
Rape and Evolutionary Theory

Not enough people understand what rape is, and, until they do . . . , not enough will be done to stop it.

—rape victim, quoted in Groth 1979 (p. 87)

By one intuitive and relevant definition, rape is copulation resisted to the best of the victim's ability unless such resistance would probably result in death or serious injury to the victim or in death or injury to individuals the victim commonly protects.¹ Other sexual assaults, including oral and anal penetration of a man or a woman under the same conditions, also may be called rape under some circumstances.

In one study, 13 percent of the surveyed American women of ages 18 and older reported having been the victim of at least one completed rape—rape having been defined as “an event that occurred without the woman's consent, involved the use of force or threat of force, and involved sexual penetration² of the victim's vagina, mouth or rectum” (Kilpatrick et al. 1992, p. i). Other surveys using slightly different definitions or different data-collection procedures have found high rates too, especially when the survey procedures have given researchers access to victims of alleged rapes not reported to the police. Kilpatrick et al. (*ibid.*, p. 6) estimate the percentage of rapes of women not reported at between 66 and 84. Of women who had experienced a rape involving penile-vaginal intercourse, from 37 to 57 percent experienced post-traumatic stress syndrome afterward—a frequency higher than that associated with any other crime against women, including aggravated assault, burglary, and robbery (Kilpatrick et al. 1987; Resnick et al. 1993).

We suggest two answers to the question of why humans have not been able to put an end to rape:

- Most people don't know much about why humans have the desires, emotions, and values that they have, including those that cause rape. This is because most people lack any understanding of the ultimate (that is, evolutionary) causes of why humans are the way they are. This lack of understanding has severely limited people's knowledge of the exact proximate (immediate) causes of rape, thus limiting the ability of concerned people to change the behavior.
- For 25 years, attempts to prevent rape have not only failed to be informed by an evolutionary approach; they have been based on explanations designed to make ideological statements rather than to be consistent with scientific knowledge of human behavior.

One cannot understand evolutionary explanations of rape, much less evaluate them, without a solid grasp of evolutionary theory. Failure to appreciate this point has caused much valuable time to be wasted on misplaced attacks on evolutionary explanations.

Assuming that the main interest of most readers of this book is the subject of rape rather than evolutionary theory per se, we now present some questions about rape that an evolutionary approach can answer:

- Why are males the rapists and females (usually) the victims?
- Why is rape a horrendous experience for the victim?
- Why does the mental trauma of rape vary with the victim's age and marital status?
- Why does the mental trauma of rape vary with the types of sex acts?
- Why does the mental trauma of rape vary with the degree of visible physical injuries to the victim, but in a direction one might not expect?
- Why do young males rape more often than older males?
- Why are young women more often the victims of rape than older women or girls (i.e., pre-pubertal females)?
- Why is rape more frequent in some situations, such as war, than in others?
- Why does rape occur in all known cultures?
- Why are some instances of rape punished in all known cultures?
- Why are people (especially husbands) often suspicious of an individual's claim to have been raped?
- Why is rape often treated as a crime against the victim's husband?

- Why have attempts to reform rape laws met with only limited success?
- Why does rape exist in many, but not all, species?
- Why does rape still occur among humans?
- How can rape be prevented?

Evolutionary Theory

The question "What is man?" is probably the most profound that can be asked by man. It has always been central to any system of philosophy or of theology. We know that it has been asked by the most learned humans 2000 years ago, and it is just possible that it was being asked by the most brilliant australopithecines 2 million years ago. The point I want to make now is that all attempts to answer that question before 1859 are worthless and that we will be better off if we ignore them completely. —Simpson 1966, p. 472

Intelligent life on a planet comes of age when it first works out the reason for its own existence. If superior creatures from space ever visit Earth, the first question they will ask, in order to assess the level of our civilization, is: "Have they discovered evolution yet?" Living organisms had existed on Earth, without ever knowing why, for more than three billion years before the truth finally dawned on one of them. His name was Charles Darwin. To be fair, others had inklings of the truth, but it was Darwin who first put together a coherent and tenable account of why we exist. —Dawkins 1976, p. 1

Many social scientists (and others) have dismissed claims such as these as evidence of a somehow non-scientific "messianic conviction" (Kacelnik 1997, p. 65). Although these quotes indicate considerable enthusiasm, the important question is whether they accurately describe the implications of the theory of evolution by natural selection. Simpson's and Dawkins's enthusiasm is warranted by the tremendous success of evolutionary theory in guiding the scientific study of life in general and of humans in particular to fruitful ends of deep knowledge.

Cause, Proximate and Ultimate

A friend of ours once told us that after a movie she returned with her date to his car in an isolated parking lot. Then, instead of taking her home, the man locked the doors and physically forced her to have sexual intercourse with him. The question addressed in this book, and the question asked us by our friend, is: What was the cause of this man's behavior?

In both the vernacular sense and the scientific sense, *cause* is defined as that without which an effect or a phenomenon would not exist. Biologists study two levels of causation: *proximate* and *ultimate*. Proximate causes of behavior are those that operate over the short term—the immediate causes of behavior. These are the types of causes with which most people, including most social scientists, are exclusively concerned. For example, if, when reading our friend's question concerning the cause of the man's behavior, you said to yourself it was because he hated women, felt the need to dominate someone, had been abused as a child, had drunk too much, had too much testosterone circulating in his body, was compensating for feelings of inadequacy, had been raised in a patriarchal culture, had watched too much violence on television, was addicted to violent pornography, was sexually aroused, hated his mother, hated his father, and/or had a rare violence-inducing gene, you proposed a proximate cause of his behavior. You probably didn't ask why your proposed proximate cause existed in the first place. That is, you probably didn't concern yourself with the ultimate cause of the behavior.

Because they refer to the immediate events that produce a behavior or some other phenotypic (i.e., bodily) trait, proximate causes include genes, hormones, physiological structures (including brain mechanisms), and environmental stimuli (including environmental experiences that affect learning). Proximate explanations have to do with how such developmental or physiological mechanisms cause something to happen; ultimate explanations have to do with why particular proximate mechanisms exist.

Proximate and ultimate explanations are complements, not alternatives. For example, the claim that millions of years of selection caused the human eye to have its current form (an ultimate explanation) is in no way contradictory to the claim that a series of rods and cones enable the eye to relay visual information to the brain (a proximate explanation). Similarly, the claim that learning affects men's rape behavior (i.e., that it is a proximate cause) does not contradict the view that the behavior has evolved.

Identifying ultimate causes, however, is important, because certain proximate explanations may be incompatible with certain ultimate explanations. This is because certain ultimate explanations specify the existence of certain types of proximate mechanisms. For example, the ultimate explanation that the human eye evolved by natural selection because it

increased our ancestors' ability to detect light requires the existence of proximate light-detection mechanisms in the eye.

No aspect of life can be completely understood until both its proximate and its ultimate causation are fully known. To understand how ultimate causes can be known, one must understand how natural selection leads to adaptations.

Natural Selection and Adaptations

Adaptations are phenotypic features (morphological structures, physiological mechanisms, and behaviors) that are present in individual organisms because they were favored by natural selection in the past. Darwin sought to explain the existence of adaptation in terms of evolution by selection. Initially, he observed the action of selection on living things in nature—a fact of natural history that is inescapable in view of the high rates of reproduction and mortality in all organisms. Later, he realized just how creative selection could be when extended over the long history of life on Earth. This retrospection is evident in the following eloquent passage from *On the Origin of Species*:

Natural selection is daily and hourly scrutinizing, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good; silently and insensibly working. . . . We see nothing of these slow changes in progress, until the hand of time has marked the long lapse of ages. (Ridley 1987, p. 87)

The biologist George Williams, in his 1966 book *Adaptation and Natural Selection*, clarified what Darwin meant when he wrote of natural selection's rejecting all that was "bad" and preserving all that was "good." First, Williams noted, these words were not used in a moral sense; they referred only to the effects of traits on an individual's ability to survive and reproduce.³ That is, "good" traits are those that promote an individual's reproductive interests. We evolutionists use the term reproductive success to refer to these reproductive interests, by which we mean not the mere production of offspring but the production of offspring that survive to produce offspring (Palmer and Steadman 1997). A trait that increases this ability is "good" in terms of natural selection even though one might consider it undesirable in moral terms. There is no connection here between what is biological or naturally selected and what is morally right

or wrong. To assume a connection is to commit what is called the *naturalistic fallacy*. In addition, Williams clarified that natural selection favors traits that are “good” in the sense of increasing an individual’s reproductive success, not necessarily traits that are “good” in the sense of increasing a group’s ability to survive.

The idea that selection favors traits that increase group survival, known as *group selection*, had become very popular before the publication of Williams’s book—especially after the publication of *Animal Dispersion in Relation to Social Behavior*, an influential book by the ornithologist V. C. Wynne-Edwards (1962). Williams’s rebuttal of the concept of group selection convinced almost every biologist who read it that Wynne-Edwards was mistaken. However, the idea that selection favors traits that function for the good of the group appears to have been too attractive for many non-scientists to give up. Not only does it remain popular among the general public; it continues to have a small following among evolutionary biologists (Wilson and Sober 1994; Sober and Wilson 1998).⁴

One cannot grasp the power of natural selection to “design” adaptations until one abandons both the notion that natural selection favors traits that are morally good and the notion that it favors traits that function for the good of the group. Only then can one appreciate the power of natural selection to design complex traits of individuals.

