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3.1. INTRODUCTION

Humans are uniquely reliant on culture as a means of adaptation. To be sure, some human variation results from genetic adaptation. Like most other animals, we adapt using individual learning. Unlike other creatures, however, humans acquire a great deal of adaptive information from other conspecifics by imitation, teaching, and other forms of "cultural transmission."

It is important to distinguish between culture and individual learning. Culture is often lumped with ordinary individual learning and other environmental effects under the heading of "nurture," to be contrasted with genes—"nature." This way of thinking is responsible for much confused thinking about the evolution of human behavior. Culture differs from individual learning because variations are acquired from other individuals. For the most part, humans do not learn their language, occupational skills, or forms of social behavior for themselves, they learn them from parents, teachers, peers, and others. Cultural variants are more like genes than are ordinary learned variants. Like genes, they are inherited and transmitted in a potentially endless chain, while variants acquired by individual learning are lost with the death of the learner.

Because culture is transmitted, it can be studied using the same Darwinian *methods* used to study genetic evolution. Human populations transmit a pool of cultural variation that is cumulatively modified to produce evolutionary change, much as they transmit an evolving gene pool. To understand cultural change we must keep track of all the processes in the lives of individuals that increase the frequency of some cultural variants and decrease the frequency of others. Of course, these processes do differ substantially from the processes of genetic evolution. Most important perhaps,

culture allows inheritance of acquired variation; individually learned variants can be taught or imitated.

Culture can also be studied using the *substantive* conclusions of Darwinism. It is plausible that natural selection has shaped the human psyche so that people tend to acquire adaptive beliefs and values, however culture may work in detail. If not, how can we account for the evolution of the complex, costly organ that manipulates culture, the human brain? To the extent that this premise is correct, human behavior can be predicted using theory drawn directly from behavioral ecology, and no special account need be taken of the processes by which people acquire that behavior. The gambit of ignoring the details of how genes, learning, and other factors actually produce adaptive behavior has proven to be very successful in the study of the behavior of other animals. The substantive use of Darwinism to understand behavior is defended in greater detail in the first two chapters of this book, and exemplified by the following chapters.

There is an irony in the history of the application of Darwinian concepts and methods to cultural evolution. Darwin (e.g., 1871) believed that the inheritance of acquired variation was a general feature of all systems of inheritance. He did not make a rigid distinction between organic inheritance and culture because he thought that habits acquired by individuals could be inherited. Darwin is often accused of biologizing culture (Alland 1985), but the truth is almost the opposite. By modern standards, Darwin had a shamelessly anthropomorphic view of the animal world. He seems to have believed that the advantages of the inheritance of acquired variation were obvious: Parents spend a lot of effort learning the details of how to behave in a local environment, and it seems a waste to dissipate this effort by requiring offspring to relearn everything anew each generation. Humans, Darwin could observe, used imitation and instruction to transmit the results of learning, and it suited his intellectual agenda to minimize the difference between humans and other animals in order to bring all organisms into the compass of his theory (Gruber 1974). It was thus easy for him to imagine that culture was the model inheritance system. The irony is that, although Darwin's view that acquired variation and natural selection interact to guide evolution is seriously wrong for the genetic system of inheritance, it is quite apt for human culture. Although after many twists and turns to correct his errors, Darwin's theory became the heart of evolutionary biology in the 1930s (Provine 1971), it was ignored by the emerging social sciences in favor of the very different progressive evolutionary schemes of Herbert Spencer and his followers.

It is only in the last few decades that biologists and social scientists have returned to try to complete the project initiated by Darwin in the *Descent*. One of the earliest and most important figures in this renaissance is Donald Campbell (1965, 1975), who argued that the general similarities of genes

and culture meant that the same methods that evolutionary biologists use to study genetic evolution would prove successful in the investigation of culture. Beginning in 1973, L. L. Cavalli-Sforza and M. W. Feldman (1981) initiated a series of theoretical and empirical investigations of culture using the techniques of population genetics. About the same time, Richard Alexander (1974) and E. O. Wilson (1975) reinvigorated the evolutionary study of humans by proposing that much of the substance of human behavior could be understood in adaptive terms no matter how it was acquired—genetically, culturally, individually learned, or a complex mixture of all three. Several workers, including ourselves, have attempted to combine the methodological and substantive questions, using models inspired by population genetics to understand how culture works as a system of adaptation (Pulliam and Dunford 1980; Lumsden and Wilson 1981; Boyd and Richerson 1985; Rogers 1989a).

In this chapter our task is to present this last, hybrid body of work. There is little doubt that the organic capacities that underlie human learning and behavior were shaped by natural selection, and thus that the behavior resulting from these capacities must have been adaptive, at least in past environments. Nonetheless, attention to the processes of cultural evolution is important for human evolutionary ecology. First, the rate at which a population adapts to changing circumstances depends on the mechanism of adaptation. Genetic adaptation by natural selection is a relatively slow process, individual learning is fast, and as we shall see, cultural adaptation may range from one extreme to the other. For some disciplines, such as archaeology, the rate of adaptation may be of great interest. Second, the rapidity of adaptation itself is a kind of adaptation to variable environments, and is of interest in its own right. Finally, we will argue at length below that cultural adaptation can yield qualitatively different outcomes than those predicted from conventional fitness optimizing theory, even if one assumes that the *capacity* for culture has been shaped solely by natural selection acting on genetic variation.

3.2. PROCESSES THAT GENERATE ADAPTATIONS

A number of processes act to change the cultural composition of a population through time. We refer to these processes as the “forces” of cultural evolution. Some are analogous to the forces of evolution operating on the genetic system—drift, mutation, natural selection, and so forth. Others have no close analog in genetic evolution. Some of these processes tend to produce adaptation in a reasonably straightforward sense. Others result in evolutionary outcomes that cannot be predicted without taking into

account the details of cultural evolution. We begin by considering processes that give rise to ordinary adaptations—that is, forces that tend to produce fitness-maximizing behavior.

3.2.1. *Guided Variation*

Because culture is acquired by copying the phenotype, culture allows the inheritance of acquired variation. Individuals acquire beliefs and values by social learning. Such culturally acquired information is often affected by individual learning during the individuals' life. People may modify existing beliefs, or even adopt completely new ones, as a result of their experiences. When such people are subsequently imitated, they transmit the modified beliefs. The next generation can engage in more individual learning and change the trait even further. When the beliefs of one generation are linked to the next by cultural transmission, learning can lead to cumulative, often adaptive, change. We say that such change results from the force of *guided variation*.

If individual learning is not to be random, there must be some rules that govern which behaviors are acquired and which are rejected. The strength and direction of guided variation depend on the nature of these learning rules. Operant conditioning provides a good example of how such rules work. An animal's nervous system causes some environmental events to be reinforcing and others aversive. The behavioral variation that individuals exhibit is shaped by such stimuli so that reinforced (generally adaptive) behaviors are retained, while those that result in aversive stimuli (normally maladaptive) disappear. Other forms of individual learning involve more complex, cognitively mediated rules. In every case, however, the kinds of traits acquired by learning depend on rules expressed in the nervous system, which were acquired genetically or during an earlier episode of cultural transmission.

Thus, the kinds of traits increased by guided variation depend on the nature of the evolutionary forces that shaped the learning rules. The case in which learning rules are genetically transmitted and shaped by natural selection is of particular interest. First, this is the primitive case and thus is important for understanding the evolutionary origin of guided variation. Second, evidence suggests that it is common in contemporary humans (Lumsden and Wilson 1981: Chapters 2 and 3; Tooby and Cosmides 1989; Cosmides and Tooby 1989). Finally, if learning rules were shaped by guided variation or some other force of cultural evolution, we then must ask how those prior learning rules were acquired. A chain of cultural rules will often end in genetically acquired traits of some kind.

Guided variation allows populations to adapt relatively quickly and effectively to changing environments. This is easiest to see when the goals of the

learning rules are closely correlated with genetic fitness. If human foraging practices are adopted or rejected according to their energy payoff per unit time (as is typically assumed in optimal foraging theory—see Chapter 6), then the foraging practices used in the population will adapt to changing environments much as if natural selection were responsible. If the adoption of foraging practices is strongly affected by consideration of prestige, say that associated with male success in hunting dangerous prey, then the resulting pattern of behavior may be different. However, there will still be a pattern of adaptation to different environments, but now in the sense of increasing prestige rather than calories.

