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# The Evolution of Ethnic Markers

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Much of the debate about human sociobiology has been framed as a binary opposition. Sociobiologists argue that evolutionary theory is useful for understanding humans because much of our behavior is currently adaptive, or was adaptive under food-foraging conditions. To be sure, they aver, culture occasionally causes human behavior to drift away from the fitness maximizing optimum, but in the long run, behaviors that have important effects on Darwinian fitness should tend to be adaptive. Critics of this view argue that the existence of culture has allowed the human species to transcend ordinary evolutionary imperatives. Culturally transmitted behavior must not be so maladaptive as to lead to the extinction of the social group, but as long as this rather weak constraint is satisfied, it is argued, people are free to elaborate their culture more or less as they please.

We believe that this dichotomy is false. Culture is neither autonomous and free to vary independently of genetic fitness, nor is it simply a prisoner of genetic constraints. Our rejection of this dichotomy is based on what we call the “dual inheritance” theory of the interaction of genes and culture (Boyd and Richerson 1985). The essential feature of this theory is that, like genes, culture should be viewed as a system of inheritance. People acquire beliefs, attitudes, and values from others by social learning, and then transmit them to others. Human behavior results from the interaction of genetically and culturally inherited information. In the theoretical models we have constructed to represent this interaction, two results stand out:

1. The cultural system of inheritance has many properties that make it quite different from the genetic system. For example, an individual can observe the behavior of a number of peers, and choose the best behavior. Such properties may often enhance genetic fitness because they allow modes of adaptation not available to noncultural species.

2. These same properties can lead to the evolution of many cultural traits that are costly divergences from those that would increase genetic fitness. Culture is an evolutionarily active part of a system that, jointly with genes and environment, can account for much of human behavioral variation.

Here we will illustrate this general argument in the context of a particular problem, the evolution of markers of group membership. One of the most striking and unusual features of the human species is that it is subdivided into ethnic groups. Barth (1969) identified what we take to be the critical feature of ethnicity: people identify themselves, and are identified by others, as members of an ethnic group based on a set of culturally transmitted characters. Some of these traits, such as language, dress style, ritual, and cuisine, appear to be arbitrary symbolic markers of ethnic affiliation, while others are more directly functional cultural traits, such as basic moral values and standards of excellence. Membership in a particular ethnic group can have important effects on an individual's economic behavior and political and social interactions.<sup>1</sup>

The interpretation of ethnic markers is controversial. Sahlins (1976) has argued that one must choose between functional explanations and nonfunctional cultural explanations of symbolic marker characters. We will show that this dichotomy oversimplifies the relationship between genetic and cultural evolution. Ethnicity provides a good example of how functional organic adaptation and symbolic cultural processes are thoroughly intertwined in human evolution. Our argument is based on an evolutionary model embodying two mechanisms that cause a population occupying a variable environment to be subdivided on the basis of ethnic markers. These mechanisms result from a pattern of enculturation in which individuals are disproportionately influenced by two kinds of people: those who are similar to themselves, and those who are successful. Even though these two mechanisms cause groups to become differentiated based on arbitrary symbolic markers in a way that could not be predicted from fitness maximization alone, they will be favored by natural selection because they allow more accurate adaptation to variable environments.

This application of dual inheritance theory emphasizes the fitness-enhancing properties of culture. We have chosen this emphasis for two reasons. First, it is interesting to try to understand why a cultural system of inheritance arose in the hominid lineage, and how that process shaped the way that culture is transmitted. Most likely, the organic capacities that allow culture to be stored and transmitted arose through the action of natural selection. In the context of this example, we are interested in why selection favored mechanisms of cultural transmission that give rise to ethnic groups. Second, the reasons that culture is adaptive are both subtle and interesting. *Even when culture is highly adaptive, it has its own evolutionary properties, and can lead to patterns of behavior that could not be understood in the absence of knowledge of how cultural processes operate.* To understand why ethnic markers allow more accurate adaptation to variable environments, one must understand how the cultural processes that give rise to ethnic differentiation operate. We have discussed the properties of cultural inheritance that lead to genetically maladaptive behavior elsewhere (Boyd and Richerson 1985). Knauff (this volume) also gives an intriguing empirical example of how the differences between genetic and cultural inheritance can give rise to behavior that is genetically maladaptive.

