological tasks, and we expect it to be manifest in real behavior. Indeed, what intelligence researchers call "general cognitive ability" or "the *g* factor" could be construed as mental fitness.

Biology students are often taught to make a very clear distinction between evolutionary fitness and physical fitness, to keep them separated by the social Atlantic that keeps professional athletes from mixing with scientists. This distinction is important

in teaching biology students to think in flexible, abstract ways about evolutionary fitness. It reminds us that evolutionary fitness is always a matter of trade-offs, or finding the optimal allocation of resources between competing demands. Physical strength is not synonymous with evolutionary fitness, because investing in larger muscles may often produce fewer offspring than investing in larger testicles, fat reserves, or brains. But the distinction makes it hard to develop good intuitions about fitness indicators, which tend to advertise fitness in both the evolutionary and the physical sense.

The Oxford biologist W. D. Hamilton has reminded his colleagues that, within a given species, physical fitness is often rather tightly linked to evolutionary fitness. In his work on sexual selection he has tried to revive a more intuitive concept of fitness in which survival and reproduction do depend on basic physical variables like health, strength, energy, and disease-resistance. Within a species, healthier, stronger animals do tend to survive better, reproduce better, and attract more mates. This correlation between evolutionary fitness and physical (or mental) fitness keeps "the survival of the fittest" from being a tautology.

Evolutionary fitness is linked to physical and mental fitness by something that biologists call "condition." In fact, an animal's "condition" is basically its physical fitness, health, and energy level. A high-fitness animal may be in poor condition due to a temporary injury or food shortage. A low-fitness animal might be in good condition due to a zoo taking very good care of it. In a science laboratory, we can disentangle condition from fitness. We can randomly assign different diets to different animals, or infect an experimental group with a communicable disease and protect a control group from that disease. But in nature, animals largely determine their own condition through their own efforts. The abilities to find food, resist disease, and avoid parasites are major determinants of condition, and major components of fitness. In nature, fitness generally correlates with condition. Good condition is thus a pretty good indicator of high fitness.

Of course, there may be droughts, disasters, food shortages, and epidemics, when all members of a population suffer from poor condition. But even then, higher-fitness animals may suffer less than lower-fitness animals do. The correlation between fitness and condition may remain, despite fluctuations in a population's average condition. In fact, fitness may sometimes be easier to assess under challenging conditions because individual differences in ability may then become more apparent. This is why romantic novels include adventure and risk: emergencies bring out the best in heroes and the worst in pretenders.

As we shall see, many fitness indicators advertise fitness by revealing an animal's condition. They are "condition-dependent" —very sensitive to an animal's general health and well-being ("condition"), and very good at revealing differences in condition between animals. This sets up a chain of relationships that will prove absolutely central to many arguments in this book: genetic mutations influence fitness, fitness influences condition, condition influences the state of fitness indicators, fitness indicators influence mate choice, and mate choice influences evolution.

From the viewpoint of an animal making sexual choices, fitness indicators are just proxies for good genes. But the sexual selection that results from mate choice does not just influence the genes for fitness. It shapes the fitness indicators themselves. These fitness indicators combine evolutionary fitness with physical fitness and mental fitness. That is the key. By trying to get good genes for their offspring, our ancestors unwittingly endowed us with a whole repertoire of very unusual fitness indicators which have come to form an important component of the human mind.

This theory of fitness indicators suggests that much of human courtship consists of advertising our physical fitness and mental fitness to sexual prospects. Physical fitness may be revealed by body shape, facial features, skin condition, energy level, athleticism, fighting ability, and dancing ability. Mental fitness may be revealed by creative story-telling, intelligent problem-solving, skillful socializing, a good sense of humor, empathic kindness, a wide vocabulary, and so forth.

Clearly, many of the traits advertised during courtship also

bring non-genetic benefits to a sexual relationship. As David Buss and others have argued, strong mates offer protection, social intelligence brings social benefits, and kindness signals commitment. Fitness-indicator theory does not deny these other benefits, but points out that they are not the only reasons for mate choice. Good genes are important too—indeed, I shall argue that some human mate preferences have been misunderstood as seeking purely non-genetic benefits, when they have actually been focusing on indicators of genetically heritable fitness.

Ms. Fitness USA

Watch enough American cable television, and sooner or later you will find a pretty good analogy for almost any intellectual revolution in evolutionary biology. For me, the revolution in sexual selection ideas in the last twenty years of the 20th century is nicely symbolized by the eclipse of the "Miss America" beauty pageant by newer, more fitness-oriented contests such as "Ms. Fitness USA." In 1980, before the Ms. Fitness contests were invented, biologists thought that most sexual ornaments were arbitrary. Ornaments supposedly evolved through the runaway process or some other arbitrary process. In this picture, the peacock's tail did not reflect any aspect of a peacock's fitness, so was not a very rational basis for sexual choice. Yet a minority of biologists became skeptical about this view that most beauty is arbitrary. Similarly, feminists protested against Miss America pageants, upset by the apparent arbitrariness of the cultural norms of beauty used by the judges. The ability to totter around in high heels and swimsuit did not seem to reflect any very significant aspect of a woman's being.

In response to such criticisms, a promoter named Wally Boyko turned the tables on the beauty contest industry by inventing the "Ms. Fitness USA" contest in 1985. This contest explicitly favors women with the highest physical fitness, not just the greatest beauty. (Indeed, the Ms. Fitness World contest, founded in 1994, is held in conjunction with the annual Arnold Schwarzenegger Fitness Weekend.) The Ms. Fitness contests include three rounds:

an evening gown round (to judge beauty, grooming, poise, and speaking ability), a swimsuit round (to judge muscle tone, body fat, and apparent fitness), and a fitness outfit round (a high-energy, 90-second display of strength, flexibility, endurance, and creativity, set to music). In the third round contestants usually do somersaults, splits, jumps, and one-handed pushups—in such a way as to make the difficult appear effortless. The whole aesthetic shifted from Miss America's soft-bodied, giggly display of femininity to a hard-boiled, active display of health. The judging criteria no longer looked quite so culturally arbitrary. Miss America contestants could improve their chances by dieting, getting silicone breast implants, dyeing their hair, and skillfully applying makeup. But Ms. Fitness contestants, such as the currently top-ranked Monica Brant, can win only by training like professional athletes with aerobics, weightlifting, stretching, sports, and healthy eating. Their physical fitness would be manifest in any culture at any point in history, regardless of minor cultural variations in the norms of beauty.

