The Role of Evolved Predispositions in Cultural Evolution

Or, Human Sociobiology Meets Pascal's Wager

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Much human behavior affected by culturally transmitted ideas—e.g., religious sentiments—does not appear to make adaptive sense. Whether sound sociobiological explanations can or cannot be given to such behavior is at the heart of debates between human sociobiologists and their critics. We argue that the debate has been miscast as a clash between mutually exclusive hypotheses, when in theory and probably in fact there are many cases that mix elements of both. When culture, using Darwinian methods, is modeled as a system of inheritance that coevolves with genes, it exhibits both adaptive properties and a series processes that give rise to maladaptive variation.

On the one hand, there is every reason to expect that cultural evolution is substantially shaped by evolved, genetically transmitted predispositions and that these predispositions often result in highly adaptive behavior. However, some kinds of beliefs are weakly affected by evolved predispositions and can have strong effects on behavior. For example, religious sentiments are carefully constructed to be difficult to challenge on the basis of empirical experience. Beliefs in rewards or punishments in an afterlife can substantially affect the behavior of people with quite utilitarian evolved goals. Once beliefs arise that are difficult to judge using evolved predispositions, processes such as group selection on cultural variation can be relatively strong. Patterns of behavior that could not be predicted without taking account of the evolutionary properties of culture can arise as a result of such "nonsociobiological" forces.

Four coevolutionary scenarios capture much of the rich behavior that is possible when genetic and cultural evolution interact: 1) Culture may be kept on a "leash" by evolved predispositions, as classical sociobiological arguments would have it; 2) the tables may be turned, and genes may be leashed by the evolution of cultural norms that affect mate choice (we present a simple model of this process); 3) harmful cultural elements with an ability to attract imitators may arise, leading to a host–pathogen type of coevolution between genes and culture; and 4) genes and culture may evolve like a system of obligate mutualists. We speculate that the last scenario is the most generally important, but that the others are common.

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We view the application of population genetical methodology to cultural evolution as a friendly amendment to human sociobiology, but one that is essential to a complete Darwinian theory of human behavior.

KEY WORDS: Cultural Evolution; Darwinian methods; Human sociobiology; Pascal; Religion.

> "Either God is or he is not." But to which view should we be inclined? Reason cannot decide this question. Infinite chaos separates us. At the far end of this infinite distance a coin is being spun which will come down heads or tails. How will you wager?
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> . . . Let us weigh up the gain and loss involved in calling heads that God exists. Let us assess the two cases: . . . [T]here is an infinity of infinitely happy life to be won, one chance of winning against a finite number of chances of loss, and what you are staking is finite. That leaves no choice; wherever there is infinity, and where there are not infinite chance of losing against that of winning, there is no room for hesitation, you must give everything.
>
> —Blaise Pascal

In fragment 418 of his *Pensees*, "The Wager," Pascal argues that rational people should choose to believe in God, even when they are unsure of whether he exists. The argument is presented in the form of Pascal's half of a dialog between himself and a rational skeptic. Pascal begins by agreeing with the skeptic that there is no rational way to determine whether God actually does or does not exist. As he puts it, "Reason cannot make you choose either, reason cannot prove either wrong." Nonetheless, he urges the skeptic, you must decide one way or the other, because you must live your life, and in doing so you must choose whether or not to behave as a Christian. Pascal then totes up the gains and losses that will result from each choice. By choosing belief, he argues, you are trading a certain but finite loss—the pleasures of the flesh during life—for the chance of infinite gain: eternal happiness. "There is no choice" Pascal urges the skeptic, ". . . wager that He does exist." While the importance of this reasoning in Pascal's midlife decision to commit himself totally to Christianity is unclear,[1] the fame and longevity of Pascal's wager testify to its appeal to others.

[1] Pascal was a practicing Christian all of his life. He was raised in a bourgeois family with conventional religious beliefs, and then as a young man, Pascal was converted to Jansenism, a Catholic sect that stressed personal faith. At the same time, however, he was a central figure in the secular life of his time. He performed physical experiments aimed at detecting the properties of gasses; he developed the first mechanical calculator, and, with Fermat, discovered the basic laws of mathematical probability. Pascal was also involved in a wealthy, sophisticated social circle, in which people valued wit, good manners, and style, and little emphasis was placed on religious values. According to one biographer (Davidson 1983), during the early 1650s, Pascal began to feel an intense conflict between his attraction to science and social intercourse and his religious belief. In 1654, he abruptly abandoned this secular life style and shortly thereafter underwent the intense conversion experience vividly described in his "Memorial." For the most part, he devoted the remainder of his life to an unsuccessful anonymous defense of Jansenism against attacks by church authorities and to charitable work amongst the poor. It is easy to imagine that the reasoning outlined in the "Wager" was important in Pascal's decision to abandon the secular social and intellectual life that he led in Paris, but there is no real evidence that this is the case.

That humans often reason and act in accord with sentiments inspired by religion and similar systems of thought is at the crux of debates about the applicability of Darwinian theory to human behavior. Much of the behavior that results from religious belief seems, on first inspection, to make little evolutionary sense. For example, in his early 30s and at the height of his scientific success, Pascal abandoned the social and intellectual life of the salons of Paris and devoted his remaining years to work among the poor and to the anonymous defense of Jansenism, an embattled doctrine favored at the Port Royal Monastery, with which he was closely associated. Neither the motivation for his acts nor their outcome seem to make sense in evolutionary terms. There are obviously many similar examples, of which the existence of celibate priesthoods is perhaps the most extreme. A number of authors have argued (e.g., Sahlins 1976) that the importance of such systems of thought falsifies the hypothesis that human behavior can be understood in terms of evolutionary theory. Because people are able to invent symbolic culture, it is argued, a non-Darwinian theory is necessary. On the other hand, a number of authors have argued that the evidence suggests that behavior inspired by religious belief can be interpreted as consistent with a Darwinian theory of behavior. For example, Boone (1983) has argued that Medieval crusading can be understood as resulting from the reduced reproductive opportunity of second sons, and Alexander (1979, p. 158) has advanced a similar explanation for celibate priesthoods. Because the patterns of variation in behavior are consistent with the adaptive interest of individuals, these authors argue, there is no need to invoke non-Darwinian explanations.

In this essay, we argue that it is not sensible to regard "sociobiological" and "cultural" explanations of human behavior as mutually exclusive hypotheses. It is likely that people acquire cultural beliefs that lead them to behave in ways that could not be predicted on the basis of ordinary Darwinian theory, and at the same time a great deal of the variation in these same behaviors can be understood in Darwinian terms. A satisfactory evolutionary account of human behavior requires first teasing apart the processes by which culture and genes affect behavior, and then understanding how they interact in the time scales of individual decisions, cultural evolution, and genetic evolution to produce the patterns of human behavior we observe.