### Models of Cultural Evolution

We define culture as information—skills, attitudes, beliefs, values—capable of affecting individuals' behavior, which they acquire from others by teaching, imitation, and other forms of social learning. A particular member of a set of attitudes, beliefs, and values will be referred to as a cultural variant. (See Boyd and Richerson 1985: chapter 3 for an extended discussion of this definition). We have adopted this definition because it focuses attention on the means by which cultural traditions are perpetuated. Culture is acquired by individuals by teaching, imitation, and other forms of social learning from other individuals, stored in individual brains, and transmitted by teaching and imitation to others.

Recently, there has been a fair amount of interest in applying concepts drawn from evolutionary biology to the problem of cultural evolution (e.g., Boyd and Richerson 1985; Campbell 1975; Cavalli-Sforza and Feldman 1981). Despite the fact that cultural and genetic evolution differ in important ways, this methodological borrowing has been fruitful because genes and culture both have population-level properties. That is, individual behavior depends in part on the cultural variation in the population from which individuals acquire cultural variants. At the same time, which cultural variants are available in the population to be acquired depends on what happened to individuals with different variants in the population in the past. For example, in every generation some individuals will invent or learn new behaviors, modifying the variants they originally imitated and transmitting the new variants to others in the process of enculturation. Cultural evolution can be viewed as a complex of sampling and modifying processes that operate iteratively on a population of variable culture-bearing individuals. That there is a very general analogy between genes and culture is a commonplace observation; what is new is the reworking of methods of analysis developed by evolutionary biologists to build a useful theory from the old analogy.

Simple mathematical models are one of the most important tools that biologists use to study population-level processes. The tradition of their use began in evolutionary biology with Wright, Fisher, and Haldane in the first part of this century, and is continued today by people like John Maynard Smith, W. D. Hamilton and many others. The goal of such models is to isolate the population-level consequences of a limited set of processes by stripping away all of the confusing detail due to other processes. For example, kin selection models address the question: when can selection favor behaviors that reduce the fitness of the individual performing them, given that they increase the fitness of other individuals affected by the behavior? In such models virtually all of the actual behavioral and ecological detail is suppressed, so that exactly the same mathematical model is applied, for example, to coalition behavior among macaques and communal nesting in scrub jays. The intent of the model is to give insight into kin selection as a generic evolutionary process, not to account for the details of particular examples of the process. Evolutionary biologists construct many such simple models, each isolating one or few processes. That a particular process is neglected in a model is not to say that it is unimportant, only that we desire to focus on something else

for the moment. This sort of theorizing is sometimes stigmatized as reductionistic. A more apt characterization would be modular. Real evolutionary phenomena are complex; except for deliberately controlled experiments, we expect to have to link many such models together to achieve a satisfactory explanation of real events.

Nevertheless, the study of the simple modules in isolation is useful because it has proven difficult to deduce the population level consequences of individual level processes using verbal reasoning alone. Population processes involve the interaction of phenomena occurring at two different levels of organization and two distinct time scales. The individual and population levels of organization interact through the sampling processes inherent in reproduction or socialization. The day-to-day ecological time scale, on which processes of change act (e.g., selective mortality), interacts with the long-run evolutionary time scale on which adaptations of particular kinds are or are not produced. Even the simplest examples of evolutionary processes are thus rather complex. Mathematics makes it relatively easy to consistently and systematically trace the implications of a given set of assumptions, even when the processes modelled are probabilistic or quantitative. Simple, but formal, models are a useful mental prosthesis to reduce the handicap of a certain kind of cognitive limitation. It is important to realize that such models serve a rather narrow function, the testing of explanations for logical consistency. While they are tremendously useful in this role, they are only a supplement to other theoretical and empirical tools in the social and biological sciences, not a replacement for them.