Some evolutionary biologists responded to the idea of arbitrary sexual ornaments in the same way that Boyko's "International Fitness Sanctioning Body" responded to the Miss America pageant. They rethought the judging criteria. Why should animals choose mates for arbitrary traits, when they can choose mates for traits that reveal their condition and fitness? Certainly, the runaway process can happen in principle, but maybe it is not so important. Maybe it creates transient sexual fashions that come and go, but it does not explain the sexual ornaments that stick around generation after generation. The ornaments that stick around should reveal some information about fitness, about good genes. Most sexual ornaments should be fitness indicators. The debate over this issue has an illuminating history.

Sexual Choice for Fitness

Sir Ronald Fisher first emphasized that animals could choose their sexual partners for high fitness by favoring certain kinds of sexual display. As we saw in Chapter 2, his 1915 paper introduced

this idea of fitness indicators. But his 1930 book barely mentioned them, and devoted more space to the idea of runaway. When runaway sank into the quicksand of scientific skepticism, Fisher's even more obscure fitness-indicator idea sank with it. The idea waited thirty-six years for rescue. George Williams revived it in his influential classic, *Adaptation and Natural Selection.* Several decades on, his description of sexual choice for fitness remains unsurpassed.

> It is to the female's advantage to be able to pick the most fit male available for fathering her brood. Unusually fit fathers tend to have unusually fit offspring. One of the functions of courtship would be the advertisement, by a male, of how fit he is. A male whose general health and nutrition enables him to indulge in full development of secondary sexual characters, especially courtship behavior, is likely to be reasonably fit genetically. Other important signs of fitness would be the ability to occupy a choice nesting site and a large territory, and the power to defeat or intimidate other males. In submitting only to a male with such signs of fitness a female would probably be aiding the survival of her own genes.

Since Williams's book became required reading for the new generation of biologists in the 1970s, the indicator idea started to catch on. It received another publicity boost when Richard Dawkins gave it a sympathetic exposition in his 1976 bestseller *The Selfish Gene.*

By the mid-1980s, biologists were seriously assessing the fitness indicator idea. The basic intuition seemed sound, but there were two technical problems so difficult that they took another ten years to resolve. One concerned the supposedly low heritability of fitness, and the other concerned the supposedly low reliability of fitness indicators. To understand how the human mind may have evolved as a set of fitness indicators, we have to understand these problems and their solution.

Why Is Fitness Still Heritable?

Fitness indicators are pointless unless individuals vary in their fitness. If we take fitness to mean the possession of good genes that can be inherited by offspring, then it seems hard to understand how evolution can allow any variation in fitness to remain. Selection is supposed to maximize fitness, driving it ever upwards. It is not supposed to permit fitness variation to persist in species just to provide an incentive for sexual choice.

To follow this argument, it is crucial to understand the difference between "inherited" and "heritable." All traits that depend on genes are inherited. But the term "heritable" is much more restrictive: it refers to the proportion of individual differences in a trait that are due to genetic differences between individuals. The concept of heritability applies only to traits that differ between individuals. If a trait exists in precisely the same form across all individuals, it may be inherited, but it cannot be heritable. It should come as no surprise that fitness is inherited, because fitness clearly depends on genes. The surprising thing is that fitness still varies between individuals in most species, and that the variation often seems to depend on genetic differences.

To see why the heritability of fitness is surprising, consider what happens in species that mate in large aggregations called "leks." *Lek* is Swedish for a playful game or party. Some birds like sage grouse congregate in these leks to choose their sexual partners. The males display as vigorously as they can, dancing, strutting, and cooing. The females wander around inspecting them, remembering them, and coming back to copulate with their favorite after they have seen enough. Leks resemble music festivals where mostly male rock bands compete to attract female groupies. In species that lek, the males usually contribute nothing but their genes. The females may never see them again, and raise their offspring as single mothers. Leks create a situation where sexual selection is extremely strong. The most attractive male sage grouse may mate with thirty females in one morning; average males usually mate with none. It is a winner-takes-all contest, and it should spread the most attractive male's genes very quickly through the population.

If the lekking females choose males for good genes generation after generation, all the males should end up being perfectly fit and identically attractive. Males of lower apparent fitness will have died unmated, their mutations having died with them. After a few generations, all the mutations that show up in fitness indicators should be gone. Only the good genes should be left. If every male has the same high fitness, there is no variation for fitness indicators to reveal. If there is no variation in genetic quality, and if genes are all that females get, there is no longer any incentive for females to be choosy about their mates. Instead of spending time and energy wandering around the lek admiring male displays, the females might as well pick randomly. The reasons for mate choice should disappear as the heritable variation in fitness disappears. According to this evolutionary logic, leks should be temporary phenomena. Yet leks still exist. Presumably, sage grouse have been gathering in leks for thousands of generations. Biologists call this the "lek paradox."

The lek paradox is the most extreme case of a general problem with the heritability of fitness. Any form of sexual selection for fitness indicators should even out genetic variation in fitness. If female choice in our species favored tall males, all males should be equally tall. If male choice favored large breasts, all females should be equally large-breasted. If both sexes favored high intelligence and beautiful faces, all humans should be equally bright and beautiful. Yet we are not. The differences remain, and they are still genetically heritable. So why would selection allow such differences to persist?

