Chapter 1

Edward O. Wilson

ON HUMAN NATURE

Thousands of species are highly social. The most advanced among them constitute what I call the three pinnacles of social evolution in animals: the corals, bryozoans, and other colony-forming invertebrates; the social insects, including ants, wasps, bees, and termites; and the social fish, birds, and mammals. The communal beings of the three pinnacles are among the principal objects of the new discipline of sociobiology, defined as the systematic study of the biological basis of all forms of social behavior, in all kinds of organisms, including man. The enterprise has old roots. Much of its basic information and some of its most vital ideas have come from ethology, the study of whole patterns of behavior of organisms under natural conditions. Ethology was pioneered by Julian Huxley, Karl von Frisch, Konrad Lorenz, Nikolaas Tinbergen, and a few others and is now being pursued by a large new generation of innovative and productive investigators. It has remained most concerned with the particularity of the behavior patterns shown by each species, the ways these patterns adapt animals to the special challenges of their environments, and the steps by which one pattern gives rise to another as the species themselves undergo genetic evolution. Increasingly, modern ethology is being linked to studies of the nervous system and the effects of hormones on behavior. Its investigators have become deeply involved with developmental processes and even learning, formerly the nearly exclusive domain of psychology, and they have begun to include man among the species most closely scrutinized. The emphasis of ethology remains on the individual organism and the physiology of organisms.

Sociobiology, in contrast, is more explicitly hybrid discipline that incorporates knowledge from ethology (the naturalistic study of whole patterns of behavior), ecology (the study of the relationships of organisms to their environment), and genetics in order to derive general principles concerning the biological properties of entire societies. What is truly new about sociobiology is the way it has extracted the most important facts about social organization from their traditional matrix of ethology and psychology and reassembled them on a foundation of ecology and genetics studied at the population level in order to show how social groups adapt to the environment by evolution. Only within the past few years have ecology and genetics themselves become sophisticated and strong enough to provide such a foundation.

Sociobiology is a subject based largely on comparisons of social species. Each living form can be viewed as an evolutionary experiment, a product of millions of years of interaction between genes and environment. By examining many such experiments closely, we have begun to construct and test the first general principles of genetic social evolution. It is now within our

reach to apply his broad knowledge to the study of human beings.

Sociobiologists consider man as though seen through the front end of a telescope, at a greater than usual distance and temporarily diminished in size, in order to view him simultaneously with an array of other social experiments. They attempt to place humankind in its proper place in a catalog of the social species on Earth. They agree with Rousseau that "One needs to look near at hand in order to study men, but to study man one must look from afar."

This macroscopic view has certain advantages over the traditional anthropocentrism of the social sciences. In fact, no intellectual vice is more crippling than defiantly self-indulgent anthropocentrism. I am reminded of the clever way Robert Nozick makes this point when he constructs an argument in favor of vegetarianism. Human beings, he notes, justify the eating of meat on the grounds that the animals we kill are too far below us in sensitivity and intelligence to beat comparison. It follows that if representatives of a truly superior extraterrestrial species were to visit Earth and apply the same criterion, they could proceed to eat us in good conscience. By the same token, scientists among these aliens might find human beings uninteresting, our intelligence weak, our passions unsurprising, our social organization of a kind already frequently encountered on other planets. To our chagrin they might then focus on the ants, because these little creatures, with their haplodiploid form of sex determination and bizarre female caste systems, are the truly novel productions of the Earth with reference to the Galaxy. We can imagine the log declaring "A scientific breakthrough has occurred; we have finally discovered haplodiploid social organisms in the one- to ten-millimeter range." Then the visitors might inflict the ultimate indignity: in order to be sure they had not underestimated us, they would simulate human beings in the laboratory. Like chemists testing the structural characterization of a problematic organic compound by assembling it from simpler components, the alien biologists would need to synthesize a hominoid or two.

This scenario from science fiction has implications for the definition of man. The impressive recent advances by computer scientists in the design of artificial intelligence suggests the following test of humanity: that which behaves like man is man. Human behavior is something that can be defined with fair precision, because the evolutionary pathways open to it have not all been equally negotiable. Evolution has not made culture all-powerful. It is a misconception among many of the more traditional Marxists, some learning theorists, and a still surprising proportion of anthropologists and sociologists that social behavior can be shaped into virtually any form. Ultra-environmentalists start with the premise that man is the creation of his own culture: "culture makes man," the formula might go. Theirs is only a half truth. Each person is molded by an interaction of his environment, especially his cultural environment, with the genes that affect social behavior. Although the hundreds of the world's cultures seem enormously variable to those of us who stand in their midst, all versions of human social behavior together form only a tiny fraction of the realized organizations of social species on this planet and a still smaller fraction of those that can be readily imagined with the aid of sociobiological theory.

The question of interest is no longer whether human social behavior is genetically determined; it is to what extent. The accumulated evidence for a large hereditary component is more detailed and compelling than most persons, including even geneticists, realize. I will go further: it already is decisive.

That being said, let me provide an exact definition of a genetically determined trait. It is a trait that differs from other traits at least in part as a result of the presence of one or more distinctive genes. The important point is that the objective estimate of genetic influence requires

comparison of two or more states of the same feature. To say that blue eyes are inherited is not meaningful without further qualification, because blue eyes are the product of an interaction between genes and the largely physiological environment that brought final coloration to the irises. But to say that the *difference* between blue and brown eyes is based wholly or partly on differences in genes is a meaningful statement because it can be tested and translated into the laws of genetics. Additional information is then sought: What are the eye colors of the parents, siblings, children, and more distant relatives? These data are compared to the very simplest model of Mendelian heredity, which, based on our understanding of cell multiplication and sexual reproduction, entails the action of only two genes. If the data fit, the differences are interpreted as being based on two genes. If not, increasingly complicated schemes are applied. Progressively larger numbers of genes and more complicated modes of interaction are assumed until a reasonably close fit can be made. In the example just cited, the main differences between blue and brown eyes are in fact based on two genes, although complicated modifications exist that make them less than an ideal textbook example. In the case of the most complex traits, hundreds of genes are sometimes involved, and their degree of influence can ordinarily be measured only crudely and with the aid of sophisticated mathematical techniques. Nevertheless, when the analysis is properly performed it leaves little doubt as to the presence and approximate magnitude of the genetic influence.

