COMMENTARY

WHY IS CULTURE ADAPTIVE?

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WHY IS culture adaptive? One of the distinctive features of the human species is the extent to which behavior is acquired by teaching and imitation. The rapid radiation of the human species into a large variety of ecological niches over a wide geographical range during the last 100,000 years suggests that this mode of adaptation may be quite effective. Until recently, however, few evolutionary biologists have attempted to identify the properties of cultural transmission that make it an effective way of acquiring behavior. Very different answers to this question have been suggested by Charles Lumsden and E. O. Wilson in *Genes, Mind, and Culture* (Harvard Univ. Press, 1981) and by H. R. Pulliam and Christopher Dunford in *Programmed to Learn* (Columbia Univ. Press, 1980).

In both of these books, culture is conceptualized in a similar way. Culture is a system of social learning. Skills or attitudes are acquired from conspecifics by teaching or imitation. Culture is therefore a system of inheritance analogous in some ways to genetic inheritance. Unlike genes, cultural transmission is coupled to ordinary learning. Variants invented or modified by one individual can be communicated to others. From this common view of culture, how-

ever, the authors develop quite divergent explanations for why culture is adaptive.

Although *Genes, Mind, and Culture* represents a much longer and more ambitious treatment of the role of culture in human evolution than does *Programmed to Learn*, Pulliam and Dunford appear to present a more interesting and plausible explanation of why culture is adpative than do Lumsden and Wilson. Each of the two views is examined below in more detail.

LUMSDEN AND WILSON'S VIEW

Lumsden and Wilson base most of their conclusions on a simple model of cultural transmission in which there are two behavioral variants, referred to as "culturgens." Every individual is assumed to learn both variants, but at any given time any particular individual actually uses only one of the two variants. They suppose that every so often each individual evaulates his behavior and with some probability stops using the variant that he currently uses, and begins using the alternative variant. This constitutes a simple model of decision making. If individuals characterized by variant 1 are more likely to adopt variant 2 than individuals characterized by variant 2 are to adopt variant 1, then the decision process (or

as they put it, the "epigenetic rule") favors those characterized by variant 2, and the usage of that variant will tend to increase in the population.

It is important to understand that this model represents cultural variation and cultural evolution in a very special way. Normally, we think of culture as skills or mental models acquired by imitation from other individuals; cultural evolution occurs when new skills or models are introduced and spread in a society. Cultural evolution does not occur instantly; rather there is a kind of "cultural inertia." If a sudden change in the environment makes the most common variant maladaptive, it is likely to remain common for a time because it is still frequently practiced and observed. If a highly valuable skill is invented, it will take a while to spread through the whole population. Lumsden and Wilson allow for cultural inertia in their models by assuming that an individual's decision to use variant 1 or 2 may depend upon the frequency of usage of the two variants in the population. For example, individuals using a "trend watcher" decision rule are more likely to use the more common behavioral variant. In a population of trend watchers, innovations will spread slowly.

The problems that exist in Lumsden and Wilson's theory are not a direct result of this approach to modeling cultural transmission. Rather, they arise because Lumsden and Wilson do not see the frequency-dependent nature of decision-making as crucial to understanding why culture is adaptive. In their Chapters 5 and 6 Lumsden and Wilson consider first the effect of culture on genetic fitness, and then the coevolution of culture and genes. In these chapters the choosing of behavioral variants is either completely independent of the frequency of usage of the behaviors or the effect of frequency is assumed to be extremely weak. Some genotypes are supposed to have a higher (frequency-independent) probability of choosing the behaviors that result in higher fitness than other genotypes. Not surprisingly, these genotypes are favored by natural selection. Lumsden and Wilson never consider how the amount of frequency

dependence may affect the adaptiveness of cultural learning.

Lumsden and Wilson seem to believe instead that the adaptive advantage of cultural learning is the same as that of ordinary learning, namely, behavioral flexibility. In discussing the adaptive advantages of culture in Chapters 1 and 7, Lumsden and Wilson stress that it makes possible more flexible behavior because individuals can choose that which is locally adaptive. In their minds, the main advantage of social learning relative to non-social learning seems to be that it eliminates the need for each individual to reinvent each behavior. The population simply acts as a kind of archive in which behaviors are stored; in each generation individuals learn all of the behaviors in the archive and then choose the behaviors that they think are appropriate for the current circumstances. They argue in Chapter 7 that the advantage of culture relative to genes is that human brains can store much more information than the human genome. Hence, culture allows a much larger archive of decision rules.