The human eye’s many physiological structures exist because they increased the reproductive success of individuals in tens of thousands of past generations. Although there are four agents of evolution (that is, four natural processes that are known to cause changes in gene frequencies of populations), selection is the only evolutionary agent that can create adaptations like the human eye. The other evolutionary agents (mutation, drift, and gene flow⁵)—cannot produce adaptations; they lack the necessary creativity, because their action is always random with regard to environmental challenges (e.g., predators) facing individuals. Selection, when it acts in a directional, cumulative manner over long periods of time, creates complex phenotypic designs out of the simple, random genetic variation generated by the three other evolutionary agents. Selection is not a random process; it is differential reproduction of individuals by consequence of their differences in phenotypic design for environmental challenges. An adaptation, then, is a phenotypic solution to a past envi-

ronmental problem that persistently affected individuals for long periods of evolutionary time and thereby caused cumulative, directional selection. Evolution by selection is not a purposive process; however, it produces, by means of gradual and persistent effects, traits that serve certain functions—that is, adaptations.

Adaptations do not necessarily increase reproductive success in current environments if those environments differ significantly from past environments. The seeds of a tree that fall on a city sidewalk are complexly designed adaptations, formed by selection over many generations in past environments, yet they have essentially no chance of surviving or reproducing in the current environment of the sidewalk. Similarly, the North American pronghorn antelope shows certain social behaviors and certain locomotory adaptations (e.g., short bursts of high speed) for avoiding species of large cats and hyenas that are now extinct (Byers 1997).

The difference between current and evolutionary historical environments is especially important to keep in mind when one is considering human behavioral adaptations. Today most humans live in environments that have evolutionarily novel components. (Modern contraception is one such component that obviously influences the reproductive success of individuals in an evolutionarily novel way.) Therefore, human behavior is sometimes poorly adapted (in the evolutionary sense of the word) to current conditions.

Evolutionary functional explanations also differ from the non-evolutionary functional explanations familiar to most social scientists. In fact, evolutionary functional explanations overcome a problem that has plagued non-evolutionary functional explanations. Non-evolutionary functional explanations are unable to explain why a particular trait has come to serve a certain function when alternative traits could also serve that function (Hempel 1959). For example, Emile Durkheim, one of the founders of sociology, tried to explain religion by stating that it functioned to maintain the social group (Durkheim 1912). That explanation, however, is unable to account for why religion, instead of numerous alternative institutions (e.g., political governments, non-religious social organizations and ideologies), fulfills this particular function. The concept of evolution by natural selection helps overcome this problem. Any gene that happens to arise by random mutation, and happens to have the effect of increasing

an organism's reproductive success, will become more frequent in future generations. Eventually, additional random mutations will also *happen* to occur in future generations and will also be favored by natural selection. Over time, this process results in functionally designed traits. Randomness (in the form of mutations) and the non-random process of natural selection combine to answer the question of why a particular trait has evolved instead of other imaginable traits that conceivably could have served the same function.

There is also the important fact that selection works only in relation to what has already evolved. The process does not start anew each time. Thus, there are many features that seem poorly designed relative to what might be imagined as a better solution. For example, the crossing of the respiratory and digestive tracts in the human throat can cause death from choking on food. It would be better design—much safer in terms of survival—if our air and food passages were completely separate. However, all vertebrates (backboned animals) from fishes to mammals on the phylogenetic tree (the tree connecting all life to a common ancestor) have crossing respiratory and digestive tracts. The human respiratory system evolved from portions of the digestive system of a remote invertebrate ancestral species, and the food and air passages have been linked in non-functional tandem ever since (Williams 1992). The crossing of passages is a historical legacy of selection's having built respiratory adaptations from ancestral digestive system features. Not itself an adaptation, it is a by-product of selection's having molded respiratory adaptation from what came before.

Similarly, any new mutation, through its bodily effect, is assessed by selection in relation to how well it performs in the evolved environment of other individuals in the population as well as in the evolved environment of the various body forms that characterize the developmental pathway of traits. Thus, what has evolved (including the existing developmental adaptations) may constrain what can evolve, or may establish certain evolutionary paths as more likely than others.

Because selection is the most important cause of evolution, and because it is the only evolutionary agent that can produce adaptations, the ultimate approach seeks to provide explanations for these seemingly purposefully designed biological traits of individuals in relation to the causal selective forces that produced them. Thus, the adaptationist approach focuses on

how an adaptation contributed to successful reproduction of its bearers in the environments of evolutionary history. The challenge in applying an ultimate or evolutionary analysis is not to determine whether an adaptation is a product of selection; it is to determine the nature of the selective pressure that is responsible for the trait. That selective pressure will be apparent in the functional design of the adaptation.

By-Products of Selection

Not all aspects of living organisms are adaptations. Indeed, Williams (1966, pp. 4–5) emphasized that “adaptation is a special and onerous concept that should be used only where it is really necessary,” and the evolutionists that Williams inspired have been well aware that a trait's mere existence does not mean that it was directly favored by natural selection. Nor is a demonstration that a trait or a character increases an individual's reproductive success sufficient evidence that the trait is an adaptation.

Not only may an increase in reproductive success be due to some evolutionarily novel aspect of the environment; an increase in reproductive success in evolutionary environments may be only a beneficial effect rather than an evolutionary function. To illustrate this point, Williams cited a fox walking through deep snow to a henhouse to catch a chicken, then following its own footprints on subsequent visits to the henhouse. This makes subsequent trips to the henhouse more energy efficient for the fox, thus potentially increasing its reproductive success. Following its own footprints back may well involve adaptations in the brain of the fox, but there is no known feature of the fox's feet that exhibits design by natural selection to pack snow. The fox's feet are clearly designed for walking and running, but they are not clearly designed for snow packing. Hence, even though snow may have been part of the past environments of foxes, there is no evidence that it acted as a sufficient selective pressure to design the feet of foxes for efficient snow packing. Snow packing and any associated reproductive success appear to be fortuitous effects of the structure of the fox's feet. That is, snow packing is not a function of any known aspect of the fox's feet. Symons (1979, p. 10) noted that “to say that a given beneficial effect of a character is the function, or a function, of that character is to say that the character was molded by natural selection to produce that effect.” Williams (1966, p. 209) stated that “the demonstration of a bene-

fit is neither necessary nor sufficient in the demonstration of function, although it may sometimes provide insight not otherwise obtainable," and that "it is both necessary and sufficient to show that the process [or trait] is designed to serve the function."⁶

As Williams emphasized, the concept of adaptation should be used only where really necessary; however, it is essential to *consider* the concept of adaptation in all cases of possible phenotypic design, because only then can it be determined if a trait has been designed by natural selection. Williams (*ibid.*, p. 10) proposed that plausibly demonstrating design by natural selection requires showing that a trait accomplishes its alleged function with "sufficient precision, economy, and efficiency, etc."⁷ Following Williams's criteria, Symons (1979, p. 11) stated that "[a] function can be distinguished from an incidental effect insofar as it is produced with sufficient precision, economy, and efficiency to rule out chance as an adequate explanation of its existence." Hence, according to the doctrine of parsimony, "if an effect can be explained adequately as the result of physical laws or as the fortuitous byproduct of an adaptation, it should not be called a function" (*ibid.*).

Similarly, drift and mutation can be ruled out as explanations of the evolutionary history of a trait when the trait shows evidence of functional design. Drift may apply only to traits that do not adversely affect reproductive success: if there are such effects, then selection will determine a trait's fate. Few traits meet the criterion of no cost to reproductive success; thus, as the biologists Richard Alexander (1979) and Richard Dawkins (1986) have explained, drift is a matter of interest primarily in the cases of phenotypic traits that do not attract adaptationists' attention in the first place.

Most mutations are deleterious and thus are in a balance with selection (selection lowering the frequency and mutation increasing it). Selection is stronger because mutation rates are very low. Thus, mutation, as an evolutionary cause for traits, may apply only to those traits that are only slightly above zero frequency in the population. Because selection is the most potent of the evolutionary agents, any explanation of the evolutionary history of a trait based on mutation or on drift must be fully reconciled with the potency of selection to bring about trait evolution.

Further evidence of adaptation may come from cross-species comparisons. First, "if related species [i.e., those sharing a recent common ancestral species] come to occupy different environments where they are subject to different selection pressures, then they should evolve new traits as adaptive mutations occur that confer a reproductive advantage under the new conditions" (Alcock 1993, p. 222). Variation among the beaks of different species of the finches Darwin found on the Galápagos Islands would be an example of such "divergent evolution." The beak types are different adaptations for eating different, species-typical foods (Weiner 1994). Second, if two distantly related species "have been subjected to similar selection pressures," they "should have independently evolved similar behavioral traits through *convergent evolution*—if the trait truly is an adaptation to that selection pressure" (Alcock 1993, p. 222). Convergent evolution is responsible for the similar shapes of fishes and marine mammals that have evolved by natural selection in the context of mobility in water.

Hence, the diversity of life has two major components: adaptations and the effects of adaptations. The latter are known as *by-products*. Adaptations are traits formed directly by selective pressures; by-products are traits formed indirectly by selective pressures.