Human social behavior can be evaluated in essentially the same way, first by comparison with the behavior of other species and then, with far greater difficulty and ambiguity, by studies of variation among and within human populations. The picture of genetic determinism emerges most sharply when we compare selected major categories of animals with the human species. Certain general human traits are shared with a majority of the great apes and monkeys of Africa and Asia, which on grounds of anatomy and biochemistry are our closest living evolutionary relatives:

- Our intimate social groupings contain on the order of ten to one hundred adults, never just two, as in most birds and marmosets, or up to thousands, as in many kinds of fishes and insects.
  Males are larger than females. This is a characteristic of considerable significance within the Old World monkeys and apes and many other kinds of mammals. The average number of females consorting with successful males closely corresponds to the size gap between males and females when many species are considered together. The rule makes sense: the greater the competition among males for females, the greater the advantage of large size and the less influential are any disadvantages accruing to bigness. Men are not very much larger than women, we are similar to chimpanzees in this regard. When the sexual size difference in human beings is plotted on the curve based on other kinds of mammals, the predicted average number of females per successful male turns out to be greater than one but less than three. The prediction is close to reality; we know we are a mildly polygynous species.
  The young are molded by a long period of social training, first by closest associations with the mother, then to an increasing degree with other children of the same age and sex.
  Social play is a strongly developed activity featuring role practice, mock aggression, sex practice, and exploration.

These and other properties together identify the taxonomic group consisting of Old World monkeys, the great apes, and human beings. It is inconceivable that human beings could be

socialized into the radically different repertories of other groups such as fishes, birds, antelopes, or rodents. Human beings might self-consciously *imitate* such arrangements, but it would be a fiction played out on a stage, would run counter to deep emotional responses and have no chance of persisting through as much as a single generation. To adopt with serious intent, even in broad outline, the social system of a nonprimate species would be insanity in the literal sense. Personalities would quickly dissolve, relationships disintegrate, and reproduction cease.

At the next, finer level of classification, our species is distinct from the Old World monkeys and apes in ways that can be explained only as a result of a unique set of human genes. Of course, that is a point quickly conceded by even the most ardent environmentalists. They are willing to agree with the great geneticist Theodosius Dobzhansky that "in a sense, human genes have surrendered their primacy in human evolution to an entirely new, nonbiological or superorganic agent, culture. However, it should not be forgotten that this agent is entirely dependent on the human genotype." But the matter is much deeper and more interesting than that. There are social traits occurring through all cultures which upon close examination are as diagnostic of mankind as are distinguishing characteristics of other animal species—as true to the human type, say, as wing tessellation is to a fritillary butterfly or a complicated spring melody to a wood thrush. In 1945 the American anthropologist George P. Murdock listed the following characteristics that have been recorded in every culture known to history and ethnography:

> Age-grading, athletic sports, bodily adornment, calendar, cleanliness training; community organization, cooking, cooperative labor, cosmology, courtship, dancing, decorative art, divination, division of labor, dream interpretation, education, eschatology, ethics, ethnobotany, etiquette, faith healing, family feasting, fire making, folklore, food taboos, funeral rites, games, gestures, gift giving, government, greetings, hair styles, hospitality, housing, hygiene, incest raboos, inheritance rules, joking, kin groups, kinship nomenclature, language, law, luck superstitions, magic, marriage, mealtimes, medicine, obstetrics, penal sanctions, personal names, population policy, postnatal care, pregnancy usages, property rights, propitiation of supernatural beings, puberty customs, religious ritual, residence rules, sexual restrictions, soul concepts, status differentiation, surgery, tool making, trade, visiting, weaving, and weather control.

Few of these unifying properties can be interpreted as the inevitable outcome of either advanced social life or high intelligence. It is easy to imagine nonhuman societies whose members are even more intelligent and complexly organized than ourselves, yet lack a majority of the qualities just listed. Consider the possibilities inherent in the insect societies. The sterile workers are already more cooperative and altruistic than people and they have a more pronounced tendency toward caste systems and division of labor. If ants were to be endowed in addition with rationalizing brains equal to our own, they could be our peers. Their societies would display the following peculiarities:

> Age-grading, antennal rites, body licking, calendar, cannibalism, caste determination, caste laws, colony-foundation rules, colony organization, cleanliness training, communal nurseries, cooperative labor, cosmology, courtship, division of labor, drone control, education, eschatology, ethics, etiquette, euthanasia, fire making, food taboos, gift giving, government, greetings, grooming rituals, hospitality, housing, hygiene, incest taboos, language, larval care, law, medicine, metamorphosis rites, mutual regurgitation, nursing castes, nuptial flights, nutrient eggs, population policy, queen obeisance, residence rules, sex determination, soldier castes, sisterhoods, status differentiation, sterile workers, surgery, symbiont care, tool making, trade, visiting, weather control.

and still other activities so alien as to make mere description by our language difficult. If in addition they were programmed to eliminate strife between colonies and to conserve the natural environment they would have greater staying power than people, and in a broad sense theirs would be the higher morality.

Civilization is not intrinsically limited to hominoids. Only by accident was it linked to the anatomy of bare-skinned, bipedal mammals and the peculiar qualities of human nature.

Freud said that God has been guilty of a shoddy and uneven piece of work. That is true to a degree greater than he intended: human nature is just one hodgepodge out of many conceivable. Yet if even a small fraction of the diagnostic human traits were stripped away, the result would probably be a disabling chaos. Human beings could not bear to simulate the behavior of even our closest relatives among the Old World primates. If by perverse mutual agreement a human group attempted to imitate in detail the distinctive social arrangements of chimpanzees or gorillas, their effort would soon collapse and they would revert to fully human behavior.

It is also interesting to speculate that if people were somehow raised from birth in an environment devoid of most cultural influence, they would construct basic elements of human social life *abinitio*. In short time new elements of language would be invented and their culture enriched. Robin Fox, an anthropologist and pioneer in human sociobiology, has expressed this hypothesis in its strongest possible terms. Suppose, he conjectured, that we performed the cruel experiment linked in legend to the Pharaoh Psammetichus and King James IV of Scotland, who were said to have reared children by remote control, in total social isolation from their elders. Would the children learn to speak to one another?