Once biologists agreed that the lek paradox was a problem, the hunt was on for evolutionary forces that could maintain variation in fitness. Two major candidates emerged. One emphasized that fitness is environment-relative; the other emphasized the ubiquity of harmful mutations that erode fitness.

Time, Space, and Fitness

We saw earlier that fitness is relative to a particular environment. Environment-relative fitness implies that if a population's environment fluctuates over time or space, then the meaning of fitness will fluctuate too. If the meaning of fitness fluctuates, and the population will not stabilize on any one set of genes that will be good in every environment, then environmental variation could maintain genetic variation.

On evolutionary time-scales, physical environments are changing all the time. The climate gets colder or hotter. Rivers shift course. Mountains rise and fall. Meteorites strike. But such physical changes are usually too slow or rare to maintain variation in fitness. Species adapt fairly quickly to changes in their physical environments, reaching a new equilibrium where all individuals should have optimal traits and high fitness.

More important is the biological environment: the other species that are evolving alongside a given population. Predators may get faster or smarter. New parasites may evolve. Viruses mutate at great speed. In the early 1980s, W. D. Hamilton and John Tooby independently developed the idea that variation in fitness could be maintained over very long periods by populations evolving interactively with their parasites. Every animal large enough for us to see has parasites. Because the parasites are smaller than their hosts, they can grow faster and breed faster—their generation time is shorter. The human generation time is about twenty-five years. For bacteria it can be as little as twenty minutes. For every generation that hosts can evolve to have resistance against parasites, parasites can evolve many generations to exploit their hosts, so parasites can adapt much faster to hosts than vice versa. From a parasite's viewpoint, the host's body is the environment to which it adapts. The host's body determines what counts as fitness for the parasite. But the converse is true as well. From the host's viewpoint, parasites are a major part of the biological environment. The capabilities of parasites determine what counts as fitness for the host. Because parasites are constantly evolving against all large-bodied animals, the biological environment is constantly changing for all such animals. Genes that are good against today's parasites might not be so good tomorrow.

In Hamilton's view, the high-speed evolution of parasites is a

major force in moving the goal posts of fitness. No large-bodied species ever reaches the hypothetical equilibrium where every individual has high fitness, because parasites always evolve faster. Hamilton saw the implications for sexual selection. Mate choice should favor fitness indicators that are especially good at revealing how individuals resist parasites like viruses, bacteria, and intestinal and skin-burrowing worms. A large, bright peacock's tail proclaims, "I have conquered my parasites. If I had not, my tail would be small, drab, and diseased-looking. If you mate with me, your offspring will inherit my resistance." In an influential 1982 paper, W. D. Hamilton and Marlene Zuk proposed that many sexual ornaments evolved as fitness indicators that signal freedom from parasites. For example, an uakari monkey's bright red face may have evolved to reveal that it is not infected by blood parasites that would cause pale-faced anemia. As long as there are parasites in the world, the meaning of fitness will vary from one generation to the next. Large-bodied species are thus chasing an optimal fitness that remains always one step ahead of them. That, in Hamilton's view, explains why fitness remains heritable in most species most of the time. Matt Ridley's book *The Red Queen* lucidly describes how arms races between parasites and hosts could maintain the incentives for mate choice.

Our ancestors had plenty of parasites and germs to worry about too: tapeworms, herpes, crab lice, common colds, malaria, stomach flu. Their communicable diseases were probably not as severe as those that arise in urban civilizations, because their population densities were much lower. They did not have plagues like medieval European cities. But every one of our hominid ancestors was probably exposed to dozens of species of fast-breeding, fast-evolving, energy-sapping organisms, from micro-parasites like viruses and bacteria to macro-parasites like head lice. The variable was not whether they had parasites, but how well they maintained their health and energy despite them. The sexual repulsion we may experience toward someone heavily infected with parasites may reflect more than a fear of contamination. It may be showing that Hamilton is right: that resisting parasites is a major part of

fitness for any large animal, and advertising that resistance is a major function of sexual ornaments.

Environments fluctuate across space as well as time. Our ancestors lived in small groups spread out over wide areas of Africa. The African continent is not one big flat savannah. Each area has slightly different weather, geology, vegetation, competitors, predators, and parasites. There are many micro-habitats. What is optimal in one area may not be optimal in another. Survival pressures vary across space, so each individual's fitness varies across space. As long as some of our ancestors migrated from one area to another in every generation, they would never evolve to the point where every individual in every area has maximum fitness relative to their local environment. Like variation in selection pressures over time, this variation in space helps explain why fitness remains heritable.

Environmental fluctuations across time and space are best at explaining why physical fitness and health remains heritable. But they are not so useful to us if our interest is in mental fitness indicators. Parasites put evolutionary pressure more on immune systems and bodies than on brains. Variations in climate from one part of Africa to another might maintain heritable variation in physical adaptations, but it is not clear why they should maintain variation in mental adaptations. To explain persistent variation in mental fitness, we need something more.

The Black Rain of Mutation

In science-fiction films and comic books, "mutations" are Faustian bargains that confer superhuman powers while damning their possessors to abnormal appearance and impaired sexual attractiveness. Spiderman was bitten by a "mutated" spider, and acquired wall-clinging powers but became alienated from his girlfriend. Monster Island apparently had high levels of mutagenic radiation, which is how Godzilla acquired his "atomic breath" that incinerates his enemies but keeps him single. This comic-book view of mutations is only half right. Mutations do undermine normal appearance and sexual

attractiveness, but they very rarely bring survival or fertility benefits.