The rate at which a population can adapt by guided variation depends on how hard it is to evaluate alternative behaviors. When individuals can easily learn that some alternative behavior is better than their existing behavior, then guided variation can transform a population very quickly. On the other hand, when it is difficult to evaluate which cultural variant is best, some people will switch from an inferior variant to a superior one, but many others will switch the other way, and the net change will be small. It may often be the case that it will be difficult to determine which variant is best, even if different variants have very different fitnesses. When learning is difficult, culture can also accumulate small learned steps over many generations, leading to larger changes than would be possible when each generation has to learn anew. Box 3.1 shows how simple mathematical models are used to make verbal arguments like this one more precise.

3.2.2. *Biased Transmission*

People do not just imitate others at random and then modify behavior on the basis of their own experience; they also pick and choose whom and what to imitate in the first place. We call this process *biased transmission*. The simplest form of biased transmission, *direct bias*, can make use of the same guiding motivations as are used in guided variation. With direct bias, there is no need to invent or reinvent the behavior concerned, but only to evaluate alternative behaviors and choose among them. If behavior is at all complex, it is much easier to evaluate available alternatives than it is to invent for oneself. Plagiarism is usually easier than invention, so the distinction between these two forces is not trivial. We will consider other forms of biased transmission below.

Again, if we suppose that selection on genes is responsible for the guiding rules behind the people's choices, direct bias will tend to cause adaptive cultural variants to spread. A seventeenth-century New Guinea population might have been exposed to American sweet potatoes for the first time when some neighbors began cultivating them. Some individuals in the population likely tried cultivating sweet potatoes, evaluating whether they were superi-

Box 3.1. A Model of Guided Variation. Mathematical models are often useful for deducing the long-run evolutionary consequences of events in the lives of individuals. Here we illustrate this idea with a simple model of guided variation. Consider some basic subsistence behavior with two cultural variants—say whether to pursue individual or cooperative foraging. To make learning useful, we assume that the environment is variable—cooperative foraging is best in some environments and individual foraging is best in others. Suppose young people acquire their initial beliefs about which mode is best in the local environment by imitation of a single adult (say children imitate their mothers). As they mature they attempt to evaluate which technique is better, say by trying out the two techniques. If such trials convince them that the other technique is superior, they switch; if not, they stick to what they learned from Mom.

Let us suppose that a population has recently moved from an environment in which cooperative foraging was favored to an environment in which individual foraging is favored. Because there are only two cultural variants we can describe the state of the population by the fraction, or "frequency," of individuals who forage individually, labeled q . Then the rate of increase in the frequency of individual foraging as a result of guided variation, Δq , will be

$$\Delta q = \alpha(p - q)$$

where α = the probability that behavior is acquired by individual learning, and p = the probability that the best behavior is chosen given that behavior is acquired by individual learning.

Notice that the frequency of individual foraging converges toward the probability that it is chosen when individuals rely on their own experience. Thus, if it is easy to discern the advantages of individual foraging, we would expect almost everybody to forage individually once the population reaches equilibrium. In contrast if it is hard to discern which is better, then many individuals may err and the equilibrium frequency of individual foraging will be lower. If "learning" is merely random ($p = 1/2$), then the equilibrium frequency is $1/2$.

The rate at which the population approaches equilibrium depends on how often individuals are convinced to switch foraging techniques based on their own experience, which is measured by α . If $\alpha = 1$, everyone learns individually, and equilibrium is reached in the first generation, and if $p = 1$, everyone who does learn for him- or herself does get the correct answer. If $\alpha = 1$ and $p = 1$, the whole population gets the new answer without error in the first generation—perfect individual learning. Smaller values of α and p indicate some reliance on social learning and errors in individual learning.

While an analysis limited to so few features of the cultural system is quite unrealistic, it does model one of its distinctive features, the inheritance of acquired variation. The hope is that the lessons of the simplified analysis remain as we add complexity.

or to existing cultivars. If, on average, individuals perceived sweet potatoes as superior, they adopted sweet potato cultivation, exposing more people to the practice and so on until it spread throughout the population.

Like guided variation, biased transmission will cause a trait to spread more rapidly if it is easy to determine that the trait is better than the alternatives. If the new sweet potatoes have substantially higher yields than older cultigens like yams, then it will be easy for horticulturalists already accustomed to evaluating alternative breeds of yams to determine that sweet potatoes are better. However, the benefits of many other very desirable traits may be hard to detect. The practice of boiling drinking water substantially reduces infant mortality due to diarrhea. Nonetheless, the practice may fail to spread because its effects are confounded by many other sources of diarrhea, because it conflicts with folk medical theory, and because the causative agents killed by boiling, bacteria, are invisible. Traits whose net beneficial effects are only apparent when averaged over substantial periods of time may be especially difficult to evaluate.

Unlike guided variation, the strength of biased transmission depends on the amount of cultural variation. Bias is a culling process analogous to natural selection. Individuals select which variants to adopt from among the variants that are available. This means the force of bias has its greatest effect when alternative variants have approximately equal frequencies, and is weak when one variant is rare. This property of direct bias is easily seen in the context of the simple model sketched in Box 3.2.

3.2.3. *Example: The Diffusion of Innovations*

Studies of the diffusion of technical innovations illustrate how the strength of guided variation and direct bias varies in response to circumstances. It is well-known that humans make extensive use of pragmatic decision-making techniques when considering adopting potentially useful innovations. Rogers (1983) reviews many studies that suggest that the perceived advantage of new technology relative to old is one of the most important variables in explaining why particular innovations spread. In conformance with the theory, people with more education and more resources are more likely to be the early adopters of innovations. The difficulty of evaluating innovations and the impact of costly errors weigh more heavily against less educated and poorer people adopting innovations on the basis of their own evaluations. They, sensibly, wait for those who can better bear the costs of independent decision-making to try them out, and imitate earlier adopters later in the cycle of innovation adoption. The very rapid rate of technical evolution at the present time is probably a result of the fact that high rates of literacy, related phenomena such as the existence of libraries, and prosperity equip

Box 3.2. A Model of Direct Bias. Let us illustrate these ideas with a very simple model of direct bias. Again suppose, as in Box 3.1, that individuals must choose between individual and cooperative foraging. As before, individuals acquire their initial beliefs from their parents. But now assume that as adults, if they encounter another person who has different beliefs, they attempt to evaluate the relative merit of their beliefs and those of the person they have encountered. If they decide the other person's beliefs are better, they switch. Then the change in frequency of individual foraging is:

$$\Delta q = 2\alpha(p - \frac{1}{2})q(1 - q)$$

The rate of increase of individual foraging is proportional to the probability that individual evaluation is decisive, just like guided variation. If $p < \frac{1}{2}$, cooperative foraging is favored; if $p > \frac{1}{2}$, individual foraging is. Unlike guided variation, the effect of direct bias is proportional to $q(1 - q)$, the amount of variation in the population. When either one of the traits is rare—(q or $(1 - q) \approx 0$)—direct bias becomes very weak. Thus even very advantageous variants will spread slowly when they are rare, assuming direct bias is the only force causing them to increase. When both variants are equally common—($q = (1 - q) = \frac{1}{2}$)—and the rate of change is a maximum for a given α and p . Also, note that in the long run, direct bias completely eliminates the inferior variant from the population, albeit very slowly toward the end, while guided variation reduces its frequency to $1 - p$. In the case of guided variation, everyone who has the right trait by inheritance can make an error in individual learning and convert back to the wrong behavior. In the case of direct bias, as the frequency of people with the favored trait goes up, fewer people observe the disfavored behavior at all, and thus fewer people are tempted to err.

many people with the capacities to make fairly effective individual decisions and to tolerate the cost of mistakes.

However, the technology of preindustrial societies can also be transformed quite rapidly. The most dramatic examples are those in which population growth leads to increased competition for resources. Exponential population growth is a very rapid process, and when it drives cultural change those processes can be rapid as well. Kirch (1984) describes the response in Polynesian societies to population growth. The Polynesian islands were apparently settled by very small groups of voyagers, and it took several hundred years for the population of larger islands to become overcrowded. However, as populations did reach these levels, considerable environmental deterioration occurred. At the same time, dense populations stimulated considerable technical innovation. On Hawaii, for example, irrigation, sophisticated dryland farming systems, and aquaculture on a considerable scale allowed for an intensification of production in response to rising populations and deteriorating resources. Although status competi-

tion between chiefs (who supervised the larger-scale economic enterprises) played an important role in the evolution of late Polynesian technology, the basic decision-making forces of direct bias and guided variation must have been major elements of the process of invention and diffusion of the technology of intensification in response to more intense competition for a diminishing stock of traditional resources.