### **A Model of the Evolution of Ethnic Markers**

The existence of ethnic groups and similarly marked social units suggests two evolutionary questions: (1) What are the processes that would cause a human population to split into two groups distinguished by cultural marker traits? and (2) could such processes give rise to cultural variation that is biologically adaptive in the sense of increasing reproductive success?

#### *Motivating the Model*

Let us approach these two questions by turning the second one around: How should natural selection have shaped the processes by which individuals acquire culture? At the very least, this way of viewing the problem ought to be appropriate for considering the origin of organic capacities that make culture possible. Consider an ancient human population that has recently expanded into a new habitat. Some individuals in the new habitat will have adopted beliefs and values that are appropriate in the new habitat, but many will share the values and beliefs with individuals in the old habitat. This lag in cultural adaptation could result from at least two factors: (1) innovation is slow and the occupation of the new habitat is recent; (2) there is an exchange of individuals between habitats, so that some individuals in the new habitat acquired their beliefs and values in the old habitat. If either of these two factors obtain, many individuals will carry variants that are appropriate in the old habitat, but not in the new one. Assuming that natural se-

lection plays a strong role in shaping cultural capacities, it will structure the acquisition of culture so that individuals in each habitat have the best chance of acquiring the set of beliefs and values that are appropriate there.

If one set of beliefs or values has easily observable advantages relative to the others, then there is an easy answer: individuals should adopt the beliefs and values that maximize reproductive success. It seems likely, however, that people commonly must choose among variant beliefs where it is quite difficult to determine which belief is most advantageous, even though the beliefs in fact differ in utility. Behavioral decision theorists (Nisbett and Ross 1980) and students of social learning (Rosenthal and Zimmerman 1978) argue from empirical evidence that the complexity and number of real decisions forces people to use simple rules of thumb. Chief among these is a heavy reliance on *imitation* to acquire most of their behavior.

Studies of the diffusion of innovations (summarized in Rogers with Shoemaker 1971) suggest that people often use two simple rules to increase the likelihood that they acquire locally adaptive beliefs by imitation. The chance that individual *A* will adopt an innovation modeled by individual *B* often seems to depend upon: (1) how *successful B* is, and (2) the *similarity* of *A* to *B*. When it is difficult to evaluate whether an innovation is sensible, imitating the successful seems like a good general rule; if the innovation is beneficial, people who use it will be more successful, on the average, than those who do not. It also seems sensible to condition adoption on similarity. If a model is very different than one's self, the model's success might not indicate that the innovation would be useful in one's own circumstances. In the interests of simplicity, we will model a situation in which success and similarity are the only adoption rules people use. As in the case of kin selection, the model is meant to yield insight into the operation of this particular pair of decision rules as their effects are integrated over individuals and time to produce evolutionary results. Since many other important processes are left out, the model is meant to apply partially and qualitatively to a great many cases, but to be a complete quantitative description of none.

How cultural populations will evolve under the influences of these two processes depends a great deal on what people use as indicators of success and similarity. Because our focus here is on the problem of the origin of a capacity for culture under the influence of natural selection, we will assume that the index of success is a correlate of genetic fitness, and that the index of similarity is a conspicuous symbolic character, like dialect, acquired from primary socializers such as parents. As far as the formal model is concerned, any standard of success or similarity can be substituted. If these assumptions are relaxed, the model may still be appropriate to understanding how ethnic groups form, but not to the problem of how such a capacity evolved in the first place. Ethnicity might be a costly by-product of some other advantage associated with ability to recognize success and similarity. The narrow interpretation we give here is not meant to prejudge these empirical issues. See Boyd and Richerson (1985: chapter 8) for a model in which the standard of success is explicitly cultural and in which it departs very sharply from what selection on genes would favor.