> I do not doubt that they *could* speak and that, theoretically, given time, they or their offspring would invent and develop a language despite their never having been taught one. Furthermore, this language, although totally different from any known to us, would be analyzable to linguists on the same basis as other languages and translatable into all known languages. But I would push this further. If our new Adam and Eve could survive and breed—still in total isolation from any cultural influences—then eventually they would produce a society which would have laws about property, rules about incest and marriage, customs of taboo and avoidance, methods of settling disputes with a minimum of bloodshed, beliefs about the supernatural and practices relating to it, a system of social status and methods of indicating it, initiation ceremonies for young men, courtship practices including the adornment of females, systems of symbolic body adornment generally, certain activities and associations set aside for men from which women were excluded, gambling of some kind, a tool- and weapon-making industry, myths and legends, dancing, adultery, and various doses of homicide, suicide, homosexuality, schizophrenia, psychosis and neuroses, and various practitioners to take advantage of or cure these, depending on how they are viewed.

Not only are the basic features of human social behavior stubbornly idiosyncratic, but to the limited extent that they can be compared with those of animals they resemble most of all the repertories of other mammals and especially other primates. A few of the signals used to organize the behavior can be logically derived from the ancestral modes still shown by the Old World monkeys and great apes. The grimace of

fear, the smile, and even laughter have parallels in the facial expressions of chimpanzees. This broad similarity is precisely the pattern to be expected if the human species descended from Old World primate ancestors, a demonstrable fact, and if the development of human social behavior retains even a small degree of genetic constraint, the broader hypothesis now under consideration.

The status of the chimpanzee deserves especially close attention. Our growing knowledge of these most intelligent apes has come to erode to a large extent the venerable dogma of the uniqueness of man. Chimpanzees are first of all remarkably similar to human beings in anatomical and physiological details. It also turns out that they are very close at the molecular level. The biochemists Mary-Claire King and Allan C. Wilson have compared the proteins encoded by genes at forty-four loci. They found the summed differences between the two species to be equivalent to the genetic distance separating nearly indistinguishable species of fruit flies, and only twenty-five to sixty times greater than that between Caucasian, Black African, and Japanese populations. The chimpanzee and human lines might have split as recently as twenty million years ago, a relatively short span in evolutionary time.

By strictly human criteria chimpanzees are mentally retarded to an intermediate degree. Their brains are only one-third as large as our own, and their larynx is constructed in the primitive ape form that prevents them from articulating human speech. Yet individuals can he taught to communicate with their human helpers by means of American sign language or the fastening of plastic symbols in sequences on display boards. The brightest among them can learn vocabularies of two-hundred English words and elementary rules of syntax, allowing them to invent such sentences as "Mary gives me apple" and "Lucy tickle Roger." Lana, a female trained by Beatrice and Robert Gardner at the University of Nevada, ordered her trainer from the room in a fit of pique by signalling, "You green shit." Sarah, a female trained by David Premack, memorized twenty-five hundred sentences and used many of them. Such well educated chimps understand instructions as complicated as "If red on green (and not vice versa) then you take red (and not green)" and "You insert banana in pail, apple in dish." They have invented new expressions such as "water bird" for duck and "drink fruit" for watermelon, essentially the same as those hit upon by the inventors of the English language.

Chimpanzees do not remotely approach the human child in the inventiveness and drive of their language. Evidence of true linguistic novelty is, moreover, lacking: no chimp genius has accomplished the equivalent of joining the sentences "Mary gives me apple" and "I like Mary" into the more complex proposition "Mary's giving me apple is why I like her." The human intellect is vastly more powerful than that of the chimpanzee. But the capacity to communicate by symbols and syntax does lie within the ape's grasp. Many zoologists now doubt the existence of an unbridgeable linguistic chasm between animals and man. It is no longer possible to say, as the leading anthropologist Leslie White did in 1949, that human behavior is symbolic behavior and symbolic behavior is human behavior.

Another chasm newly bridged is self-awareness. When Gordon G. Gallup, a psychologist, allowed chimps to peer into mirrors for two or three days, they changed from treating their reflection as a stranger to recognizing it as themselves. At this point they began to use the mirrors to explore previously inaccessible parts of their own bodies. They made faces, picked bits of food from their teeth, and blew bubbles through their pursed lips. No such behavior has ever been elicited from monkeys or gibbons presented with mirrors, despite repeated trials by Gallup and others. When the researchers dyed portions of the faces of chimpanzees under anesthesia, the apes subsequently gave even more convincing evidence that they were self-aware. They spent more time at the mirrors, intently examining the changes in their appearance and smelling the fingers with which they had touched the altered areas.

If consciousness of self and the ability to communicate ideas with other intelligent beings exist, can other qualities of the human mind be far away? Premack has pondered the implications of transmitting the concept of personal death to chimpanzee, but he is hesitant. "What if, like man," he asks,

> the ape dreads death and will deal with this knowledge as bizarrely as we have? . . . The desired objective would be not only to communicate the knowledge of death but, more important, to find a way of making sure the apes' response would not be that of dread, which, in the human case, has led to the invention of ritual, myth, and religion. Until I can suggest concrete steps in teaching the concept of death without fear, I have no intention of imparting the knowledge of mortality to the ape.

And what of the social existence of the chimpanzees? They are far less elaborately organized than even the hunter-gatherers, who have the simplest economic arrangements of all human beings. Yet striking basic similarities exist. The apes live in troops of up to fifty individuals, within which smaller, more casual groups break off and reunite in shifting combinations of individuals over periods as brief as a few days. Males are somewhat larger than females, to about the same degree as in human beings, and they occupy the top of well-marked dominance hierarchies. Children are closely associated with their mothers over a period of years, sometimes even into maturity. The young chimpanzees themselves remain allied for long periods of time; individuals on occasion even adopt younger brothers or sisters when the mother dies.

Each troop occupies a home range of about twenty square miles. Meetings between neighboring troops are infrequent and usually tense. On these occasions nubile females and young mothers sometimes migrate between the groups. But on other occasions chimpanzees can become territorial and murderous. At the Gombe Stream Reserve in Tanzania, where Jane Goodall conducted her celebrated research, bands of males from one troop, encroaching on the home range of an adjacent, smaller troop, attacked and occasionally injured the defenders. Eventually the residents abandoned their land to the invaders.