Sometimes the diffusion of improved practices proves exceedingly slow. Bettinger and Baumhoff (1982) describe the case of the several-century-long episode of the expansion of Numic speaking (Shoshone, Ute, Mono) peoples across the Great Basin of North America. The Numic speakers made intensive use of high-processing-time plant resources, such as grass seed, for their subsistence. Because this strategy supported relatively denser populations that also exploited higher-quality game and plant resources, previous populations that restricted themselves to the high-quality resources were displaced (see Chapter 6 for the optimal foraging theory that in part underpins this analysis). What kept the people being displaced from adopting Numic technology to defend themselves against the slow incursion of the Numics? Bettinger and Baumhoff argue that the key cultural trait was not the processing technology itself, which was relatively simple and widely known, but a social-organizational innovation that placed greater value on women and women's labor. In general, the utility of various subsistence techniques is easy to observe and evaluate. Alternative variants can be tested and retained or discarded as experience dictates. The consequences of social organizational variables are often harder to observe. What sort of woman should a man marry? How many should he attempt to marry? How should he treat her? The consequences of such decisions are worked out over an entire lifetime and few people get to make more than one or two experiments. It makes sense that people should rely more on tradition with regard to social organization and less with regard to subsistence techniques, even when, as perhaps with the pre-Numic peoples, clinging to traditional social organization results in displacement.

3.3. CULTURE AS AN ADAPTATION

If the massive use of culture is, like bipedalism and large cheek teeth, a distinctive human trait, what adaptive role does it play and how did a capacity for it evolve? In this section we try to understand the circumstances under which culture is superior to genetic transmission and individual learning as a means of adaptation. Understanding culture as an adaptation is important for two reasons: First, the usual approach to this problem is an anthropocentric rush to judgment. It is assumed that culture is an inherently superior mode of adaptation, and the question reduces to the breakthroughs

required to achieve it. It is salutary to reverse this presupposition. Darwin erred; the inheritance of acquired variation is rare in nature. What is so *wrong* with culture that it should be really conspicuous in only one species? Second, below we will argue that some cultural processes may lead to "maladaptive" outcomes, but only if guided variation and direct bias are weak forces. Thus, it is important to know under what conditions selection might favor a strong reliance on social learning.

3.3.1. The Advantage of Cultural Adaptation in Variable Environments

To understand the evolution of social learning we ask: What sorts of selective pressures might have favored the expansion of a capacity for social learning? When will a tendency to depend on an inherited tradition become important relative to genetically inherited patterns of behavior, or a combination of genes plus individual learning?

As we have already noted, social learning is similar to both individual learning and genetic inheritance. Individual learning is a pure system of phenotypic adaptation to environmental contingencies, but the acquired adaptation perishes with the individual learner. A pure system of inheritance (genetic or cultural) does not allow the individual any flexibility, but the fitness consequences of heritable variation cause the population to become adapted. Social learning allows both modes of adaptation. This mixed mode of adapting has two distinct advantages.

First, social learning may be favored because it allows individuals to avoid costs associated with learning. Individual learning may often be costly; it takes time and energy, exposes the organism to risk, and may require a larger brain. Rogers (1989a) analyzes a simple model in which there are two types of individuals—individual learners who evaluate alternative behaviors and choose the best one, and social learners who copy the behavior of a randomly chosen individual from the previous generation. He assumes that occasionally the environment changes from generation to generation. If individual learning is more costly than social learning, then social learners always increase in frequency when they are rare since they are virtually certain to acquire the best behavior without bearing the costs of individual learning. However, as social learners become more common, fewer people are learning for themselves and errors begin to accumulate in the population. Those that merely copy have a greater chance of copying another social learner, and thus acquiring an inferior behavior learned in a different environment. Rogers shows that at equilibrium there is always a mix of social and individual learners—the greater the environmental variability the lower the frequency of social learning. This model also has the

property that the average fitness of the equilibrium mix of social and individual learners is the same as a population composed only of individual learners. Culture is favored by selection, but it does not increase average fitness. The equilibrium mix of social and individual learning is an ESS (see 2.2.3).

Second, social learning may be favored because it allows individuals to avoid learning errors. Virtually all learning mechanisms allow the possibility of error. Consider, for example, an individual trying to decide which of two foraging techniques is better. She tries them both out, and chooses the one that yields the highest return. In a noisy world, small samples may often yield erroneous results—the technique with the higher return in the sample may have a lower return over the long run. Costs and errors may be linked, since making learning more sophisticated and costly will tend to reduce errors. Social learning can reduce the importance of such errors by allowing individuals to be more selective in their use of learned information. A social learning forager can use a rule like: Try out the two techniques and if one yields twice as much as the other adopt that technique; otherwise use the technique that Mom used. The use of such a rule will reduce the number of learning errors; however, it will also slow down the rate at which the population adapts. We have analyzed a simple model that incorporates this idea, which is sketched in Box 3.3 (see Boyd and Richerson 1988b, 1989a, for more detailed analysis). This model suggests that at equilibrium (the ESS) individuals always depend on a mix of social and individual learning, and the average dependence on social learning increases as the environment becomes less variable in either time or space. Unlike Rogers's model, the equilibrium population has higher average fitness than a population that depends only on individual learning; the cultural system for the inheritance of acquired variation is adaptive in changing environments.

So far, we have ignored genetic adaptation. We have seen that cultural inheritance is favored as environments become less variable. However, these are exactly the conditions under which selection will allow a population to adapt genetically to changing environments. What if we compare a system of genetic transmission plus individual learning with a cultural transmission system plus learning for the same subsistence trait? We have done such an analysis for a model that is conceptually similar to the one just presented, but using a different detailed structure (Boyd and Richerson 1985: Chapter 4). This model shows that the inheritance of acquired variation is favored relative to genetic inheritance plus individual learning unless the environment is either nearly constant or nearly random. In the context of this model, the range of environments under which culture or a similar system should be favored is rather broad.

This family of models gives as much support as a simplified theoretical model can to our intuitive argument. A cultural system of inheritance

Box 3.3. *The Optimal Dependence on Culture.* Consider the same model of guided variation as presented in Box 3.1. Now, however, we assume that the learning rules that govern acquisition of subsistence technique are genetically variable. The question is: How will natural selection acting on this variation shape the learning rule?

Suppose that the fitness of each behavior in each environment is given by the following matrix:

| | Fitness associated with | |
|----------------|-------------------------|-------------------|
| | Cooperative foraging | Solitary foraging |
| Dry conditions | $W + \delta$ | W |
| Wet conditions | W | $W + \delta$ |

where W represents a baseline of fitness having to do with things other than choice of subsistence, and δ is the component of fitness due to subsistence choice. The environment varies from generation to generation. The probability that parent's and offspring's environments differ is m . When $m = 0$, the environment never changes; when $m = 1/2$, the environment varies randomly on the time scale of a generation.

To consider the evolution of learning, we need to model learning in a little more detail than we did in Box 3.1. Suppose that the individual evaluates the two alternatives by trying each method and comparing their net yields. Let the observed difference between the net yields of individual foraging and cooperative foraging in a particular trial be x . Thus if $x > 0$, the net yield from solitary foraging is greater. However, due to the finite sample and the noisiness of the world, x will vary from trial to trial, even in the same environment. Thus, sometimes individuals will achieve a higher yield with the technique that is inferior on the average. We assume that individuals deal with this problem as a statistician might—they begin by acquiring an initial technique by imitating another individual; then they switch to the other technique only if the difference in yield is greater than a threshold value d , which we assume is genetically determined and variable. Individuals with larger values of d require more convincing evidence to switch and thus tend to rely on social learning more when compared with individuals characterized by smaller values of d .

As is illustrated in Figure 3.1, increasing d decreases the probability α that the individual learning trial will be decisive, but it increases the probability p of acquiring the best foraging technique given that individual learning is decisive. If d is made small, individuals will act as if they have great confidence in their own experience. However, if S , the noisiness of the environment, is large, they will very frequently adopt the wrong strategy by mistake. A large d avoids the possibility of making a mistake, but it will cause individuals to be more likely to depend on social learning. If the environment has recently changed this may be deleterious.