Is the evolution of ethnic markers possibly an adaptive result of using these two rules in cases where more direct decision rules are too costly to use? It is fairly obvious that if most people adopt beliefs or values modeled by successful people, beliefs or values that lead to success will spread. It seemed possible to us that coupling a propensity to imitate the successful with a propensity to adopt the beliefs and values of those who are similar to oneself might cause groups occupying different habitats to become culturally isolated from each other because it would cause whatever cultural markers that are used to judge similarity to diverge in the two populations. To check the cogency of this intuition, we analyzed the following model.

### *Formalizing the Intuition*

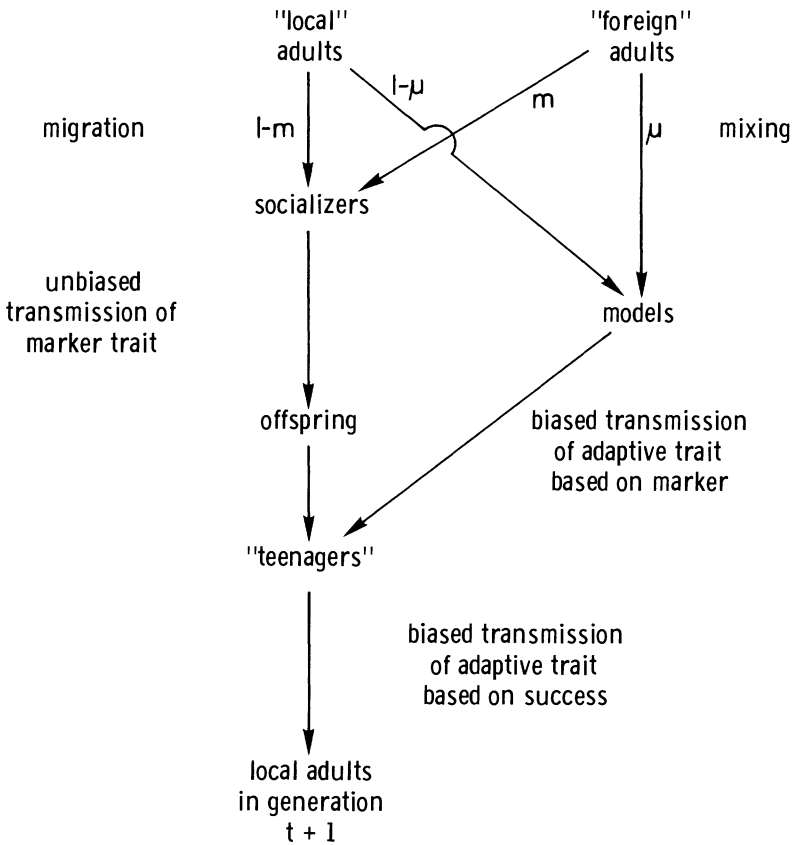
Real environments and real means of exploiting them are complex. However, we think that the cogency of intuitions can be evaluated using quite simple models. Accordingly, we imagine that there are two ecological niches that differ according to the optimal value of an adaptive character. For example, suppose that there are two habitats, one moist and one dry. The adaptive character could be a belief that affects the extent to which a person relies on stock raising as opposed to cultivation. This belief might be the extent to which an individual believes that cattle ownership is an intrinsic measure of a person's worth as a human being. In the dry habitat the most successful subsistence strategy might be pure pastoralism, and thus the optimal value of the adaptive character is a heavy valuation of cattle. In the moist habitat the most successful strategy might involve mostly horticulture, and a lesser valuation of cattle might lead to a more successful subsistence strategy.