Like primitive human beings, chimpanzees gather fruit and other vegetable foods primarily and hunt only secondarily. The difference between their diets is one of proportion. Where all of hunter-gatherer societies considered together derive an average of 35 percent of their calories from fresh meat, chimpanzees obtain between 1 and 5 percent. And whereas primitive human hunters capture prey of any size, including elephants one hundred times the weight of a man, chimpanzees rarely attack any animal greater than one-fifth the weight of an adult male. Perhaps the most remarkable form of manlike behavior among chimpanzees is the use of intelligent, cooperative maneuvers during the hunt. Normally only adult males attempt to pursue animals—another humanoid trait. When a potential victim, such as a vervet or young baboon, has been selected, the chimpanzees signal their intentions by distinctive changes in posture, movement, and facial expression. Other males respond by turning to stare at the target animal. Their posture is tensed, their hair partially erected, and they become silent—a conspicuous change from the human observer's point of view, because chimpanzees are ordinarily the noisiest of animals. The state of alertness is broken by a sudden, nearly simultaneous pursuit.

A common strategy of the hunter males is to mingle with a group of baboons and then

attempt to seize one of the youngsters with an explosive rush. Another is to encircle and stalk the victim, even while it nervously edges away. At the Gombe Stream Reserve an enterprising male named Figan tracked a juvenile baboon until it retreated up the trunk of a palm tree. Within moments other males that had been resting and grooming nearby stood up and walked over to join the pursuit. A few stopped at the bottom of the tree in which the baboon waited, while others dispersed to the bases of adjacent trees that might have served as alternate routes of escape. The baboon then leaped onto a second tree, whereupon the chimpanzee stationed below began to climb quickly toward it. The baboon finally managed to escape by jumping twenty feet to the ground and running to the protection of its troop nearby.

The distribution of the meat is also cooperative, with favors asked and given. The begging chimpanzee stares intently while holding its face close to the meat or to the face of the meat eater. It may also reach out and touch the meat and the chin and lips of the other animal, or extend an open hand with palm upward beneath his chin. Sometimes the male holding the prey moves abruptly away. But often he acquiesces by allowing the other animal to chew directly on the meat or to remove small pieces with its hands. On a few occasions males go so far as to tear off pieces of meat and hand them over to supplicants. This is a small gesture by the standards of human altruism but it is a very rare act among animals—a giant step, one might say, for apekind.

Finally, chimpanzees have a rudimentary culture. During twenty-five years of research on free-living troops in the forests of Africa, teams of zoologists from Europe, Japan, and the United States have discovered a remarkable repertory of tool use in the ordinary life of the apes. It includes the use of sticks and saplings as defensive weapons against leopards; the hurling of sticks, stones, and handfuls of vegetation during attacks on baboons, human beings, and other chimpanzees; digging with sticks to tear open termite mounds and "fishing" for the termites with plant stems stripped of leaves and split down the middle; prying open boxes with sticks; and lifting water from tree holes in "sponges" constructed of chewed leaves.

Learning and play are vital to the acquisition of the tool-using skills. When two-year-old chimpanzee infants are denied the opportunity to play with sticks their ability to solve problems with the aid of sticks at a later age is reduced. Given access to play objects, young animals in captivity progress through a relatively invariant maturation of skills. Under two years of age they simply touch or hold objects without attempting to manipulate them. As they grow older they increasingly employ one object to hit or prod another, while simultaneously improving in the solution of problems that require the use of tools. A similar progression occurs in the wild populations of Africa. Infants as young as six weeks reach out from their mother's clasp to fondle leaves and branches. Older infants constantly inspect their environment with their eyes, lips, tongues, noses, and hands, while periodically plucking leaves and waving them about. During this development they advance to tool-using behavior in small steps. One eight-month-old infant was seen to add grass stems to his other toys—but for the special purpose of wiping them against other objects, such as stones and his mother. This is the behavior pattern uniquely associated with termite "fishing"—by which the apes provoke the insects into running onto the object and then quickly bite or lick them off. During play, other infants prepared grass stalks as fishing tools by shredding the edges off wide blades and chewing the ends off long stems.

Jane Goodall has obtained direct evidence of imitative behavior in the transmission of these traditions. She observed infants watch adults as they used tools, then pick the tools up and use them after the adults had moved away. On two occasions a three-year-old youngster was seen to observe his mother closely as she wiped dung from her bottom with leaves. Then he picked up leaves and imitated the movements, even though his bottom was not dirty.

Chimpanzees are able to invent techniques and to transmit them to others. The use of sticks to pry open food boxes is a case in point. The method was invented by one or a few individuals at the Gombe Stream Reserve, then evidently spread through the troop by imitation. One female new to the area remained hidden in the bushes while watching others trying to open the boxes. On her fourth visit she walked into the open, picked up a stick, and began in poke it at the boxes.

Each tool-using behavior recorded in Africa is limited to certain populations of chimpanzees but has a mostly continuous distribution within its range. This is just the pattern expected if the behavior had been spread culturally. Maps of chimpanzee tool-using recently prepared by the Spanish zoologist Jorge Sabater-Pi might be placed without notice into a chapter on primitive culture in an anthropology textbook. Although most of the evidence concerning invention and transmission of the tool-using methods is indirect, it suggests that the apes have managed to cross the threshold of cultural evolution and thus, in an important sense, to have moved on into the human domain.

This account of the life of the chimpanzee is meant to establish what I regard as a fundamental point about the human condition: that by conventional evolutionary measures and the principal criteria of psychology we are not alone, we have a little-brother species. The points of similarity between human and chimpanzee social behavior, when joined with the compelling anatomical and biochemical traces of relatively recent genetic divergence, form a body of evidence too strong to be dismissed as coincidence. I now believe that they are based at least in part on the possession of identical genes. If this proposition contains any truth, it makes even more urgent the conservation and closer future study of these and the other great apes, as well as the Old World monkeys and the lower primates. A more thorough knowledge of these animal species might well provide us with a clearer picture of the step-by-step genetic changes that led to the level of evolution uniquely occupied by human beings.

