

T E N

The Sociobiology of Human Behavior: Extrapolations and Speculations

"Know thyself"
SOCRATES

More than two thousand years after the Socratic injunction, we are still strangers to ourselves. The scientific study of human behavior has traditionally been the province of social science: psychology, sociology, and anthropology, and, whereas great advances have certainly been made, there can be little doubt that *Homo sapiens* is not yet understood. Will sociobiology help? When Mark Twain was asked a difficult question: "I was gratified to be able to answer promptly, and I did" he wrote in *Life on the Mississippi*. "I said I didn't know." At this point, no one knows whether the perspective of evolutionary biology will shed light on our own social behavior, but it seems worth trying.

It may be argued that human behavior is so complex that biology will oversimplify and hence mislead. On the other hand, if human sociobiology is worth pursuing, it may be precisely *because* of that complexity. The task of unraveling such a difficult creature as *Homo sapiens* is so awesome that the social sciences need all the help they can get. They should leave no stone unturned, no tool unused in pursuit of anything that might offer further insight; and, considering the explanatory and predictive power of evolutionary theory when applied to the social behavior of other living things, application of this evolutionary approach to human behavior seems eminently sensi-

ble. If biology seems arrogant in seeking to include humans within its scope, think of the greater arrogance of a social science that refuses help when it is offered.

Actually, biological approaches to human behavior are not altogether novel. For example, in recent years there has been a spurt of interest in human ethology. This approach has been characterized by direct observation of people behaving in natural situations, free of any experimental contrivance (Blurton-Jones, 1972; McGrew, 1972). Beyond this, researchers have begun applying ethology's conceptual baggage of *releasers*, *fixed action patterns*, and *innate releasing mechanisms* to the study of human behavior (Eibl-Eibesfeldt, 1975). Efforts of this sort may well prove valuable, but it is at least possible that even greater insights will ultimately be achieved by combining the observational approach of ethology with the predictive tools of modern sociobiology. Thus, a worthwhile endeavor for students of human sociobiology would be the making and testing of predictions based on the assumption that individual human beings behave in such a manner as to maximize their inclusive fitness.

Because this territory is almost entirely unexplored, the approach in this chapter will be frankly speculative, suggesting some direct applications of the principles of sociobiology to a new species, ourselves. The preceding nine chapters have presented empirical observations concerning the sociobiology of nonhuman animals as well as the fundamentals of theory. Such theory has not been developed with any particular species in mind, and it may well be generalizable to all living things. This chapter will be especially concerned with exploring possible implications for human social behavior, *assuming* that our species follows these same general rules. This caveat is important. We are going to play "Let's Pretend", and see where it takes us. In other words, if the Central Theorem of Sociobiology holds for humans, and we tend to behave so as to maximize personal, inclusive fitness, then what? We can begin by making predictions that may ultimately be confirmed or refuted. At least, it is a start.

In nearly all cases these will be real predictions; their validity is simply unknown. The future should provide exciting oppor-

tunities for evaluating these and other extensions of sociobiological thought.

Some Problems and Justifications

Humans are unique among animals, both in terms of their characteristics as objects for scientific scrutiny and also in terms of the social consequences of such efforts. Objections have been raised to the application of sociobiology to human behavior, much of it directed against Harvard zoologist, Edward O. Wilson, whose book, *Sociobiology: The New Synthesis*, crystallized many of the issues and served as a rallying point for both proponents and opponents; see Allen et al. (1976) for a particularly vigorous attack. Criticism appears to be focused on two major themes: The social and political implications of human sociobiology and the question of scientific validity for such research. These are important and emotion-packed issues, and they warrant attention before proceeding with the meat of this chapter. Like sociobiology itself, the controversy involves complex issues that can only be touched upon here.

Concern has been expressed that human sociobiology represents racism in disguise: This is simply not true. Sociobiology deals with biological universals that may underlie human social behavior, universals that are presumed to hold cross-culturally and therefore cross-rationally as well. What better *antidote* for racism than such emphasis on the behavioral commonality of our single species?

Sociobiology searches for the biological foundations of social behavior. When evaluations of this sort are made for human behavior and supporting evidence is presented, this may be misread as somehow *condoning* the behaviors in question. Again, this is nonsense: Ethical judgments have no place in the study of human sociobiology or in any other science for that matter. What is biological is not necessarily good, assuming here that human social behavior is in fact found to have a valid evolutionary substrate. Diseases are part of our biology; this does not imply that they are good. We study pneumococci, seek-

ing further understanding of how they are put together and why they do what they do; this does not imply that we approve of pneumonia. Some critics have even gone so far as to advocate the suppression of research in human sociobiology. Restraints upon research and attempted prohibitions against inquiry smack of totalitarianism and book burning; they should be anathema to a free society. Human sociobiology will hopefully proceed and with adherence to scientific validity alone. There must be no forbidden knowledge. "Knowledge humanely acquired and widely shared, related to human needs but kept free of political censorship, is the real science for the people" (Wilson, 1976). Science is neither good nor bad of itself; only the socially mediated disposition of such knowledge is susceptible to moral judgment. And yet science can be misused.

Unfortunately there are no easy solutions to this dilemma. The conceptual tools of sociobiology have been employed successfully on nonhuman animals, and this can only whet the appetites of those of us who recognize how little we understand our own species. Most biologists are committed to the proposition that a herring gull is well worth knowing in its own right. But so is *Homo sapiens*. We are unlikely to deny ourselves the same analytic attention we lavish on other species, and there is no reason why we should.

Another criticism of human sociobiology that is essentially ethical or, rather, political in nature is that it tends to portray social systems as natural and therefore provides support for their continuance. Critics have furthermore pointed out that the systems being supported tend to be those within which sociobiologists, as private citizens, are functioning successfully—capitalist, sexist, etc. First, we have already emphasized that *biological* and *good* are not synonymous. Furthermore, concern with adaptive significance need not imply a Panglossian view that "all is for the best in this best of all possible worlds". Population geneticists have employed the concept of *adaptive landscape* in which populations are seen as isolated specks on a complex, multidimensional landscape of numerous peaks of different shape and height, separated by valleys. The peaks represent adaptation, and so the greater the altitude of

any population, the greater its average fitness. Populations move upwards to greater fitness by natural selection operating upon each component individual; they may also fall over a cliff, i.e., become extinct. But these movements are essentially blind. Therefore an individual or a species has no idea where it is relative to the rest of the landscape and accordingly cannot tell if it would be better off (more fit) on a different peak entirely. Because its predominant movement is upwards, it may be restricted indefinitely to a small hillock, unable to attain a much larger, more adaptive, mountain nearby from which it is separated by an uncrossable valley. For this reason, it has been suggested that maximum adaptation may require the addition of occasional nondirected, random movements, i.e., genetic drift, in order for populations to escape from their adaptive prisons to the greater heights of enhanced fitness (Wright, 1969).