The basic elements of our argument are as follows:

Cultural variation is shaped by evolved psychological predispositions. Along with most sociobiologists, we believe that human choices, including choices among alternative beliefs and values are shaped by evolved goals. People strive to avoid hunger, attain sexual gratification, achieve control over others, and so on. We assume that such predispositions affect people's decisions to adopt particular beliefs and that culture is shaped by these predispositions in such a way that much cultural variation can be understood as a indirect product of Darwinian processes, especially natural selection.

Because the spread of some kinds of beliefs is weakly affected by

evolved predispositions, other processes may be important in cultural evolution. Unlike most sociobiologists, we think that the spread of many kinds of beliefs cannot be strongly influenced by evolved predispositions because it is difficult or impossible for individuals to determine which of many alternatives best serve the evolved goals, even when alternative beliefs differ markedly in this respect. We argue below that religious beliefs are good examples. Therefore, such beliefs may evolve under the influence of a variety of other kinds of processes that frequently lead to the spread of beliefs that could not be predicted on the basis of ordinary Darwinian theory. For example, it is plausible that religious beliefs may spread because they enhance the stability of groups.

Religious faith and similar beliefs can affect behavior even if it is assumed that people strive to satisfy evolved goals. First, individuals with different beliefs about the world may make different choices even if they have the same goals. Suppose that all people were purely selfish and valued only personal satisfaction. Nonetheless, selfish individuals who believe in an omniscient God who punishes sinners would be more likely to behave morally than those who think they need only avoid human detection. Second, the behavior of individuals who hold such beliefs may affect the decisions of others who do not. For example, people with religious beliefs often exercise sanctions and confer rewards on others; a private atheist may choose the priesthood and preach the faith because of the prestige and wealth conferred on priests by the devout.

If the cultural environment is taken as given, much behavioral variation may still be explained in ordinary Darwinian terms. Because behavior results from the interaction of culturally acquired beliefs and the attempt to satisfy evolved goals, we expect that much behavioral variation can be explained in terms of evolved goals. If, for example, first sons have more to lose by joining the Crusades than do second sons, then second sons will be more likely to choose to join even if eldest sons' beliefs in Christianity are equally fervent.

Over the long run of hominid evolution, cultural variation must have influenced what predispositions evolved. Humans are a species highly specialized in the use of culture—or social learning, to use the psychologist's term—as a means of acquiring adaptive information. Much of our psychological structure must have evolved in response to the oppportunities and constraints imposed by the peculiarities of the cultural inheritance system. We believe that we can only understand what sorts of genetically evolved predispositions are likely to have arisen in hominid evolutionary history by taking account the evolutionary properties of culture.

These assertions will be fleshed out in three sections. First, we will review the sociobiologist's argument about how human culture is shaped by evolved and genetically transmitted predispositions. Then we will consider how other processes may affect cultural variation in the context of a particular example, the belief that virtue is rewarded in an afterlife, and how

this belief can in turn affect how people attempt to satisfy evolved goals. Finally, we will argue that the ideas presented in the example generalize to many other cases of the interaction of evolved predispositions and cultural evolution.

1. THE ROLE OF EVOLVED PREDISPOSITIONS IN SHAPING CULTURAL VARIATION

Human sociobiologists differ about whether cultural variation within and among contemporary human groups is adaptive. Some (Alexander 1979; Betzig 1986; Turke 1984; Durham 1976) believe that a greal deal of contemporary variation *is* adaptive, i.e., that one can generally predict variation in behavior by determining the variation in fitness maximizing behavior. Of course, they admit that exceptions exist: Mistakes occur, many behaviors have little impact on fitness, and even important traits may temporarily drift away from the fitness optima. In general, however, these authors believe that cultural differences represent adaptation. Others, including Daly and Wilson, Tooby and Cosmides, and Barkow in their contributions to this issue, argue that behavior represents an adaptation to the social and ecological conditions that confronted Pleistocene food foragers (see also Konner 1982; van den Berghe 1981). According to this view, some cultural variation may be adaptive because the relevant aspects of the environment have not changed very much. There will be much behavior that is not fitness maximizing under current conditions because the environment imposed by farming and industrial life is so different from food foraging, but we can still understand human behavior in terms of the outmoded evolved predispositions interacting with contemporary environments.

Two ideas unify these disparate views. First, with very few exceptions (Lumsden and Wilson 1981, Chap. 6; Freedman 1979, Chap. 9), human sociobiologists reject the idea that significant genetic variation underlies behavioral variation among contemporary humans. Important cultural changes can occur in a very short time, and important cultural differences are maintained between adjoining human groups despite substantial amounts of gene flow. It is very difficult to believe that behavioral variation on these temporal and spatial scales can be explained by genetic variation (Boyd and Richerson 1985, pp. 155–157). In fact, given the high degree of morphological similarity between contemporary and late-Pleistocene humans, it is easy to believe that humans have had very similar genetically evolved predispositions for the last few tens of thousands of years. Similarly, the existence of art and stylistic variation in artifacts (Marshack 1976; Isaac 1976) during the same period supports the "psychic unity" of humans on this time scale.

The second, related idea is that cultural variation among contemporary humans has been shaped and channeled by evolved predispositions. According to this view, people do not uncritically acquire the beliefs, values,

and attitudes that characterize the people around them. Instead, evolution has equipped people with psychological mechanisms that cause them to be predisposed to acquire beliefs, values, and attitudes that either are presently fitness enhancing or were fitness enhancing under Pleistocene food foraging conditions. Most sociobiologists would probably agree on the basic nature of these mechanisms; people are endowed with evolved goals. They fear death, avoid hunger and discomfort, value sexual gratification, and social approval, and so on. Through various mechanisms (not necessarily conscious ones) people attempt to evaluate alternative beliefs, values, and attitudes, and then adopt the variants that best satisfy these genetically inherited goals, as evaluated by genetically inherited cognitive capacities. People may acquire secondary cultural dispositions and cognitive skills, but the primary genetic ones are fundamentally responsible for the trajectory of cultural evolution.

Sociobiologists differ about the nature and specificity of the psychological mechanisms that they think shape cultural variation. Those who argue that contemporary behavior is usually adaptive imagine that a small number of quite general psychological mechanisms maintain behavior near the fitness optimum in a wide range of different environments, including contemporary industrialized societies (e.g., Flinn and Alexander 1982). Those who doubt that current behavior is adaptive tend to envision a larger number of mechanisms that are more specific to the environment of Pleistocene food foragers (e.g., Tooby and Cosmides, this issue). To simplify our prose, we will summarize all of these mechanisms by saying that people are predisposed to acquire beliefs that satisfy "evolved goals."

The invariant evolved predispositions posited by human sociobiologists lead to cultural variation because they bias cultural evolution in different directions in different environments. The beliefs, values, and attitudes that lead to reproductive success (a long comfortable life, many wives or children, and so on) may be quite different in different environments. For example, very different kinds of subsistence skills and social organizations characterize traditional African societies living in savannahs and in moist tropical highlands. It seems that nomadic pastoralism and fierce individualism are adaptations to the savannah while sedentary cultivation and socially aware conformity succeeds in the fertile, densely settled highlands. In both cases, the argument is that people are able to assess which beliefs and attitudes lead to success in a particular environment, and then tend to adopt those beliefs and attitudes.