To summarize the argument to this point; the general traits of human nature appear limited and idiosyncratic when placed against the great backdrop of all other living species. Additional evidence suggests that the more stereotyped forms of human behavior are mammalian and even more specifically primate in character, as predicted on the basis of general evolutionary theory. Chimpanzees are close enough to ourselves in the details of their social life and mental properties to rank as nearly human in certain domains where it was once considered inappropriate to make comparisons at all. These facts are in accord with the hypothesis that human social behavior rests on a genetic foundation—that human behavior is, to be more precise, organized by some genes that are shared with closely related species and others that are unique to the human species. The same facts are unfavorable for the competing hypothesis which has dominated the social sciences for generations, that mankind has escaped its own genes to the extent of being entirely culture-bound.

Let us pursue this matter systematically. The heart of the genetic hypothesis is the proposition, derived in a straight line from neo-Darwinian evolutionary theory, that the traits of human nature were adaptive during the time that the human species evolved and that genes consequently spread through the population that predisposed their carriers to develop those traits. Adaptiveness means simply that if an individual displayed the traits he stood a greater chance of having his genes represented in the next generation than if he did not display the traits. The differential advantage among individuals in this strictest sense is called genetic

fitness. There are three basic components of genetic fitness: increased personal survival, increased personal reproduction, and the enhanced survival and reproduction of close relatives who share the same genes by common descent. An improvement in any one of the factors or in any combination of them results in greater genetic fitness. The process, which Darwin called natural selection, describes a tight circle of causation. If the possession of certain genes predisposes individuals toward a particular trait, say a certain kind of social response, and the trait in turn conveys superior fitness, the genes will gain an increased representation in the next generation. If natural selection is continued over many generations, the favored genes will spread throughout the population, and the trait will become characteristic of the species. In this way human nature is postulated by many sociobiologists, anthropologists, and others to have been shaped by natural selection.

It is nevertheless a curious fact, which enlarges the difficulty of the analysis, that sociobiological theory can be obeyed by purely cultural behavior as well as by genetically constrained behavior. An almost purely cultural sociobiology is possible. If human beings were endowed with nothing but the most elementary drives to survive and to reproduce, together with a capacity for culture, they would still learn many forms of social behavior that increase their biological fitness. But as I will show, there is a limit to the amount of this cultural mimicry, and methods exist by which it can be distinguished from the more structured forms of biological adaptation. The analysis will require the careful use of techniques in biology, anthropology, and psychology. Our focus will be on the closeness of fit of human social behavior to sociobiological theory, and on the evidences of genetic constraint seen in the strength and automatic nature of the predispositions human beings display while developing this behavior.

Let me now rephrase the central proposition in a somewhat stronger and more interesting form: if the genetic components of human nature did not originate by natural selection, fundamental evolutionary theory is in trouble. At the very least the theory of evolution would have to be altered to account for a new and as yet unimagined form of genetic change in populations. Consequently, an auxiliary goal of human sociobiology is to learn whether the evolution of human nature conforms to conventional evolutionary theory. The possibility that the effort will fail conveys to more adventurous biologists a not unpleasant whiff of grapeshot, a crackle of thin ice.

We can be fairly certain that most of the genetic evolution of human social behavior occurred over the five million years prior to civilization, when the species consisted of sparse, relatively immobile populations of hunter-gatherers. On the other hand, by far the greater part of cultural evolution has occurred since the origin of agriculture and cities approximately 10,000 years ago. Although genetic evolution of some kind continued during this latter, historical sprint, it cannot have fashioned more than a tiny fraction of the traits of human nature. Otherwise surviving hunter-gatherer people would differ genetically to a significant degree from people in advanced industrial nations, but this is demonstrably not the case. It follows that human sociobiology can be most directly tested in studies of hunter-gatherer societies and the most persistent preliterate herding and agricultural societies. As a result, anthropology rather than sociology or economics is the social science closest to sociobiology. It is in anthropology that the genetic theory of human nature can be most directly pursued.

The power of a scientific theory is measured by its ability to transform a small number of axiomatic ideas into detailed predictions of observable phenomena; thus the Bohr atom made modern chemistry possible, and modern chemistry recreated cell biology. Further, the validity of a theory is measured by the extent to which its predictions successfully compete with

other theories in accounting for the phenomena; the solar system of Copernicus won over that of Ptolemy, after a brief struggle. Finally, a theory waxes in influence and esteem among scientists as it assembles an ever larger body of facts into readily remembered and usable explanatory schemes, and as newly discovered facts conform to its demands: the round earth is more plausible than a flat one. Facts crucial to the advancement of science can be obtained either by experiments designed for the purpose of acquiring them or from the inspired observation of undisturbed natural phenomena. Science has always progressed in approximately this opportunistic, zig-zagging manner.

In the case of the theory of the genetic evolution of human nature, if it is ever to be made part of real science, we should be able to select some of the best principles from ecology and genetics, which are themselves based on the theory, and adapt them in detail to human social organization. The theory must not only account for many of the known facts in a more convincing manner than traditional explanations, but must also identify the need for new kinds of information previously unimagined by the social sciences. The behavior thus explained should he the most general and least rational of the human repertoire, the part furthest removed from the influence of day-to-day reflection and the distracting vicissitudes of culture. In other words, they should implicate innate, biological phenomena that are the least susceptible to mimicry by culture.

These are stern requirements to impose on the infant discipline of human sociobiology, but they can be adequately justified. Sociobiology intrudes into the social sciences with credentials from the natural sciences and, initially an unfair psychological advantage. If the ideas and analytical methods of "hard" science can be made to work in a congenial and enduring manner, the division between the two cultures of science and the humanities will close. But if our conception of human nature is to be altered, it must be by means of truths conforming to the canons of scientific evidence and not a new dogma however devoutly wished for.

Incest taboos are among the universals of human social behavior. The avoidance of sexual intercourse between brothers and sisters and between parents and their offspring is everywhere achieved by cultural sanctions. But at least in the case of the brother-sister taboo, there exists a far deeper, less rational form of enforcement: a sexual aversion automatically develops between persons who have lived together when one or all grew to the age of six. Studies in Israeli kibbutzim, the most thorough of which was conducted by Joseph Shepher of the University of Haifa, have shown that the aversion among people of the same age is not dependent on an actual blood relationship. Among 2,769 marriages recorded, none was between members of the same kibbutz peer group who had been together since birth. There was not even a single recorded instance of heterosexual activity, despite the fact that the kibbutzim adults were not opposed to it. Where incest of any form does occur at low frequencies in less closed societies, it is ordinarily a source of shame and recrimination. In general, mother-son intercourse is the most offensive, brother-sister intercourse somewhat less and father-daughter intercourse the least offensive. But all forms are usually proscribed. In the United States at the present time, one of the forms of pornography considered most shocking is the depiction of intercourse between fathers and their immature daughters.