In addition to snow packing by fox feet, another example of a by-product is the red color of human arterial blood (Symons 1987a,b). This trait did not arise because of selection in the context of blood-color variation among individuals. That is, redness of arterial blood did not cause individuals with arterial blood of that color to become more frequent in succeeding generations. Instead, selection acting in other contexts gave rise to the trait as an epiphenomenon of adaptations. Human arterial blood is red for two proximate reasons: the chemistry of oxygen and hemoglobin in blood, and human color vision. Hence, the ultimate causation of the color of blood lies in the selective pressures that produced the chemical composition of human blood and human color vision.

Another example of a by-product is the higher death rate of males relative to females among humans of all ages (Alexander 1979; Trivers 1985; Wilson and Daly 1985; Geary 1998). The higher male mortality is not an adaptation; it is an incidental effect of sex-specific adaptations. The adap-

tations are in males' and females' bodies, including their brains. For example, various traits motivate male humans, relative to female humans, to engage in riskier activities. The ultimate cause of these male adaptations is a human evolutionary history of stronger sexual selection acting on males than on females.⁸

When one is considering any feature of living things, whether evolution applies is never a question. The only legitimate question is how to apply evolutionary principles. This is the case for all human behaviors—even for such by-products as cosmetic surgery, the content of movies, legal systems, and fashion trends.

The crucial legitimate scientific debate about the evolutionary cause of human rape concerns whether rape is a result of rape-specific adaptation or a by-product of other adaptations. That is, does rape result from men's special-purpose psychology, and perhaps from associated non-psychological anatomy, designed by selection for rape, or is rape an incidental effect of special-purpose adaptation to circumstances other than rape? We two authors, having debated this question for more than a decade (Palmer 1991, 1992a,b; Thornhill and Thornhill 1992a,b), agree that it may eventually be answered by determining whether or not rape is the result of special-purpose psychological mechanisms that motivate and regulate men's pursuit of rape in itself. We also agree that enough now is known about the ultimate evolutionary causes of human rape that an evolutionary approach can contribute significantly to prevention of the act.

But how can an ultimate explanation of why men rape help prevent future rapes? The answer is that ultimate evolutionary explanations have unique power in both a theoretical and a practical sense. In terms of theory, only selection can account for the creation and the maintenance of adaptations. Even complete identification of all proximate causes of an adaptation could not explain the genesis and the persistence of that adaptation. However, an ultimate explanation of a biological phenomenon can account for all proximate causes influencing the phenomenon, whether the phenomenon is an adaptation or an incidental effect of an adaptation. Thus, ultimate explanations are more general in that they are more inclusive of causation. As a result, ultimate explanations have enormous practical potential: if evolution by individual selection is truly the general theory of life, it should lead to the best insights about proximate causes,

and identifying proximate causes is the key to changing human behavior (e.g., eliminating rape).

That an ultimate evolutionary approach can serve as a guide for research into proximate causes has been shown repeatedly in investigations of non-human organisms. Indeed, this approach has revolutionized those investigations (Krebs and Davies 1993; Alcock 1997). It is also revolutionizing the study of human behavior (Alexander 1987; Wright 1994; Pinker 1997; Geary 1998; Buss 1999).

Evolutionary theory contributes to the study of proximate causation in two ways.

First, it leads to the discovery of new biological phenomena whose proximate causes are unknown. For example, the evolutionary psychologists Leda Cosmides and John Tooby (1992) have found that the human brain contains a mechanism designed specifically to detect cheating in social exchanges. The discovery of such a "cheater-detection" mechanism was the result of an understanding of the evolutionary concept of reciprocal altruism originally developed by the biologist Robert Trivers (1971). Similarly, evolutionary theory has led to the discovery of specific patterns of nepotism. This knowledge has resulted from studies directed by the fundamental evolutionary concept of kin selection: individuals perpetuate their genes not only by producing offspring but also by aiding relatives, including offspring (Hamilton 1963, 1964; Alexander 1987; Chagnon and Irons 1979; Betzig et al. 1988; Betzig 1997; Crawford and Krebs 1998). Relatives contain a high proportion of identical genes, and the closer the kinship relationship the higher the genetic similarity. What are the proximate cues by which individuals identify their relatives and distinguish categories of relatives? "Social learning" is the general answer (Alexander 1979; Palmer and Steadman 1997). Children are taught who their relatives are by their parents and their other relatives and through association with them during upbringing, and are encouraged by their adult relatives to be altruistic toward them (especially close kin). But what is the precise nature of the learning schedules involved in the ontogeny (development) of an individual's nepotistic behavior? This question would never have been asked had not evolutionists first successfully predicted the patterns of nepotistic behavior. After the social-learning aspects of nepotism are understood, the proximate physiological mechanisms in the brain that cause humans to

feel closer to and more generous toward close relatives can be investigated. Also, we may someday know the locations of human genes (another category of proximate causation), which, in conjunction with the environment, construct proximate mechanisms of kin recognition and discriminative nepotism.

The second way in which evolutionary theory interacts with the identification of proximate causes is even more direct and important. Evolutionary theory can tell investigators what proximate mechanisms are most likely to be found, and therefore where any investigation of proximate causation should begin. For example, evolutionary theory has provided unique directions for investigations of child abuse, child neglect, and infanticide (Daly and Wilson 1988). Evolutionary predictions regarding parental investment have directed researchers to multiple proximate causes of child maltreatment: resources available for successfully rearing offspring; paternity certainty and genetic relatedness of parent to offspring generally; health, sex, and status of offspring; age of parent; birth order.⁹

The example of child abuse also demonstrates the ability of an evolutionary approach to identify the proximate causes of both adaptations and by-products. In this case, it is not child abuse or infanticide per se that was favored by selection in human evolutionary history. The adaptations concern what Daly and Wilson (1988) call "child-specific parental solicitude" or "discriminative parental solicitude," which evolved because they increased the number of surviving offspring in a parent's lifetime relative to parents who invested indiscriminately in children generally. These are species-wide psychological adaptations that cause some parents to show love to all their children more or less equally, or to love some children and neglect (or even abuse or kill) others. The power of an evolutionary approach in identifying these factors is illustrated by Daly and Wilson's observation (1995, p. 22) that "living with a stepparent has turned out to be the most powerful predictor of severe child abuse risk yet discovered, but two decades of intensive child abuse research conducted without the heuristic assistance of Darwinian insights never discovered it." We suggest that the evolutionary approach can make a similar contribution to the identification of the proximate causes of rape. Specifically, we suggest that an understanding of the evolved differences between male and female sexuality can lead to identification of the proximate causes of rape. In-

deed, the ability of an ultimate evolutionary approach to direct research to the proximate causes of rape may be the key to lowering the frequency of rape.

Adaptations Are Functionally Specific

An understanding of the ultimate cause of adaptations can provide specific ways of preventing rape because adaptations are themselves specific.

In a paper titled "If we're all Darwinians, what's the fuss about?" Donald Symons (1987a) pointed out that the difference of opinion between traditional social scientists and the evolutionary anthropologists, biologists, and psychologists who were inspired by Williams's book *Adaptation and Natural Selection* does not concern whether or not the brain is designed by selection. The idea of psychological (brain) adaptation is almost certainly compelling to anyone who accepts that the rest of the human body has evolved by Darwinian selection. Indeed, the notion that the rest of the body could have been designed by selection without selection's simultaneously acting on the brain and the nervous system that control the body is absurd. To those who accept the notion of evolution, it is clear that the human brain must contain evolved structures that process environmental information in a manner that guides feelings and behavior toward ends that were adaptive in past human environments. Similarly, a moment's reflection on the evolution of the human opposable thumb—whose name implies both a structure and the movement (behavior) of that structure—should resolve any remaining controversy as to whether human physical behavior (muscle-induced motion) has evolved. All this means that the explanations of human behavior put forth by the social scientists who accept evolution (the vast majority) are implicitly evolutionary explanations. Hence, according to Symons (p. 126), "perhaps the central issue in psychology is whether the mechanisms of the mind are few, general, and simple, on the one hand, or numerous, specific, and complex, on the other." Symons goes on to say that "for all their differences, theories that purport to explain human affairs in terms of *learning*, *socialization*, or *culture*, and so on seem to have one thing in common: they assume that a few generalized brain/mind mechanisms of association or symbol manipulation underpin human action" (p. 139). We suggest that one reason that many social scientists have not learned evolutionary theory is

that they have mistakenly assumed that adaptations are so general as to be of little significance.

Special-Purpose and General-Purpose Adaptations

Defined more precisely than above, adaptations are mechanisms that Darwinian selection "designed" because they provided solutions to environmental problems faced by ancestors (Williams 1966, 1992; Symons 1979; Thornhill 1990, 1997a). Providing these solutions is the "function" of adaptations (Williams 1966).

Although most people consider physical traits to be distinct from psychological (or mental) traits, this is a mistake. The brain, even if one calls it the psyche, is a physiological component of the body. In fact, the brain is the component of physiology and anatomy that controls the rest of physiology and anatomy via environmental information processing. Hence, when evolutionary psychologists speak of evolved "psychological mechanisms," they are actually postulating physiological mechanisms in the nervous system that, at the present stage of scientific knowledge, can only be inferred from patterns of behavior (Palmer 1991, 1992a,b).