For those who see politics in every aspect of the natural world, perhaps the preceding is an argument for anarchy, at least in limited doses. But, on a more sober level, this model shows how evolutionary biology does *not* claim that all phenotypes must represent fitnesses that are absolutely maximal. Thus, sociobiologists are not necessarily apologists for the status quo; the whole issue is a red herring. In fact, historians of science might well find this debate amusing. When evolution by natural selection was originally proposed, it met strong resistance from the entrenched European political and social establishment. Evolution implies movement and susceptibility to change. It sees the living world in a constant state of flux, as opposed to the static system of divine creation. Coming on the heels of the American and French Revolutions, such a radical world view was distinctly uncomfortable for the powers-that-be. Now, purveyors of evolutionary thought are accused of defending social intransigence. How strange.

In the hope of avoiding further confusion, an important distinction should also be made at this point: the difference between *analogy* and *homology*. Structures are analogous if they serve similar functions, often because of similar selective pres-

ures. The wings of a bird and of an insect are classic examples: Both are flapped in the air and both contribute to flying. But the similarity is superficial only. An insect's wing derives from an out-folding of the body wall, whereas a bird's wing is derived from the same bone structures that give rise to a bat's wing or a man's arm. These latter structures are all homologous: They possess an underlying similarity based on common evolutionary descent. Like the wings of birds and insects, similar behaviors of human and nonhuman animals may represent analogy and nothing more, or, like the wings of birds and bats, they may be homologous as well. Basically, our ignorance on this important matter is due to the fact that human behavior derives from many possible sources. If a particular pattern resembles that found among nonhuman animals, it may occur among humans almost entirely as a function of learning and social tradition, in which case it is analogous only. To be homologous, it would have to derive from the action of similar genes.

This poses a serious problem for the study of human sociobiology, because we cannot experimentally manipulate genes and vary environments at will among humans so as to isolate causative factors, as we can among nonhumans. Therefore we must content ourselves with descriptions of what actually occurs in human behavior, often being unable to parcel these phenotypes to social experience or evolution. For example, among certain Eskimo societies, it is customary for the very old to sacrifice themselves in times of famine. This is in accord with sociobiologic predictions, particularly the biology of altruism. Thus, kin selection could evolve this tendency when it increased the reproductive success of surviving relatives. Furthermore we would expect that old people especially would be selected for such behavior, because their ratio of benefit to cost is high; they are likely to have many relatives who benefit. Simultaneously, because of their senescence they have little potential reproductive future; i.e., low cost associated with their act. On the other hand, such behavior may also result from cultural tradition, spread among Eskimo families because it is adaptive, that is, families with such traditions are more likely to succeed and to

generate additional families with similar traditions than others whose cultural practice precludes geriatric self-sacrifice.

Accordingly, culture can mimic biology and vice versa; and it may be difficult or even impossible to establish the precise relevance of natural selection in such cases. However we can use our understanding of the selective process to predict adaptive behaviors; our strongest evidence for the legitimacy of human sociobiology may well be the documentation of cross-cultural behavioral universals. Thus, because there is no way to eliminate culture as a confounding variable, the next best thing may be to examine human behavior in a wide array of societies. This would essentially be an experiment in which our biological nature as the species *Homo sapiens* was held constant, while cultural practices were permitted to vary.

The persistence of common patterns, despite a diversity of cultural overlays, may reflect underlying biological tendencies consistent with but not proving the action of natural selection. Such evidence would be particularly cogent if these universals conformed to the predictions of evolutionary theory; ideally, these predictions should be generated without any advance knowledge of what is really true. In each case, the particular pattern may be interpretable in proximate terms as the outcome of particular cultural factors, but consistent findings could also at least suggest an ultimate, biological reason for *why* these cultural factors exist and why *Homo sapiens* responds to them as they do, rather than in some different way.

The Eskimo example may provide an opportunity for the evolution of altruistic behavior through genetic assimilation in conjunction with kin selection. Assume that geriatric self-sacrifice is initially a phenomenon of cultural tradition and nothing else. Selection could then operate upon the *susceptibility* to such teachings, assuming here, that susceptibility genes of this sort exist. Eventually, the behavior could be genetically incorporated and thereafter maintained by kin selection. When biology and culture are confounded, we cannot yet identify the root cause, but we can and should continue to speculate and gather evidence, so long as we do both with open minds.

The Hebraic prohibition against eating pork is a clear-cut

example of an adaptive, culturally mediated behavior; it undoubtedly reduces the incidence of trichinosis, and it undoubtedly is not genetic in origin. But there is at least the possibility that even dietary preferences have some underlying genetic basis. Among human populations such as Orientals and Australian aborigines who consume few or no dairy products, the enzyme lactase, which acts to digest the sugar lactose found in milk, tends to be missing (Kretchmer, 1973). As a result, the milk sugar, lactose, cannot be digested, and ingestion of milk commonly causes intestinal distress. Cultural practices may have selected for the presence of lactase among herding peoples; or the fortuitous presence or absence of the relevant genes may have predisposed different societies to different cultural norms. Certainly just because something is adaptive does not mean that it must be biological even if it accords with sociobiologic prediction. But it is equally true that being cultural does not require that it cannot be biological *as well*.

Sociobiology relies heavily upon the biology of male-female differences and upon the adaptive behavioral differences that have evolved accordingly. Ironically, mother nature appears to be a sexist,* at least where nonhuman animals are concerned. There may or may not be similar biological underpinnings of sexism in human societies; we do not know. Certainly, analysis and evaluation of male-female differences in human behavior should not be construed as supporting its propriety. Human sociobiology seeks to explore our nature, not to legitimize our foibles. Once again, it seems scientifically appropriate and ethically responsible to employ theory to make testable predictions. If reality accords with theory, this does not prove anything, because social and cultural factors may mimic the action of natural selection regarding sex differences in behavior just as with Eskimo altruism. Human social behavior is the product of many interacting factors and it is certainly unlikely that sexism is entirely biological. But it also may not be entirely cultural. One way of shedding more light is to make some predictions and try to interpret the realities.

*Sociobiology is sexist if sexism is recognition of male-female *differences*; however, it does not imply that either sex is *better*.

A final, political concern of sociobiology's opponents is that it represents an inimical form of biological *determinism*. This worry may derive largely from confusion of genetic determinism with genetic *tendencies*, and it also leads into the primary scientific complaint against human sociobiology.

*Genetic Predispositions and Human Behavior, or
Why Is Sugar Sweet?*

Evolution operates by changes in gene frequencies over time, and natural selection is the means by which adaptation is achieved. Because evolution can operate upon a phenotype, including behavior, only if some correlation exists between that phenotype and the genotype, any consideration of adaptive aspects of human behavior must assume that genetics plays at least some role in mediating human behavior. But this is not to claim that we are involuntary automatons, prisoners of our DNA. Thus, we may be predisposed to behave in a certain manner without being at the mercy of heredity.

Male stickleback fish have a red breast in the spring when courtship and mating occur. Such males respond with automatic aggression toward other males, so long as they also possess a red breast. Indeed, the intruder need not even be recognizable to us as a fish at all; almost any red object will produce this genetically coded response, and this will occur even if the animal has been kept in total isolation and therefore has had no opportunity to learn the behavior. Such rigidly stereotyped, mouse-trap-type responses are common among nonhuman animals, especially invertebrates, fish, reptiles, and birds, but not in humans. We do not experience anything like this genetically mediated automaticity of response. We may feel vague and general inclinations to respond in certain ways, but such tendencies can be overridden consciously and modified drastically by our experience.