Since the late 1980s, many biologists have been coming around to the view that fitness remains heritable mostly because new mutations are constantly arising and causing trouble. As we saw before, mutations almost always lower fitness. The more mutations an individual carries, the lower its expected fitness. To avoid mutational meltdown and extinction, selection had to be potent enough to eliminate those mutations at the same average rate at which they arose. (As we saw, Eyre-Walker and Keightley estimated that at least 1.6 harmful new mutations per individual every generation have been arising in our lineage for the last several million years.)

In most species for most of the time, almost all of the natural selection and sexual selection consists simply of removing harmful new mutations and maintaining the status quo. Selection is mostly conservative and stabilizing. Very rarely does selection favor a new mutant, because only rarely is a mutated gene better than the existing gene at helping an organism survive and reproduce. These rare occasions attract the biologist's attention because they are the times when evolution—genetic change in a species—can occur. But for the rest of the time, there is a tension between selection and mutation. Selection tends to maintain adaptations in their current effective form, while mutation tends to erode them into a chaotic, ineffectual mess.

The Brain as a Target for Mutation

For simple traits that depend on just a few genes, selection is pretty good at eliminating mutations. Each mutation is likely to cause such dramatic change that natural selection rapidly eliminates it. But for very complex traits, like human brains, that grow through the interaction of many genes, mutations are harder for selection to eliminate. There are more genes vulnerable to mutation in the first place, and selection's effects get diluted across more genes. This decreases selection's power to eliminate mutations on any one gene. With mutation stronger and selection weaker, complex traits are less likely to be perched on the peak of perfection.

Genetic variation is more likely to be manifest in complex traits. This makes complex traits like the human brain better fitness indicators.

Imagine all the DNA in our 23 pairs of chromosomes laid end to end in a single strip. The DNA from a single human cell would be about six feet long, and contain about 80,000 genes. Imagine that the genes involved in growing a particular trait are lit up in bright green, and that each gene has a tiny chance of having a mutation that turns the green light red. For a very simple trait like skin color, there might be only half a dozen lights sprinkled along the six-foot length of DNA. It is very unlikely that any of them would be red. For a moderately complex trait like the shape of the human face, there might be several hundred lights. It is likely that a few of them might be red. For a very complex organ like the human brain, there might be tens of thousands of lights. Our DNA would light up like a Christmas tree. Although the proportion of red lights would still be very low, the absolute number would be much higher. The brain would give much better information about mutation load and fitness, because it gives mate choice a wider window on a larger sample of our DNA. (The larger the sample of genes, the more accurate the estimate of mutation load.) This is what biologists mean by the "mutational target size" of a trait: the proportion of the genome that is involved in a trait's development determines the proportion of all mutations that are visible in the trait.

At the moment, nobody knows exactly how many of our genes are involved in growing our brains. Geneticists sometimes estimate that about half of our genes are involved in brain development, and about a third might be active only in the brain. If this guess is about right (and we shall know within a decade or two whether it is), then the mutational target size of the human brain is about half the human genome. The brain probably has a larger mutational target size than any other organ. Of all the new mutations that mess up something during human development, half of them mess up something in the human brain.

If mutations maintain most of the variation in fitness that we

see, then the organs with the largest mutational target sizes will make the best fitness indicators. The human brain should make a very good fitness indicator indeed. Its vulnerability to mutation is precisely why sexual choice mechanisms should evolve to pay attention to its performance.

In the rest of this book, I shall take the heritability of fitness for granted. The expectation that fitness should not be heritable was based on theoretical arguments developed in the 1930s. Those arguments are contradicted by the evidence. Wild populations show large amounts of genetic variation. Biologists routinely find individual differences in reproductive success in the wild, differences which are often genetically heritable. Fitness remains heritable in most species for most of the time. It seems likely that a lot of this continuing heritability is due to the continual rain of mutations. Some biologists even wonder how selection can possibly be strong enough to eliminate all these new mutations, and keep the species from falling apart. Fitness-eroding mutations are ubiquitous, and usually stick around for a fairly long time. There is always a tension between mutation and selection. And there are always fluctuations in fitness across time and space which keeps fitness heritable. These are just the facts of life. Mate choice evolves to deal with them.

How to Advertise Fitness

Fitness is like money in a secret Swiss bank account. You may know how much you have, but nobody else can find out directly. If they ask the bank, the bank will not tell them. If they ask you, you might lie. If they are willing to mate with you if your capital exceeds a certain figure, you may be especially tempted to lie. This is what makes mate choice difficult. The supposedly low heritability of fitness was one argument against the importance of fitness indicators in sexual selection. The other problem is the potentially low reliability of fitness indicators. An animal trying to find a high-fitness mate is in the position of an attractive gold digger seeking a millionaire. She has incentives to mate only with a male who offers high genetic or financial capital. But every male has incentives to pretend to be richer than he is, to attract more mates. What is a poor girl to do?

Anita Loos's classic 1925 novel *Gentlemen Prefer Blondes* suggested one good strategy. The blonde protagonist Lorelei Lee forced her suitors to spend vast amounts of money on her, to show how much they really had. Her suitor Gus Eisman may have called himself "the Button King," but who can say whether his business is really profitable? Miss Lee was not the brightest button ever to baffle "Doctor Froyd" in Vienna, but she understood the principle of costly display. If a man can afford to dress as well as a peacock, he is probably not poor. If he gives you a very large diamond, he is likely to be rich. The more they can spend, the more they must have.

Lorelei was not the first to realize this, of course. Thorstein Veblen's *Theory of the Leisure Class* introduced the idea of "conspicuous consumption" in 1899. Veblen argued that in modern urban societies, where strangers come and go, people increasingly advertise their wealth by ornamenting themselves with costly luxuries. Where nobody knows anyone else's true wealth directly, conspicuous consumption is the only reliable signal of wealth. Sociologists and economists understood this logic immediately. Capitalist consumerism evolved in part as a set of wealth indicators.