Elsewhere (Boyd and Richerson 1988b, 1989a) we have determined the evolutionarily stable value of α , which we label α^* . Figure 3.2 illustrates the results of this analysis. The relative importance of social and individual learning depends upon two things: the noisiness of the

(Box 3.3. Continued)

environment (more generally, the difficulty of accurate individual learning) and the degree of similarity of the average environmental condition from generation to generation. If there is a reasonable degree of resemblance between parents' and offspring's environments and individual learning is fairly inaccurate, strong dependence on social learning can be favored. This simplified analysis is extended in various ways in the papers cited above, and this essential behavior does not change.

combining individual and social learning ought to provide adaptive advantages in environments with an intermediate degree of environmental similarity from generation to generation. This is the regime where the faster tracking due to the evolutionary force of cumulative, relatively weak, low-cost individual learning pays off most. Most individuals can depend primarily on tradition, yet the modest pressure of individual learning is sufficient to keep culture "honest."

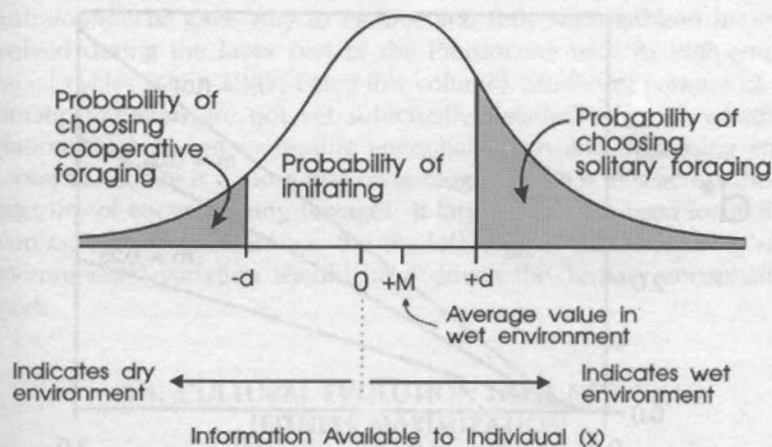


Figure 3.1. The effect of the learning threshold (d) on the probability of acquiring the best behavior by individual learning or tradition. The curve shows the probability of obtaining a given estimate x of the average difference in yield between the two environments ($2M$) from the small sample of years a young person experiences before choosing his strategy, assuming that environment is actually wet. If x exceeds $+d$, the young person ignores tradition and chooses the strategy best for a wet environment, solitary foraging. If x is less than $-d$, he mistakenly chooses the best strategy for a dry environment, cooperative foraging. If x is between $-d$ and $+d$, the young person follows tradition (adopts mother's strategy). The width of the bell-shaped curve gives the variability of the individual's estimate. When the variability of the sample is large compared to the average difference between environments, most individuals will find it difficult to determine the best strategy. Note that for the value of S illustrated, the probability of choosing the wrong strategy will be quite high unless the d interval is fairly wide; individuals should have only modest confidence in their own experience in this case.

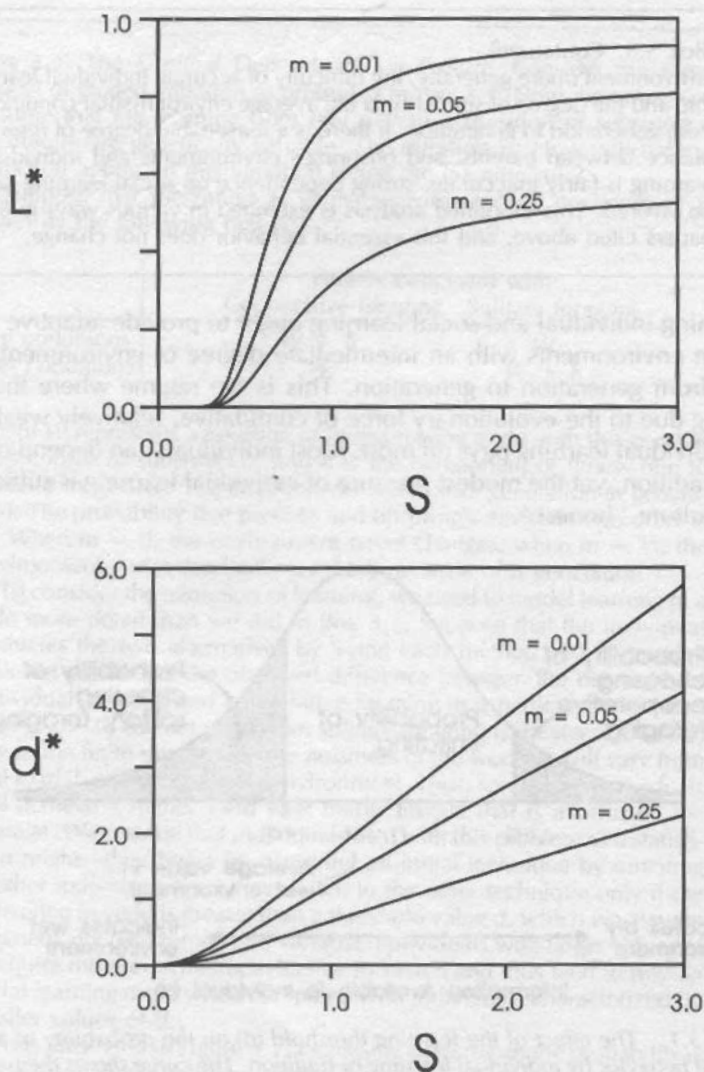


Figure 3.2. The equilibrium values of d^* (the learning threshold) and α^* (the fraction of a population acquiring a trait by individual learning) as a function of information quality (S) for three values of environmental variability (m). The upper panel plots the evolutionary equilibrium value of d^* , as a function of the quality of information available from individual learning (S), for three levels of environmental variability measured by the probability of parents' and offsprings' environments being different (m). The lower panel plots the fraction of the population that acquires the trait by individual learning at evolutionary equilibrium (α^*) as a function of S for the same three values of m . Individual learning becomes less important and therefore cultural transmission becomes more important as the quality of information from experience deteriorates (S increases) and the environment becomes more stable (m decreases).

Existing data do not allow a critical empirical test of this adaptive rationale for culture. Two lines of inquiry might be pursued to develop such tests. First, many animals seem to have simple capacities for social learning (Zentall and Galef 1988). Two animals for which social learning is apparently quite important are rats (Galef 1988) and pigeons (Lefebvre and Palametta 1988). These are weedy generalists that certainly have to adapt to variable environments. If a broader comparative study of animal social learning showed a significant correlation between environmental variability and capacities for social learning, the models would be supported. Second, humans are an extreme example of "encephalization" (brain enlargement), but many other animal lineages show more moderate encephalization during the Tertiary Epoch (the last 65 million years, Jerison 1973; Eisenberg 1981). At least the last 2 million years of the Pleistocene Era seem to have much more variable climates than the past (Shackleton and Opdyke 1976). It is perhaps not a coincidence that highly cultural hominids arose during the Pleistocene. The beginnings of the enlargement of the neocortex to the contemporary human scale began about the beginning of the Pleistocene as *Australopithecus* gave way to *Homo*, and fully sapiens-sized brains only evolved during the latter part of the Pleistocene with its high-amplitude glacial cycles (Klein 1989; Foley this volume). Studies of patterns of paleoclimatic variation are not yet sufficiently detailed to know whether the relationship between increasing encephalization and increasing environmental variability is a close one on geological time scales across the broad spectrum of encephalizing lineages. If large brains are used for individual learning and social learning, the models suggest that increasing rates of environmental variation should have driven the Tertiary encephalization trends.

3.4. CULTURAL EVOLUTION NEED NOT YIELD FITNESS MAXIMIZATION

Thus far we have seen how the forces of guided variation and direct bias can cause cultural evolution to mimic the results of genetic evolution. At equilibrium, individuals will act as if they chose the behavior that maximizes fitness. It may be that this behavior actually evolved over many generations as a result of guided variation and direct bias. However, for many purposes this fact will be irrelevant, and it will be possible to predict behavior based on fitness maximization.

Other forms of cultural adaptation are not so simple. In this section we argue that there are processes of cultural adaptation that (1) lead to different outcomes than would be predicted based on fitness maximization, but (2) are nonetheless favored by natural selection because they make social learning more effective.

3.4.1. Natural Selection of Cultural Variation

Natural selection can act on cultural variation to produce evolutionary change in the same way that it acts on genetic variation. For natural selection to occur there must be variation and variants must differ in ways that affect the number of copies of each variant that are present in the next generation (see 2.2.1). Many culturally transmitted traits have substantial effects on fitness. Belonging to a pronatalist religion tends to increase fecundity, and belonging to an abstemious one tends to increase survival. Thus, if religious beliefs are transmitted from parents to offspring, selection on cultural variation can produce adaptations in the metric of genetic fitness.