PULLIAM AND DUNFORD'S VIEW

Pulliam and Dunford's perspective is quite different. For them the primary puzzle is how an organism determines what behaviors are adaptive. In a spatially or temporally varying environment, it is clearly useful to be able to develop the locally adaptive phenotype. But how does the organism determine what that phenotype might be? Clearly there are many ways, but in most species these processes share the same general features. The organism inherits criteria that determine what feels good and what feels bad; feelings of security and satisfaction are good, and feelings of fear and hunger are bad. It also inherits generalized behavior patterns and modes of learning; quail associate gastric distress with foods that are visually novel, while rats associate the same symptoms with foods with novel tastes. The organism tries a variety of behaviors and retains those which are associated with rewarding sensations. In this way, complex patterns of behavior appropriate to the local condition can be generated.

The problem with this kind of trial and error learning, as Pulliam and Dunford note, is the cost of errors. The cost of errors made during the course of learning and the cost of developing the cognitive machinery necessary to avoid errors are the price of phenotypic flexibility. Pulliam and Dunford suspect that these costs are often quite substantial. This leads them to consider short-cuts to learning—ways in which an organism can accomplish phenotypic flexibility without paying the full cost of learning.

One way of avoiding the costs of learning is to simply pick some older individuals and imitate what they do. If the locally adaptive behavior is more common than other behaviors, then imitation will provide an efficient alternative to trial and error learning. Pulliam and Dunford do not think that cultural learning completely replaces trial and error learning; rather, ordinary learning causes individuals to show some weak tendency to modify the behavior that they acquired culturally, and in the direction of what is locally adaptive. The tendency is weak because learning is costly. Nonetheless, acting over time, the combination of learning and cultural transmission can cause the frequency of the locally adaptive variants to increase.

This vision of social learning is very different from that of Lunsden and Wilson. For Pulliam and Dunford, the frequency-dependent nature of cultural transmission is fundamental. Imitation is adaptive precisely because it greatly reduces the need to evaluate alternative behaviors. It does so because the probability of acquiring any behavior depends crucially on the frequency of that behavior among individuals available as models for imitation, and upon weak learning processes that help insure that models generally have adaptive skills.

In the last two chapters of their book, Pulliam and Dunford argue that because the cultural inheritance system is only weakly influenced by learning, culture can respond independently to evolutionary forces, and therefore cultural inheritance can lead to the evolution of behaviors that are maladaptive in terms of genetic fitness. They illustrate this argument with the case of culturally

transmitted patterns of altruistic behavior. They show that when patterns of cultural transmission differ from those of genes, selection can favor different patterns of altruistic behavior than would be predicted based on maximizing inclusive fitness. For Pulliam and Dunford, a capacity for cultural inheritance is a specialized adaptation entailing a complex mixture of adaptive costs and benefits, likely to be favored in some instances but not others.

THE IMPORTANCE OF THE DIFFERENCES
BETWEEN THE TWO VIEWS: AN EXAMPLE

One of Lumsden and Wilson's central claims is that natural selection should cause the genes that control the decision process to evolve rapidly. We believe that this conclusion is a direct result of their view of the adaptive advantages of culture, and that if one looks at the same question from Pulliam and Dunford's perspective, one will arrive at very different conclusions.

Lumsden and Wilson introduce genetic variation into their model by assuming that a single genetic locus (with two alleles) affects the probability of switching usage from one cultural variant to the other. Individuals who are homozygous for one of the alleles switch from one variant with a constant probability of one half. They refer to this homozygote as the *tabula rasa* genotype. Individuals who are homozygous for the other allele have a probability greater than one half of switching from the deleterious cultural variant to the favored cultural variant, and a probability also greater than one half of remaining with the favored variant. Thus, this homozygote, which they refer to as the *bias* genotype, has a genetic predisposition to use the cultural variant favored by natural selection.