If quiet, romantic little coffee houses are not regularly the scene of passionate lovemaking under the tables, it is generally not because the biological inclinations aren't there; the patrons simply are also responding to cultural taboos that at least in this

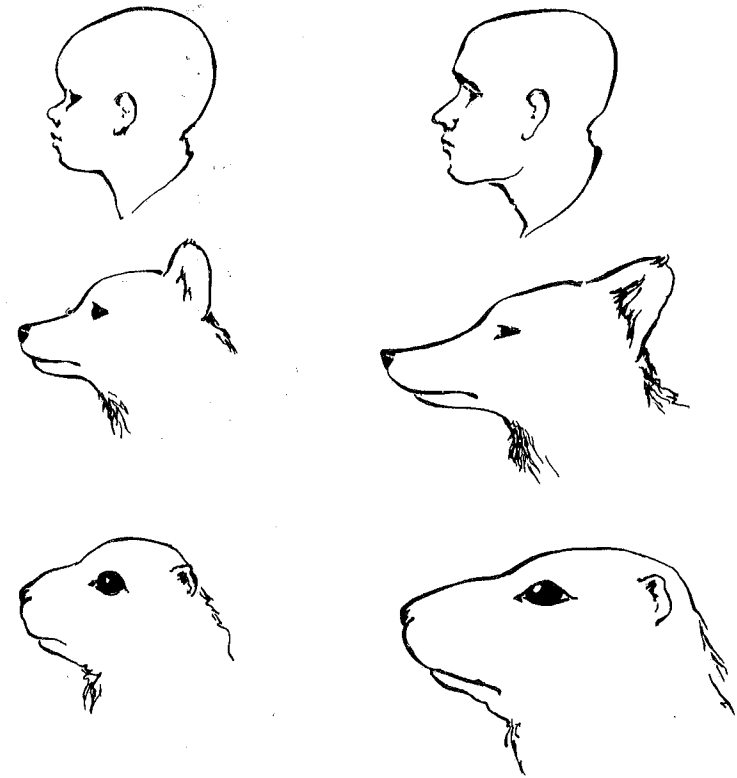


FIGURE 10.1 GENERALIZED SENSITIVITY TO BABYISH FEATURES. Humans typically feel more inclined to cuddle and care for individuals who possess certain features such as blunt stubby body parts and relatively large eyes and head compared to the rest of the body. (ILLUSTRATION BY D. COOK)

situation are stronger. But the fact that such inclinations can be suppressed does not mean that they do not exist. For example, humans have almost certainly been under intense selective pressure for responsiveness toward their infants. Although we do not possess the automatic inborn response patterns used by so many nonhuman animals in recognizing their young, we may well be responsive to certain general physical patterns that characterize infants: Large eyes, rounded features, unsteadiness of gait, etc. (FIG. 10.1). We can force ourselves to remain unresponsive to such patterns, but the very fact that force is required suggests a natural inclination in the other direction.

In suggesting possible adaptive predispositions in human behavior, this is the type of system sociobiology has in mind: A flexible, modifiable and perhaps rather fragile set of inclinations but a potentially significant part of our biology, quite possibly grounded in the evolutionary wisdom of our past.

This approach is clearly at variance with many other views of human nature. Simone de Beauvoir described human beings as *l'être dont l'être est de n'être pas* [the being whose essence is having no essence]. Behaviorism is one of the dominant schools of American psychology; part of *its* essence is captured in the following, oft-quoted challenge from J. B. Watson (1930), its prime mover.

Give me a dozen healthy infants, well-formed, and my own specified world to bring them up in and I'll guarantee to take any one at random and train him to become any type of specialist I might select—doctor, lawyer, artist, merchant-chief and yes, even beggarman and thief, regardless of his talents, penchants, tendencies, abilities, vocations, and race of his ancestors.

Choice of a profession may well be more specific than the genetic predispositions that sociobiologists would claim. In an evolutionary perspective, the only concern of all human behavior is the production of other humans. Behaviors evolve when they confer greater fitness than their alternatives, although in many cases the route from behavior to fitness may be tortuous and the adaptive significance obscure. However this is not to say that our behavior is necessarily directed by our genes. As explained earlier, DNA is only a blueprint, a potential for constructing something whose actual appearance may vary dramatically as a function of the materials available to do the job. Not only that; even after a behavioral structure is completed, it may assume a dramatically different shape from one situation to the next. Nevertheless some correlation always exists between genes and behavior, even human behavior. It may be precise, as in the nervous system wiring that produces the blink reflex in response to sudden loud noises. Or it may be diffuse and therefore almost entirely dependent upon environmental influences, as in the case of personality. It may be nothing more than a re-

striction of potential: A human being cannot develop the personality of a seahorse, just as a seahorse cannot be loving, happy, greedy, jealous, or schizophrenic in the same sense that we can.

Practitioners of human sociobiology therefore do *not* necessarily advocate biological determinism of human behavior. The difference between determinism and genetic *influence* is the difference between shooting a bullet at a target and throwing a paper airplane; the paper airplane is acutely sensitive to environmental influences such as wind, and its ultimate path is not entirely predictable by the thrower. The great evolutionary biologist, Julian Huxley, warned against "nothing butism," the idea that because humans are animals, it necessarily follows that we are nothing but animals. This is important advice, but it also applies in the other direction: We should beware the notion that humans are nothing but the outcome of their experiences. It stretches credulity to imagine that *Homo sapiens* is unique among animals in possessing no biological components relevant to social behavior. If nothing else, we must possess a genetically mediated *capacity* for culture, learning, language, etc. in the same sense that wolves have the capacity of developing complicated dominance relationships. Furthermore, we lack the capacity to perform accurate long-distance migration, found in many birds, just as herring gulls are incapable of forming political parties or writing a symphony. The next step, at which many sociologists, psychologists, and anthropologists will doubtless balk, is to identify predispositions for the learning of particular things, the acquisition of cultural traits that, despite their diversity, demonstrate a certain functional, adaptive, consistency. In some cases, learning may be minimal or even largely unnecessary; in others, it may be overwhelmingly important. In any event, sociobiology enables us to postulate an end toward which these diverse means might be directed: Much of human behavior may be adaptive; i.e., it may maximize the inclusive Darwinian fitness of each individual.

Unfortunately, most of the thought concerning genetic aspects of human behavior has been highly emotional and hence, extremist in each direction. On the one hand, many social scien-

tists advocate that humans are born as "tabula rasa", blank slates with infinite potential to become anything at all, depending only on experience. On the other end of the spectrum is extreme genetic determinism, in which free will and the capacity for self-betterment is denied, and we are literally prisoners of our heredity. As usual in such outlandish debates, the truth doubtless lies somewhere in between (Dobzhansky, 1976). For our purposes, this means that we are justified in assuming an *influence* of genetics in human behavior, although not necessarily a controlling influence. Sociobiology's approach is to ask natural selection about the expected direction of that influence.