To represent these assumptions mathematically, we suppose that each individual's subsistence strategy can be characterized by a single number labeled  $A$ . This can be thought of as an index of the extent to which individual's beliefs lead them to depend on stock raising. The habitats are labeled 1 and 2, and the optimal values of  $A$  in those habitats are  $\theta_1$  and  $\theta_2$ . The more that an individual's adaptive character deviates from the optimum in his or her habitat, the lower on average will be his or her success (and genetic fitness). More mathematical detail is given in the appendix. In terms of the example introduced above,  $\theta_1$  might be the value of  $A$  that corresponds to mostly pastoralism, and  $\theta_2$  mostly horticulture. In what follows we will sometimes refer to the adaptive character as the amount of pastoralism in order to make the presentation less abstract. The reader should keep in mind, though, that the adaptive trait is not meant to refer to any specific situation. Rather it is meant to formalize the idea that different beliefs and values are more or less adaptive in different environments.

We assume, further, that each individual is characterized by an arbitrary neutral "marker" character. For example, the marker trait might be an index of dialect, such as the extent to which people pronounce  $r$ 's. It is arbitrary and neutral in the sense that many dialect variants with no direct effect on adaptive success are possible, although, as we shall see, there may be very strong indirect effects

of marker traits upon fitness. Once again we will assume that the marker trait can be described by a single number, labeled  $M$ . Thus, in the context of the model, each individual's culturally acquired beliefs can be described by a pair of numbers,  $A$  and  $M$ .

We assume that these two cultural traits are transmitted according to the life cycle shown in Figure 1. This life cycle is meant to reflect the fact that children, adolescents, and young adults have different patterns of enculturation. Individuals acquire their *marker* trait (i.e., their dialect) at an early age from a set of primary socialization agents (socializers). They acquire their *adaptive* trait at a later age by observing the behavior of a much wider range of individuals whom we will refer to as models. Socializers need not be biological kin; *the key assumption is only that the amount of mixing between habitats is much greater for models than for socializers* ( $u \gg m$ ). As we shall see, this condition allows the differentiation of marker traits, hence a sense of ethnic distinctiveness, to build up in the local environment. We further assume that dialect is acquired through a process of



**Figure 1.**  
Assumed life cycle of cultural transmission.



faithful copying. That is, on average, people acquire the dialect of the community in which they were raised. We formalize this idea by assuming that each naive individual has the opportunity to observe the behavior of  $n$  socializers. Naive individuals then adopt a weighted average of the dialect of  $n$  socializers as their own dialect. The fact that socializers may have different weights is meant to represent the idea that some individuals may be more important in transmission than others, due to kinship, social status, or some other factor.

In later phases of the life cycle, the adaptive trait is not acquired through faithful copying. Rather, the acquisition of the adaptive trait is biased by two processes. When individuals initially acquire their adaptive trait from models as teenagers, they are predisposed to imitate individuals who have similar marker traits (i.e., have similar dialects). This idea is represented mathematically by assuming that the basic influence of a model (due to social role and the like) is reduced as the difference between the individual's and the model's marker trait increases (in absolute value). Subsequently, individuals modify both their adaptive and marker traits by imitating the successful individuals among their local young adult peers. We represent this idea mathematically by assuming that individuals select one peer to imitate and weight this peer's modifying influence in proportion to his or her success.

Our goal is to use the model to study how these transmission and choice processes might change the distribution of culturally transmitted variation in a population through time. In particular, we want to know whether different values of the marker trait will come to predominate in the two habitats, and whether this difference ensures that more people acquire the locally adaptive trait. The first step is to describe the nature of the cultural variation present in the population at some point in time. To do this we use the joint distribution of the two traits in the population. This distribution simply specifies the fraction of the population that is characterized by each pair of values,  $A$  and  $M$ . The shape of such a distribution can be summarized by five numbers. The two means give the "position" of the distribution. For example,  $\bar{A}$  tells us the degree to which, on average, the population relies on stock raising. The two variances describe the spread of the distribution. For example, a large variance of  $A$  would mean that there were a wide range of subsistence techniques in use in the population. The covariance tells us the extent to which the two traits are correlated. A nonzero covariance means that individuals who rely largely upon pastoralism tend to have a similar dialect, and that this is different from the dialect most commonly used by horticulturalists.