Based on this model Lumsden and Wilson then go on to show that the biased allele will increase very rapidly in frequency. They propose a rule of thumb, which they call the "thousand-year rule," to the effect that human populations that exist in the same environment for roughly 1000 years should have genes that cause individuals to preferentially acquire the locally favored phenotypic variants. Lumsden and Wilson do not

explicitly apply this to the question of the differences between human groups. The model upon which the 1000-year rule is based assumes a single population in an unchanging environment. However, it is easy to interpret them (Maynard Smith and Warren, 1982) as implying that human populations that are separated for more than 1000 years should be expected to be genetically differentiated at loci that control the learning process. Indeed, it is difficult to imagine what other interpretation of this rule would make sense.

Let us consider the same question using a model in the spirit of Pulliam and Dunford's approach. Consider a population that is divided into two subpopulations that live in different habitats. Like Lumsden and Wilson, we will suppose that there are two culturally transmitted variants, 1 and 2. In subpopulation 1, the culturally transmitted variant 1 is favored relative to 2 by an amount $(1 + s):1$. In subpopulation 2, variant 2 is favored by an amount $(1 + s):1$. During each generation, after selection takes place, a fraction m of each subpopulation emigrates and is replaced by immigrants from the other subpopulation. In this model, some naive individuals will be exposed to cultural parents with maladaptive cultural variants who have immigrated from the other subpopulation.

Suppose there are three haploid genotypes that affect the cultural transmission process. For simplicity, assume that each naive individual is exposed to n potential models who are chosen at random from the subpopulation. Individuals with genotype 0 simply choose a random individual from among the n models and imitate that individual's behavioral variant. This means that if there are j individuals with cultural variant 1 in a set of models, the probability that an individual with genotype 0 will acquire cultural variant 1 is simply j/n. We will call this the *tabula rasa* genotype. Notice that our *tabula rasa* genotype chooses a model to imitate at random; Lumsden and Wilson's *tabula rasa* genotype chooses a behavior at random.

The other two genotypes choose models in a biased fashion. Individuals characterized by genotype 1 are predisposed to acquire

variant 1. If they are exposed to models characterized by both cultural variants (i.e., $0 < j < n$), the probability that they acquire cultural variant 1 is $j/n + b$, where b is a small positive number. Individuals characterized by genotype 2 are predisposed to acquire variant 2. If they are exposed to both cultural variants, the probability that they acquire variant 1 is $m/(n-b)$.

If Lumsden and Wilson's conclusion about the genetic differentiation of human groups is robust, the two *biased* genotypes should be able to replace the *tabula rasa* genotype. Based on the model outlined above, one can easily show that the *tabula rasa* genotype will decrease in frequency whenever the following condition holds:

$$[q_1 - q_2] \ \{(1-p)ps\} \ b > z$$

where q_1 and q_2 are the frequencies of the genotypes 1 and 2 in subpopulation 1, p is the frequency of cultural variant 1 in subpopulation 1, and z is a measure of the costs
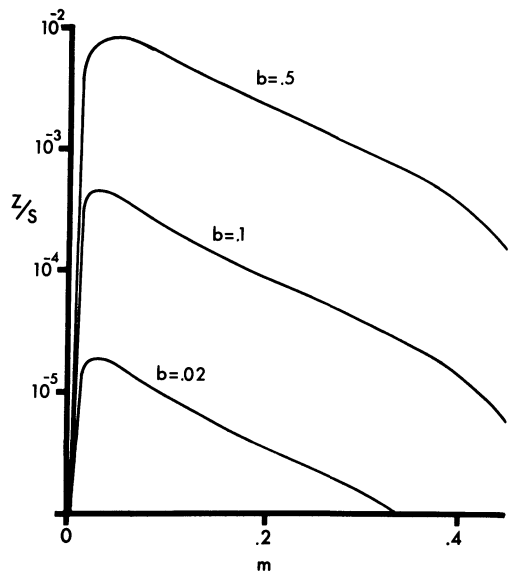

FIG. 1.

The threshold values of z/s necessary for the *tabula rasa* genotype to increase for three values of the bias parameter b as a function of the amount of migration between the two populations on a logarithmic scale. The parameter s = .1 in all three cases. (See text for explanation of symbols.)

associated with the bias measured in terms of fitness. As is shown in Fig. 1, the costs of bias must be 100 to 1,000,000 times smaller than the difference in fitnesses between the cultural variants in order for *biased* genotypes to increase in frequency. Clearly, the forces favoring the genetic differentiation of cultural learning rules are very weak in this model.