Social scientists are likely to be uncomfortable with this approach, based as it is upon the notion of genetically influenced, although not genetically determined, behavioral predispositions. However such thinking is not really novel for social science: The role of genotype is basic to the theories of the great developmental psychologist Piaget (1973), with his emphasis upon the adaptive unfolding of strategies for dealing with experience, and Chomsky's conception of an underlying "innate deep structure" in human language (1972). Both of these approaches recognize a biological substrate for behavior. But it is one thing to identify certain underlying givens in the human repertoire; it is quite another to use evolutionary theory to explain the reason for these givens and then to go even further and predict the existence of other tendencies, perhaps some not yet identified. This is the unique promise of sociobiology.

In many cases, genetic influences upon our behavior are so subtle that we take the results for granted—it sometimes takes considerable mental effort to step back from our behavior and view ourselves objectively. For example, why is sugar sweet? Of course, chemists have identified similarities in the molecular structure of those compounds we call sugars. But sweetness does not reside in these molecules; rather, it is in our taste buds, our response to these substances. To an ant eater, sugar is not desirable eating, but of course ants are a different matter. To us, ants taste bitter. Why the difference? Our primate ancestors probably ate a great deal of fruit, which is more nutritious when

it is ripe and rich with sugars. We were therefore selected for responding positively to the taste of those chemicals that characterize ripe fruit. Accordingly sugar tastes sweet to us; an articulate giant panda would probably say the same about bamboo shoots.

In a sense humans are unique among animals in that our behaviors appear liberated from the tyrannical demands of biology, mediated by natural selection. We can substitute personal satisfactions for adaptive significance. But carry this thought one step farther: What behaviors do we find satisfying, and why? Sex, good food, rest, the respect of others, physical comfort, personal power and autonomy, coordinated and successful movements (athletics, dancing), the accomplishments of ourselves and our offspring, all these pleasures contribute eventually to our own fitness, and therefore we have been selected to engage in them. We find them sweet.

Armed with the intellectual paraphernalia of sociobiology, and cautioned as to the uncertain role of genes in human behavior, let us now attempt a preliminary, speculative and predictive excursion into human sociobiology.

Mate Selection

Assuming that human behavior has been selected to maximize inclusive fitness, we would expect to see evidence of this in choice of a mate. Sexual attractiveness of a potential partner is not different from sweetness of a potential food: The quality is not inherent in the subject perceived but, rather, in the perceiver. Just as with our choice of foods, we should choose mates that are good for us. Therefore, insofar as we have been selected for positive responses to certain physical characteristics of potential mates, selection would favor those individuals preferring mates who conferred maximum reproductive success upon the discriminating partner. The situation is analogous (homologous?) to sexual selection in other animals (Chapter 6): Individuals are most fit if they make the best choice. Therefore,

we could predict a positive correlation between physical viability, general health, and other indicators of reproductive potential among members of each sex and those characteristics perceived as attractive by members of the opposite sex. Regularity of features, smoothness of complexion, optimum stature (neither too short nor too tall), good physique, all of these things count, and for good reason. Among the secondary sexual characteristics of women, breasts help nourish offspring, although within normal limits breast size is not correlated with milk production, and hips of a certain minimum width facilitate childbirth. In this regard the traditional Mother Earth Goddess of antiquity may come closer to biological appropriateness than does today's chic svelte look. If in earlier times, plumpness implied command of resources, in American society at least, it no longer does. Even this change in cultural norm is at least not maladaptive because modern medicine has relaxed the biological requisites for reproductive success: we have hospitals, cesareans, and baby bottles.

All human societies have prohibitions against incest between siblings and between parents and offspring. Social scientists commonly interpret these universals as due to the potential for family disruption inherent in sexual rivalry between close relatives (Levi-Strauss, 1969). Of course close breeding would also reduce the fitness of the participants because of the reduced viability of the offspring produced. Like the Jewish dietary laws, incest avoidance is cultural. It is also adaptive. However, it goes further in being universal and therefore suggesting genetic predispositions. The anthropological literature on incest avoidance systems is immense; for a biological perspective, see Fox (1972).

Humans are mammals. We therefore experience the same differences between male and female parental investment as most other animals (see Chapter 6). Extrapolating from the theory, men should accordingly be sexual aggressors. Men should also compete among themselves for the sexual favors of women, and women should in turn be selected for assessing men in large part by the quality of the reproductively relevant

resources they control. It may be significant that women tend to concentrate their reproductive interests upon men who are socially, economically, and educationally above them (Blake, 1971).

Savoir-faire and the capacity to command respect from others are characteristics of men that have long been valued by women. The reverse is much less prevalent and, in fact, too much competence and accomplishment by a woman is often threatening to a prospective male partner unless his ego is especially secure. Successful single women often face a problem in that their range of prospective mates tends to be limited to those above them in the socioeconomic scale. This adaptive tendency for women to marry up (hypergamy) would occur even when reproduction is not intended or even if it is consciously excluded. Thus, such basic adaptive inclinations as hypergamy may be insensitive to personal conditions (i.e., intentional childlessness), which are themselves too recent to have been acted upon by natural selection.

Similar tendencies among animals often result in sexual bimaturism (Chapter 6) and indeed, it is almost universal in human societies that men are older than their mates; furthermore, puberty occurs earlier in girls than in boys. Older men are more likely to control resources of value to a reproducing female and, given this correlation, selection could easily result in female preference for a degree of male maturity. There is nothing very peculiar in a 70-year-old man marrying a 25-year-old woman. Even if tongues wag, there may be a grudging unconscious recognition that both could be maximizing their fitness. A young man with an old woman seems much more inappropriate.

In fact, similarly adaptive human predispositions could be responsible for the prolongation of reproductive potential in men relative to women. Female fertility ends at menopause, roughly at 45 to 55 years of age. In contrast, men can father children at any age. The physical strains of childbearing may have selected against reproduction by older women, especially if they are able to enhance their inclusive fitness by contributing indirectly to

the eventual reproductive success of existing children, grandchildren, and other relatives. Increased fragility with increasing age thus adds to the cost of reproducing, while at the same time an accumulation of wisdom and experience adds to the ultimate reproductive benefit that grandmothers, great-aunts, etc., can provide, even if they now assume a nonreproductive role themselves. In contrast, the physical cost of sex is minimal to men; they do not get pregnant. This, combined with the general correlation of age with control of resources and the presumed female preferences with which this correlation is associated, could select for the relatively prolonged sexual potency of men.

The polygyny threshold model of female mate selection (Chapter 6) suggests that maximization of female fitness requires discriminative mate selection. Nonhumans apparently achieve this by weighing the disadvantages of sharing a male's attention against the advantage of good resource quality often provided by an already-mated male. Among polygynous human societies the number of wives allotted to a man is a function of resources; i.e., he cannot have more wives than he can adequately support. This phenomenon appears to be entirely cultural, but it is also adaptive, and the parallels with other animals are striking. In addition, younger men in human polygynous societies are almost invariably monogamists, if they are mated at all. Polygyny is reserved for the older men who control greater resources.