The next step is to see how the distributions of  $A$  and  $M$  in the two populations change through a single generation. To do this we must determine how events in the lives of individuals change the distribution of cultural variants in the population. First, we assume that when the generation begins, the means and variances that describe the distribution of cultural variants in the population are at some initial values. Then we construct submodels to represent individual movement from population to population and the two forms of biased imitation. The effects of each individual's behavior on the properties of the population are very small, but aggregated over all individuals they may cause an appreciable change by the

beginning of the next generation. *It is this part of the model that does the important work of linking individual- and population-level processes.* In what follows we provide a qualitative description of the most important effects of each process. A formal description is given in the appendix.

*Faithful copying* leaves the mean value of the marker trait,  $M$ , in each habitat unchanged. This result follows from the assumption that naive individuals faithfully copy the marker of their socializers, who are in turn an unbiased sample of the previous generation.

*Mixing* of individuals between the environments creates covariance between the adaptive character and the marker character in the populations of models, even if there was no association before mixing in either habitat. To see why, suppose that in habitat 1 people have beliefs that cause them to depend more on pastoralism than do people in habitat 2. This means that the value of  $\bar{A}$ , the mean value of the adaptive trait, is larger in habitat 1 than in habitat 2. Now suppose that the values of  $\bar{M}$ , the mean values of the marker trait, in the two habitats are different—for example, individuals in habitat 1 might be more likely to pronounce their  $r$ 's. Then a model drawn from habitat 1 will be more likely to have large values of  $A$  and  $M$ , while a model from habitat 2 will tend to have small values. Thus, models who practice pastoralism will tend to pronounce their  $r$ 's, and those who practice horticulture will tend not to, even if there was no association between the two traits in either habitat before mixing. Mixing also moves the mean values of  $A$  and  $M$  in the two habitats toward each other. If no other processes affect the means, the populations in both habitats will eventually be characterized by the same values of  $A$  and  $M$ , even though the habitats are quite different.

*Biased transmission based on similarity* causes the mean value of the adaptive trait among individuals who have just acquired their adaptive trait to be closer to the mean in their habitat before mixing than the mean adaptive trait among their models. By imitating the adaptive trait of people who are like themselves with regard to the marker trait, naive individuals reduce the chance that they will imitate a model drawn from the other habitat. Thus, this form of a biased imitation has the effect of reducing the amount of mixing. The strength of this effect depends on the difference between the mean marker trait in the two habitats. If the dialects are not very different, biased imitation based on similarity will have little effect. If the dialects are quite different, the result will be to substantially reduce the effect of mixing.

*Biased transmission based on success* moves the mean value of the adaptive trait toward the optimum in both habitats *and* causes the mean values of the marker traits in the two habitats to diverge from each other. Suppose that in habitat 1 individuals who rely mostly on pastoralism are more successful on the average than individuals who rely mostly on horticulture. Then individuals whose beliefs cause them to rely more on pastoralism will be more likely to be imitated, and such beliefs will spread. The same process will cause the mean value of the marker traits to diverge because of the covariance between the marker trait and the adaptive trait that is induced by mixing. Suppose that individuals who rely on pastoralism tend to pronounce their  $r$ 's. Then, the practice of imitating successful

people will cause the pronunciation of *r*'s to spread, because successful people will tend to pronounce their *r*'s.