What advantage do the incest taboos confer? A favored explanation among anthropologists is that the taboos preserve the integrity of the family by avoiding the confusion in roles that would result from incestuous sex. Another, originated by Edward Tylor and built into a whole anthropological theory by Claude Lévi-Strauss in his seminal *Les Structures Elémentaires de la Parenté*, is that it facilitates the exchange of women during bargaining between social

groups. Sisters and daughters, in this view, are not used for mating but to gain power.

In contrast, the prevailing sociobiological explanation regards family integration and bridal bargaining as by-products or at most as secondary contributing factors. It identifies a deeper, more urgent cause, the heavy physiological penalty imposed by inbreeding. Several studies by human geneticists have demonstrated that even a moderate amount of inbreeding results in children who are diminished in overall body size, muscular coordination, and academic performance. More than one hundred recessive genes have been discovered that cause hereditary disease in the undiluted, homozygous state, a condition vastly enhanced by inbreeding. One analysis of American and French populations produced the estimate that each person carries an average of four lethal gene equivalents; either four genes that cause death outright when in the homozygous state, eight genes that cause death in fifty percent of homozygotes, or other, arithmetically equivalent combinations of lethal and debilitating effects. These high numbers, which are typical of animal species, mean that inbreeding carries a deadly risk. Among 161 children born to Czechoslovakian women who had sexual relations with their fathers, brothers, or sons, fifteen were stillborn or died within the first year of life, and more than 40 percent suffered from various physical and mental defects, including severe mental retardation, dwarfism, heart and brain deformities, deafmutism, enlargement of the colon, and urinary-tract abnormalities. In contrast, a group of ninety-five children born to the same women through nonincestuous relations were on the average as normal as the population at large. Five died during the first year of life, none had serious mental deficiencies, and only five others had apparent physical abnormalities.

The manifestations of inbreeding pathology constitute natural selection in an intense and unambiguous form. The elementary theory of population genetics predicts that any behavioral tendency to avoid incest, however slight or devious, would long ago have spread through human populations. So powerful is the advantage of outbreeding that it can be expected to have carried cultural evolution along with it. Family integrity and leverage during political bargaining may indeed be felicitous results of outbreeding, but they are more likely to be devices of convenience, secondary cultural adaptations that made use of the inevitability of outbreeding for direct biological reasons.

Of the thousands of societies that have existed through human history, only several of the most recent have possessed any knowledge of genetics. Very few opportunities presented themselves to make rational calculations of the destructive effects of inbreeding. Tribal councils do not compute gene frequencies and mutational loads. The automatic exclusion of sexual bonding between individuals who have previously formed certain other kinds of relationships—the "gut feeling" that promotes the ritual sanctions against incest—is largely unconscious and irrational. Bond exclusion of the kind displayed by the Israeli children is an example of what biologists call a proximate (near) cause; in this instance, the direct psychological exclusion is the proximate cause of the incest taboo. The ultimate cause suggested by the biological hypothesis is the loss of genetic fitness that results from incest. It is a fact that incestuously produced children leave fewer descendants. The biological hypothesis states that individuals with a genetic predisposition for bond exclusion and incest avoidance contribute more genes to the next generation. Natural selection has probably ground away along these lines for thousands of generations, and for that reason human beings intuitively avoid incest through the simple, automatic rule of bond exclusion. To put the idea in its starkest form, one that acknowledges but temporarily bypasses the intervening developmental process, human beings are guided by an instinct based on genes. Such a process is indicated in the case of brother-sister intercourse, and it is a strong possibility in the other categories of incest taboo.

Hypergamy is the female practice of marrying men of equal or greater wealth and status. In human beings and most kinds of social animals, it is the females who move upward through their choice of mates. Why this sexual bias? The vital clue has been provided by Robert L. Trivers and Daniel F. Willard in the course of more general work in sociobiology. They noted that in vertebrate animals generally, and especially birds and mammals, large, healthy males mate at a relatively high frequency while many smaller, weaker males do not mate at all. Yet nearly all females mate successfully. It is further true that females in the best physical condition produce the healthiest infants, and these offspring usually grow up to be the largest, most vigorous adults. Trivers and Willard then observed that according to the theory of natural selection females should be expected to give birth to a higher proportion of males when they are healthiest, because these offspring will be largest in size, mate most successfully, and produce the maximum number of offspring. As the condition of the females deteriorates, they should shift progressively to the production of daughters, since female offspring will now represent the safer investment. According to natural-selection theory, genes that induce this reproductive strategy will spread through the population at the expense of genes that promote alternative strategies.

It works. In deer and human beings, two of the species investigated with reference to this particular question, environmental conditions adverse for pregnant females are associated with a disproportionate increase in the birth of daughters. Data from mink, pigs, sheep, and seals also appear to be consistent with the Trivers-Willard prediction. The most likely direct mechanism is the selectively greater mortality of male fetuses under adversity, a phenomenon that has been documented in numerous species of mammals.

Let me now try to answer the important but delicate question of how much social behavior varies genetically *within* the human species. The fact that human behavior still has structure based on physiology and is mammalian in its closest affinities suggests that it has been subject to genetic evolution until recently. If that is true, genetic variation affecting behavior might even have persisted into the era of civilization. But this is not to say that such variation now exists.

Two possibilities are equally conceivable. The first is that in reaching its present state the human species exhausted its genetic variability. One set of human genes affecting social behavior, and one set only, survived the long trek through prehistory. This is the view implicitly favored by many social scientists and, within the spectrum of political ideologies that address such questions, by many intellectuals of the left. Human beings once evolved, they concede, but only to the point of becoming a uniform, language-speaking, culture-bearing species. By historical times mankind had become magnificent clay in the hands of the environment. Only cultural evolution can now occur. The second possibility is that at least some genetic variation still exists. Mankind might have ceased evolving, in the sense that the old biological mode of natural selection has relaxed its grip, but the species remains capable of both genetic and cultural evolution.