People often acquire beliefs and values from individuals other than their parents. Such "asymmetric" cultural transmission makes adaptive sense. Direct bias is more effective if naive individuals survey many models before they make up their minds whose trait to adopt. If Dad is a poor hunter, why not observe the strategies of several other men before making up your mind how you will approach the problem? Thus, selection may favor a tendency to imitate nonparental individuals.

When cultural variation is transmitted nonparentally, natural selection may favor genetically maladaptive cultural variants. Whenever individuals are culturally influenced by grandparents, teachers, peers, and so on, natural selection acting on cultural variation can favor the increase of behaviors that increase the chance of attaining such nonparental roles. When the traits that maximize success in becoming a parent are different from those which maximize success as a teacher, priest, or grandparent, natural selection acting on cultural variation can cause genetically maladaptive traits to spread. In most past societies, various risks ensured that few people lived to see their grandchildren. Surviving to grandparental age might require being unusually cautious, more cautious than would be optimal from a genetic fitness point of view. Too-cautious behaviors might easily spread throughout a society if grandparents play any significant role in socialization. This effect is easily seen in a simple model—see Box 3.4. The result is intuitively reasonable and is robust to the relaxation of many of the special assumptions of this simple model (Boyd and Richerson 1985:Chapter 6).

Example: The Demographic Transition. Human demography may provide examples of this effect. Many urban populations, especially elite populations, throughout recorded history seem to have reproduced at rates below replacement despite an economic capacity to out-reproduce nonelites (Knauff 1987). Ancient cities were like tar pits, drawing country folk into their alluring but disease-ridden precincts. The modern demographic transitions that occurred in Europe at various times from the beginning of the

Box 3.4. *Natural Selection on Cultural Variation.* Suppose that, in some given society, people acquire (culturally) beliefs about the existence of an afterlife in which believers are rewarded. For simplicity, further suppose that there are only two variants—believers and unbelievers. Children acquire their beliefs by imitating one parent and one priest. Parents and priests have different weights in socialization processes, such that the importance of parents can be measured as A and of priests as $1 - A$. Beliefs in an afterlife will affect the chance that their bearer will become a priest or a parent. Let the relative superiority of one variant of the trait at helping their bearers become parents or priests be v and w , respectively. Suppose that believers are more likely to become priests than unbelievers, and thus w is a small positive fraction. Further suppose that believing reduces the likelihood of becoming a parent, and v is a small negative fraction.

The change in the frequency of people who value piety, Δq , is approximately

$$\Delta q \approx q(1 - q)(Av + (1 - A)w)$$

Thus, one of the two beliefs will increase at the expense of the other. Which one depends on the relative magnitude of their effects on life chances and the weight of parents versus priests in what children learn. For example, belief in an afterlife will increase whenever $Av + (1 - A)w > 0$. We might suppose that parents are rather more important in socialization than are priests, so that A is larger than $1 - A$ (say 0.75 and 0.25, respectively). However, becoming a priest may be a more selective process than becoming a parent—almost all priests are believers, while there are many parents of each type. If so, w will be a larger positive fraction than v is a negative one (say 0.1 versus -0.01). If so, $Av + (1 - A)w$ may be positive even if the importance of priests in socialization is relatively small. In our example, the value is $+0.0175$. It is only necessary that becoming a priest is sufficiently more selective to compensate. (See Richerson and Boyd (1984) for details of the analysis. Some generalizations are examined in Boyd and Richerson 1985:Chapter 6.)

nineteenth century onward are another striking example. As people have become wealthier in the industrialized countries, they have tended to lower their fertility and completed family sizes to replacement or even below. This reverses the correlation between wealth and reproductive success often found in rural pastoral and agricultural societies (see Chapters 11 and 12). Coale (1986) has collected some examples of strong fertility control and population declines among rural populations in Europe before the main transition, but these are rather isolated cases, because only urban societies could draw enough cultural recruits to sustain a demographic transition given premodern rates of mortality. Other fertility-controlling subcultures seem to have simply gone extinct.

At least for the modern European transition, a good case can be made for the spread of low-fertility norms due to their effects at promoting cultural success. The modernization of Europe greatly increased the social complexity of European societies. Many new professions arose that were allocated on the basis of achievement, rather than upon inherited rank as was common in premodern Europe. Professional educators to serve the need for universal literacy are one example. Professional entrepreneurs are another. Many of these new roles besides the formal teaching ones carried responsibility for education. Entrepreneurs and business managers had an important role in training factory workers, clerks, and so forth for the new occupations of the industrial era.

Relative to the previous agrarian society, European modernization must have resulted in more nonparental transmission from more competitively selected individuals. Modern data (Terhune 1974) suggest that raising children who are likely to be successful in competition for such roles conflicts with having a large family. Children who do well in school and acquire similar skills for professional and entrepreneurial competition require considerable parental investment. Many readers will be familiar with the conflicts between having families, especially large families, and the demands of modern careers. It seems likely that the occupants of the new competitive roles tended to be drawn from a fraction of the population that already valued small families within which greater investments of parental effort per child were possible. As the weight of "teachers" in cultural transmission increased, and as these roles became allocated on the basis of achievement rather than inheritance, low-fertility norms could spread to the whole population.

Similarly, Knauf suggests, preindustrial cities could draw their population from the countryside despite being demographic "black holes" because of the cultural dominance of the city over the rural population. City elites tended to define the norms and values of the whole society because of their dominance of governmental, economic, and spiritual institutions effective in nonparental transmission of culture, and hence to draw replacement personnel from among members of the demographically successful countryside "infected" with these values.

3.4.2. *Why Selection May Allow Culture to Deviate*

The fact that natural selection may favor genetically maladaptive traits does not mean that cultural evolution will necessarily result in maladaptive outcomes. Many core beliefs and values are usually acquired from parents and other close relatives, and selection on variants so transmitted will tend

to favor genetic-fitness-maximizing behavior. Even if selection acts to increase the frequency of maladaptive beliefs, the effect may be unimportant if direct bias and guided variation are sufficiently powerful to keep genetically maladaptive variants at low frequency. Suppose, for example, natural selection acting on cultural variation favors a belief in a god who rewards the pious in heaven, and that this belief causes people to have families that are smaller than the genetic optimum, either because they join religious orders, or because they devote resources to support the church. Family sizes still might be optimal if the effect of selection is counteracted by direct bias. The evolved predispositions that underlie direct bias (e.g., sexual desire and a love for children) might cause people to reject these religious beliefs, or at least to obey them mainly in the breach.

On the other hand, direct bias and guided variation may often fail to counteract the effects of selection on non-parentally transmitted variation because it is too difficult to determine which beliefs best serve the individual's genetic interest. Earlier we showed that the optimal reliance on cultural transmission depends on the cost of learning and the likelihood of learning errors. When it is difficult to determine which of two variants is best, learning is costly and error prone, and therefore natural selection acting on genes favors a heavy reliance on cultural transmission. Does God exist? If He does, and He rewards the pious, some evolved predispositions—fear of death, love of comfort—may overbalance the desire for a large family and lead people preferentially to adopt the practices sanctioned by religion. But determining whether God exists and exactly what He (She, They) expects of us has proven to be very difficult over the millennia.

The idea of a god who rewards the pious 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 effective? 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(s) should one marry? What mixture of devotion to work 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 concerning 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. 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 the information collected from the environment.

As the effect of direct bias and guided variation 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. 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. However, it is also likely that cultural variation often responds to selection for behaviors that conflict with genetic fitness. Selection on genes that regulate the cultural system may still favor cultural transmission, because *on average* it does better than genes could do alone.

These ideas are consistent with much behavioral variation both within and among societies being genetically adaptive. In 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 the religious beliefs of the rich and the poor are equally fervent. The same argument applies to variation among societies. People are more likely to become a celibate in a society where they can enhance their relatives' reproductive success because celibates are admired, wealthy, or powerful than in one in which such people are recruited by poor, despised religious minorities that restrict opportunities for nepotism.