This result has a simple intuitive explanation. For biased transmission to be strongly favored by selection, there must be significant probability that offspring will be exposed to both behavioral variants. Because cultural transmission is frequency-dependent in our model, selection tends to increase the frequency of the locally favored cultural variant. This means that if sufficient variability is to be maintained for bias to be favored, migration must be a strong force relative to selection. However, a genetically transmitted habitat-specific transmission bias will be favored relative to a *tabula rasa* allele only if the allele that leads to a bias appropriate to a particular habitat is more common in that habitat than the allele that is biased in favor of the other cultural variant. For this condition to hold, migration must be weak relative to the selection acting on the *bias* alleles. The intensity of selection on the alleles affecting bias is always less than the intensity of selection on the cultural variants themselves, because some individuals who are predisposed to acquire variant 1 nonetheless acquire variant 2, and vice versa. Thus, if migration is strong enough to create sufficient cultural variation for bias to be favored, selection will not be strong enough to cause the *bias* alleles to have different frequencies; if migration is weak enough to allow genetic differentiation, selection will eliminate the cultural variability that is needed for bias to be useful.

Our result differs from that of Lumsden and Wilson because we suppose that the *tabula rasa* genotype chooses a parent at random and accurately imitates the parent's behavior. In terms of Lunsden and Wilson's model, we are assuming that the *tabula rasa* decision rule is frequency-dependent. If migration is weak relative to selection, then selection plus accurate unbiased transmission increases the frequency of the locally

favored variant to the point where there is little benefit to having biased transmission. Thus, if bias is costly, the *tabula rasa* genotype will be favored. In contrast, Lumsden and Wilson suppose that the *tabula rasa* genotype chooses a behavior at random. Thus, there is no way in their model that favored variants can increase, no way that culture can act as a short-cut to learning. The only evolutionary options that exist are more or less effective frequency-independent decision rules. Not surprisingly, the more effective rules are favored.

In our simple model, with just pure frequency-dependent transmission of cultural variation, the only force acting to increase the frequency of the locally favored cultural variant is selection. This mode of cultural transmission merely acts as a substitute for genetic adaptation. It is not intrinsically a better or worse mode of adaptation. The combination of weak general-purpose biases and frequency-dependent transmission, however, can be more adaptive than genetic transmission or unbiased cultural transmission. For example, suppose there is a genotype that is predisposed to imitate the models with the locally adaptive behavior in both habitats. That is, suppose that in habitat 1 the probability that this general-purpose *bias* genotype acquires variant 1 is $j/(n + b)$, and in habitat 2 it acquires variant 2 with probability $j/(n + b)$. Such a general-purpose genotype will replace the *tabula rasa* genotype whenever

$$\{(1-p)ps\}\ b > z$$

When migration is strong, this is clearly a much weaker condition than before. Thus, for a given cost of making decisions, general-purpose capacities to learn are more likely to evolve than habitat-specific decision rules. We believe that this result is also likely to prove robust. Elsewhere (Boyd and Richerson, 1983), we show that individual learning combined with cultural transmission can be superior to genetic transmission combined with learning in some kinds of temporally varying environments.

CONCLUSION

Genes, Mind and Culture is not flawed as an evolutionary analysis of culture because it

gets the "wrong answer"—that genes play a direct part in human behavior—nor because the idea that culture's main function is to act as an archive is itself implausible. Rather, its main flaw is that Lumsden and Wilson neglect the dynamic properties of cultural inheritance when they come to consider its adaptive advantages. This leads to an overly simplified view of culture; one which seems to us to cause Lumsden and Wilson to overestimate the role of genetic variation in explaining human differences. Pulliam and Dunford's approach is more interesting because it links the adaptive advantages of culture to the dynamics of cultural inheritance. This view leads to a more complex picture of cultural evolution in which the benefits of cultural transmission are inseparable from its tendency to create novel, and sometimes maladaptive, evolutionary processes. Because it is richer in possibilities, Pulliam and Dunford's approach seems to us more likely to be able to explain the diversity of culturally transmitted behaviors in the human species.

In the last analysis, however, both books are valuable because they represent earnest attempts to solve an interesting, important, and neglected evolutionary problem, the interaction of genetic and cultural inheritance during the course of human evolution. It is far too early to tell whether the perspectives outlined in these two books will ultimately prove fruitful. Such views of the adaptive significance of culture need to be developed and tested further in a climate free of ideologically motivated criticism.

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