The idea that cultural variation has been shaped by evolved propensities allows human sociobiologists to make some kinds of general predictions about human behavior. This task seems straightforward for those who think that cultural variation is currently adaptive; the beliefs and values that predominate in a particular culture should be the ones that maximize reproductive success in the environment at hand. For those that think that culture is shaped by goals that were appropriate in food foraging conditions, the

task is a bit more complicated: First, they must understand what past conditions were like, then deduce what kinds of predispositions would maximize fitness under those conditions, and finally predict the effect of the antique predispositions in contemporary environments. In either case, making predictions often requires detailed knowledge of relationship between cultural variation and variation in reproductive success in particular environments, either past or present. However, there are many beliefs and values that would seem to be maladaptive in any environment. This fact allows human sociobiologists to make general predictions about human cultural variation. For example, as Cosmides and Tooby argue in their contribution to this issue, predispositions that lead to unreciprocated altruism toward unrelated people will never be favored by natural selection under any assumptions about the environment. If one accepts this argument, then it follows that beliefs that cause people to behave unselfishly toward nonrelatives should never predominate in any human culture, because evolved predispositions will cause people to reject such beliefs.

We think that the sociobiological views we have outlined are, in principle and probably in fact, incomplete. While evolved predispositions must be *among the most important influences* on culture, they *cannot be the only processes* that cause some cultural variants to spread and others to become extinct. Moreover, there are good reasons to believe that for some kinds of traits, these additional processes are more influential than those that result from evolved goals. This fact causes the interaction of genes and culture to be a coevolutionary process of some complexity. The example in the next section and the generalization of it in the following one are meant to show how the reciprocal influences of cultural variation and evolved predispositions can be important in explaining contemporary human behavioral variation and, in the deeper past, how the processes of cultural evolution might have structured the genetic evolution of some predispositions in the first instance.

2. A MODEL OF THE EVOLUTION OF THE BELIEF THAT VIRTUE IS REWARDED IN AN AFTERLIFE

With these ideas in mind, let us now consider how the belief that virtue is rewarded in an afterlife might evolve. We are not interested here in belief in an afterlife per se; it is easy to understand how an evolved fear of death might lead to the spread of this idea. Nor are we interested in public compliance with religious practice; there are many practical reasons to appear to conform to widely held dogma. Rather, we want to consider how it might come to be that significant numbers of people really believe that individuals who behave unselfishly on earth live forever in a paradise after death, while those who behave selfishly, perish (or worse, suffer forever in a hell).

The belief in rewards in an afterlife is interesting because it is plausible that in an attempt to satisfy evolved goals, believers will be more likely to behave unselfishly, on the average, than unbelievers. For the sake of argument, let us suppose that people have evolved preferences for longevity, personal comfort, and lots of healthy children and relatives. To keep things simple, let us further suppose that there are only two kinds of people, atheists who do not believe that virtue is rewarded in an afterlife and believers, who do. In any behavioral choice, believers must balance the short-run costs in terms of reduced comfort, and perhaps numbers of offspring, against the long-run gains in comfort and longevity that will result in the hereafter. The worldly atheist does not face this trade-off. Thus it seems likely that, all other things being equal, the believer is more likely to choose the monastery or distribute his wealth among the poor than the atheist, even though both believer and atheist are assumed to be trying to satisfy the same evolved goals. These differences in behavior do not result from different evolved predispositions. Rather, believers and atheists have very different notions of what the world is empirically like. Of course, many factors other than religious conviction affect the choices of any particular individual. For example, in a society with primogeniture, second sons might have many fewer opportunities to have children than first sons. Thus, we would expect second sons (if we control for piety) to be more likely to choose to become monks.[2]

The evolution of a belief in reward in an afterlife is problematical because it is hard to see how attempting to satisfy evolved predispositions will guide the choice of whether to believe in an afterlife or not. From the point of view of an individual attempting to achieve evolutionary goals such as long life, personal comfort, and so on, the answer depends on which belief is true. If unselfish behavior is rewarded during an afterlife, it is best to choose one's behavior accordingly, and vice versa. The problem, of course, is there there is no easy way to test claims about the supernatural.

Christianity, for example, is elaborately justified by rational arguments and emotional appeals designed to disarm the most intelligent skeptic and remove this system of belief from the possibility of empirical disconfirmation. Even such an intellectual giant as Pascal could be convinced to choose to believe in an eternal reward, and then act on this belief. Because the reality of reward in the hereafter is immune to any objective evaluation, it seems to us that the likelihood that people will adopt or not adopt this belief will only be weakly affected by evolved propensities like those discussed above.

If our argument is correct so far, and if the only processes causing cultural change were due to a biased social learning mechanism requiring

[2] By using the example of religion (with Pascal's Christianity in specifically in mind) for illustration here, we do not mean to imply that religion is always required for unselfish behavior, nor that religion is always associated with unselfish behavior. It is interesting, however, that moral codes are so often embedded in supernatural belief systems. Rappaport (1979) and Campbell (1975, 1983) provide interesting recent discussions of this phenomenon, which we attempt to model in more detail than is possible here in Boyd and Richerson (1985, Chap. 8).

empirical proofs, then frequency of the belief in reward in the hereafter in the population would change only very slowly, if at all. Some atheists would take some natural phenomena as confirming the existence of the afterlife, while some believers would despair for lack of convincing proofs. We would expect that the net effect of such decisions on the fraction of the population that believed would be relatively small, and, therefore, neither belief would spread rapidly at the expense of the other.

However, it is easy to imagine a variety of other social processes that could cause some beliefs to become commoner and other beliefs to become rarer. For example, it is plausible that the involvement of religious orders in charity and education, within limits, increases the number of believers in a group. The propensity of believers to obedience and public service may well increase the political stability of groups with such a role for religion. Therefore, groups with a greater fraction of believers are more likely to persist. Over time, this process of cultural group selection will, all other things being equal, cause the belief in reward in the afterlife to spread. Whether this actually occurs depends on a variety of factors. However, it is clear that if these are the only two processes generating cultural change, then as the effect of evolved goals becomes weaker, selection among groups will become more important. Group selection is but one of a variety of processes that can shape cultural variation in ways that are not directly explicable in terms of evolved goals. (See Boyd and Richerson 1985, Chaps. 6–8, for a discussion of several such processes.) We will refer to these as "nonsociobiological" processes because they do not play any important role in the usual sociobiological views of cultural change.