The reader should note that either possibility—complete cultural determination versus shared cultural and genetic determination of variability within the species—is compatible with the more general sociobiological view of human nature, namely that the most diagnostic features of human behavior evolved by natural selection and are today constrained throughout the species by particular sets of genes.

These possibilities having been laid out in such a textbook fashion, I must now add that the evidence is strong that a substantial fraction of human behavioral variation is based on genetic differences among individuals. There are undeniably mutations affecting behavior. Of these changes in the chemical composition of genes

or the structure and arrangement of chromosomes, more than thirty have been identified that affect behavior, some by neurological disorders, others by the impairment of intelligence. One of the most controversial but informative examples is the XYY male. The X and Y chromosomes determine sex in human beings; the XX combination produces a female, XY a male. Approximately 0.1 percent of the population accidentally acquires an extra Y chromosome at the moment of conception, and these XYY individuals are all males. The XYY males grow up to be tall men, the great majority over six feet. They also end up more frequently in prisons and hospitals for the criminally insane. At first it was thought that the extra chromosome induced more aggressive behavior, creating what is in effect a class of genetic criminals. However, a statistical study, by Princeton psychologist Herman A. Witkin and his associates, of vast amounts of data from Denmark has led to a more benign interpretation. XYY men were found neither to be more aggressive than normal nor to display any particular behavior pattern distinguishing them from the remainder of the Danish population. The only deviation detected was a lower average intelligence. The most parsimonious explanation is that XYY men are incarcerated at a higher rate because they are simply less adroit at escaping detection. However, caution is required. The possibility of the inheritance of more specific forms of predisposition toward a criminal personality has not been excluded by this one study.

In fact, mutations have been identified that do alter specific features of behavior. Turner's syndrome, occurring when only one of the two X chromosomes is passed on, entails not just a lowered general intelligence but a particularly deep impairment in the ability to recall shapes and to orient between the left and right on maps and other diagrams. The Lesch-Nyhan syndrome, induced by a single recessive gene, causes both lowered intelligence and a compulsive tendency to pull and tear at the body, resulting in self-mutilation. The victims of these and other genetic disorders, like the severely mentally retarded, provide extraordinary opportunities for a better understanding of human behavior. The form of analysis by which they can be most profitably studied is called genetic dissection. Once a condition appears, despite medical precautions, it can be examined closely in an attempt to pinpoint the altered portion of the brain and to implicate hormones and other chemical agents that mediated the change without, however, physically touching the brain. Thus by the malfunctioning of its parts the machine can be diagrammed. And let us not fall into the sentimentalist trap of calling that procedure cold-blooded; it is the surest way to find a medical cure for the conditions themselves.

Most mutations strong enough to be analyzed as easily as the Turner and Lesch-Nyhan anomalies also cause defects and illnesses. This is as true in animals and plants as it is in human beings, and is entirely to be expected. To understand why, consider the analogy of heredity with the delicate construction of a watch. If a watch is altered by randomly shaking or striking it, as the body's chemistry is randomly transformed by a mutation, the action is far more likely to impair than to improve the accuracy of the watch.

This set of strong examples, however, leaves unanswered the question of the genetic variation and evolution of "normal" social behavior. As a rule, traits as complex as human behavior are influenced by many genes, each of which shares only a small fraction of the total control. These "polygenes" cannot ordinarily be identified by detecting and tracing the mutations that alter them. They must be evaluated indirectly by statistical means. The most widely used method in the genetics of human behavior is the comparison of pairs of identical twins with pairs of fraternal twins. Identical twins originate in the womb from a single fertilized ovum. The two cells produced by the first division of the ovum do not stick together to produce the beginnings of the fetus but instead separate to

produce the beginnings of two fetuses. Because the twins originated from the same cell, bearing a single nucleus and set of chromosomes, they are genetically identical. Fraternal twins, in contrast, originate from separate ova that just happen to travel into the reproductive tracts and to be fertilized by different sperm at the same time. They produce fetuses genetically no closer to one another than are brothers or sisters born in different years.

Identical and fraternal twins provide us with a natural controlled experiment. The control is the set of pairs of identical twins: any differences between the members of a pair must be due to the environment (barring the very rare occurrence of a brand-new mutation). Differences between the members of a pair of fraternal twins can be due to their heredity, their environment, or to some interaction between their heredity and environment. If in a given trait, such as height or nose shape, identical twins prove to be closer to one another on the average than are fraternal twins of the same sex, the difference between the two kinds of twins can be taken as prima facie evidence that the trait is influenced to some degree by heredity. Using this method, geneticists have implicated heredity in the formation of a variety of traits that affect social relationships: number ability, word fluency, memory, the timing of language acquisition, spelling, sentence construction, perceptual skill, psychomotor skill, extroversion-introversion, homosexuality, the age of first sexual activity, and certain forms of neurosis and psychosis, including manic-depressive behavior and schizophrenia.

There is a catch in these results that render them less than definitive. Identical twins are regularly treated alike by their parents, more so than fraternal twins. They are more frequently dressed alike, kept together for longer times, fed the same way, and so on. Thus in the absence of other information it is possible that the greater similarity of identical twins could, after all, be due to the environment. However, there exist new, more sophisticated techniques that can take account of this additional factor. Such a refinement was employed by the psychologists John C. Lochlin and Robert C. Nichols in their analysis of the backgrounds and performances of 850 sets of twins who took the National Merit Scholarship test in 1962. Not only the differences between identical and fraternal twins, but also the early environments of all the subjects were carefully examined and weighed. The results showed that the generally closer treatment of identical twins is not enough to account for their greater similarity in general abilities, personality traits, or even ideals, goals, and vocational interests. The conclusion to be drawn is that either the similarities are based in substantial part on genetic closeness, or else environmental factors were at work that remained hidden to the psychologists.

My overall impression of the existing information is that *Homo sapiens* is a conventional animal species with reference to the quality and magnitude of the genetic diversity affecting its behavior. If the comparison is correct, the psychic unity of mankind has been reduced in status from a dogma to a testable hypothesis.