Psychological mechanisms can be characterized as either *special-purpose* or *general-purpose* on the basis of the kind of information they process to accomplish their function. Information that is *domain-specific* (for example, that will help an individual acquire a proper diet or a mate with high reproductive potential) is, by definition, special-purpose. If the information processed to accomplish a goal is ecologically general, the mechanism is, by definition, general-purpose. Thus, we can imagine a general-purpose mechanism that evaluates a broad range of items (food items, potential mates, rocks) in terms of their quality.

Hypothetically, adaptations could range from very general to very specific. For example, a mechanism that used the same information to obtain a good diet and a mate with high reproductive potential would not be as general-purpose as a mechanism that used the same information to solve those problems and also the problem of finding safe places to sleep. On the other hand, finding a mate with high reproductive potential might involve a number of even more specific mechanisms. For example, among humans there seem to be separate, specific psychological mechanisms that

have evolved to discriminate health, age-related cues, and parenting ability in a potential mate (Symons 1979, 1995; Thornhill and Møller 1997; Townsend 1998).¹⁰

Hence, what is at question is not whether psychological mechanisms are general-purpose or special-purpose; it is their degree of specificity. Many social scientists believe that humans possess only a few very general psychological mechanisms; evolutionary psychologists posit many very specific mechanisms. This evolutionary perspective is akin to many cognitive scientists' long-standing assumption of the modularity of mind (Gazzaniga 1995).

There are three reasons why evolutionary psychologists argue that the human brain must be composed of many specialized, domain-specific adaptations.

The first is that **the environmental problems our evolutionary ancestors faced were quite specific**. Since adaptations are solutions to these specific environmental problems that impinged on ancestors during evolutionary history, they should be equally specific. Selection should have led to special-purpose adaptations because such adaptations can better solve specialized problems.

Any environmental problem that is typically solved by organisms could be used to illustrate the issue of specificity. Vision, for example, may at first appear to present only the very general problem of viewing one's environment. However, "vision" and "environment" are actually general words for complex phenomena. "Vision" entails solving many specific problems: color, black and white, depth, edges, distance, available light, and so on. Which of these problems an organism solves, and in what manner, will depend on very specific variables in the environment in which the organism's ancestors lived. Hence, the eyes, brains, and nervous systems of various species respond only to certain colors, shapes, and movements, and these vary greatly among species in correspondence to the features of the environments that impinged on the past reproductive success of individuals of the various species. For example, some cells in the European toad's eye "respond most to long, thin objects that move horizontally across the toad's visual field," and this specific design "becomes clear if one imagines how they would respond to a nearby moving worm" (Alcock 1993, pp. 134, 135). Furthermore, an individual animal's environment often is spe-

cific not only to the species but also to the individual's age and sex. Vision stems from many specialized psychological adaptations, each designed to process specific environmental information.¹¹ An eye is a collection of many special-purpose psychological adaptations. Evolutionary psychologists expect the same to be true of an organism's other adaptations.

The second reason why human psychological adaptations are expected to be special-purpose is that **much of successful human behavior depends on environmental circumstances that are variable** (Symons 1987a).¹²

The existence of environmentally dependent behavioral flexibility is often mistakenly used by social scientists to argue *against* the existence of specialized brain structures. "Many writers seem to believe that behavioral flexibility somehow implies the existence of simple, amorphous mental structures," Symons (1987a, p. 127) notes. He continues: "There is a litany in the literature of anthropology that goes something like this: Human beings have no nature because the essence of the human adaptation is plasticity, which makes possible rapid behavioral adjustments to environmental variations. This litany, however, has the matter backwards: Extreme behavioral plasticity implies extreme mental complexity and stability; that is, an elaborate human nature. Behavioral plasticity for its own sake would be worse than useless, random variation suicide. During the course of evolutionary history the more plastic hominid behavior became the more complex the neural machinery must have become to channel this plasticity into adaptive action."

A *facultative* response to the environment (that is, a conditional response that depends on specific environmental variables) evolves when the environment changes within the lifetime of an individual in a way that significantly influences reproductive success. The capacity to learn is one such response. The human social environment is one of change, and the portion of human psychology that is involved with social learning is large. This is probably an evolutionary outcome of selection in the context of changing social conditions within the lifetimes of individuals, coupled with an inability to solve a learning task by experimentation or trial-and-error learning; under this scenario, social learning evolves (Humphrey 1980; Alexander 1989). However, learning will generate *maladaptive* behaviors (behaviors that decrease the reproductive success of the individual) unless special-purpose mental mechanisms guide and bias learning and behavior along paths that are adaptive.

We humans are social strategists par excellence (Wright 1994), and our social behavior is apparently unique in the degree of its plasticity. This unique behavioral plasticity requires not only that human psychology consists of many specialized mechanisms but also that it be much more diverse and complex in structure than the psychology of any other organism.

The third reason that human psychological adaptations are expected to be special-purpose rather than general-purpose is that **our knowledge of the functional design of non-psychological adaptations indicates that they are special-purpose**. The human body, for example, is not a single general-purpose adaptation; it is a bundle of innumerable specific adaptations designed to solve specific challenges to reproduction in past environments. Indeed, those who accept the reality of evolution realize that species-specific non-psychological adaptations are what allow biologists to distinguish species morphologically, physiologically, and developmentally. If adaptations were general-purpose, differences among species (including differences in behavior) would not exist, and thus the discipline of taxonomy (the classification of organisms) would not exist. It is also sex-specific adaptations, psychological and otherwise, that allow researchers to describe sex differences, and it is age-specific adaptations, psychological and otherwise, that make the field of developmental biology possible.

Many social scientists apparently fail to realize that it is species-specific *psychological* adaptations that allow biologists to distinguish species *behaviorally*. Not only is it unreasonable to think that the human psyche will be an exception to the general pattern of specific adaptations; there is increasing evidence from behavioral studies and from neuroscience that the human psyche is composed of adaptations that process specialized information.

In 1989 the cognitive neuroscientist Michael Gazzaniga reviewed the evidence that aspects of human cognition are structurally and functionally organized into discrete units ("modules") that interact to produce mental activity. Gazzaniga summarized his review as follows: ". . . when considering the various observations reported here, it is important to keep in mind the evolutionary history of our species. Over the course of this evolution efficient systems have been selected for handling critical environmental challenges. In this light, it is no wonder there are specialized systems (modules) that are active in carrying out specific and important assignments." (1989, p. 951) As is evident from this summary, Gazzaniga

had been led by empirical evidence to the conclusion that the human psyche is made up of many specialized adaptations.

Of course, to demonstrate the implausibility of the assumption that there are only a few very general psychological adaptations is not to demonstrate the existence of very specialized adaptations. Similarly, the existence of specialized adaptations in the frog brain is not evidence that similar specialized adaptations exist in the human brain. But evidence of specialized adaptations in the human brain is abundant. Symons (1987b, 1992), Cosmides and Tooby (1987, 1989), Barkow et al. (1992), Buss (1994, 1999), Gazzaniga (1995), Pinker (1997), and many others have amassed human behavioral evidence that the specific nature of ecological problems applies to environmental information-processing problems as much as it applies to other related problems, and thus that human psychological mechanisms appear to be domain-specific in function.¹³

Although evolutionists debate the exact degree of specificity of the psychological mechanisms of the human brain (Symons 1987b, 1992; Alexander 1990; Turke 1990), essentially all of them are in agreement that the brain is much more specialized than is implied by a certain class of social scientists. As the evolutionary anthropologist Paul Turke (1990, p. 319) notes, "with the exception of some outdated behaviorists, . . . we all have been working towards understanding the nature of the more or less specific mechanisms that constitute the human psyche."

Biology, Learning, and Ontogeny

Social scientists commonly assert that cultural learning is not biological, evidently because they inaccurately equate "biological" with "genetic." In reality, every aspect of every living thing is, by definition, biological, and everything biological is a result of interaction between genes and environmental factors. Without this understanding, it is not possible to understand how domain-specific adaptations of the human brain develop and how they are involved in learning.

Even an individual cell—the most fundamental building block of any larger organism—is a product of genes *and* certain aspects of the environment (e.g., various chemicals). Certain changes in either the genes or the environment change a cell (and may even end its existence). As an organism continues to develop, genes will create new cells only when they inter-

act with certain additional environmental triggers, and differences in the developmental environment will produce a variety of cells (muscle cells, nerve cells, and so on). This constant intertwining of genetic and environmental factors continues throughout the life of the organism. The environmental factors include not only a multitude of things external to the individual (oxygen, water, nutrients, other individuals, and so on) but also the environment within the developing individual (e.g., other cells, tissues, organs). And these cells, tissues, and organs themselves are products of their own gene-environment interactions.