When nonsociobiological processes such as cultural group selection shape cultural variation instead of evolved goals, the result can be that most people will choose to behave in ways that one would not predict based on ordinary evolutionary theory. Let us suppose that selection among groups has caused believers to become much more common than atheists. Assuming that behaviors that result from belief (such as charity, defense of the faith, and chastity) cause believers to have lower fitness on the average than atheists, the average behavior in the population would not be predicted through a straightforward application of sociobiological theory. Moreover, believers may be prone to exercise sanctions and confer rewards on others. Crusading, defending obscure doctrines, acts of Christian charity, entrance into a convent, and the like may, on average, serve the evolved goals of private nonbelievers if these behaviors are rewarded by believers. This does not mean that human behavior has somehow transcended biology. It simply means that to understand human behavior, evolutionary theory must be modified to allow for the complexities introduced by social learning.

These ideas are consistent with much variation both within and among societies being in line with sociobiological predictions. On the view proposed here, people strive to satisfy evolved goals, but in the context of culturally acquired beliefs. Thus, *if the cultural context is taken as given, we would*

expect that much variation in behavior would be explicable in sociobiological terms. For example, we would expect that a believer's decision to join a monastery will be influenced by what he or she must give up in order to do so. A wealthy woman may well be more likely to enter a convent than a poorer one if it is customary to marry hypergynously, even if their religious beliefs are equally fervent. The same argument applies to variation among societies. A celibate can more likely enhance his relatives' reproductive success in a society in which celibates are admired, wealthy, or powerful than in one in which such people are recruited by poor and despised religious minorities.

It is also possible religious beliefs could have influenced the evolution of predispositions. Clearly, the specific doctrines of particular religions are relatively short-lived and are unlikely to have large effects on the evolution of genes. However, supernatural beliefs are a cross-cultural universal (Wallace 1966, p. 4). Most such belief systems include theories of reward and sanction by supernatural personalities or forces either in this life or an afterlife (Wallace 1966, pp. 56–57). The earliest archaeological evidence for the ceremonial treatment of the dead predates the emergence of anatomically modern humans (Solecki 1971). Such rituals usually occur today in the context of religion, so perhaps cultural beliefs in supernatural rewards and punishments have been a near universal feature of the social environment of genes for tens of thousands of years. If group selection has commonly acted on such beliefs over this span of time, humans might well be genetically predisposed to behave altruistically.[3]

3. GENERALIZATION: CULTURE AS A PROBLEM IN COEVOLUTION

The idea of an afterlife with infinite rewards is only an especially striking example of a much larger class of cultural variation about which it is difficult and costly to apply evolved predispositions to make adaptive choices in real environments. The natural world is complex, hard to understand, and variable from place to place and time to time. Is witchcraft real? What causes malaria? What are the best crops to grow in a particular location? Are natural events affected by human pleas to their governing spirits? The relationship between cause and effect in the social world is often equally hard to discern. What sort of person should one marry? What mixture of devotion to work

[3] Darwin (1874, Chap. 4, 5) thought that a sense of sympathy and sensitivity to the opinion of others were ancient social instincts developed to a high degree in humans by selection based on competition and conflict between tribes. He seeemed to believe that much of variation between tribes leading to this group selection was due to differences in customs, although his notion of "inherited habits" does not make the modern sharp distinction between genetic and cultural variation. Darwin himself was thus the first to hypothesize that basic human predispositions could evolve in response to our imitative capacity combined with group selection. We will sketch a modernized variation of his hypothesis below.

and family will result in the most happiness or the highest fitness? People can make some intelligent guesses about such decisions, but, compared to the variation we observe in others' behavior, the number of alternatives we can investigate in any detail is quite limited. Even if individuals are willing to devote substantial effort to particular decisions, each of us faces too many decisions to make costly investigations before making all of them. The picture that emerges from behavioral decision theory (Nisbett and Ross 1980) is that people commonly rely on simple, often misleading rules of thumb to make complex decisions. Cosmides and Tooby's paper in this issue illustrates a similar kind of phenomenon. People seem to be quite skilled at making logical inferences in one problem domain, but the skill does not generalize to other, logically equivalent domains. Human decision-making skills seem empirically to be a compromise between the rewards of accurate judgments and the costs imposed by enlarging the cognitive apparatus and increasing information collected from the environment.

When the determination of which beliefs best satisfy evolved goals is costly or difficult, unbiased imitation may be an adaptive response to variable environments. We have investigated theoretical models in which both social and individual learning are possible, and we asked what mix of the two will be favored by selection (Boyd and Richerson 1983, 1985, Chap. 4). According to our analysis, the answer depends mainly on the kind of environment in which the population exists and on the relative costs and error rates of social and individual learning. When imitation is easy and accurate compared to individual learning, and when environmental change from generation to generation is neither too rapid nor too slow, individuals will be best off depending mostly on imitation. This result is quite intuitive. When environments change substantially from generation to generation, what those of the parental generation have learned is of little use to their offspring, and mostly individual learning is favored. In very slowly changing environments, any form of individual learning is useless because natural selection on cultural or genetic variation is sufficient to keep adaptive variants in high frequency without such a costly, error-prone process. Pure imitation (or genetic transmission) is favored. In the intermediate environments with moderate changes from generation to generation, a relatively weak, low-cost disposition to learn is effective in keeping the adaptive trait at high frequency. The strategy favored by selection is to imitate a traditional behavior, make a few observations of the environment, and make marginal adjustments in the imitated behavior as indicated by the observations. In intermediate environments, this strategy balances the chance of imitating an outdated tradition with the cost and possibility of error due to individual learning.

As the effect of evolved goals on cultural change weakens, culture becomes more and more like a system of inheritance. Much of an individual's behavior is a product of beliefs, skills, ethical norms, and social attitudes that are acquired from a set of other people by social learning. To predict

how an individual will behave, one must have knowledge about his or her cultural milieu. This does not mean that the evolved predispositions that underlie individual learning become unimportant. Indeed, without them, cultural evolution would be uncoupled from genetic evolution and would provide none of the fitness-enhancing advantages that must have favored the evolution of capacities for culture.

To the extent that important components of culture are acquired by imitation and only weakly influenced by evolved goals, it follows that the culture can only be understood by taking account of its population-level properties. Ernst Mayr (1982, pp. 487–488) argues that Darwin's greatest contribution to science was not his theory of natural selection, but the method he used to deduce it. Mayr calls this method "population thinking." In brief, population thinking means that evolutionary change is understood in terms processes that affect the heritable variation contained in a population. The cultural traits that we observe in a society, like the genes that we observe in a population, are the long-run result of of the repeated action of evolutionary forces and transmission patterns. Individual choices (not necessarily conscious) will tend to increase the frequency of beliefs and attitudes that serve evolved goals. However, when the effect of evolved goals is weak, the chance that other population-level processes will play a role becomes greater. Group selection acting on cultural variation is one such process. Such processes may sometimes serve evolved goals, and other times not. Sociobiologists believe that selection acting on genes will tend to alter predispositions to ensure that culture does serve fitness goals, at least in the very long run. However, in our view, the cost of the powerful, general, decision-making predispositions necessary to ensure that culture always serves fitness goals is likely to be greater than tolerating some fitness-reducing cultural traits. Even in the long run, cultural organisms will still face the trade-off between the information economizing virtue of social learning and the various costs implied by a degree of blindness in imitation.