It took biologists another three-quarters of a century to apply the same principle to sexual selection for fitness indicators. As we saw earlier, in 1975 Israeli biologist Amotz Zahavi argued that many animal signals—including sexual ornaments—evolved as advertisements of the animal's fitness. He suggested that the only reliable way to advertise one's true fitness is to produce a signal that costs a lot of fitness. This explains why sexual ornaments are so often large, extravagant, costly, and complicated. The peacock's tail is not just a cheap, transient advertisement visible only to peahens. It is heavy, encumbering, hard to grow, hard to preen, and highly visible to predators. Peacocks have to drag it around everywhere they go. Unfit peacocks might be able to grow large tails, but they would not be strong enough to carry them while finding food,

or fast enough to escape from predators. Only highly fit peacocks can afford very large tails.

Therefore, if a female sees a male sporting a very large tail, she can be confident that he has high fitness, and that his good genes could be passed on to her offspring. Since very fit peacocks tend to have fit sons and daughters that are more likely to survive and reproduce, peahens benefit by choosing big-tailed peacocks. Their preferences for larger-than-average tails can spread. Conversely, peahens that preferred shorter-than-average tails did not leave many descendants to inherit their misguided preference, because their offspring were less fit than average. Sexual selection favors both the preference for costly sexual displays and the displays themselves.

Zahavi suggested that most sexual ornaments are "handicaps": they advertise true fitness by handicapping an individual with a survival cost. He also argued that handicaps should be the only evolutionarily stable kinds of sexual ornament, because they are the only ones that convey the information about fitness that individuals really want when making sexual choices. His paper unleashed a storm of protest. The handicap idea seemed absurd. Throughout the late 1970s the handicap principle was attacked by almost every eminent evolutionary theorist. Surely sexual selection could not have an intrinsic drive to produce wasteful displays that impair survival?

Apparently, most biologists in the 1970s had not read Thorstein Veblen. They did not make the connection between conspicuous consumption to advertise wealth and costly sexual ornaments to advertise fitness. Without that connection it was hard to see how Zahavi's handicap principle could work (or rather, which of the several possible versions of it might work). How could sexual selection favor fitness indicators that impaired an animal's survival prospects? How could mate choice favor a costly, useless ornament over a cheaper, more beneficial ornament? (Why should a man give a woman a useless diamond engagement ring, when he could buy her a nice big potato, which she could at least eat?)

A clever peahen able to read Veblen might propose that, for the good of the species, peacocks should stop this mad waste. Suppose, for example, that each peacock agreed to wear a little hat showing a number between one and ten that revealed his actual fitness (perhaps a composite score of health, strength, fecundity, intelligence, and screeching ability). The problem with this system of quality-signs is that there would be no effective way to police it. Low-fitness peacocks would lie, because they could attract better mates by lying—they would all proclaim a perfect ten. Zahavi realized that the signaling system has to be self-policing. It has to include a range of sexual signals that differ in cost, and thus differ in affordability by individuals of different fitness, by virtue of which they honestly reveal their fitness.

The handicap principle suggests that prodigious waste is a necessary feature of sexual courtship. Peacocks as a species would be much better off if they didn't have to waste so much energy growing big tails. But as individual males and females, they have irresistible incentives to grow the biggest tails they can afford, or to choose sexual partners with the biggest tails they can attract. In nature, showy waste is the only guarantee of truth in advertising.

The handicap principle was also rejected initially because most biologists did not know about economists' research into costly signaling. During the 1960s, game theorists working in economics departments did a lot of work on what makes signals reliable, given incentives to lie. They developed something called signaling theory, which distinguishes two kinds of signal. There are signals that incur a significant cost or commitment, which can therefore be reliable indicators of someone's intentions. And then there are signals that cost nothing, which are called "cheap talk." Economists realized that cheap talk is not to be trusted. It does not commit someone to a course of action. It does not reveal their capabilities. It means nothing, because it costs nothing. If a car company proclaims "We will defend our share of the four-door market at all costs," that is just cheap talk and hot air. But if the company spends a billion dollars building a factory specialized for four-door car production, their proclamation carries some weight.

The factory is not just a capital investment—it is also a strategic signal. It deters competitors from entering the same market niche by reliably revealing the company's financial strength and strategic commitment. In fact, the more (wasteful) excess capacity the factory has, the better a strategic signal it is. Likewise, proclaiming "I have a straight flush" in poker carries less credibility than placing a large bet on one's hand. This costly-signaling principle became so widely accepted among economists in the 1960s that signaling theory withered for lack of controversy.

Advertising Within One's Budget

It took biologists about fifteen years to accept Zahavi's handicap principle. Much of that time was spent clarifying what kinds of handicaps could evolve and what kinds could not. Since handicaps are basically fitness indicators, the debate over handicaps helped lay the foundation for the modern theory of fitness indicators.

A handicap cannot usually evolve if it commits all the males to producing a costly signal regardless of their true fitness. This would be like all men buying a five-carat diamond engagement ring regardless of their salaries. Such a fixed-cost strategy is not sensible for anybody—all the poor men would go bankrupt and starve before their wedding day, while the super-rich men would be indistinguishable from the moderately rich men. The same problems explain why we rarely see sexual ornaments in nature that are produced by all males to an equal degree. A handicap gene that committed all low-fitness males to produce a very costly sexual ornament would simply kill them all. The handicap would help females to recognize high-fitness males, but the females could not tell which of the high-fitness males was best. Mathematical models and simulations suggest that this sort of fixed-cost handicap cannot evolve under reasonable conditions.

Handicaps can evolve much more easily if they are a little more sensitive to an animal's fitness level. A gene that says "spend 50 percent of your disposable energy on courtship dancing" could easily spread through a population if females appreciate dancing.