The interaction of genes and environment in development is too intimate to be separated into "genes" and "environment." Not only is it meaningless to suggest that any trait of an individual is environmentally or genetically "determined"; it is not even valid to talk of a trait as "primarily" genetic or environmental. However, since "biological" actually means "of or pertaining to life," it is quite valid to claim that any phenotypic trait of an organism is biologically, or evolutionarily, determined (Daly and Wilson 1983, chapter 10; Oyama 1985). Genes per se are not evaluated by selection. Instead, it is the interaction of genes and environment that selection evaluates. When a given interaction produces a trait that promotes individual reproduction more than an alternative trait created by a different gene-environment interaction, the genetic underpinning of the reproductively superior trait increases in frequency in the population. When selection acts in a directional manner over a long period of time, gene frequencies change, gene-environment interactions change, and new adaptations spread. Adaptations, then, as Tooby and Cosmides (1990a) and others have emphasized, are manifestations of *evolved* gene-environment interactions. Thus, the environmental and the genetic causes acting during development are not only equally important and inseparable; in addition, they are specific and non-arbitrary. Both the environmental and the genetic causes reflect evolutionary history, and equally so.

Biological or evolutionary determinism is not equivalent to biological inevitability. Indeed, the accretion of scientific knowledge about how traits develop, with equal causal input from genes and from environment, makes it more likely that traits can be altered by changing one or more of their developmental causes.

The degree to which differences between individuals are due to differences in genes—known as *heritability*—is expressed as the proportion of the variation among individuals with regard to a certain trait that is attributable to genetic rather than environmental variation (Falconer 1981). For example, difference between individual humans in height has a heritability index as high as 0.9 in some human populations (Bodmer and Cavalli-Sforza 1976). This means that about 90 percent of the difference in height between individuals is due to genetic differences, and about 10 percent to differences in environment (nutrition, disease, etc.). However, the height of any individual is the result of an inseparable interaction of genes and environmental factors. Hence, height (like all aspects of living things) is “biologically determined,” because it is the product of both genetic and environmental factors.

That heritability is a very different concept than inheritance is evident from the fact that inheritance occurs in the absence of heritability. For example, although two hands are normally inherited from one’s parents, hand number is not a heritable trait—that is, there is essentially no genetic variance underlying hand number. In times past, hand number in humans was under strong selection, and that greatly reduced genetic variation affecting the development of this trait. In other words, the genes that encode for two hands are virtually fixed in humans.

Thus, Michael Crichton’s *Jurassic Park* is truly fictional. Even if someone were to obtain the fossilized DNA of extinct dinosaurs, transferring those genes to an iguana egg would not yield a dinosaur. The genes of a *Tyrannosaurus rex* could express themselves adaptively only in the environment of a *T. rex* egg, then in that of a *T. rex* embryo, fetus, hatchling, and adult—an environment that is as extinct as *T. rex* itself.

Learning

Social scientists often treat learning as a distinctive—indeed, even a non-biological—phenomenon. They also view it as a complete, or an essentially complete, explanation of behavior. In fact, however, learning is only a specific type of gene-environment biological interaction. It is, therefore, one type of proximate cause—to be more specific, one type of developmental cause.

Both learned and non-learned “innate” behaviors are products of gene-environment interactions. Either requires interaction between genes and a vast number of things in the environment. These two types of behaviors are distinguished only by whether or not one specific *identified* aspect of the environment is among the environmental factors that must be present for the behavior to occur.

We call a behavior “learned” when we have identified a specific experiential factor as necessary for its occurrence. For example, it is because we have identified that one must pick up a bow and shoot an arrow several times before one is likely to hit a target that we call archery a learned behavior. Similarly, “innate” behaviors require previous interactions with many specific environmental factors during the development of the organism. The word ‘innate’ only connotes that certain environmental exposures are *not* necessary in order for the behavior to occur. For example, the sucking behavior of newborn infants is often called innate because it doesn’t require the specific previous environmental influence of exposure to a nipple. But this use of ‘innate’ overlooks the fact that the behavior requires the presence of many other environmental factors.

Rather than implying that *no* environmental factors are necessary, “innate” actually implies that specific environmental factors necessary for the behavior to occur have not been identified. Hence, it connotes behaviors and other traits for which *particular* experiences can be ruled out as developmental causes, but not *all* environmental causes. Conversely, “learned” implies only that specific identified environmental factors necessary to the occurrence of the behavior have been identified, not that such environmental factors are sufficient for the behavior to occur.

The modern view of development means that psychological adaptations, including those that affect human sexuality, have been designed by selection during our evolution to process specific, non-arbitrary information in the environment. Such design is the case whether a psychological adaptation requires experiences with environmental stimuli commonly referred to as “learning” or whether it is influenced only by other experiences during ontogeny that do not fit standard definitions of learning (Symons 1979, pp. 17–21). Individuals whose psychological mechanisms did not guide behavior, feelings, development, hormone release, and so on adaptively in human evolutionary history are no one’s evolutionary an-

cestors. Adaptive psychological traits of individuals that increased in frequency during human evolution had one essential property that made them, and not alternative traits, successful in withstanding selection: They helped individuals reproduce successfully in ancestral environments because they contributed to the solution of specific environmental problems.

Perception and processing of arbitrary environmental information by psychological features will lead to psychological changes and behavioral effects that provide ineffective responses to environmental challenges that cause selection. Thus, each psychological adaptation (and each non-psychological adaptation) has evolved because of a precise, specific, *non-arbitrary* relationship between genes and environment. Learning abilities and underlying psychological mechanisms cannot be isolated from genes, adaptation, and our evolutionary past.

Culture

Is the socially learned behavior known as culture still biological and subject to the only general biological theory—evolution by selection? A common justification for rejecting evolutionary explanations of human behavior is that it is not, and that hence it requires an entirely different approach. This view was expressed recently by the feminist biologist Anne Fausto-Sterling (1997, p. 47): “I have found it useful to try to separate discussions of sociobiological approaches to the study of animal behavior from the application of such approaches to human behavior. I do this, not because I believe in a special, non-evolutionary creation for humans. Rather, I think that the evolution of culture has enormously complicated the task of understanding human behavior and development.”

Although culture certainly hasn't simplified the task of understanding human behavior and development, has it really removed some human behaviors from the realm of biology and evolutionary explanation? Are some human behaviors biological and others not? The feminist biologist Victoria Sork (1997, p. 89) refers to “gender differences in human society—some of which are biologically based, and some of which are culturally based.” The confusion here is the same one we pointed out in our discussion of heritability. Yes, some differences in behavior between individuals could be due entirely to cultural influences that have affected

their behavior. But that is very different from saying that an individual's culturally influenced behavior is due entirely to environmental causes and hence is not biological. An individual's cultural behavior is still a product of gene-environment interactions. And the individual can learn nothing without underlying adaptation for learning.

Most social scientists use the word ‘culture’ when referring to socially learned behavior (Flinn 1997). Although culture is often asserted to involve mental states, and sometimes asserted to involve only mental states, we know that we are dealing with culture only when we observe certain kinds of behavior or their consequences. The realization that culture is behavior places it clearly within the realm of biology, and hence within the explanatory realm of natural selection.

That culture is socially learned behavior means only that the causes of the behavior include, not that they are limited to, learning experiences involving other human beings (Steadman and Palmer 1995). Just as some people use the word ‘learned’ to refer to the subset of behavior for which we have identified a specific necessary environmental factor, some use the word ‘cultural’ to refer to the subset of learned behavior for which we have identified that a specific necessary environmental factor is another person.

Speaking a language, for example, is clearly a cultural behavior, because the environmental influences leading to its occurrence *include* social learning. It does not follow, however, that “cultural evolution can facilitate the transmission of behaviors from one generation to the next as well as within a generation without any genetic basis” (Sork 1997, p. 109). Although learning experiences involving members of the same species are necessary for language acquisition, they are far from sufficient for it. Among the other necessary proximate precursors to speaking a language is a set of specialized brain structures forming at particular stages of development that are themselves the ultimate product of a long history of natural selection and the proximate product of complex gene-environment interactions during ontogeny (Pinker 1994). Hence, although language is cultural, it is still just as biological, and just as subject to evolutionary influences, as the human eye.

The parent-offspring resemblance that has typified language, and until a few thousand years ago nearly all other aspects of culture, is typically referred to as *tradition*. Cultural traditions result when both environmental

and genetic influences on the trait are repeated across generations. Specific genes and specific environments interact during development to produce adaptations in young humans that enable them to learn a language from others. Genes are passed in the gametes of parents. Male and female gametes unite to form the zygote. The genes of the developing individual interact with the environment—that is, with everything external to the specific genes being expressed during development: cytoplasm, nourishment, the developing individual itself, other genes. The gene-environment interaction results in nervous-system adaptations that make possible the perception and processing of information. Genetic and environmental influences also construct the emotional and cognitive adaptations¹⁴ of the brain, including those involved in the copying of behavior and the highly specialized mechanisms designed to copy language. If the social learning (copying) involves English in parent and offspring generations, there will be parent-offspring resemblance and the behavior of speaking English can be said to have been inherited.

As evidence that *both* genetic and environmental influences must be transmitted in order for language to be inherited, consider what factors eliminate the inheritance of language. Suppose that a young child of English-speaking parents is adopted and then raised in an environment in which only French is spoken. In this case, the speaking of English is not inherited, because the language spoken in the environment during certain stages of development was not repeated in the environment of the offspring. Now suppose that a child raised by its parents in an environment in which only English is spoken does not learn English despite the opportunity. In the latter case, the child may have received genes not expressed in the parents (recessive genes)—for example, the child may be deaf as a result of such genes.