When cultural evolution is conceived of in these methodologically Darwinian terms, the relationship between cultural and genetic evolution is a coevolutionary one. Ehrlich and Raven (1964) introduced the term "coevolution" to describe the evolutionary interaction between insects and their host plants. More recently, this term has been applied to any situation in which evolutionary change of two or more species is coupled (Futuyma and Slatkin 1983, Chap. 1). The most interesting cases of coevolutionary systems are those in which the evolutionary trajectory of either one of a pair of species cannot be understood without considering the evolutionary trajectory of the other. For example, one cannot understand the evolution of poisonous plant compounds without considering the evolving ability of insects to detoxify these compounds, and vice versa.

The relationship between genetic and cultural evolution is coevolution-

ary in two different senses.[4] On very long-time scales, the kinds of the genotypes that are favored by natural selection will depend on the kinds of cultural variants that characterize populations. Similarly, the kinds of cultural variants that spread under the influence of both sociobiological and nonsociobiological processes will depend on the genetic characteristics of the population as well as upon the environment. Thus, we cannot understand cultural change without knowing the nature of genetically inherited predispositions that affect which cultural traits are adopted. Nor can we predict genetic change without understanding the kinds of beliefs and values that are present in a population.

On shorter time scales, cultural variants, whose evolution is mainly controlled by evolved predispositions, will coevolve with cultural variants whose evolution is mainly guided by nonsociobiological processes. For example, impractical extremes of fashion in clothing may be limited or reversed by a return to fashion of clothes that are utilitarian, comfortable, and cheap. The evolution of many cultural traits will be strongly influenced by evolved goals. These traits will evolve much as if they were under the influence of natural selection; variants which best satisfy the evolved goals will increase in frequency. However, the kinds of variants which are perceived as satisfying evolved goals will depend on many other cultural traits, including those that evolve under the influence of nonsociobiological processes may not increase the frequency of traits that satisfy evolved goals. Draper's paper in this issue is an excellent example of how cultural belief systems can affect decisions about behavior central to genetic fitness, including sexual activity, marriage patterns, and investments in offspring. In what follows we will refer to the coevolutionary process at both time scales as the coevolution of genes and culture. The reader should keep in mind that on short time scales it is the gene's agents—cultural traits under the strong influence of evolved predispositions—that are actually coevolving with other cultural traits that are affected more strongly by nonsociobiological forces.

The following scenarios all seem to us to be plausible outcomes of gene-culture coevolution for at least some sets of traits:

Culture on a Genetic Leash

Some form of this scenario is envisioned to be the most important one by human sociobiologists. As Lumsden and Wilson (1981, p. 13) describe it:

[4] We do not treat a third type of coevolution explicitly in this paper, although it is implied in our discussions of group-selected cultural traits. When human societies become differentiated either spatially (as among hunters and gatherers) or by social roles (as in complex societies), they may evolve much like two separate species as far as cultural traits are concerned—e.g., elites in complex societies may evolve much like predators or parasites to increase their fitness at the expense of subordinate classes. The victimized groups may in turn evolve behaviors to minimize the burden of elites. See McNeill (1982, vii) for a brief discussion of this analogy. Barkow (this issue) discusses this problems under the rubric "elites appropriate." No formal Darwinian models have yet been constructed to examine this problem.

> Over a period of generations the population is unstable against invasion by genetic mutants that program epigenetic rules biasing individuals toward assimilation of relatively adaptive [culturgen] sets. The epigenetic rules will then tend to channel cognitive development toward certain culturgens as opposed to others. . . . [G]enetic natural selection operates in such a way as to keep culture on a leash.

Similar metaphors are invoked by a variety of writers. Durham (1978) argues that culture will be kept "on track" of genetic fitness, Alexander (1979, p. 79) that a cultural instruction must be a "vehicle of genetic replicators" and Barkow in this issue that an "elastic band" of psychological processes tend to pull cultures toward fitness-enhancing patterns.

We have analyzed a number of theoretical models in which we assumed that inherited predispositions act to control cultural evolution. As we described above, the basic outcome is just as adherents of the culture-on-a-leash scenario predict. The cultural variants that are favored by the rule do tend to prevail, and selection can optimize such rules with respect to genetic fitness. We think that these models are useful for understanding how a capacity for culture would have arisen in an acultural lineage. The culture-on-a-leash scenario nicely illustrates how selection on genetic predispositions can take advantage of the special properties of cultural transmission to increase fitness.

Genes on a Cultural Leash

While the culture-on-a-leash scenario undoubtedly captures an important part of the coevolutionary relationship between the two systems, it incomplete and thus misleading. When the interests of two species are strongly opposed, coevolution can become an "arms race." For example, selection on a parasite species will favor better means for overcoming its host's defenses, while selection on the host will favor better defenses. Sometimes one species or the other will win such an arms race; parasites might tend to win arms races with their host because they typically have shorter generation times. Suppose that an antagonistic pattern of coevolution between genes and culture arose, and culture won an arms race, completely "domesticating" genes. Such an outcome is certainly conceivable.

Cultural evolution could come to control evolved predispositions in two ways. First, on a short time scale, cultural evolution may generate norms, ideology, and systems of reward and punishment that are capable of misleading, suppressing, and finessing evolved predispositions. The model outlined in the appendix shows how a culturally inherited female preference for mating with culturally prestigious, polygynous males can spread in a population even when it lowers female fertility. Interestingly, even in the long run, genetic predispositions to correct for this sort of mating preference system will not necessarily evolve because of the success of prestige preferring females' sons in the culturally defined mating game. To take another

example, giant modern military organizations appear to function by tapping men's capacities for loyalties to small groups of fellows (Kellett 1982). Cultural evolution during the last 5,000 years has created systems of military organization that develop, in squad to regiment-sized units, a sense of solidarity and willingness to engage in acts of desperate courage, the capacity for which must have evolved in much simpler societies. Mass armies can be created and function well, but only by traditions of military organization that partly use and partly suppress predispositions that, by themselves, would dissolve such armies into natural loyalty groups of tens to a few thousand men at most. The role of religious ideas in turning human intellectual capacities and behavior to the service of perpetuating systems of religious ideology was the point of our example of rewards in the afterlife. Campbell (1975, 1983) has elaborated a hypothesis along these lines to explain the development of urban civilizations on a psychological substratum adapted for much smaller scale societies.