More generally, we think it is plausible to view genetic and cultural evolution as a tightly coupled coevolutionary process in humans. In some cases, forces like guided variation and direct bias will be based on genetic variation, strong, and expressed in the environments under which selection produced the guiding rules. In such cases, fitness will be increased by the presence of the cultural system, and behavior may be accurately predicted without explicit reference to the dynamics of cultural evolutionary processes. In other cases, the decision-making forces will be weak, or expressed in a cultural environment that distorts their effects. In these cases, even when the cultural system does act to increase fitness, it will be necessary to account for cultural effects in more detail.

3.4.3. Indirect Bias

A similar argument can be made for two other bias forces, *indirect bias* and *frequency-dependent bias*. These forms of biased transmission allow individuals to better their chance of acquiring adaptive behavior, but at the same time give rise to processes that may not always result in fitness-maximizing behavior.

Indirect bias results when individuals use some traits, for example, those connoting prestige, as an indicator of whom to choose as a cultural model. Once chosen, one may imitate many characteristics of an admired other without further bias. If variants of these latter traits are correlated with the variants of the indicator trait, the correlated variants will increase due to this indirect bias. This process may favor ordinary adaptations and these rules are effective at economizing on information costs. Indirect bias may also allow cultural variation to respond to evolutionary forces in ways that can, under some circumstances, yield different outcomes than would be predicted based on fitness maximization models that ignore cultural inheritance.

There are often likely to be easily visible traits that are correlated with fitness, such as wealth, even when the exact behaviors that contribute most to fitness are very hard to evaluate. In such cases, it makes sense to imitate everything that wealthy people do in an effort to acquire the traits that make them wealthy, but without actually trying to determine exactly how wealth is produced. Irons (1979a) presented evidence from a group of Iranian Turkomen pastoralists that showed social status and biological reproductive success to be strongly correlated. High-status men had larger herds and more wealth, and translated these economic advantages into more wives and more and healthier children. As Borgerhoff-Mulder notes in Chapter 11, a number of studies have documented a similar correlation in other subsistence societies. If wealth partly derives from subsistence or social skills that can be acquired by imitation, it makes adaptive sense to imitate the wealthy. The assumption that wealth is correlated with adaptive behavior is perhaps generally correct; if so it would be sensible to imitate wealthy people even if it is not always very clear just what components of wealthy people's behavior are adaptive.

Studies of the diffusion of innovations (Rogers 1983) document that people use prestige systems in a sophisticated way to acquire new traits. Especially in the case of the poor and less educated, whose ability to bear the costs of direct evaluation of innovations is limited, people tend to adopt the practices of "opinion leaders" of higher status. However, it is people of high *local* status who are preferentially imitated, not socially distant elites whose life situation is very different from potential adopters. When informa-

tion about a novel behavior is difficult or expensive to acquire, the simple rule, Imitate the most successful people whose general situation is roughly comparable to mine, is likely to be an effective mechanism for acquiring adaptive traits so long as the correlation between cultural and biological success is high. A poor Turkomen herdsman is probably well advised to imitate the herd management practices of his wealthier neighbors and ignore the advice of technical experts whose recommendations may derive from principles developed in Colorado, Switzerland, or New Zealand. The wealthy man, who perhaps can read manuals for himself and can afford to make a few mistakes in search of a high-payoff new method, is more likely to make effective use of such technical experts.

The indirect bias force can lead to dynamics that are similar to runaway sexual selection. Darwin (1871) believed that mate-choice sexual selection (see Chapter 11) was responsible for the maladaptive elaboration of secondary sexual characters such as the feather displays of male peacocks. When there is mate choice based on some visible trait, a trait that was originally correlated with fitness might become wildly exaggerated as evolution comes to respond more to the choice process itself than to ordinary natural selection. This subject remains controversial in evolutionary biology, but in theory this mechanism can operate (Lande 1981; Pomiankowski 1988) and seems to account for otherwise mysterious characters such as the elaborate penises of many insects (Eberhard 1985). The indirect bias process works in a similar way except that individuals choose their cultural parents in addition to their mates based on criteria such as indicators of prestige. Models show that the runaway dynamic is also possible in the case of indirect bias (Boyd and Richerson 1985:Chapter 8). We have argued that many phenomena ranging from maladaptive fads and fashions to group-functional religious beliefs to symbolically marked boundaries between groups might result from the properties of indirect bias (Boyd and Richerson 1987, 1990a; Richerson and Boyd 1989).

3.4.4. *Frequency Dependent Bias*

Guided variation, direct bias, and natural selection on parentally transmitted variation will tend to cause the most adaptive behavior to be more common than alternative behaviors. Thus, when it is difficult or costly to determine which variants are adaptive, it may be best to bias imitation in favor of the commonest type in the population. Recall the aphorism, When in Rome, do as the Romans do. We label this process *frequency-dependent bias*. Humans are widely suspected of conformity in their behavior, and this bias rule is quite plausibly important.

Frequency-dependent bias may cause group selection to be a more important process in cultural evolution than it seems to be in genetic evolution

(see 2.2.2). Consider a large population subdivided into many smaller, partially isolated groups. Frequency-dependent bias reduces variation within groups because rarer variants are less likely to be imitated and therefore to become even rarer. At the same time, frequency-dependent bias increases variation between groups because immigrants entering a group will be rare and also subject to discrimination in transmission. For this reason, group selection may be more important in shaping cultural variation than it is in shaping genetic variation. If so, group level adaptations may be more common in the human species than in other species (Boyd and Richerson 1982, 1985:Chapter 7, 1990b).

Example: Cooperation among Nonrelatives. Human societies exhibit much more cooperation than is typical of vertebrate societies. This tendency is most marked in the complex societies of the last few millennia, where the degree of division of labor, amount of altruistic self-sacrifice, and coordination of complex activities rival and exceed that of the advanced social insects (Campbell 1983). Even the simplest hunting and gathering societies are much more complex and cooperative than the societies of any other social mammal. The human sexes cooperate in an extensive division of labor between hunting and gathering. There is much sharing of food and other resources, especially within bands. Relatively peaceful, cooperative relations are generally maintained between several bands that share a common language and culture, numbering a few hundred to a few thousand individuals. By contrast, even among our closest relatives the chimpanzees, the sexual division of labor is absent, food sharing (other than mothers with offspring) is minimal, and political cooperation is restricted to the handful of closely related males that form the core of a troop (Goodall 1986).

In other animal societies, patterns of cooperation are well explained by kin selection and reciprocal altruism. For example, the complex societies of the social insects are based on kin selection. Only a few closely related individuals are reproductively active in the colony, and the cooperating sterile workers are their offspring (Wilson 1975). The best documented cases of reciprocal altruism, involve pairs of individuals, as in the example of the species of "cleaner" fish and shrimps that eat ectoparasites from the mouths and gills of larger fish (Trivers 1971).

It is an open question whether either of these two mechanisms is sufficient to explain the scale of cooperation observed in even the smallest-scale human societies. The problem with explanations based on kin selection is that humans cooperate with nonrelatives in large-scale societies. Van den Berghe (1981) has proposed that kin selection will account for patterns of cooperation observed in small-scale societies, and that cooperation in complex societies is the result of a cognitive mistake. The empirical problem with reciprocal altruism is that there are no known cases of large-scale cooperation attributable to reciprocity (unless humans are such). Alexander

(1987) proposed that human cooperation is supported by complex webs of "indirect reciprocity" that is restricted to humans because only our species has the cognitive sophistication to keep track of the complex webs of interactions that result.

Darwin (1871) was first to advance the notion that human societies might be subject to group selection, although he was not generally attracted to such explanations. Hamilton (1975) has elaborated this hypothesis, especially in connection with warfare as an agent of effective selection between groups. The empirical problem with this hypothesis, it seems to us, is that human groups are genetically open systems. As Chagnon et al.'s (1970) data for the Yanomamo suggest, groups that are successful in warfare often incorporate female and juvenile captives, and marriage across ethnic boundaries is common in any case. In the famous case of the Nuer expansion in the Sudan in the nineteenth century, wholesale capture and ordinary marriage of the defeated and surrounded Dinka was the demographic mainstay of the expansion (Kelly 1985). In small-scale societies, individuals in groups defeated in war typically disperse to other groups where they have relatives or other connections. These sorts of patterns, if they are indeed general, are those that will tend to reduce any genetic differences between groups and increase genetic heterogeneity within groups. As noted in Chapter 2, lack of genetic isolation of groups is the main difficulty with group selection.