Furthermore, much of human courtship can be interpreted as providing opportunities for mutual assessment, analogous (homologous?) to one of the suggested functions of courtship among nonhuman animals. Expenditure of money on dinners, flowers, movies, or gifts provides a means of displaying financial resources and willingness to dispense them. Dancing and athletics demonstrate physical prowess, along with the display of trophies or other symbols of successful rites of passage. Living-together arrangements permit assessment of sexual compatibility.

I have pointed out (Chapter 6) that the biology of male-female differences predisposes males of most species to sexual

aggressiveness, advertisement, and availability, while females are selected for discrimination and sales resistance. Humans are perfectly good animals in terms of their reproductive biology and the necessarily high parental investment required of women compared with that of men. Accordingly our species may also demonstrate the same adaptive difference in male-female reproductive strategies, albeit modified by such cultural phenomena as laws, moral norms, and experiences during childhood. Prostitutes are nearly always female in every culture; pornographic books and movies are directed almost exclusively at men; men are readily seduced by explicit sexual advances whereas women are more likely to be influenced by a romantic setting, some indication of genuine commitment by the man, etc.

A man's sperm represents very little investment; a woman's egg, while small itself, may have enormous significance to her. Given the peculiar biology of *Homo sapiens*, males probably maximize their fitness by a degree of reproductive, parental, commitment to their mate(s). However, optimum male strategy would include remaining susceptible to additional copulations, so long as they did not require further investment. Women may also have been selected for an interest in copulations outside the pair-bond but, because of their greater involvement in the consequences of such activity, women should be more fussy than men. Men are predicted to feel more threatened by the sexual activities of their women than women should feel as a result of sexual dalliance by their men. In terms of Darwinian fitness, men *are* threatened more than women by out-of-pair-bond copulations by their partner. In effect, I am suggesting a potential biological basis for the double standard. Once again, I am *not* suggesting that what is biological must also be ethically right, or unavoidable. With the current changes in social tradition and the perfection of birth control, we can certainly expect dramatic changes in such traditional behavior patterns. It will be interesting to see what evolves from modern society. We can afford equality of sexual behavior only when the biological consequences of such behavior are equal, but so long as women, not men, get pregnant, some differences can be predicted.

Responses to Behavior of the Mate

Few decisions are irrevocable. The behavior of mates toward each other can be expected to vary with many factors, especially as situations change and as life experiences provide further information regarding the partner. Relevant information could include actual changes in physical condition, behavioral predispositions, etc., or more accurate assessment of existing factors, if either partner had previously received an inaccurate impression of the other. These inaccuracies could be due to deceit, insufficient perceptiveness, or both. In any case, sociobiology suggests that one essential criterion could underlie the patterning of responses to the behavior of one's mate: The consequences of such responses or the failure to respond for the fitness of the individual concerned. Thus, mate A should be particularly sensitive to any characteristic of mate B, either physical or behavioral, that has important consequences for the inclusive fitness of mate A. Furthermore, the response of mate A should be such as to enhance or maintain his (or her) personal fitness and not that of B.

Sociobiology accordingly predicts, for example, that divorce or its equivalent correlates closely with any substantial decrement to successful reproduction. Failure to consummate a marriage is often sufficient cause for annulment, and impotence and infertility have historically been a cause of marital breakdown. Among kittiwake gulls, over 60% of the pairs retain their mates of the previous season (Coulson, 1966). These old married couples begin reproduction several days earlier than "newly weds". They appear to benefit from the increased coordination that comes with mutual familiarity. But "divorce" also occurs: Pairs that failed to hatch any young the previous year are three times as likely to change partners as are those that bred successfully. This represents an adaptive strategy: Find a new mate if you and your old mate are reproductively incompatible. It would be interesting to learn whether divorces

among humans are more likely following the death of a young child, for example.

Let us assume that the major biological function of man-woman pair-bonding is the production of successful offspring. Love, companionship, and sexual satisfaction can all be seen as proximate means of achieving this ultimate end. We seek them and find them pleasurable for the same reason we find sugar sweet. This certainly explains the prevalence of couples remaining together for the sake of the children, even when the adults are personally dissatisfied. Of course, such adult self-sacrifice is ultimately selfish, in that offspring are the primary vessels carrying the adult genotype, their most direct route to Darwinian fitness and evolutionary success.

Significantly, decreased reluctance to divorce in present day America correlates with increased availability of day-care centers and other forms of substitute parenting. It is axiomatic that divorce is easier when there are no children. Admittedly, this commonplace observation may reflect true altruism by the parents or the selfish recognition of the increased burden of single parenting. But it may also represent our own deep-seated awareness that such an action often runs counter to the biologically appropriate reproductive strategy of an animal whose offspring have a long period of dependency. For the same reason that sugar tastes sweet, we can expect divorce to taste bitter, especially if there are children.

What about the sociobiology of cuckoldry? The male response to apparent female adultery in mountain bluebirds (Chapter 3) reflects an adaptive male response, aggressive intolerance. This strategy is biologically appropriate, as long as replacement females are available and the chances of rearing a brood are high and/or if the threat of such response causes the potential adulterer to have second thoughts. No information is currently available regarding the *female* response to *male* adultery among animals, although I predict it to be significantly less intense. This is because females of every species enjoy an enormous biological advantage: They know that they will share 50% of their genes with each of their offspring. Males lack this

assurance. Accordingly, the philandering husband is no great disgrace, as long as he also provides adequately for his domestic obligations. His fitness may be high. The cuckolded husband, on the other hand, is an object of ridicule. His fitness is probably low.

Sociobiology predicts that human males are therefore significantly more intolerant of infidelity by their wives than wives are of their husbands. Violent crimes are often precipitated by domestic infidelity and it is no secret and should be no surprise that adultery is punished with particular severity in male-dominated societies. Significantly, socially approved wife sharing among unrelated men occurs only in certain societies, such as some Eskimos, in which the rigor of the natural environment makes cooperation of greater value than absolute confidence of genetic relatedness. Finally, the marital system of commitment and fidelity may provide a means of mutual restraint, with each partner threatening potential infidelity in the event of such behavior by the other.

On one level, this discussion of human sexuality in terms of strategies for the maximization of fitness may appear to be missing the boat. Sex is great fun. That's why we do it, isn't it? In fact, our pleasure in sex is but another example of the "why sugar is sweet" argument; the enormous satisfaction of sex may be viewed as a trick by natural selection to ensure that we reproduce. But beyond this we humans are unique among animals in the additional use we make of sex. Sex is an expensive endeavor, and it is energetically demanding and exposes the participants to increased likelihood of predation. On the other hand, it is adaptive in serving reproduction, and clearly that is why it is done. And among nonhuman animals, that is virtually the only reason. They copulate almost exclusively with regard to reproduction; sex is a serious, businesslike activity, performed when there is a high probability of offspring being produced. On the other hand, humans appear to be unique in that we engage in *nonreproductive* sex; unlike other animals, human sexual activity is not limited to distinct breeding seasons or special periods of receptivity (estrus or heat in other mammals)

correlating with ovulation by the female. Human sexuality has essentially been liberated from its domination by hormones, and accordingly we engage in sex throughout the calendar, if not around the clock.