Second, on a longer time scale, culture is a source of decision rules with potentially important genetic consequences. Cultural norms often specify what sort of a person is a suitable mate and what sorts of behaviors deserve rewards and punishments. Cultural universals and near universals are likely to have been a part of the environment of human genes for so long as to have been an important component of selection on genetic predispositions. Barkow (1980) discusses this general process under the rubric "genetic assimilation of culture"—e.g., the anatomy of the human vocal tract is a genetic adaptation to life in a world where command of an elaborate symbolic communication system is important for survival and reproduction. A more controversial but theoretically unproblematic example is human altruism. Even in the smallest-scale human societies that we know, food sharing and other examples of altruism (Kaplan and Hill 1985) are much better developed than in any other mammal, with the possible exception of naked mole rats (Jarvis 1981). If our models indicating the relative ease with which culture can become group selected are realistic, it may be that people have long lived in cultures where cooperation with distantly related individuals is common. Cultural rewards for acceptably sociable conduct, and punishment for the kinds of aggression common in most primates, might have selected for individuals with a more docile temperament and a willingness to cooperate outside the immediate family.

Selfish Memes and Epidemiological Models

There need be no permanent winner in an antagonistic coevolution, an endless "moving target" arms race is possible, as between many diseases and their hosts. One difference between the cultural and genetic inheritance systems is that cultural traits are acquired piecemeal from many individuals over a considerable period. This rather loosely integrated system of inheritance is prone to produce cultural fragments that reproduce at the expense

of the individual's other genetic and cultural traits. Cavalli-Sforza and Feldman (1981, p. 33) note the formal resemblance of the spread of innovations and the spread of infections, and they adopt their descriptive terminology for varieties of cultural transmission (vertical, oblique, horizontal) from epidemiology. An empirical study of the spread of heroin addiction describes the close resemblance of its dynamics to the spread of disease that requires intimate contact (Hughes and Crawford 1972). Addiction is spread along chains of close friendship. Addicts remain infectious only in the early stages of addiction, while the pleasurable aspect of the drug still outweighs the manifest disability of advanced addiction. Only a limited population of susceptible individuals is at risk of acquiring the addiction even if exposed. Many simple epidemiological principles probably apply to pathological cultural traits—e.g., parents notice that the incidence of minor microbial infections and various obnoxious habits in children increase together when they first go to school. Crowded classrooms of young susceptibles are the ideal environment for the spread of pathogens of both types by horizontal transmission among the children!

Dawkins' (1982) idea that evolution is best understood from the point of view of the minimal selfish heritable unit is heuristic in this context. Because of the constraints of meiosis, mutant genes normally have little opportunity to increase their reproductive success at the expense of the rest of the genome. Nevertheless, segregation distorting and sex ratio distorting genes are known. Viral pathogens may evolve from broken fragments of DNA that acquire a means of horizontal transmission. The extensive noncoding DNA in eukaryotes might be a product of selfish, vertically transmitted genes.

The extensive imitation of nonparental individuals multiplies the opportunity for this sort of pathology to arise in the cultural system. On the other hand, imitating only parents considerably reduces the effectiveness of biased transmission based on evolved predispositions and has other costs (Boyd and Richerson 1985, pp. 188–190). Thus, reducing the possibility of cultural pathogens arising by eliminating nonparental transmission would forego some of the most potent adaptive advantages of cultural transmission. We speculate that a primary genetic and secondary cultural system of defense are required to manage the burden of cultural pathogens. Some evolved predispositions are likely adapted to protect humans from adopting pathogenic cultural traits, much as skin and mucous membranes provide substantial protection from microbes—e.g., many pleasurable intoxicants are bad tasting or mildly sickening to the uninitiated. No doubt, our sensory machinery thus provides some defense against the use of such substances. But the transmission of cultural traits among peers especially leads to the potential for rapid evolution of mechanisms to defeat such slowly evolving defenses. For example, a number of pathogenic cultural traits, such as smoking, drinking, and heroin addiction, take advantage of evolved senses of pleasure as routes of infection. The reports of pleasure and proselytizing

attitudes of the freshly addicted can easily overcome the discomforts produced by one's first cigarette, the rough taste of whiskey, or the poke of a needle in susceptible individuals. Evolving a genetic defense against such pleasure-producing substances would probably involve a slow and possibly costly reorganization of the nervous system to eliminate their pleasurable effects. Given the wide variety of natural toxicants that could be substituted for an obsolete one, defense against such pathologies requires some form of rapidly evolving protection analogous to the immune system. Empirically, the moral strictures of religious belief, transmitted mostly from parents to offspring, do seem to be effective in protecting youths from "victimless" crimes (Jensen and Erickson 1979). Also, older adults who have survived "infection" by such traits, or who have observed their destructive effect in others, are analogous to the recovered, immune class of standard epidemiological models. Such recovered individuals likely tend to socialize their children and others against the deleterious practice. (Of course, unless pathological ideas are lethal, they will also be transmitted vertically as long as they are present.)

Genes and Culture as Obligate Mutualists

The tremendous success of the human species suggests that the coevolution of genes and culture is mostly mutualistic. This might be the result of a genetic leash on culture keeping cultural variation perfectly domesticated. But a more complex scenario is also quite plausible. Suppose that the processes allowing culture a leash on genetic evolution also operate. Genetic fitness may be improved by some changes in the cultural environment and improved still further if changes in inherited predispositions encourage cultural changes in the same direction that initially improved genetic fitness. This would be the recipe for the evolution of a mutualism if we were speaking of two species, and the analogy with gene-culture coevolution is reasonably apt. If each of the two leash scenarios is plausible enough taken by itself, that both can act together is an obvious deductive consequence. Certainly, the basic natural history of humans squares with this scenario; major flaws in either people's genes or their culture are extremely deleterious. There is a division of labor between the cultural and genetic systems of inheritance, both furnishing inherited information that is essential to survival and reproduction. We have already alluded to what we think is the most fundamental reason for this division of labor—the cultural transmission system provides information cost economies in certain kinds of spatially and temporally varying environments. This is an unusual division of labor to serve as the basis for a mutualism, although it bears a resemblance to the mutualism of bacteria and plasmids where plasmids have been the vector for acquiring drug resistance in many types of bacteria.

Elaborating our examples of the evolution of altruistic predispositions owing to group selection on cultural variation provides an illustration of how

a mutualistic coevolution might work. The cultural leash favoring more altruistic genetic predispositions (or providing the means to finesse selfish and nepotistic ones) could very well increase genetic fitness by harvesting fruits of cooperation not directly accessible to genes via kin selection and reciprocal altruism. From the cultural point of view, genes have been domesticated in the service of a group-selected cultural unit. However, from the genetic point of view, selfish genes have merely used their leash on cultural evolution to concoct an efficient system to police a extensive, generalized system of reciprocal altruism. That is, all other things being equal, the extensive cooperation in human societies ought to be susceptible to invasion by more selfish genotypes, eventually reducing human sociality to something like the common primate norm. This invasion is prevented, in this scenario, by group-selected cultural norms that detect and penalize any such invading genotypes; genes are rescued from their own Hobbesian tendencies by a cultural Leviathan—happily so, too, for the genetic leash on cultural evolution may well keep the Leviathan sufficiently benevolent to increase fitness substantially above what it would be in its absence. (The adaptive perfection implied here should be taken with a large grain of salt. Theoretical work to date on coevolutionary models suggests that coevolution does not always maximize fitness, and when it does maximize fitness, it may not maximize measures of adaptedness like population size. See Roughgarden 1979, Chap. 23; Slatkin and Maynard Smith 1979.)