It would be just like the cultural rule invented by the De Beers diamond cartel that insists, "Spend two months of your salary on your engagement ring." Costly signals that take fitness budgets into account evolve much more easily than do costly signals that ignore budgets. Sensitivity to this budget constraint is called "condition-dependence" by most biologists. It could equally be called "fitness-dependence," to reflect the intuition that fitness indicators should be fitness-dependent. Alan Grafen showed that condition-dependent indicators could evolve, giving Zahavi's handicap principle much more credibility.

This sort of condition-dependence seems intuitive when you think of examples. Better-fed animals can afford to grow larger sexual ornaments. Most energetic animals can afford to exert more effort in courtship. Stronger animals can afford to fight other strong animals in ritualized contests. Faster animals can afford to taunt predators from a closer distance. Animals with better memories can afford to learn a large repertoire of courtship songs. Animals with higher social status can afford to act more confident and relaxed around their peers.

Such condition dependence is one of the most important concepts in sexual selection today. It protects low-fitness animals from incurring the costs of sexual ornamentation and courtship if they do not feel up to it. If you are a really unfit peacock, you are not forced to grow a huge tail that will kill you through exhaustion within a week; instead you can grow a drab little tail and hope for the best. Compared to sexual ornamentation that grows on the body, courtship behavior is even more flexible and condition-dependent. If you are a human feeling really ill, you do not have to go to the Ministry of Sound nightclub with your significant other and dance all night after taking lots of drugs. If you are in poor aerobic condition you do not have to run the Olympic marathon and die of heatstroke. If you are not very bright you do not have to go to Stanford Business School and fail. Condition-dependence lets us choose our battles.

Condition-dependence is equally useful at the high end of the fitness scale, for it enables one to tailor the amount one spends on

fitness indicators to one's fitness level. This helps the extremely fit to distinguish themselves from the very fit. It spreads out the apparent differences between individuals so that their fitness is easier to judge. Condition-dependence makes mate choice easier because it lets one infer fitness directly from the apparent costliness of a courtship display.

An Infinite Variety of Waste

Zahavi's handicap principle and the idea of condition-dependence are different perspectives on the same thing. The handicap idea emphasizes that sexual ornaments and courtship behaviors must be costly in order to be reliable fitness indicators. Their cost can take almost any form. They can increase risk from predators by making an animal more conspicuous with bright colors. They can increase risk from germs by impairing an animal's immune system (which many sex hormones do). They can burn up vast amounts of time and energy, like bird song. They can demand a huge effort to obtain a small gift of meat, as in human tribal hunting.

As with Veblen's conspicuous consumption principle, the form of the cost does not matter much. What matters is the prodigious waste. The waste is what keeps the fitness indicators honest. The wastefulness of courtship is what makes it romantic. The wasteful dancing, the wasteful gift-giving, the wasteful conversation, the wasteful laughter, the wasteful foreplay, the wasteful adventures. From the viewpoint of "survival of the fittest," the waste looks mad and pointless and maladaptive. Human courtship even looks wasteful from the viewpoint of sexual selection for non-genetic benefits, because, as we shall see, the acts of love considered most romantic are often those that cost the giver the most, but that bring the smallest material benefits to the receiver. However, from the viewpoint of fitness indicator theory, this waste is the most efficient and reliable way to discover someone's fitness. Where you see conspicuous waste in nature, sexual choice has often been at work.

Every sexual ornament in every sexually reproducing species could be viewed as a different style of waste. Male humpback whales waste their energies with half-hour-long, hundred-decibel songs that they repeat all day long during the breeding season. Male weaverbirds waste their time constructing ornamental nests. Male stag beetles waste the matter and energy from their food growing huge mandibles. Male elephant seals waste a thousand pounds of their fat per breeding season fighting other elephant seals. Male lions waste countless calories copulating thirty times a day with female lions before the females will conceive. Male humans waste their time and energy getting graduate degrees, writing books, playing sports, fighting other men, painting pictures, playing jazz, and founding religious cults. These may not be conscious sexual strategies, but the underlying motivations for "achievement" and "status"—even in preference to material sources—were probably shaped by sexual selection. (Of course, the wasteful displays that seemed attractive during courtship may no longer be valued if they persist after offspring arrive—there is a trade-off between parental responsibilities and conspicuous display.)

The handicap principle suggests that in each case, sexual selection cares much more about the prodigious magnitude of the waste than about its precise form. Once the decision-making mechanisms of sexual choice get the necessary information about fitness from a sexual display, everything else about the display is just a matter of taste. This interplay between waste and taste gives evolution a lot of elbow room. In fact, every species with sexual ornaments can be viewed as a different variety of sexually selected waste. Without so many varieties of sexual waste, our planet would not be host to so many species.

Evolving Better Indicators

The late 1990s have brought an ever-deeper understanding of fitness indicators in sexual selection theory. Biologists such as Alan Grafen, Andrew Pomiankowski, Anders Moller, Rufus Johnstone, Locke Rowe, and David Houle have pushed the idea of condition-dependence deeper into the heart of sexual selection, relating it to

the heritability of fitness arguments and the idea of mutation selection balance. Indicator theory is still developing very quickly, and no one has yet had the final word. However, I am especially intrigued by some ideas that Rowe and Houle developed about condition-dependence in a 1996 paper, because they seem most relevant to the human mind's evolution.

In Rowe and Houle's model all fitness indicators start out as ordinary traits. Each trait has certain costs. Higher-fitness individuals have larger energy budgets, so are better able to bear these costs. Initially, a trait may be favored by sexual choice because of some random runaway effect. But once it is favored, individuals with more extreme, costlier versions of the trait will spread their genes more successfully. This sexual selection increases average fitness in the population, because the trait acts as a weak fitness indicator. But here is the crucial point: the sexual selection also puts pressure on the trait to recruit a larger share of the individual's energy budget for itself. Individuals who allocate a low proportion of their fitness to the sexually favored trait will lose out to those who allocate a lot. As the sexually favored trait grabs a larger share of an organism's resources for itself, it becomes ever more dependent on the organism's total fitness budget. The trait turns from a cheap ordinary trait into a true handicap with large costs—in other words, its condition-dependence increases. And the increasing condition-dependence becomes an ever more valuable source of information about fitness. In this way, sexual selection has turned an ordinary trait into a really good fitness indicator.