Group selection based on cultural variation is a possible explanation for the evolution of human cooperation. Frequency-dependent bias may maintain enough cultural variation between groups for group selection to be important. It has the by-product of discriminating against rare variants in the population. Thus, a fair amount of immigration of less altruistic individuals (say from bands defeated in war) will not convert a more altruistic group to a less altruistic one. As long as the less altruistic variants are a minority, the conformity effect acts as a powerful impediment to this variant's increase despite assuming the usual within-group advantage to less altruistic behavior. This mechanism does not even require the demographic annihilation of groups with too few altruists, merely their disruption and dispersal of their members. So long as it is rare for such dispersal events to tip more altruistic populations over the threshold where the less altruistic variant begins to increase, between-group selection can be a potent force (Boyd and Richerson 1982, 1985:Chapter 7).

None of these hypotheses is completely implausible. Our theoretical studies of reciprocity in large groups, including models incorporating Alexander's idea of indirect reciprocity and models of punishment, suggest that reciprocity should be restricted to quite small groups (Boyd and Richerson 1988a, 1989b, in press b). Even in groups as small as 6–10, reciprocity is much more difficult to get started in a population than it is when only pairs

interact. The models also indicate that a synergistic combination of kin selection and reciprocity does not tend to make it easy to get reciprocity started when rare in larger groups, unlike the case for pairs. However, this area is still poorly explored, and it may be that strategies as yet unmodeled will be more effective. It is certainly possible that some combination of kinship and reciprocity can explain cooperation in small-scale, face-to-face societies. Campbell (1983) argues that cultural group selection is only necessary to explain the levels of cooperation and integration in the complex, large-scale societies of the last few thousand years. These societies are so large as to involve extensive cooperation among largely anonymous masses of people. It is harder to see how kin altruism and reciprocity can knit these societies into workable complexes than in the case of hunting and gathering societies where much of the political power may reside in 100 or so adult males, who cooperate for the most part in coresidential groups of only 10 or so. Critical theoretical and empirical work is only beginning on this important problem.

3.5. RELATIONSHIP TO OTHER VIEWS

3.5.1. *Human Sociobiology*

The publications of Alexander (1974) and Wilson (1975) mark the advent of human sociobiology. Although neither of these works was primarily concerned with human behavior, both insisted that the rapidly developing evolutionary theory of ecology and social behavior was applicable to the human species. Much of the work in this book has been stimulated by this claim, and, as you have read in Chapters 1 and 2, the commonest method of studying human behavior is the use of fitness optimization and ESS models. Oversimplifying somewhat, human sociobiology has mainly added a genetic evolutionary component to classical rational-choice models (Hirshleifer 1977; Boyd and Richerson 1985:157–166).

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 great deal of contemporary variation is adaptive, that is, that one can generally predict variation in behavior by determining what is fitness maximizing. 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 adaptations. Others, including Tooby and Cosmides (1989) and Barkow (1989), 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. However, 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. We can still understand human behavior in Darwinian terms, but only as the result of now outmoded evolved predispositions interacting with contemporary environments. Symons (1989) has labeled proponents of these two hypotheses *Darwinian anthropologists*, and *Darwinian psychologists*, respectively.

Our view is both something like Darwinian anthropology and something like Darwinian psychology. From the former perspective, apparent departures from fitness-optimizing behaviors can be viewed as fitness optimizing under a constraint of information cost. Like most adaptations, a capacity for culture has costs as well as benefits. Culture is peculiar only in that some of the costs of having culture are tolerating its evolutionary activity. Ordinary learning will often lead to maladaptive behavior because unless it is easy to learn, individuals will often, more or less at random, learn the wrong thing. In the case of culture, the errors made will tend to be systematic rather than random, but so long as the systematic errors are less costly than the unsystematic ones, natural selection will favor capacities for culture. Since all evolutionary optimization arguments involve constraints (see 2.2.4), the costly-information argument could be subsumed under Darwinian anthropology.

On the other hand, the key postulate of Darwinian psychology (Barkow 1989; Cosmides and Tooby 1989) is that departures from the expectations of simple models can be traced to specific evolved psychological mechanisms acting in specific environments. The costly-information argument similarly suggests that a tendency to depend upon nonparental transmission, the use of conformist transmission, and so forth must, averaged over many societies and long periods of time, be adaptive. These mechanisms, a propensity for which might well be organic, only go wrong in some times and places. We suspect that there is nothing magical about the hunting and gathering past. Even in such societies the evolutionary dynamics of culture likely mattered because culture helped people to adapt to an environment that was highly variable in space and time. If so, all the considerations of information cost constraints we have discussed would have applied. It seems unlikely that a static "environment of evolutionary adaptedness" would have favored the evolution of culture capacities in the first place since culture is mainly an advantage in variable environments. However, it is certainly plausible that some kinds of departures from basic fitness-optimizing expectations may have become more dramatic since agriculture so changed the subsistence

and social environment of human populations. It is easy to imagine that the institutions of complex societies are built willy-nilly using a psychology adapted for hunting and gathering.

3.5.2. *Darwinism Is Consistent with Many Views of Human Nature*

The idea that the human psyche has been shaped by natural selection allows human sociobiologists to make general predictions about human behavior. Darwinian anthropologists think that the beliefs and values that predominate in a particular culture should be the ones that maximize reproductive success in the environment at hand. Darwinian psychologists 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 atavistic predispositions in contemporary environments. In either case, making predictions often requires detailed knowledge of the relationship between behavioral variation and variation in reproductive success in particular environments, either past or present. However, there are many behaviors that would seem to be maladaptive in any environment, so both kinds of Darwinians are prepared to agree about a range of general predictions.

Most human sociobiologists agree that the following two principles are necessary consequences of this argument:

No group-beneficial explanations. Human behavior can never be explained in terms of group benefits. Selection should have shaped the human psyche so that individuals' choices increase their reproductive success and that of their relatives, either in contemporary environments or under Pleistocene foraging conditions. In neither case should selection favor behaviors because they benefit a social group. Any observed group benefits must be side effects.

No mentalism. Human behavior is only proximally, not ultimately, the result of cultural rules. Selection should have shaped the human psyche so that individuals constantly modify their behavior in their own interest. Human behavior cannot be explained in terms of cultural history. Rather, it must be explained in terms of the pragmatic consequences for survival and reproduction. This means that behavioral differences between groups are usually the result of environmental or technological differences, not of history.

These two principles are *deductions*, consequences of the belief that natural selection has shaped psychological predispositions that govern human behavior, and given an understanding of what kinds of outcomes are favored by selection. We believe that these deductions do not necessarily follow from Darwinian premises. There is little doubt that the human psyche *was shaped by natural selection*. However, *if our view of culture and its*

evolutionary origin are correct, this fact does not force us to accept either of these two principles. It is possible that an evolved psychology could cause the evolution and spread of group-beneficial beliefs and values *because* they are group beneficial. It is also possible that an evolved psychology could cause people to adhere to culturally acquired rules, even though those rules are not in their immediate interest, and therefore that sometimes it may be necessary to explain human behavior in terms of cultural history.

We believe that Darwinian theory is a rich source of models of cultural change. It can play a broadly unifying role in the social sciences; its methods of evolutionary analysis should not be viewed as committing one to narrow conclusions about human behavior. The two sociobiological principles mentioned above are in conflict with a great deal of thinking in the social sciences. Thus, human sociobiologists are in the position of saying to whole schools of social science: "If you took the trouble to learn a little about evolution, you would see that your whole view of society and how it works is obviously and egregiously wrong." In contrast, if our view of culture is correct, these are questions for empirical investigation. Human behavior may or may not be purely selfish or bound by cultural rules, depending on the factors discussed above. Thus the debate between human sociobiologists and their critics can be a matter of empirical test rather than dogma. In what follows we illustrate this argument with two examples.

Group-Level Functionalism. In the social sciences, there is a long tradition of explaining behavior in terms of group-level functions (e.g., Vayda and Rappaport 1968). The insistence of some human sociobiologists that group selection cannot occur (see Chapter 2) has made it seem to some observers as if Darwinian approaches are inherently incapable of offering group functionalist explanations. Rappaport (1987), in a retrospective discussion of his classic (Rappaport 1968) study of ritual and warfare in New Guinea, is unmoved by the arguments of human sociobiologists, arguing that the evidence that humans have group-level functions is virtually inescapable. We believe cultural evolutionary models furnish the tools to investigate such controversies. If humans are unique in the animal world in some behavior, the processes of cultural evolution are a plausible candidate to explain the difference, since we are unique in our reliance on culture. As we noted in section 3.4.4, conformist transmission effects can set up the preconditions for group selection to operate. This or other cultural mechanisms offer testable hypotheses that might account for why humans cooperate on such a large scale without reproductive suppression of the mass of society's members. Studies of the degree to which people really do conform when they acquire cultural traits relevant to cooperation, and of the degree to which between-group cultural variation is actually maintained, should resolve this question.