The basic natural history of the human species gives provisional support this view. Most of the great variety of niches that humans have exploited during the last few tens of thousands of years have depended on cooperation, especially cooperation between males and a division of labor, initially based on sex. Even in the simplest societies that we know of, these principles of social organization are elaborated quite beyond the range of variation encountered in other primates. Kinship and face-to-face pairwise reciprocity are important variables in human social organization, but human propensities to cooperate also seem to be extended in ways that are better predicted by cultural evolutionary models.

4. CONCLUSION

We regard the coevolutionary view of human evolution presented in this essay as a friendly Darwinian amendment to ordinary sociobiological hypotheses. To our consternation, chagrin, and confusion, we have sometimes been read as proposing that cultural evolutionary processes are independent of the genetic evolutionary process. Alexander (1979, p. 79) describes us as arguing that "their separate modes of inheritance lead to an uncoupling of their [genetic and cultural] directions of change." Barkow, in a draft version of his introduction to this symposium issue, classified us with others as viewing culture as a "semi-independent system of inheritance." For similar

characterizations see Daly (1982), Flinn and Alexander (1982), and Durham (1982). We do think that culture differs in its evolutionary properties from genes and that it plays an active role in human evolution, but we certainly do not view genetic and cultural evolution as generally uncoupled. "Semi-independent" is perhaps closer; the term captures the sense that genes and culture are mechanically distinct systems of inheritance. However, the mutual influence of genes (via evolved predispositions) and culture on one another means that the coupling between the two inheritance systems is quite strong in all of the coevolutionary scenarios sketched above. It is true that coevolution with cultural processes can lead to evolutionary outcomes that seem quite odd from the point of view of simple deductions from genetic fitness alone, but this is usually because interactions between the two systems are strong, not weak.[5]

Aside from confusion that we may have introduced by our descriptions of our models, there is understandable reason to resist approaching the relationship between genes and culture as generalized coevolution problem: Coevolutionary processes are intrinsically complex, and the theory necessary to understand them is more difficult than when only one "species" is involved. We are on record as favoring the use of the simplest useful models to explore even such complex topics. The question is, what are the simplest useful models? When key evolutionary parameters like the relative genetic fitness of different phenotypes depend on the frequency of cultural traits in a population, and when these cultural traits evolve partly under the influence of nonsociobiological forces, attempts to use heuristic arguments based on fitness optimization are very likely to founder. If the mutualistic and epidemiological coevolutionary scenarios are as generally important as we believe they are, it will not be possible to neglect these complexities. We hope that our own theoretical efforts demonstrate that useful progress can be made with the gene-culture coevolution problem, despite these complexities. We certainly do not advocate the nihilistic viewpoint that evolutionary interaction between genes and culture is hopelessly complex. Rather, we think that exciting, rapid progress in developing a Darwinian theory of human behavior along coevolutionary lines is likely, even if final answers to all controversial questions lie in the distant future. Recall that evolutionary biology is full of unsolved problems a century and a quarter after the *Origin*.

Despite having made the best apology we can for the dual inheritance view, we would like to end this essay with a plug for unvarnished sociobiological reasoning in its several forms. We still know very little about the complexities of gene-culture coevolution and one of the most useful hypothesis-generating techniques available is to ask what genetic fitness might have favored, setting some or all cultural complexities aside. Such hy-

[5] We do describe one process, in which a certain range of symbolic cultural variation might have real evolutionary independence (Boyd and Richerson 1985, pp. 273–274), but this is a rather special case, and it should be completely untroubling to an orthodox sociobiologist.

potheses serve three purposes. First, given that evolved predispositions are likely to be important in human behavior, a quite significant fraction of human behavioral variation may be explained by such hypotheses. This is especially true if culture is taken as given, or its effects removed by statistical controls. The work of Daly and Wilson reported in this issue is a promising example of such a use. Second, asking what sorts of cognitive capacities associated with cultural transmission and its control would maximize genetic fitness is a useful way to identify the evolutionary benefits of the cultural system for acquiring information. We have made extensive use of this technique, and we applaud its similar use in empirical contexts as illustrated by Cosmides and Tooby's paper in this issue. Finally, the attempt to construct sweeping theories of adaptive functionalism on the model of Alexander's (1979) and Lumsden and Wilson's (1981) efforts is also useful, at the very least, for comparative purposes; it is useful to have the implications of the most extreme genes-hold-the-leash models worked out as theoretical reference points. We would only say that it is equally useful to have the implications of extreme cultural hypotheses worked out in the same detail for the same reasons.

APPENDIX

To see how culture can, in effect, domesticate the genome, consider the following very simple model. The essential feature of the model is that the evolution of a cultural trait that affects female mate choice is under the control of a nonsociobiological force. Males are characterized by a culturally transmitted trait that affects the proportion of their time and energy that they invest in child rearing versus attaining a prestige roles. The trait has two variants: ambitious individuals, and familial individuals. Ambitious individuals devote more of their time and energy to achieving social prominence than do familial individuals; conversely, ambitious individuals invest less effort in raising their children. Females are characterized by a cultural trait that affects their choice of husbands. One kind of female prefers ambitious males while the other kind is not affected by this particular male attribute and mates at random. We have adopted the following model of mate choice introduced by Seger (1985).

Cultural variant of female	Probability that husband is	
	Ambitious	Familial
Random	m	$1 - m$
Preferring	$m(1 + g(1 - m))$	$(1 - m)(1 - gm)$

where m is the frequency of ambitious males in the population of potential

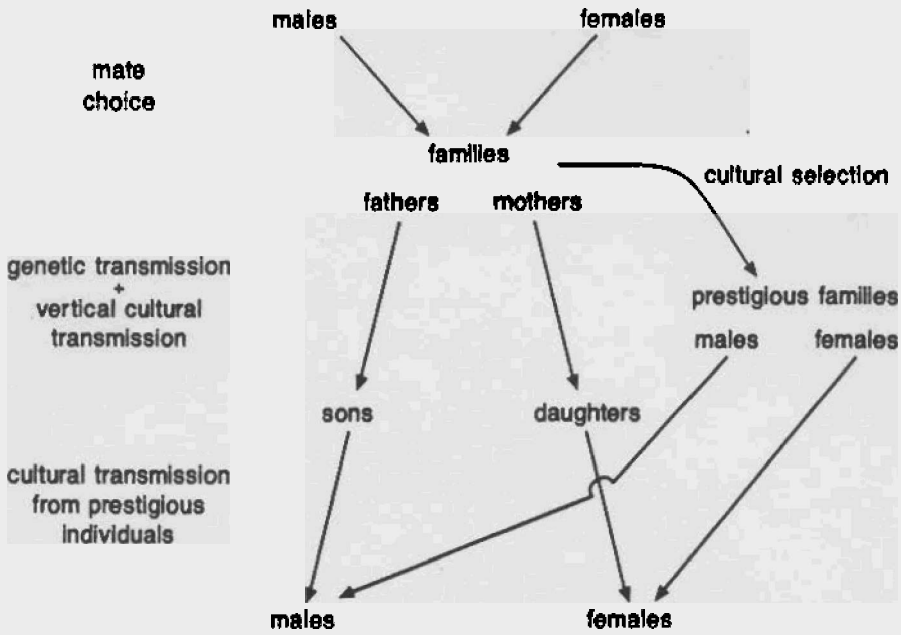

FIGURE 1. The life cycle assumed in the model of the evolution of female preference for prestigious males.

husbands, and the parameter g is a measure of the strength of the female preference. It can be interpreted as the probability that a female will choose an ambitious male when she is confronted with a choice between an ambitious male and a familial one.