The fitness indicator does not just recruit an increased share of an organism's energy: it also makes itself dependent on an increased proportion of an organism's genes. Rowe and Houle call this process "genic capture." The indicator captures a larger amount of information about an individual's genetic quality. Typically, this might work by a trait evolving a little bit more complexity, recruiting some of the genes that influence growth and development processes already evolved for other adaptations. This genic capture process makes the fitness indicator a window

on an animal's genome. As the window grows wider through genic capture, the indicator lets an observer see a larger amount of all the genetic variation in fitness with the population, making it easier to choose mates for their good genes. Good fitness indicators give sexual choice a panoramic view of a potential mate's genetic quality.

It is not clear yet exactly how genic capture works, and this feature of Rowe and Houle's model needs further research. If it does work, and if the human brain's complexity evolved in part through genic capture, then there is an interesting implication. It would explain why so many unique human mental abilities look to some biologists like "spandrels," mere side-effects of other adaptations. Stephen Jay Gould has argued that most of our uniquely human capacities did not evolve for specific adaptive functions, but emerged as side-effects of already-existing brain circuits and learning abilities. Like most evolutionary psychologists, I find that argument weak for many reasons—for example, it fails to explain why other large-brained species such as dolphins, whales, and elephants did not invent paleontology or socialism.

However, Gould's argument may have this grain of truth: the human brain's distinctive power is its ability to advertise a lot of the computational abilities that were already latent in the brains of other great apes. This does not mean that music, art, and language came for free just because an ape brain tripled in size. But it might mean that when sexual selection seized upon the ape brain as a set of possible fitness indicators, the genic capture process recruited a lot of pre-existing brain circuitry into human courtship behavior. It made that brain circuitry more manifest in courtship behavior, more condition-dependent, and more subject to sexual choice. Our brains may look like a set of spandrels, but they look that way only because our mental fitness indicators are so efficient at advertising the brain's many abilities. (Of course, fitness indicators are different from spandrels because they evolved through sexual selection to have a specific courtship function, whereas spandrels, by definition, do not have any specific evolved function.)

Mental Traits as Fitness Indicators

Fitness indicator theories like Rowe and Houle's model can help us to understand the evolution of the human mind. Our capacities for music, art, creativity, humor, and poetry do not look like ordinary adaptations are supposed to look. Evolutionary psychologists like John Tooby, Leda Cosmides, David Buss, and Steven Pinker have developed some rules for recognizing mental adaptations. If a human mental trait evolved through natural selection for some specific function, it is supposed to show small differences between people, because selection should have eliminated maladaptive variation long ago. It is supposed to show low heritability, because selection should have eliminated all genes other than the optimal ones long ago. It is supposed to be efficient and low in cost, because natural selection favors efficient problem-solving. And it is supposed to be modular and specialized for solving a particular problem, because modular specialization is the efficient way to engineer things.

Fitness indicators violate all these criteria. If a mental trait evolved through sexual selection as a fitness indicator, it should show large differences between people. It evolved specifically to help sexual choice discriminate in favor of its possessor at the expense of sexual rivals. Fitness indicators can show high heritability because they tap into genetic variation in fitness, and fitness usually remains heritable. For fitness indicators to be reliable, they have to be wasteful, not efficient. They have to have high costs that make them look very inefficient compared with survival adaptations. Finally, fitness indicators cannot be totally modular and separate from other adaptations, because their whole point is to capture general features of an organism's health, fertility, intelligence, and fitness. The peacock's tail appears to fit this profile as a fitness indicator, and many human mental abilities do as well.

To traditional evolutionary psychologists, human abilities like music, humor, and creativity do not look like adaptations because they look too variable, too heritable, too wasteful, and not very modular. But these are precisely the features we should expect of fitness indicators. If a human mental trait shows large individual differences, high heritability, high condition-dependence, high costs, and high correlations with other mental and physical abilities, then it may have evolved through sexual selection as a fitness indicator.

If we make an inventory of what the human brain can do, we find two general themes: very few of the ancient mental abilities that we share with other apes look like fitness indicators, but many mental abilities unique to humans do look like fitness indicators. There are probably thousands of psychological adaptations in the human mind. The vast majority are shared with other species. Some evolved hundreds of millions of years ago and are shared with thousands of species. Some evolved only a few million years ago and are shared only with other great apes. We have exquisitely efficient mechanisms for regulating our breathing, controlling our limbs, keeping our balance, seeing colors, remembering spatial locations, learning foraging skills, being kind to offspring, feeling pain when injured, remembering faces, making friends, punishing cheats, perceiving social status, estimating risks, and so forth. Steven Pinker has explored many of these mechanisms in his book *How the Mind Works*. When I propose a shorthand slogan like "the human mind evolved through sexual selection," I do not mean that sexual selection shaped all of these adaptations that we share with other primates. Of course, about 90 percent of our psychological adaptations evolved through standard natural selection and social selection to solve routine problems of surviving and living in groups. Evolutionary psychology has proven very good at analyzing these adaptations.

My interest is in the psychological adaptations that are uniquely human, the 10 percent or so of the brain's capacities that are not shared with other apes. This is where we find puzzling abilities like creative intelligence and complex language that show these great individual differences, these ridiculously high heritabilities, and these absurd wastes of time, energy, and effort. To accept these abilities as legitimate biological adaptations worthy of study, evolutionary psychology must broaden its view of what an adaptation should look like. At the moment, too many scientists

are mis-describing effective fitness indicators like music and art as if they were nothing more than cultural inventions or learned skills. Their expression certainly depends on cultural traditions and years of practice, but other species with different genes cannot learn to do them no matter how hard they might try. If one banishes all these fitness indicators to the realm of "culture," then it does not look as if sexual choice had much impact on the human mind's evolution. But if one accepts fitness indicators as legitimate biological adaptations, then one starts to see the tracks of sexual selection all over our minds.