But for what has it been liberated? One guess is that our novel use of sex relates to the unique problem posed by our utterly dependent infants. Human infants are totally helpless and require the committed attention of one parent, invariably the woman, since she is also adapted to nourish her newborn. It would certainly help if there was a daddy around to hunt, scavenge, defend the female and her child, etc. Given that, during our evolutionary development, offspring were more likely to be successful if they received the committed assistance of at least two adults, selection would favor any mechanism that kept the adults together. Sex may be such a device, selected to be pleasurable for its own sake, in addition to its procreative function. This would help explain why the female orgasm seems to be unique to humans; among other animals, reproduction is the only goal, and satisfaction per se is irrelevant. In addition, loss of estrus among humans contributes to sexual consistency that may in turn help maintain a stable pair-bond. This interpretation, while admittedly speculative, is clearly at odds with the traditional Vatican argument that nonreproductive sex is somehow animalistic and dehumanizing. Sex for its own sake may in fact be one of the few biological distinctions of our species, a uniquely human attribute.

Strategies of Being a Parent

I have already discussed a study of parental defense in Alpine accentors (Chapter 7). These small birds show increased bravery in defense of their offspring as the latter grow older, an adaptive strategy because with increased age the chances of further reproduction decline, rendering the offspring at hand increasingly important to the fitness of the parent(s). Similarly, white-crowned sparrows of the *pugetensis* subspecies that are

capable of renesting show less parental defense than does the *gambelli* subspecies with only one brood per season and no second chance (Chapter 7).

Considerations of this sort yield several predictions concerning human parental behavior. Thus, abortion is generally viewed with increasing repugnance as the embryo becomes older. We have relatively few qualms about destroying a just-fertilized egg but feel differently about a seven-month fetus. The older the offspring and the greater the investment, the greater the defense. Killing or abandoning a newborn baby is usually even more difficult. After all, the mother has felt the child grow and develop, and there are powerful proximate mechanisms operating to ensure continuation of parental care once so much has been invested. Extend the analysis: If parents were forced to choose between their newborn baby and their three year old, the three year old would almost certainly win. The older child has successfully completed a hazardous time, infant mortality being relatively high, and it therefore represents a better bet for evolutionary success than does the newborn. A decision in its favor would therefore be adaptive for the parents. Certainly in most cultures, little fuss is occasioned by the death of an infant, as opposed to adult mortality.

Of course, one might argue that this choice has nothing to do with adaptive strategies and the maximization of Darwinian fitness; we choose the three year old because we have grown to love it, whereas we hardly know the infant. But that is the point: Why do we *grow* to love a child? Maybe because the older the child, the more value it represents in terms of our evolutionary future. Like love between adults, parental love is highly adaptive. In biological terms, parents who decide to invest preferentially in such offspring will ultimately produce more successful offspring than will parents who follow an alternative strategy; i.e., the former will be more fit and such tendencies could therefore be selected. In this case, we identify as *love* the proximate mechanism ensuring such tendencies. Human love, then, could be a universal behavioral means to a biological end.

Let us assume that human parents demonstrate solicitude toward their children according to the basic formulations of kin

selection (Chapter 4): Given that genetic relatedness between the parent and each child is equal, solicitude toward each child should vary inversely with the risk to the parents' reproductive success via other born or unborn offspring and relatives. In addition, parental solicitude should vary directly with the extent to which the assisted child will benefit reproductively by each investment. Thus, a deformed or defective child should generally receive little investment or even suffer infanticide. This is the predominant pattern throughout most human societies. An older child who has survived the dangers of infant mortality should warrant greater investment than one less likely to provide an evolutionary return. Similarly, we should reserve our greatest antagonisms toward unrelated individuals, especially when they have achieved maximum reproductive value, at adolescence (Emlen, 1966).

Parental investment has been defined as any behavior that increases the chances of survival and reproduction by offspring at the cost of the parents' ability to invest in other offspring (Chapter 6). Parents with less future reproductive potential should therefore be selected for greater parental investment in current offspring. There is good evidence for such a tendency among animals; witness the *gambelli* versus *pugetensis* white-crowned sparrows, and a similar pattern can be predicted among humans. For example, compare the decisions made by two women, pregnant for the first time, and both hypothetically faced with the choice of saving themselves or their baby. One woman is 19 and the other is 38 years old. Most women in these situations would probably save themselves, but older women should also be significantly more inclined to save their baby than would younger women.

Like the *pugetensis* sparrows, a young human can have other babies and her best strategy under this situation would therefore be to "cut bait"; by contrast, the older woman, like the *gambelli* sparrow, would likely be sacrificing her only reproductive potential and should be reluctant to do so. Interestingly, most American hospitals take special note if a newborn is the first offspring of an older mother. The presence of other, dependent offspring introduces complications: It should reduce the

likelihood of maternal self-sacrifice. It would be adaptive to sacrifice the infant if the failure to do so would endanger the ultimate success of other children to whom the mother is equally related. Our hypothetical mother would therefore be acting in accord with constraints that are ultimately selfish, conferring maximum Darwinian fitness by way of optimizing investment in her offspring.

Of course, such concerns are not limited to women although they would probably be more strongly developed than among men. This is because of the greater female parental investment, the restricted age range of female reproductive potential, and the unique nutritive role of mothers. To some extent, fathers could also be expected to vary their behaviors as a function of fitness considerations, although the uncertainty of genetic relatedness adds a degree of diffuseness to the strategic evaluations. The exemptions of fathers of young children from military service may reflect at least in part an appreciation that such individuals may be less inclined to risk themselves for other causes.

Assuming once again that human behavior has evolved to maximize individual fitness, interactions with others should be patterned with regard to genetic relatedness; see the discussion of kin selection in Chapter 4. This has implications for differential male-female parental strategies. Women have the primary child-care roles in all human societies. Men are significantly less concerned with infants and children. Cultural determinists will claim this to be a function of socialization, but this does not explain the universality of such tendencies. The one commonality shared by Alaskan Eskimos, Australian aborigines, African Bushmen and Wall Street businessmen is their biological heritage; one aspect of that heritage is that males of virtually all animal species must have less confidence in their paternity than females have in their maternity. Females know that they share 50% of their genes with their children, while males must take the female's word for it. It is therefore adaptive for females to invest heavily in the well-being of the children. Males are predicted to be less predisposed in this direction, especially because the solicitous tendencies of women

enable such male "irresponsibility" without any decrement in the male's fitness via his presumed offspring. The woman can be counted upon to take care of the kids. She will lactate; he will not.

What will he do? Like the male hoary marmots inhabiting a highly social colony (Chapter 7), the human male can maximize his fitness by interacting with other adults. By competing with other males, he can retain access to his female and also possibly attract additional mates. This line of reasoning thus provides further support for the "biology of the double standard" argument presented above, and it also suggests why women have almost universally found themselves relegated to the nursery while men derive their greatest satisfaction from their jobs. For example, reversion to standard sexual division of labor has even occurred in Israeli *kibbutzim*, despite an overt ideological commitment to behave differently (Tiger and Shepherd, 1975).