These two traits are transmitted according to the life-cycle diagrammed in Figure 1. We begin a generation just before mate choice when the frequency of ambitious males is m, and f is the frequency of preferring females. There are four possible matings that occur with the frequencies given in the following table:

Cultural variant		
Female	Male	Probability that mating occurs
Preferring	Ambitious	$M(A/P) = fm(1 + g(1 - m))$
Preferring	Familial	$M(F/P) = f(1 - m)(1 - gm)$
Random	Ambitious	$M(A/R) = (1 - f)m$
Random	Familial	$M(F/R) = (1 - f)(1 - m)$

We assume that polygyny is possible. This means that, assuming that there are equal numbers of males and females in the appropriate age classes, ambitious males will have more than one wife, on the average, any time there are preferring females in the population.

Next we consider the frequency of the male and female cultural variants among children. Children acquire their initial cultural variants from their parents—boys get their beliefs about the importance of attaining prestige roles from their father, and girls get their beliefs about what kinds of men make desirable husbands from their mothers. Because male beliefs affect investment in offspring, the average number of children raised by each wife of an ambitious male ($2F_A$) will be smaller than the average number of children raised by wives of familial males ($2F_F$). Thus the frequency of ambitious sons, m', is:

$$m' = \frac{F_A[M(A/P) + M(A/R)]}{F_A[M(A/P) + M(A/R)] + F_F[M(F/P) + M(F/R)]} \tag{1}$$

Similarly, the frequency of preferring daughters, f', is:

$$f' = \frac{F_A M(A/P) + F_F M(F/P)}{F_A[M(A/P) + M(A/R)] + F_F[M(F/P) + M(F/R)]} \tag{2}$$

As they mature, children modify their beliefs by imitating prestigious adults—young men imitating prestigious men, and young women imitating the wives of prestigious men. There are a variety of plausible situations that could cause this to occur. For example, it could simply be an advertising effect—by investing in public prominence, ambitious men are simply more salient and therefore more likely to influence others. Or, in a "big man" system, prestigious males might "buy" influence by accumulating wealth that is then distributed to others in return for influence. This is a highly nonsociobiological force in cultural evolution; for related models see Boyd and Richerson (1985, Chap. 8). We assume that people will adopt the belief of a prestigious role model with probability h and retain the belief acquired as a child with probability $1 - h$. Then the frequency of the ambitious males after this second episode of cultural transmission, m'', is:

$$m'' = (1 - h)m' + hm^* \tag{3}$$

where m^* is the frequency of ambitious males in prestige roles. Similarly, the frequency of preferring females after cultural transmission, f'', is;

$$f'' = (1 - h)f' + hf^* \tag{4}$$

where f^* is the frequency of preferring females whose husbands occupy prestige roles.

Because ambitious males invest more in attaining prestige roles, they are more likely to be successful. In particular, the probability that an ambitious male attains a prestige role is V_A; the probability for a familial male is V_F, where $V_A > V_F$. Then the frequency of ambitious males among prestigious men, m^*, is:

$$m^* = \frac{mV_A}{(1 - m)V_F + mV_A} \tag{5}$$

and the frequency of preferring females among wives of prestigious males, f^*, is:

$$f^* = \frac{V_A M(A/P) + V_F M(F/P)}{V_A[M(A/P) + M(A/R)] + V_F[M(F/P) + M(F/R)]} \quad (6)$$

Combining equations (1)–(6) yields two recursions specifying how the various events in the life cycle of individuals change the frequency of ambitious males and preferring females over the course of a single generation. What really interests us, however, is what happens in the long run. One approach to answering this question is to find the values of f and m that are stable equilibria—i.e., the frequencies of ambitious males and preferring female that, once reached, will persist indefinitely.

First consider a population in which there no ambitious males and no preferring females, i.e., when $f = 0$ and $m = 0$. This equilibrium is the result that one would predict based on ordinary Darwinian theory—selection should favor females who prefer males who maximize female fecundity (Kirkpatrick 1985) and thus also familial males. This equilibrium is unstable whenever

$$(1 - h)(F_A/F_F - 1) + h(V_A/V_F - 1) > 0 \quad (7)$$

This expression says that a population consisting of all familial males and random females will be stable as long as the effect of fecundity selection weighted by the importance of parents in cultural transmission is greater than the selection process that culls among potential prestigious individuals weighted by the importance of prestigious individuals in cultural transmission. If ambitious males are much more likely to attain prestige positions than familial males, or if prestigious individuals play a large role in enculturation, the equilibrium will be unstable.

Next, consider a population that is all ambitious males and all preferring females, i.e., when $f = 1$ and $m = 1$. It turns out that this equilibrium is stable whenever the first equilibrium is unstable, i.e., when inequality (7) is satisfied. Thus, if an individual's attainment of prestigious roles is strongly affected by whether or not he is ambitious, or if prestigious people are important in cultural transmission, the long-run evolutionary result is one that would not be predicted based on Darwinian theory—females prefer males who reduce their fitness.

One obvious response to this argument is that such an equilibrium is not evolutionarily stable. In the short run, it will be eroded by the action of evolved goals. Young females will look around and see that prestigious females have fewer children and choose not to marry ambitious men, and this will eventually lead males to choose to be familial. In the longer run, natural selection willl favor genes that reduce the importance of prestigious people in cultural transmission. The thing that makes this model interesting is that this argument is not necessarily correct; once this equilibrium is

reached, the preferring females have more grandchildren than those who mate at random as long as:

$$\frac{g}{1+g} > 2(F_A/F_F - 1) \tag{8}$$

This can occur because females who marry ambitious males have ambitious sons who acquire more wives. When relation (8) is satisfied, this effect overbalances the reduced fecundity due to the lower investment of ambitious males. Interestingly, Kirkpatrick (1985) has shown that this "sexy son" effect cannot work for genetic evolution. We believe that it does work here because of the effect of the nonsociobiological force due to selection during the attainment of prestige roles (modeled by Eq. 5).

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