When inheritance is properly considered as a phenotypic phenomenon caused by both genetic and environmental causes, there can be no confusion about how cultural behavior is inherited.¹⁵ There is no fundamental difference in the mechanisms of inheritance of cultural and non-cultural behavior, nor is there a difference between the mechanisms of inheritance of cultural behavior and the mechanisms of inheritance of physiology and morphology. Inheritance occurs—like begets like, traits breed true—when

and only when both genetic and environmental influences are repeated between generations.

This approach provides an answer to the question about the relationship between culture and biology that has dominated much of the history of social science (Freeman 1983; Brown 1991). Claims that cultural inheritance is independent of biological inheritance, whether made by non-evolutionary social scientists or by evolutionary biologists (Dawkins 1976; Boyd and Richerson 1978, 1985; Pulliam and Dunford 1980), are erroneous. Culture is not the “superorganic” force that some social scientists have claimed it to be. Nor, as the philosopher Daniel Dennett (1995) has pointed out, does culture consist of ideas (also called *memes*) that parasitize minds independent of psychological (biological) adaptation, as certain biologists have claimed. Such claims are simply inconsistent with modern knowledge of how inheritance and development work.

Gregor Mendel discovered the role of genes in inheritance, but of course he did not discover inheritance itself. That like begets like was known long before Mendel. Parent-offspring resemblance in socially learned behavior requires psychological mechanisms—mechanisms that are produced by gene-environment interaction during development. Innate behavior, learned behavior, and cultural behavior are all products of brains. Brains are products of gene-environment interactions. Gene-environment interactions are subject to natural selection.¹⁶

However, a given cultural behavior cannot be automatically assumed to increase current reproductive success, nor can it be assumed to have been designed by natural selection (even though our *capacity* for culture clearly was). Cultural behavior, like all behavior, should be expected to show evidence of adaptation, and thus direct selection for the behavior, only to the extent that both the genetic and the environmental influences on that behavior have been replicated across generations for the long periods of time needed for effective selection. Since we use the word ‘tradition’ to refer to such enduring cultural behavior, it is to the extent that cultural behavior is traditional that it is expected to show evidence of selectionist design.

The greater the number of generations in which a cultural behavior has been replicated, the greater is the probability of evidence of design. At one extreme are certain cultural behaviors, such as an individual’s adoption of

a new hairstyle, that show no evidence of design by natural selection. Although a hairstyle is a by-product of numerous underlying psychological adaptations (perhaps concerning status, mate preferences, and/or visual acuity), a particular new hairstyle in itself cannot be considered an adaptation. At the other extreme are cultural behaviors that may have been copied for hundreds or even thousands of generations, thus implying the replication of both the genes involved and the environmental influence of the behavior of other individuals in each generation. In addition to language, such extremely traditional cultural behaviors include aspects of child care (feeding and caring), systems of kinship identification (kin terms, descent names, clan markings), techniques for manufacturing stone tools, hunting strategies, religious rituals, mating practices, and systems of punishment.

Although there is much variation in traditions, the universal presence of kin terms, religious rituals, and languages (Brown 1991; Steadman and Palmer 1995; Steadman et al. 1996) suggests the role of species-typical adaptations in all these behaviors. Thus, although culture can change much faster than adaptations (as a result of changes in the environmental factors that contribute to the cultural behavior), cultural traditions and their underlying psychological mechanisms also show obvious signs of adaptation. For example, a multitude of new words may enter a language during a short period of time, while language itself remains a highly adaptive, evolved vehicle for communication.

Like any aspect of phenotype, any cultural behavior—whether designed by natural selection or merely a by-product of other adaptations—may be currently non-adaptive, and even maladaptive, as a result of environmental influences that are novel with respect to the historical environments in which the mechanisms responsible for the cultural behavior evolved. Just as some of the pronghorn antelope's social behaviors are not currently adaptive but are adaptations to extinct predators, many human adaptations, both behavioral and physiological, are not currently adaptive.

Even when cultural change and adaptation do not coincide, applying evolutionary principles to human behavior is still valid. Human psychological mechanisms of social learning are still the products of a long history of selection, and they still affect the cultural behavior of individuals—even when they produce novel, non-traditional cultural be-

havior. The cultural behavior of individuals is *never* independent of the human evolutionary history of selection for individual reproductive success.

Consciousness

Although there is considerable debate over the exact function of consciousness, and some debate over whether it is an adaptation or a by-product, there is no scientific reason for assuming that consciousness is anything other than an aspect of our evolved biology.

One hypothesis, proposed by the evolutionary psychologist Nicholas Humphrey (1980) and by the biologist Richard Alexander (1989), is that conscious awareness permits quick adaptive adjustments of social striving based on the perception of how well one is doing in social competition. The *consciousness adaptation* stores information on how others view one and helps one build and evaluate alternative scenarios that may promote one's success in the social arena. Humphrey and Alexander suggest that the most important aspect of the design of consciousness may be its usefulness for solving social problems that resemble, but differ slightly from, the social problems that were consistently faced in ancestral environments. Such new social problems are often evolutionarily unique combinations of the non-unique social variables that have been repeatedly encountered in human evolutionary history. For example, having to compete with other individuals of a certain age and sex for a resource such as mates is a task that was faced innumerable times by our ancestors, but the exact combination of the sexual variables we face on any given day may be unique. If consciousness is the result of our evolutionary history, it is almost certainly composed of special-purpose mechanisms for information processing (Alexander 1989, 1990; Turke 1990) that aid in solving problems composed of evolutionarily unique combinations of variables.

As an illustration of how consciousness processes information, consider an argument between two academics: A, who understands evolutionary biology, and B, who doesn't. Assume that each wants to win the argument. Suppose A is being interviewed by B for a job in a traditional social science department. Suppose that during the interview B argues that, because human behavior is cultural, it is independent of biology (and, therefore, A should not be hired). Knowing that many people erroneously equate biol-

ogy with genetics, A launches into a long speech about gene-environment interactions, ontogeny, and psychological adaptations and looks for signs of comprehension from B—nods, affirmative grunts, perhaps even a smile. When no such responses are forthcoming, the now-perspiring A consciously searches her memory for statements that have produced signs of understanding in the past and hence may do so again. Detailed descriptions of the visual systems of frogs and references to the statistics on child abuse by stepparents spill forth. At one point, A even attempts to draw on a napkin a diagram illustrating an optical illusion that involves the edges of black squares. (See note 13.)

The point we wish to make is that this particular line of disagreement was not a part of the environment of human evolutionary history. It is evolutionarily novel. In this case, however, both individuals process *specific* information in their social-striving mechanisms. Each uses specific information about how the other has responded to his or her comments to decide on the next line of argument to use. Furthermore, they both use specific psychological procedures to construct specific arguments that relate this feedback to information that they learned in the course of their training in their respective fields. In this way, consciousness adaptations generate many kinds of secondary mechanisms or procedures that are used in social striving. Those mechanisms or procedures involve specific information—for example, that B sees “biological” and “cultural” as alternatives, but A doesn’t. Furthermore, both participants process some of the same specific information. Their consciousness adaptations can be viewed as rules of conscious striving—and here “rules” means *specified procedures*, which implies special-purpose mechanisms. For example, the willingness of each individual to engage in and continue in the argument will depend on the perceived benefit to each party. This aspect alone, however, requires the processing of detailed, specific information, which typically differs considerably between individuals. This example illustrates that the psychological phenomena surrounding consciousness can be viewed as depending on specific information, and therefore as based on special-purpose mechanisms.

2

The Evolution of Sex Differences

Harbor seals are monogamous, and the males and the females are nearly equal in size. In contrast, male elephant seals are much heavier and longer than females, and a male elephant seal may inseminate as many as 100 females. Furthermore, the pronounced differences between the brains of male and female elephant seals produce vastly different sex-specific behavior patterns throughout their lives. For example, there are male-female differences in diet and in migration patterns. Perhaps the most striking sex-specific behavior among elephant seals, though, is the violent physical confrontations between males during the mating season.

The male-female differences in the brains, other body parts, and behavior of elephant seals are attributable to the simple fact that males and females in ancestral populations faced very different obstacles to reproduction. Hence, over thousands of generations, Darwinian selection favored different adaptations in males and females.

To understand why selection produced such different male-female adaptations in elephant seals but lesser differences between the adaptations of male and female harbor seals requires an understanding of what Darwin called sexual selection: the selection of traits that increase the quantity and/or the quality of an individual’s mates rather than increasing the individual’s ability to survive. Not incidentally, an understanding of sexual selection is also necessary to an understanding of the differences between the adaptations of male and female humans, and thus to a complete understanding of rape.

all else being equal, the more a woman's reproductive success would have contributed to the genetic success of her mate or her relatives in evolutionary history, the greater the suffering of those individuals is likely to be after she is raped.

In an evolutionarily informed post-rape counseling and treatment program for victims and their significant others, the counselors would understand the proximate causes of the psychological pain and would direct the victims and their significant others to the sources of that pain. Psychotropic medications might be employed (selectively and cautiously, so as not to eliminate the defense that psychological pain provides). The victim's age, the change in her value to her mate and her family, the credibility of her rape report, and the paternity concerns of her mate would be taken into account. By acknowledging what is unique about the psychological pain surrounding rape and by addressing the anticipated magnitude of the pain, the evolutionary approach can focus therapy where it is most needed. Finally, such a program would inform the victim about cues that may increase the probability of rape, thus helping her avoid being raped again.