The Hominid That Wasted Its Brain

To sum up the last few sections, I think that the handicap principle casts a new light on the human brain. Everyone who proposes a theory about the brain's evolution mentions its costs. Our brains are only 2 percent of our body weight, but they consume 15 percent of our oxygen intake, 25 percent of our metabolic energy, and 40 percent of our blood glucose. When we spend several hours thinking really hard, or just conversing with people whose opinion matters to us, we get hungry and tired. Our brains cost a lot of energy and effort to run. Usually, theorists argue that these costs must have been balanced by some really large survival benefits, otherwise the brain could not have evolved to be so large and costly. But that survivalist argument holds only as long as one ignores sexual selection.

If we view the human brain as a set of sexually selected fitness indicators, its high costs are no accident. They are the whole point. The brain's costs are what make it a good fitness indicator. Sexual selection made our brains wasteful, if not wasted: it transformed a small, efficient ape-style brain into a huge, energy-hungry handicap spewing out luxury behaviors like conversation, music, and art. These behaviors may look as if they must be conveying some useful information from one mind to another. But from a biological viewpoint they might signify nothing more than our fitness, to those who might be considering merging their genes with ours.

The better our ancestors become at articulating their thoughts, the deeper the principles of wasteful sexual signaling could reach into their minds. By favoring fitness indicators, sexual choice demanded courtship behavior that stretched the mind's capacities. It demanded that which is difficult. It forced the human brain to evolve ever greater condition-dependence, and ever greater sensitivity to harmful mutations. It asked not what a brain can do for its owner, but what fitness information about the owner a brain can reveal.

Are Fitness Indicators Immoral?

The idea that the human mind evolved as a bundle of fitness indicators does not sit comfortably with contemporary views of human nature and human society. In fact, it violates at least eight core values commonly accepted in modern society. Variation in fitness betrays our belief in human equality. The heritability of fitness violates our assumption that social and family environments shape most of human development. Loudly advertising one's fitness violates our values of humility, decorum, and tact. Sexual status hierarchies based on fitness violate our belief in egalitarian social organization. The idea that people sort themselves into sexual pairs by assessing each other's fitness violates our romantic ideal of personal compatibility. The conspicuous waste demanded by the handicap principle violates our values of frugality, simplicity, and efficiency. The sexual choice mechanisms that judge individuals by their fitness indicators violate our belief that people should be judged by their character, not the quality of their genes. Finally, it seems nihilistic to propose that our capacities for language, art, and music evolved to proclaim just one message that has been repeated loudly and insistently for thousands of generations: "I am fit, my genes are good, mate with me." A mind evolved as a set of fitness indicators can sound like a fascist nightmare.

How is it possible for one biological concept to affront so many of our fundamental values? It seems quite astounding that a scientific idea should so consistently fall on the wrong side of the

ideological fence. I think it is no coincidence. Look at it this way: our human norms and values developed as reactions to patterns of natural human behavior that we decided should be discouraged. If a great deal of human behavior consists of advertising one's fitness, and if many ways of doing that impose social costs on others, and if moral norms develop to minimize social costs, then a lot of moral norms should be aimed directly against the irresponsible use of fitness indicators. We value humility precisely because many people are unbearable braggarts who try to flaunt their fitness indicators so relentlessly that we cannot hold a decent conversation. We value frugality because so many people embarrass everyone with their ostentatious displays of luxuries, and waste limited resources that others need. We value egalitarianism because it protects the majority from aspiring despots intent on power and polygyny.

These norms do not just fall randomly from the sky. They emerged as moral instincts and cultural inventions to combat the excesses of sexual self-advertisement and sexual competition. Our moral aversion to fitness indicators may tempt us to reject them as an important part of sexual selection. But if we reject them, then it is hard to see how our moral norms evolved in the first place. It is possible, perhaps even necessary, to admit that much of human behavior evolved to advertise fitness, while simultaneously realizing that the essence of wisdom and morality is not to take our fitness indicators too seriously. This is not to say that our capacities for wisdom and morality are cultural inventions that liberate us from the imperatives of our genes. Our moral instincts may be just another set of evolved adaptations. It is not a question of "us" overriding our genetic predispositions, but of using one set of predispositions to overrule others—just as our evolved desire to preserve our looks can override our evolved taste for fat and sugar.

Another response to such worries is to point out that practically every theory of human mental evolution sounds like a fascist nightmare when we compare it with our comfortable modern lives and our political ideals. According to the Machiavellian intelligence theory, our minds evolved to lie, cheat, steal, and

deceive one another, and the most cunning psychopaths became our ancestors by denying food, territory, and sexual partners to kinder, gentler souls. Richard Alexander's group warfare theory suggests that our minds evolved through genocidal violence, with larger-brained ancestors killing off smaller-brained competitors. The theory that human genes and human cultures co-evolved sounds slightly less bloody in the abstract, but it sounds that way only because it fails to specify any selection pressures that could have actually shaped anything. In terms of survival selection, what it boils down to is the view that those with brighter brains learned better technologies to grab resources before those with dimmer brains could, leaving the dimmer brains to starve, die of infectious disease, or be eaten by predators.

No theory of human origins can avoid the fact that evolution depends on reproductive competition, and competition means that some individuals win and some lose. With survival selection, the losers die. With sexual selection, the losers merely get their hearts broken (as their genes die out). If one demands moral guidance from a theory of human evolution, one is free to pick which of these options sounds better. Personally, I think that scientific theories should try to account for facts and inspire new research, rather than trying to conform to contemporary moral values.