Like a male red-winged blackbird struggling to defend a territory capable of transforming him from a bachelor to a polygynist, the male human may well have been selected for behaviors that maximize his fitness. According to this line of reasoning, success in male-male competition indicates and/or generates resources ultimately attractive to women for which men will therefore compete. For their part, women then choose these resources because they in turn will be selected to bestow their reproductive favors in accordance with the maximization of *their* fitness. Hypergamy should therefore correlate with polygyny, and it does. Of course, as with other behaviors, modern twentieth century life would have greatly diffused these more primitive, biologically generated tendencies, but they may well persist nonetheless, taking different forms in different cultures.

Such differences in male-female attachment to family versus vocation could derive in part from hormonal differences between the sexes. The maternal hormones prolactin and progesterone are intimately concerned with care of young in most vertebrate species, although there is no clear-cut evidence for such a relationship in *Homo sapiens*. If it did hold, it would constitute *proximate* causation; for the *ultimate*, evolutionary cause, we ask,

why should child care be the concern of female hormones? For the same reason that vertebrate aggressiveness is largely the concern of male hormones; for the same reason that sugar is sweet.

Successful parents, insofar as evolution is concerned, are those that become grandparents. Grandparents share one-fourth of their genes with their grandchildren. For the same reason that men and women differ in the confidence of their genetic relatedness to their offspring, grandparents or, rather, grandmothers are certain to be related to the offspring of their daughters, whereas they must rely upon the honor of their daughters-in-law for the offspring of their sons. Grandparents would therefore be predicted to invest more heavily in their daughters than in their daughters-in-law. Why is it usually the mother's parents who help out most when the new baby arrives? On the other hand, patrilocal residence is the most common human living arrangement (van den Berghe, 1975); the bride moves in with the family of her husband. In this manner, the in-laws with less genetic security can oversee their investment. It would also be interesting to know whether pressures for avoiding extramarital intercourse are exerted particularly by in-laws, those with the most to lose.

Of course sociobiology holds that, when parents invest in their offspring, it is because such investment increases the likelihood that they will become grandparents; i.e., evolutionary success, fitness, is ultimately measured by the production of genetically related descendants. The reproductive performance of children should therefore be a major concern of parents. Significantly, young couples often describe parental pressure as a major factor positively influencing their own decision to have children. Of course their parents *naturally* want to become grandparents. The evolutionary perspective of sociobiology suggests why this may be.

We can also make specific predictions. For example, parental concern that each offspring reproduce should to some extent vary inversely with the number of such offspring. The spoiled only child is a well-known phenomenon. We may have been selected to lavish resources on our children in proportion to

how much they represent our only chance at long-range reproductive success. This is not to deny parental love in large families, but it is probably no coincidence that the glow of grandparenthood like that of parenthood tends to diminish with repeated kindling.

The sociobiological theory of parent-offspring conflict (Chapter 7 and Trivers, 1974) provides numerous opportunities for predictions concerning human behavior, based once more upon the assumption that individuals will be selected for the maximization of their inclusive fitness. Children should therefore be selected to demand more parental investment than the parents will be selected to give, and weaning conflict can be expected, for example, with regard to both the amount and duration of nursing. The child wants a lot of milk; where this is necessary for offspring success, the parents also want the child to get it. However, parents want to invest in other offspring as well, and the nursing child can therefore be expected to disagree over the amount and duration of nursing.

Of course offspring would lose fitness if they were too selfish. Excessive gluttony would contribute little if at all to their personal success and, besides, offspring stand to gain fitness from the reproductive success of their siblings in exactly the same sense as the altruistic turkeys and the Tasmanian native hens (see Chapter 4). Genes for extreme selfishness relative to siblings would therefore be selected against by the consequent decline in inclusive fitness, unless the personal reproductive advantage they confer exceeded twice the disadvantage they inflict upon their brothers and sisters (because siblings share half their genes, on the average).

This line of reasoning suggests many interesting predictions. For example, a child's willingness to forego additional parental investment should be to some extent a function of its genetic relatedness to its other siblings. In families or societies where siblings are successively produced by the same parents, children should engage in less parent-offspring conflict with regard to the duration and amount of parental investment than in situations where different, unrelated males successively father the offspring. Similarly, greater offspring-offspring conflict would

be expected among half-siblings, the offspring of one man's unrelated wives, than among full siblings.

Furthermore, older parents should experience less parent-offspring conflict than younger parents. This is because the former have less future reproductive potential than the latter and would therefore be less strongly selected for withholding investment from their current offspring. On the other hand, weaning conflict should predictably increase during the development of each child as (1) it becomes increasingly competent to survive without the disputed investment, (2) its increased size requires proportionately more of that investment, and (3) the parent becomes increasingly prepared to invest in subsequent offspring. It is interesting that minimization of parent-offspring conflict over lactation and nursing is institutionalized in many human societies through a postpartum sex taboo until the nursing infant is weaned.

Children would be expected to employ psychological rather than physical tactics in attempting to induce more parental investment than would be in the best interests of the parents themselves. This derives from the obvious physical disadvantage of the offspring. Given that offspring will be selected for the use of such tricks, parents will be selected for the ability to discriminate true need from those demands that would increase offspring fitness at the cost of parental fitness. Previous experience with children might benefit parents in their ability to make this distinction. Therefore experienced parents should be relatively more successful at winning parent-offspring conflicts (Trivers, 1974).

Behaviors characteristic of earlier developmental stages should serve as an effective tactic in generating parental investment, because parent-offspring conflict is expected to be less intense when the offspring are younger. The psychological phenomenon of regression to infantile behavior could therefore have its roots in such a system (Trivers, 1974). Offspring would also be selected for sensitivity to their own needs when these needs relate to their own fitness and to their parents' inclinations concerning future investment in them. Thus, the evolutionary perspective suggests that living things behave with a

degree of "enlightened self-interest" not usually attributed to them. For example, several studies have examined the effects of mother-infant separation on the behavior of rhesus monkeys; such research may be of practical significance for understanding and predicting the often-traumatic consequences of forced separation in humans (Bowlby, 1973). Specifically, when rhesus mothers are removed from their infants and then reunited, the infants spend significantly more time huddling with the mother and demanding attention than they did before separation (Hinde and Spencer-Booth, 1971). Furthermore, the more frequent the separations, the greater the infant demands for maternal attention. In contrast, when mother-infant separation occurs by removing the *infant*, rather than the mother, then the infant is less demanding of maternal attention when they are eventually reunited (Hinde and Davies, 1972). This difference may seem puzzling: why should it make such a difference to the infant whether the separation is caused by removal of the mother or of the infant? In either case, the separation is the same. However, an evolutionary perspective suggests an answer. Separation caused by departure of the infant is less likely to indicate maternal negligence than is separation caused by departure of the mother. Therefore, infants should be relatively unconcerned about the former, whereas when they have some reason to doubt their mothers' devotedness to them, it would be adaptive for them to behave in a manner that will reduce the likelihood of such separations occurring in the future. Sociobiology thus offers a rather new perspective on parent-offspring interactions, one that is based upon the notion that each individual is ultimately motivated by considerations of their own evolutionary self-interest: it sheds new light on old problems.