Whether evolutionarily informed therapy programs would alleviate the psychological pain generated by rape is an empirical question, as is who might benefit most from such programs. We hope, nonetheless, that such programs will be forthcoming. A therapy program that maintains that men rape because they collectively want to dominate women will not help a victim to understand why her attacker appeared to be sexually motivated, why her husband or boyfriend may view the attack as an instance of infidelity, why she can no longer concentrate enough to conduct her routine life effectively, or why her father wants to keep the attack secret. Programs based on ignorance of what is creating the victim's post-rape problems seem as useless as those based on the Freudian psychodynamic theory of rape.

We have mentioned the Freudian proposal that women desire to be raped. In addition, Freudian theory proposes that young human males wish to copulate with their mothers, and that, when this desire is unresolved, it produces sexual deviance in male adulthood, female rape victims being substituted for the mother (Freud 1933).¹ Evolutionarily informed people realize that pursuit of rape by women and incestuous psychology in men such as Freud posited cannot possibly have evolved. Those trying to help rape victims and their significant others need to have reality on their side.

12

Conclusion

The reason why the friend we mentioned in chapter 1 asked us about the causes of rape was that she was suffering. She hoped that our answer to her question would reduce her pain, would help her to avoid a recurrence of the event that caused the pain, and would help to prevent others from experiencing similar pain. The answers she had been given previously—that sex had been irrelevant to the act, that the man had been motivated by desires to control and dominate her, that a patriarchal culture had given the man these desires through childhood socialization, that rape was a means by which all men controlled the lives of all women in order to maintain the patriarchal culture, and that her appearance was not a factor in her chances of being raped again—were based on the social science explanation, and they seemed to fail to account for several things. Why, if he had not been sexually motivated, had the man used tender compliments in his attempts to initiate sexual acts throughout the evening? Why, after the rape, had he apologized for having resorted to physical restraint and to threats of further force? Why, if her appearance was not relevant to her chances of being raped again, was she now reluctant to dress as attractively as she had in the past?

The choice between the social science explanation's answers and the evolutionarily informed answers provided in this book is essentially a choice between ideology and knowledge. An evolutionary approach to rape provides the following answers to the questions we posed in the first chapter.

Why are males the rapists and females (usually) the victims?

This question can be answered at each of the two complementary levels of causation in biology: the ultimate and the proximate. We will begin

with the ultimate, which is the more general and encompassing level of causation.

Males and females, both juvenile and adult, faced many sex-specific obstacles to reproductive success during human evolutionary history. As a result, selection favored different adaptations in the two sexes. Sexual selection—the primary kind of selection that explains the sex differences that lead to rape—is the differential reproductive success of individuals due to their trait differences that affect mating success (measured by mates' survival, parental investment, and reproductive capacity, and, in males, also by number of mates and by successful fertilization of eggs in competition with the sperm of other males). Sexual selection's action on each sex is governed by the relative parental investment of the sexes. Parental investment consists of the parental materials and services that determine the number and the survival of offspring; thus, it is the commodity for which each sex competes in the competition for mates. In humans, the parental investments of the two sexes may sometimes be nearly equal; however, the minimum parental investment for offspring production by a male is trivial: a few minutes of mating and the small amount of energy needed to place an ejaculate in a female's reproductive tract. The female must invest all the time and energy required for gestation, birth, and lactation.

The sex difference in the minimum parental investment is the key to understanding the sex-specific historical selection that gave rise to rape. Given the small investment of males and thus the low cost of each male mating, sexual selection favored males who achieved high mate number. As a result, men show greater interest than women in variety of sex partners and in casual sex without investment or commitment. Selection on females favored careful mate choice that allowed them to expend their precious parental investment under the circumstances most conducive to the production of viable offspring. Female adaptations for mate selection fall into two categories: (1) preference for males with status and resources, which evolved because such males provided material benefits to females and their offspring, and (2) preferences for males with physical markers in behavior and body of genetic benefits, which evolved because they increased the survival chances of a female's offspring.

Human rape arises from men's evolved machinery for obtaining a high number of mates in an environment where females choose mates. If men

pursued mating only within committed relationships, or if women did not discriminate among potential mates, there would be no rape. The two leading evolutionary hypotheses for the existence of human rape behavior are (1) that rape is an incidental effect (a by-product) of men's adaptation for pursuit of casual sex with multiple partners and (2) that rape is an adaptation in and of itself. According to the first hypothesis, rape was indirectly sexually selected. According to the second, rape was directly selected because rape itself promoted success in competition for mates. Mutation-selection balance, drift, and other ultimate causes other than selection are not consistent with the data on rape's common occurrence and its high cost to rapists. Data also disconfirm general explanations of rape that are based solely on evolutionarily novel environments.

Ultimate explanations pertain to evolutionary agents that account for the existence of biological traits. Distinguishing the two leading ultimate hypotheses for rape empirically would require additional research along the lines discussed in chapter 3. Existing data do not allow a strong conclusion one way or another. It is entirely clear, however, that rape is centered in men's evolved *sexuality*.

The proximate causes of rape include genes, environmental cues, ontogeny, learning, physiology, and psychological and behavioral responses to environmental stimuli. The importance of evolutionary theory for reducing rape lies in its ability to identify likely proximate causes, which may enable individuals to eliminate the immediate factors that bring about rape. Therefore, we have emphasized the importance of identifying the developmental cues that construct the adaptation responsible for rape as well as the cues that activate this adaptation after its ontogenetic construction.

Why is rape a horrendous experience for the victim?

Mate choice was a fundamental means of reproductive success for females in human evolutionary history. Thus, rapists' circumvention of mate choice has had extremely negative consequences for female reproductive success throughout human evolutionary history. The psychological pain that rape victims experience appears to be an evolved defense against rape. The pain focuses the victim on the rape and on the negative changes it has brought about in her life, thus helping her to solve current problems (e.g.,

her mate's divestment and suspicions) and to avoid being raped again. Women also appear to have psychological adaptations other than mental pain that also defend against rape, such as avoiding contexts with elevated risk of rape when at the point of maximum fertility in the menstrual cycle.

The females who outreproduced others and thus became our ancestors were individuals who were highly distressed by rape.

Why does the mental trauma of rape vary with the victim's age and marital status?

From biological (evolutionary) theory, we can predict that the negative reproductive consequences faced by rape victims in evolutionary history depended on their age and on their pair-bond status. Since only reproductive-age females can get pregnant from rape, females of reproductive age and those with investing mates are predicted to have experienced the greatest negative consequences. Males of species in which males engage in parental effort have been selected to invest in their own offspring because cuckoldry was, in human evolutionary history, a persistent problem that lowered or eliminated a male's offspring production. A female with an investing mate faced the prospect of losing some or all of the mate's investment as a result of his concern about rape's effect on his paternity. Research shows that females of reproductive age and married women indeed exhibit more psychological pain after rape than other females. That mental pain is a variable response rather than an invariant one is predicted on the ground that mental pain historically entailed costs to reproductive success (such as distraction from other important life events) as well as reproductive benefits.

Why does the mental trauma of rape vary with the sex acts?

The epitome of circumvention of female mate choice is insemination by an unwanted mate. If such insemination results in pregnancy, it leads the female to expend her limited parental investment in a maladaptive manner. Research indicates that rapes that include copulation give rise to more psychological pain in female victims than non-copulatory sexual assaults. This pattern is driven by the greater pain of reproductive-age females, who during human evolutionary history had the most to lose (in terms of lowered reproductive success) from insemination by rapists.

Why does the mental trauma of rape decrease as physical injuries increase?

The answer to this question is related to men's evolved desire to invest in offspring they have sired rather than in offspring born to their mates but sired by other men. A rape is less threatening to a man's paternity than a consensual affair. That a partner has indeed been raped is less ambiguous if there are visible signs that she resisted. Thus, evolutionary theory predicts that raped women with visible signs of having resisted will experience less post-rape mental anguish, and indeed this is a strong pattern in women's response to rape trauma.¹

Why do young males rape more often than older males?

Sexual selection on males for mate number has endowed boys and men with a much greater risk proneness than is seen in human females. The risk proneness of male humans peaks in young adulthood (Wilson and Daly 1985). So does that of females, but they are much less risk prone than males (Campbell 1995). Both peaks stem from sexual selection's favoring maximal risk taking when the competition for entering the breeding population is most intense: at the onset of adulthood. Males have been strongly sexually selected to pursue resources and climb the social ladder at this stage because success in these pursuits positively affected male reproductive success in human evolutionary history (Alexander 1979; Weisfeld 1994). That men's sexual interest and impulsiveness peak early in adulthood is also due to past sexual selection. The combination of the two peaks—that of risk taking and that of sexual desire—accounts for the fact that young men rape more.

Why are young women more often the victims of rape than older women or girls?