The analysis presented so far only tells us what will happen to the distribution of cultural variants in the two habitats over the course of one generation. Normally, such changes will be quite small, there will be competing effects, and the direction of change will be dependent on several interacting factors. Our goal is to find out what will happen to the population over the long run. To accomplish this goal, we use various techniques to iterate the equations that describe the change over one generation. *These techniques allow us to accomplish the second difficult step of evolutionary reasoning, the connection of short-time scale ecological processes with their eventual evolutionary results.* Assuming that the amount of mixing of primary socializers is small enough that it may be neglected, two important results emerge from such an analysis. Starting with a single, nearly uniform population that comes to occupy two habitats: (1) the mean value of the adaptive trait in each habitat approaches the optimum, and (2) the mean values of the marker trait in the populations become quite different. These general properties are illustrated by the numerical simulation of the model shown in Figure 2.

These qualitative results make sense in the light of the processes described above. The mean value of the adaptive trait is affected by two forces—mixing

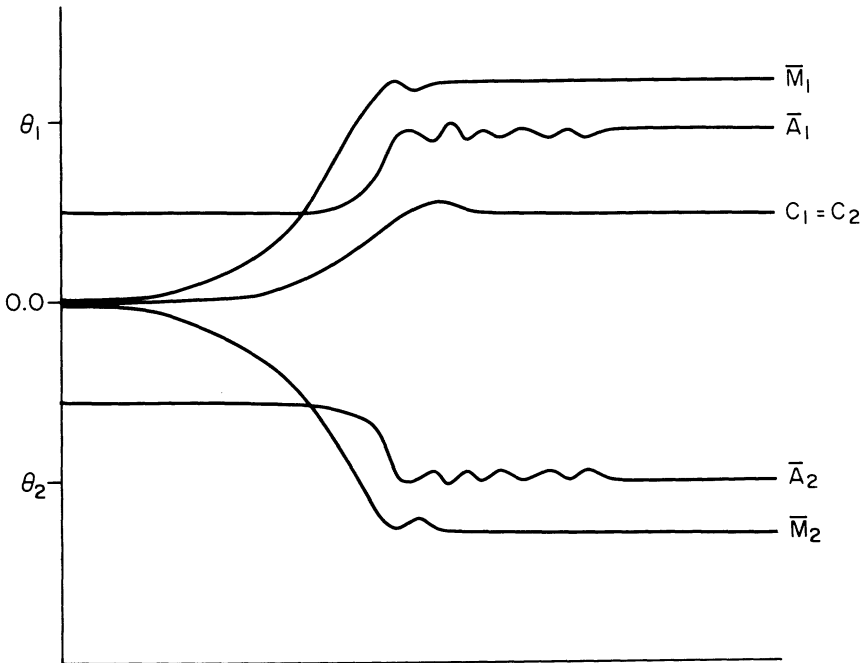


Figure 2.

Representative trajectory of the mean value of the adaptive character, the marker character, and the covariance between the two characters in the two habitats.

causes the mean in the two habitats to approach each other, while biased cultural transmission based on success causes the means to approach the optimum in each habitat. The impact of mixing depends on the difference between marker trait means both because increasing this difference increases the covariance created by mixing, and because it makes biased transmission based on similarity more effective in causing people to imitate models with more adaptive variants. Thus, increasing the difference in the mean marker traits will cause the mean adaptive trait in each habitat to move toward the optimum. This in turn will cause marker trait means to diverge. This positive feedback cycle will come to a halt only when the mean adaptive trait stops changing, which occurs when the adaptive trait in each habitat is at the optimum.

These results suggest that subdivision of a population into culturally semi-isolated groups based on arbitrary symbolic traits such as dialect can result from using the success and similarity choice rules. The same analysis also indicates that the tendency to imitate similar individuals can be genetically adaptive. Consider an individual who does not use similarity as a criterion in weighting potential models for the adaptive trait. On average, such an individual will acquire a value of the adaptive trait that is farther from the optimum in his or her habitat than an individual who does use similarity. If, as we have assumed, the criteria by which success is judged are correlated with reproductive success, then individuals who use similarity to bias their enculturation will have higher fitness than those who do not. If one further assumes that the nature of the imitative process is affected by heritable genetic variation, then natural selection will give rise to a cultural transmission system that is biased in favor of imitating culturally similar individuals.