According to the sociobiology of parent-offspring conflict, parents and offspring are expected to disagree over the "behavioral tendencies of the offspring insofar as these tendencies affect related individuals" (Trivers, 1974). For example, parents have an evolutionary interest in preventing their offspring from engaging in a selfish act that harms a full sibling, whereas the offspring are selected for persistence in such behavior so

long as the performer benefits from it more than one-half as much as the recipient is harmed, because full siblings have, on the average, one-half of their genes in common. The same potential conflict exists with regard to more distant relatives as well, when the genetic relatedness of parent-to-relative and child-to-relative is asymmetric. For example, parents share one-fourth of their genes with their nieces or nephews, while their offspring share only one-eighth of their genes with these same individuals (their cousins), adults should therefore have a greater interest than their offspring in discouraging selfishness and encouraging altruism among cousins.

Psychologists have traditionally viewed early socialization as a process of *enculturation* during which the offspring are simply instructed in the details of their parents' culture for the benefit of all. Clearly, the preceding discussion is greatly at variance with this approach. Given their conflicting evolutionary strategies, we can predict that parents will attempt to induce offspring to behave more altruistically than would be in the children's best interests and that the latter should resist these efforts, tending toward a degree of egoistic behavior that should in turn be resisted by the parents. However, parents have a big edge: Existing adult culture is presumably of some adaptive value, at least as indicated by the fact that its practitioners have survived and succeeded in producing children. In addition, because of their greater experience, parents probably do have something of value to impart to their children. Offspring should therefore be selected for susceptibility to adult teaching. In turn, parents might be expected to take advantage of this vulnerability on the part of their children by exaggerating the significance and importance of their teaching, while using such teaching to further their own manipulation of their offspring. It is therefore not surprising that the prevalent view of socialization, in which children are pictured ideally as passive recipients of parental beneficence, is one that is supported by adults! (Trivers, 1974).

In fact, a great deal of actual parent-offspring conflict may be illuminated by Trivers' approach. Common parental exhortations include going to bed early, studying hard at school, not

fighting with siblings, refraining from gambling, drinking, or premarital sex, and learning to share. All these are either directly altruistic (prepare the child for future altruism, increase the likelihood of others reciprocating with altruism toward relatives) or reduce the expenditure of time and/or energy required of the parents. Children often disagree with these parental prescriptions, considering them to be unpleasant, excessively moral, and/or generally a drag. This may well emanate in part from their adaptive unconscious perception that such actions would maximize their parents' fitness rather than their own. Enlightened self-interest may work wonders in generating cooperative children.

According to sociobiologic theory, children are only a special case of our evolved propensity for leaving genetic representation in future generations. We share more genes with our children than with our nieces or nephews, more with the latter than with second cousins, etc. But these differences are quantitative, not qualitative. Parental behaviors should therefore constitute only a special case of generalized concern for the success of our relatives. The family organization in current American society may actually constitute an aberration in terms of our biological history and evolved propensities, in that the nuclear family is restricted to parents and their children. When the children mature, they typically leave the family circle, often in search of educational opportunities, jobs, a spouse, etc., and establish their own nuclear family. Contrast this with the usual pattern of primitive, nonindustrialized societies: Children tend to remain near their parents, and their offspring in turn are brought up in an environment of grandparents, uncles, aunts, cousins, etc.

Assuming that evolution has favored both the expenditure and receipt of kin investment, our present system of relatively isolated nuclear families may well generate substantial stresses upon all concerned. The frustration of grandparents who must content themselves with occasional long-distance telephone calls and eagerly sought Christmas visits may reflect their forced inability to fulfill a major biological satisfaction. Maiden aunts and bachelor uncles are similarly deprived, although they

may not consciously recognize it. For their part, parents in isolated nuclear families may well be laboring under stresses that are novel to our biology. Life was certainly not easy for our remote ancestors. But having evolved in small social groups in which genetic relatedness was undoubtedly quite high, we as parents probably enjoyed considerable assistance from our relatives when it came to the obligations of child rearing. Such assistance was beneficial to all concerned. Older individuals were experienced and knowledgeable in child care, while juveniles and adolescents profited by the training. Finally, the dependent children themselves doubtless gained by the arrangement. Modern domestic strains can be somewhat alleviated by babysitters, day-care centers, and, possibly, communal living arrangements, but for the most part our turning from biology may have robbed child rearing of much of the serenity it once possessed.

In addition, extended-family societies provide an excellent opportunity for evaluating the applicability of inclusive fitness theory to human social behavior. Most of them have unilineal descent; i.e., they are either patrilineal, tracing kin relationships through the father's line, or matrilineal, through the mother's. Given that genetic relatedness is equivalent in both cases, the question is whether the cultural rule of ignoring all but one line of descent predicts altruistic behavior better than does actual biological relatedness. The evidence is simply not in, and the question remains open.

Altruism and Such

We have discussed the biology of altruism among nonhuman animals (Chapter 4), specifically excluding any consideration of internal motivation or cognition. In contrast, the social science literature on human altruism revolves almost entirely around such notions. In this brief section let us apply a sociobiological approach to human altruism, suggesting possible adaptive predispositions in *Homo sapiens*. Once again, this is not to deny a role for learning or social tradition in mediating such behavior;

factors of this sort are entirely compatible with underlying genetically influenced tendencies as well. The value of sociobiology's evolutionary approach is that it allows predictions of possible behavioral universals or at least a common substructure rooted in our biology.

The theory of kin selection has great potential relevance to human behavior. In fact, it suggests a coherent theory for the biology of nepotism. It provides a straightforward answer to the puzzle of why we tend to favor our relatives. Sociobiology's prediction is that we should be selected to show altruism toward others in direct proportion to how closely related they are to us genetically. Insofar as the Central Theorem of Sociobiology holds for us, the relationship $k > 1/r$ (Chapter 4) should hold for human altruism. We should be willing to suffer greater risks in aiding individuals who are more closely related and should withhold aid to more distantly related individuals, unless the risk to our personal, Darwinian fitness is also proportionately lower. Similarly, we should require that a distant relative be in greater need, derive a higher benefit from our act, in order for us to render the same assistance that we would dispense to a closer relative in less dire straits. Anxious parents may inquire eagerly as to whether their children need more money at college, whereas, in general, assistance to a second cousin might be forthcoming only in greatest emergency and even then only after it is requested.

Assuming equivalent genetic relatedness to all recipients (equal r), our willingness to disperse altruism should vary directly with the benefit in fitness to the recipient and inversely with the cost in fitness to the altruist. Appeals for the needy emphasize how much good can be done with so little cost: "Only one dollar provides milk for a month". Similarly, costs are lowest for the potential altruist when his or her personal reproductive potential is lowest; there is little to lose. Older, post-reproductive people should therefore be particularly inclined to assist others. If they have many potential beneficiaries that are also relatives, their attention would be especially directed toward them. The need to help or to be needed should be strong in all *Homo sapiens*, and feeling useless should be painful