Fertility is strongly related to age in women but not in men. In Western countries, menarche usually occurs between the ages of 10 and 13 (Barber 1998). Women's fertility declines markedly after age 30 and drops to zero at menopause. Men's fertility begins at puberty and remains high into the fifties or even later, with no abrupt cessation

comparable to menopause. The sex difference in fertility schedules gives women a narrow window of opportunity for offspring production. This had tremendous evolutionary consequences in humans, and it led to selection on males for preferring young women as mates. This preference is manifested in men's pursuit of consensual and non-consensual sex. Young women are the focus of men's sexual interest, whether the context is prostitution, pornography, marriage, romantic affairs, or rape. Men's focus on visual indicators of youth is due to the fact that a female's mate value is largely manifested in her bodily signals of fertility. A male's mate value, in contrast, is spread across bodily features, resources, and status.

Why is rape more frequent in some situations, such as war, than in others?

Humans (including rapists), like all animals, pay attention to costs and benefits when making decisions. Rape by conquering soldiers is common because the benefits are high (many young women are available) and because the costs are low (the women are vulnerable; the rapists are anonymous and relatively free from sanctions against rape). Cost-benefit considerations also go part of the way toward explaining why modern societies have relatively high rape rates. In such societies, young women rarely are chaperoned and often encounter social circumstances that make them vulnerable to rape. Moreover, anonymity is more prevalent, and the sanctions against rape are less effective deterrents, in modern societies than in traditional human environments, where individuals are more likely to be known to others.

Why does rape occur in all known cultures?

The capacity to rape is attributable ultimately to selection and proximately to ontogeny and adaptation. Rape behavior arises from elements of men's sexual nature—their sexual psychology. This psychology is characteristic of men in general, but not of pre-pubescent boys. It is reliably generated during development across a wide range of rearing environments.

Why are some instances of rape punished in all known cultures?

Rape within the rapist's own social group (known as *in-group* rape and usually defined by kinship in traditional societies) is punished across human societies because it has negative consequences for the reproductive success of all whose reproductive interests overlap with those of the victim, including her relatives, her mate, and her mate's relatives. Sanctions against in-group rape take the form of codified rules (law) and unwritten rules that protect the interests of those who make and enforce them. The rules and other forms of teaching are directed at controlling men's sexual desires.

Why are people (especially husbands) often suspicious of the victim's claim to have been raped?

The husband of the victim is looking for evidence of an unambiguous rape that the woman tried to avoid to the best of her ability—an act that is less threatening to his paternity than either a consensual affair or a rape that the woman did not resist strongly. In his suspicions, the husband is unconsciously assessing the cost of the rape to him and whether he should desert the mate or continue to invest in her and her offspring. Significant social allies of the victim other than her husband are also gaining information about the rape's impact on their reproductive interests through their suspicions. On theoretical grounds, they are expected to adjust their investment in the victim according to the same criteria that her husband uses.

Intuition that some women use false accusations, gossip, rumor, and ostracism of others to obtain resources and other social benefits may also play a part in suspicion toward claims of rape. Indeed, women do use these tactics more than men. Men rely more on direct forms of competition, such as intimidation and aggression. Humans are socially astute because of past selection for analysis of social behavior, which contains many predictive elements that are also products of past selection.

Why is rape often treated as a crime against the victim's husband?

Men are selected to control the sexual behavior of their mates and of their sisters and daughters. Control of mates serves the purpose of protecting

paternity; control of female relatives is intended to make them more attractive to discriminating men with resources. Because in human evolutionary history only males could be cuckolded, a female's mate value depended greatly on how much paternity reliability she could provide. Rape of a woman, therefore, is viewed as a cost to the men whose reproductive interests she is expected to serve.

Why have attempts to reform rape laws met with only limited success?

To date, attempts to reform rape laws have not taken into account various evolved human intuitions about human behavior. This is true of all aspects of the reform movement, including expanding the definition of rape, eliminating the requirements that rape be corroborated by other persons and that proof of the victim's resistance be provided, and disallowing consideration of the victim's sexual history.

Humans are selected to define rape in a specific way because, as discussed just above, the events involved in the sexual act affect the woman's value to her male and female social allies. Much the same is true of rape corroboration, victim resistance, and victim sexual history. Furthermore, intuition about women's use of sexual allegations for self-gain may tend to block reform of the laws.

Why does rape exist in many, but not all, other species?

The vast majority of species show the same sex differences in sexuality that humans show: relative to females, males are more eager to mate, show less discrimination about mating partners, and pursue sexual variety without commitment. Females, on the other hand, are very choosy about mates. All these species have an evolutionary history of a high degree of polygyny. A very small percentage of species practice monogamy, but even in these species the stronger sexual selection for high mate number (attributable to the trivial minimum investment by males) creates virtually the same male sexual features seen in highly polygynous species, with "monogamous" males seeking extra-pair copulation. (A fraction of species show sex-role reversal, the males choosing mates and the females competing for multiple mates. Sex-role reversal arises out of the rare cir-

cumstance in which males contribute more parental investment than do females.)

Although males of essentially all species exhibit sexual psychological adaptations for obtaining a high number of mates, rape is not universal across animal species. It is, however, common. Most of the attempts to theorize about the ecological variation that creates selection for rape are very recent. Recent research by biologists examining selection for and against rape focuses on ecological factors that affect rape's benefits and costs, such as whether or not females are distributed spatially in ways that make them vulnerable to males (for example, whether they form female-female social alliances against coercive males, and whether they live within range of protective relatives). Also, how well adapted females are against rape in the coevolutionary race with rapist males appears to be relevant to the selection on males to rape. Another factor is the cost of rape to females and to rapist males when the degree of force used lowers female survival (Clutton-Brock and Parker 1995).

Some of the same factors that select for or against rape across species may be relevant to the conditional use of rape by men across human societies (Smuts and Smuts 1993). Protection of women by family members and husbands may be especially important in inhibiting rape; structural barriers such as chaperoning may also help.

Why does rape still occur among humans?

In chapter 1 we suggested two reasons for why it has not yet proved possible to eliminate rape: First, social scientists and people in general have such a limited understanding of ultimate causation that they fail to see how evolutionary theory can contribute to an understanding of rape's proximate causes. Dawkins (1986), Alexander (1987) and Pinker (1997) have discussed some possible reasons for this difficulty, including ideological biases and the fact that thinking about ultimate causation requires us to envision vast stretches of historical time when we are designed only to understand short-term causal factors. We have emphasized the role of ideological bias, but certainly there is reason to think that other factors often play important roles. Second, most attempts to eliminate rape have been based on the social science explanation, which is fundamentally ideologi-

cal rather than empirical and which hence contains many fundamental inaccuracies.

Biologists are in a position to inform others about how evolution applies to humans. Biologists have deep understanding of ontogeny and of the theory of evolution, both of which deny the dichotomies for traits of individuals (e.g., learned vs. genetic) that have misled and misguided social scientists' research on rape. In addition, the existence of rape across many animal species is one of the many evidentiary blows biology has dealt to the social science explanation, which insists that rape is not natural, not evolved, not biological, uniquely human, and attributable to "culture" (a non-biological entity that works its magic through children's arbitrary socialization). The existence of the same differences between the sexes in humans and in most other animals is another blow to the notion that rape is just about cultural causation, since relatively few of the non-human species have any socialization of offspring at all, much less sex-differentiated socialization.

Recently some social scientists have asserted that the entire "animal literature" does not count. Polaschek et al. (1997, p. 128) suggest that this literature is "seriously flawed in both what is observed and the interpretations made" and that it reveals "a male-centered view." Polaschek et al. cite Gowaty's 1992 paper "Evolutionary biology and feminism" as supporting their claim. In a few sentences they discount all evidence for rape in non-human species and dismiss all the data on the evolution of sexual differences²—findings that, in fact, are clearly relevant to an understanding of human behavior, as we have explained. Polaschek et al. go on to criticize the evolutionary view of rape on the ground that men's strong desire for partner number is cultural rather than biological. This too reflects a fundamental misunderstanding of the fact that culture is biology. We would not be surprised to hear social scientists suggest, next, that insects, other arthropods, other invertebrates, and most vertebrates are somehow being influenced during development by music videos, television, and movies.

How can rape be prevented?

Among the important implications of the biological understanding of rape is that programs meant to educate people about rape should be revised so as to stop spreading the notion that rape is not sex but violence. Both

young men and young women should be taught about male and female sexuality (particularly male sexuality) and about risk factors for rape. Men should be informed of the penalties for rape. Structural barriers to rape should be considered, and efforts to change evolved biases about rape accusations should be considered. Finally, changes in the law with regard to rape and related matters should be based on scientific knowledge.

Though we have not advocated specific methods of punishing rapists, we have stressed the value of punishment for changing human behavior, keeping in mind that some claims of rape are false and that false conviction is possible. Voters must decide what is a suitable punishment for rape. Science has nothing to say about what is right or wrong in the ethical sense. Biology provides understanding, not justification, of human behavior. Biological knowledge is useful to a democratic society to the extent that it can be used to achieve goals that people decide are appropriate. These goals are typically based on ideological considerations. Whereas many ideological issues (e.g., abortion, conservation, taxation) involve a great deal of disagreement, it is safe to say that the vast majority of people are against rape. This being the case, it is our hope that concerned people will begin making use of the knowledge that evolutionary biology provides in order to reduce the incidence of rape and to better deal with this horrendous crime's effects on its victims and their significant others.