History and Diffusion. It is interesting to note that the Darwinian project is far from complete in biology. However, disputes are conducted within a broadly Darwinian framework, which does provide a language of communication at the minimum. The recent dispute over the relationship between the long-run fossil record (macroevolution) and the small-scale changes studied by most evolutionary biologists (microevolution) is an example (see also section 5.2). Some paleontologists (e.g., Valentine, 1973) think that the conventional processes of microevolution, when combined with the known evolution of the earth due to plate tectonics, can account well for the fossil record. Others (e.g., Gould 1982) suppose that biological processes that operate over very long time scales are required to account for the fossil record.

The social sciences have long dealt with similar disputes (Vayda and Rappaport 1968; Renfrew 1984; Nelson and Winter 1982 have good discussions of this issue). To what extent can we account for human behavior in terms of responses to immediate environmental contingencies, and to what extent must we consider the effects of history and diffusion? We have already seen that Darwinian psychologists and Darwinian anthropologists give different answers to this question. Are the differences between, say, contemporary Americans and Japanese primarily a result of adaptation to contemporary local circumstances, or to the fact that these societies have developed historically in near isolation and hence have developed very different solutions to the same problems? Both effects are obviously important, and for some traits one or the other explanation clearly predominates. The linguistic differences between Americans and Japanese are almost wholly a product of a long independent history, while the similarities of industrial technology are the result of conscious borrowings and independent inventions of very similar procedures for common purposes.

The most interesting cases are subtler traits, such as social organization. The Japanese have adopted many Western social institutions, such as parliamentary democracy, yet they remain distinctively Japanese in many respects. Some people in Western nations are intensely interested in adopting those features of Japanese social organization that are responsible for their successes in industrial production, but it is not clear just what needs to be copied to replicate this success. In the worst case, we might imagine that the Japanese tendencies to be very good at industrial production but relatively poor at industrial innovation are strongly linked, so that neither society can acquire the strengths of the other without accepting its weaknesses.

Theoretical investigation of this question is still in its infancy, but the general form it will take is easy to see. For historical factors to be important, there must be constraints that prevent evolutionary optima from being reached quickly (on the evolutionary time scale), or there must be processes that multiply equilibria so that different societies can get stuck at different

optimal points. Historians (e.g., McNeill 1963) often picture the last 10,000 years of human history as the working out of the potential inherent in the development of agricultural modes of subsistence. The incipient agricultural societies of 10,000 years ago did not advance to the industrial level in a few generations mainly because the innovations required to create such societies occurred sporadically in different locations. Considerable time was required for each innovation, such as iron metallurgy, to diffuse widely and stimulate the next logical step. In our terms, this hypothesis implies that forces like direct bias and guided variation are relatively weak, and that the uncritical transmission of a cultural tradition is a strong effect. On the other hand, it might be that social organizational factors are more important than invention of technology *per se*. Models of the evolution of cooperation in large groups suggest that many different strategies and combinations of strategies can be ESSes, that there are inherently many different stable forms that human social organization might take (Boyd and Richerson 1988a). If, as Marx argued, technical innovations tend to upset existing social arrangements, then the need for social innovation to accompany technical innovation will act as a substantial brake on the latter. Interestingly enough, strong optimum-seeking forces like direct bias and guided variation will *slow* the rate of evolution when there are multiple ESSes because it will be harder for chance effects to help societies slide from a lower local optimum to a higher one. Only some form of group selection between societies or subsocieties (like classes) will be effective in spreading superior innovations, and this may be a slow process (Boyd and Richerson 1990b). Thus, there are several rather different potentially satisfactory explanations for the long-run historical patterns we observe. (For a longer version of this argument, see Boyd and Richerson in press a.)

These examples illustrate one of the important virtues of Darwinian theory: It can be used to capture many different kinds of explanations in a common framework that makes pointed and critical comparison possible. This makes it an unparalleled device for communication between schools and disciplines in the social sciences (as it is in biology). It is a mistake to identify Darwinism too closely with its substantive discoveries in biology, such as the importance of natural selection and the dubiousness of group selection, especially when the application is to a rather peculiar organism like humans with a peculiar system of inheritance like culture. The application of Darwinian methods to culture does not commit one to the adaptationism that results from the simplest models of natural selection. At least to speak for our own experience, conceiving of Darwinian models of (substantively) "un-Darwinian" hypotheses, analyzing simplified versions of them, and considering the implication of the results clarifies complex long-disputed issues such as the possibility of group functions and the role of historical explanations. We believe that such theoretical clarification will

make empirical tests more efficient and thus the ultimate resolution of such questions possible.

3.6. SUMMARY

The main aim of this chapter has been to show that cultural evolution is a Darwinian process. Culture is like genes in the sense that information about how to behave is transmitted from individual to individual. Each individual "samples" the culture of the past by observing others or by being taught, and then potentially becomes sampled in turn. But in many other respects, culture is unlike genes. One or many cultural "parents" may be sampled instead of only two, for example. The most fundamental structural difference between genes and culture is that cultural inheritance is a system for the inheritance of acquired variation. Individuals' capacity for learning and decision-making is harnessed directly to the cultural transmission system in ways that apparently do not exist in the case of genes.

The differences between the genetic and cultural systems gives rise to interesting scientific problems. How does the cultural evolutionary process work? How does it interact with the genetic evolutionary process to produce adaptations? What are we to make of apparently maladaptive cultural practices?

The most important difference between the evolutionary processes of the genetic and cultural systems is the existence of decision-making forces in the cultural system. It is not only the survival and fecundity of variant individuals that causes evolutionary change in the cultural system. The decisions that people make as they learn for themselves or decide whom to imitate or what behaviors to adopt also affect cultural evolution.

The decision-making forces—guided variation and the various forms of biased transmission—are what gives the cultural system of inheritance an adaptive advantage in certain kinds of variable environments, according to the theoretical analysis described in section 3.3.1. When individual learning is coupled to the possibility of transmission by imitation, the cultural system can track environmental fluctuations more quickly than can genes, and at a lesser information cost (or with fewer errors) than relying entirely on individual learning. It is optimal to depend mostly on imitation when learning is costly or error prone, and when the environment does not change too rapidly. Even in this case, the small amount of individual learning is important; it causes the population to track the changing environment more effectively than genes, and can give the cultural inheritance system a considerable advantage over the more familiar genes-plus-individual-learning system. *Human diet choices, for example, may well be closer to optimal than they otherwise would be due to this effect.*

In addition to making ordinary adaptive processes more efficient, the existence of culture may have contributed to qualitatively new human adaptations. Human eusociality is an example. We hypothesize that cultural processes like conformist transmission permit a measure of group selection on cultural variation. The food sharing and division of labor of hunting and gathering bands appears to have been crucial to the extraordinary geographical expansion of the human species during the Pleistocene. The demographic success of complex societies is clearly dependent on cooperation and the division of labor. Culture may be the analog of the peculiar "haplodiploid" system of sex determination in the ants, bees, and wasps that makes sisters more related to each other, and hence prone to the evolution of sterile-worker eusociality. Conformist transmission can raise cultural "relatedness" far above genetic relatedness, even in large groups. Note that in a group in which the cultural environment has evolved to favor altruistic behavior, genetic impulses to altruism might be favored by mate selection. Those with a genetic predisposition to altruism may have had greater mating success.

Finally, there is no guarantee that all cultural traits will be adaptive from the genetic point of view. As the theoretical analysis described in section 3.4.1 shows, the existence of nonparental transmission, among other things, gives culture a measure of evolutionary activity in its own right. When the decision-making that might more closely control cultural evolution is costly, genetic fitness is best served by a system that tolerates some deviance from genetic fitness optimization. Better some systematic cultural deviations from fitness optima than more severe random ones due to individual error.

A quite suggestive case can be made that the theoretically arresting cases of novel human adaptations and unique kinds of maladaptations due to culture are also real and important. But only suggestive! The amount of critical fieldwork and experimentation that has been undertaken to test these ideas is still quite small. We as yet know far less about cultural evolutionary processes and their interactions with the genetic system than we know about ordinary organic evolution. It is an interesting historical paradox that we know least about evolutionary processes in the animal whose evolution interests us most.