I also believe that it will soon be within our power to identify many of the genes that influence behavior. Thanks largely to advances in techniques that identify minute differences in the chemical products prescribed by genes, our knowledge of the fine details of human heredity has grown steeply during the past twenty years. In 1977 the geneticists Victor McKusick and Francis Ruddle reported in *Science* that twelve hundred genes had been distinguished; of these, the position of 210 had been pinpointed to a particular chromosome, and at least one gene had been located on each of the twenty-three pairs of chromosomes. Most of the genes ultimately affect anatomical and biochemical traits having minimal influence on behavior. Yet some do affect behavior in important ways, and a few of the behavioral mutations have been closely linked to known biochemical changes. Also,

subtle behavioral controls are known that incorporate alterations in levels of hormones and transmitter substances acting directly on nerve cells. The recently discovered enkephalins and endorphins are protein-like substances of relatively simple structure that can profoundly affect mood and temperament. A single mutation altering the chemical nature of one or more of them might change the personality of the person bearing it, or at least the predisposition of the person to develop one personality as opposed to another in a given cultural surrounding. Thus it is possible, and in my judgment even probable, that the positions of genes having indirect effects on the most complex forms of behavior will soon be mapped on the human chromosomes. These genes are unlikely to prescribe particular patterns of behavior; there will be no mutations for a particular sexual practice or mode of dress. The behavioral genes more probably influence the ranges of the form and intensity of emotional responses, the thresholds of arousals, the readiness to learn certain stimuli as opposed to others, and the pattern of sensitivity to additional environmental factors that point cultural evolution in one direction as opposed to another.

It is of equal interest to know whether even "racial" differences in behavior occur. But first I must issue a strong caveat, because this is the most emotionally explosive and politically dangerous of all subjects. Most biologists and anthropologists use the expression "racial" only loosely, and they mean to imply nothing more than the observation that certain traits, such as average height or skin color, vary genetically from one locality to another. If Asians and Europeans are said to differ from one another in a given property, the statement means that the trait changes in some pattern between Asia and Europe. It does not imply that discrete "races" can be defined on the basis of the trait, and it leaves open a strong possibility that the trait shows additional variation within different parts of Asia and Europe. Furthermore, various properties in anatomy and physiology—for example, skin color and the ability to digest milk—display widely differing patterns of geographical ("racial") variation. As a consequence most scientists have long recognized that it is a futile exercise to try to define discrete human races. Such entities do not in fact exist. Of equal importance, the description of geographical variation in one trait or another by a biologist or anthropologist or anyone else should not carry with it value judgments concerning the worth of the characteristics defined.

Now we are prepared to ask in a more fully objective manner: Does geographical variation occur in the genetic basis of social behavior? The evidence is strong that almost all differences between human societies are based on learning and social conditioning rather than on heredity. And yet perhaps not quite all, Daniel G. Freedman, a psychologist at the University of Chicago, has addressed this question with a series of studies on the behavior of newborn infants of several racial origins. He has detected significant average differences in locomotion, posture, muscular tone of various parts of the body, and emotional response that cannot reasonably be explained as the result of training or even conditioning within the womb. Chinese-American newborns, for example, tend to be less changeable, less easily perturbed by noise and movement, better able to adjust to new stimuli and discomfort, and quicker to calm themselves than Caucasian-American infants. To use a more precise phrasing, it can be said that a random sample of infants whose ancestors originated in certain parts of China differ in these behavioral traits from a comparable sample of European ancestry.

There is also some indication that the average differences carry over into childhood. One of Freedman's students, Nova Green, found that Chinese-American children in Chicago nursery schools spent less of their time in approach and interaction with playmates and more time on individual projects than did their European-American counterparts. They also displayed interesting differences in temperament:

Although the majority of the Chinese-American children were in the "high arousal age," between 3 and 5, they showed little intense emotional behavior. They ran and hopped, laughed and called to one another, rode bikes and roller-skated just as the children did in the other nursery schools, but the noise level stayed remarkably low and the emotional atmosphere projected serenity instead of bedlam. The impassive facial expression certainly gave the children an air of dignity and self-possession, but this was only one element affecting the total impression. Physical movements seemed more coordinated, no tripping, falling, bumping or bruising was observed, no screams, crashes or wailing was heard, not even that common sound in other nurseries, voices raised in highly indignant moralistic dispute! No property disputes were observed and only the mildest version of "fighting behavior," some good natured wrestling among the older boys.

Navaho infants tested by Freedman and his coworkers were even more quiescent than the Chinese infants. When lifted erect and pulled forward they were less inclined to swing their legs in a walking motion; when put in a sitting position, their backs curved; and when placed on their stomachs, they made fewer attempts to crawl. It has been conventional to ascribe the passivity of Navaho children to the practice of cradleboarding, a device that holds the infant tightly in place on the mother's back. But Freedman suggests that the reverse may actually be true: the relative quiescence of Navaho babies, a trait that is apparent from birth onward, allows them to be carried in a confining manner. Cradleboarding represents a workable compromise between cultural invention and infant constitution.

Given that humankind is a biological species, it should come as no shock to find that populations are to some extent genetically diverse in the physical and mental properties underlying social behavior. A discovery of this nature does not vitiate the ideals of Western civilization. We are not compelled to believe in biological uniformity in order to affirm human freedom and dignity. The sociologist Marvin Bressler has expressed this idea with precision: "An ideology that tacitly appeals to biological equality as a condition for human emancipation corrupts the idea of freedom. Moreover, it encourages decent men to tremble at the prospect of 'inconvenient' findings that may emerge in future scientific research. This unseemly anti-intellectualism is doubly degrading because it is probably unnecessary."

I will go further and suggest that hope and pride and not despair are the ultimate legacy of genetic diversity, because we are a single species, not two or more, one great breeding system through which genes flow and mix in each generation. Because of that flux, mankind viewed over many generations shares a single human nature within which relatively minor hereditary influences recycle through ever changing patterns, between the sexes and across families and entire populations. To understand the enormous significance of this biological unity, imagine our moral distress if australopithecine man-apes had survived to the present time, halfway in intelligence between chimpanzees and human beings, forever genetically separated from both, evolving just behind us in language and the higher faculties of reason. What would be our obligation to them? What would the theologians say—or the Marxists, who might see in them the ultimate form of an oppressed class? Should we divide the world, guide their mental evolution to the human level, and establish a two-species dominion based on a treaty of intellectual and technological parity? Should we make certain they rose no higher? But even worse, imagine our predicament if we coexisted with a mentally superior human species, say *Homo superbus*, who regarded us, the minor sibling species *Homo sapiens*, as the moral problem.