### Discussion

The model presented here suggests that the modes of cultural transmission that give rise to ethnically subdivided populations are adaptive because they allow populations to more accurately track a heterogeneous environment. Similar processes may favor the development of symbolically marked caste, class, occupational, and professional subgroups within complex societies. The process of imitating people like oneself sets up a self-reinforcing process, which causes subpopulations occupying different habitats, or pursuing different economic strategies in the same environment, to become culturally isolated. This in turn allows the mean value of the adaptive trait in each habitat to converge to the optimum. A population using only transmission based on success would adapt much less quickly to a variable habitat.

It is noteworthy that this mode of adaptation is closed to animals that lack a capacity for culture. Such differences between genetic and cultural evolution ought to be reflected in basic differences between the natural history of humans and other animals. It is interesting in this regard that the human species occupies a much broader range of habitats than any other mammalian species. Consider the primates: If all baboons are classified as belonging to a single species, then it is

the primate species with the widest geographical range, a substantial fraction of sub-Saharan Africa. Our closest relatives, chimpanzees and gorillas, are restricted to the tropical forests of Africa. In contrast, even with only hunting and gathering technology, humans occupied virtually every terrestrial habitat.

Most contemporary theories of speciation hold that a population must occupy more than one ecological niche in order for speciation to occur (Templeton 1981). Once a portion of a population has adapted *genetically* to a particular niche, selection will favor mechanisms that prevent mating with individuals living in some other niche, because the offspring that result from such matings will be inferior in both niches. Whether multiple niches are sufficient, or some additional factor, such as an isolating barrier, is necessary is not completely clear. The data from other primate species suggests, however, that typical primate species occupy much smaller ranges than the human species, presumably because reproductive barriers were favored by selection as successful primates extended their ranges to sufficiently different habitats.

Unlike other mammals, humans acquire massive amounts of adaptive information culturally. Perhaps it is not coincidental that symbol-using humans of the late Pleistocene became very widely distributed for a biological species. The processes modeled here, by allowing the protection of culturally transmitted adaptations to local conditions without genetic isolation, can be considered a cultural substitute for speciation. There are undoubtedly many aspects of cultural transmission that allow adaptation to a wide range of habitats. However, it does seem plausible that the fact that the human species is divided into distinct groups that are culturally isolated from each other may play a role in allowing humans to be culturally polymorphic and thus to occupy such a wide range of ecological niches. This intuition is reinforced by studies like those of Frederik Barth, which suggest that contemporary ethnic groups often occupy different ecological niches.

This interpretation illustrates, in the context of a rather simple model, how adaptive modes of cultural transmission lead to outcomes that could not be predicted without taking cultural processes explicitly into account. Even if one assumes that the criteria by which success is judged are coincident with reproductive success, it is only the properties of cultural transmission that allow populations to adapt rapidly to a variable environment. An adaptive outcome—the differentiation of local groups with regard to marker traits—can only be understood in terms of cultural processes. We believe that this argument ought to be very interesting to cultural anthropologists. *We have not had to leave the confines of adaptationist assumptions to show how the properties of culture play a fundamental role in human evolution.*

It should also be noted, however, that once the use of such rules as success and similarity arise, selection on genes underlying the capacity for culture may not be able to prevent the violation of adaptationist assumptions. For example, processes closely related to those modeled here can lead to the runaway evolution of marker and preference traits, which then have no adaptive or functional explanation (Boyd and Richerson 1985: chapter 8). It is easy to imagine that the adaptive uses of cultural markers are common enough so that selection on genes has

maintained a cognitive capacity to use them, despite the runaway process carrying some to maladaptive extremes. We are convinced that complexities of this sort are a pervasive feature of the coevolutionary process that links genes and culture. To the extent that this idea is correct, any attempt to reduce the problems of human evolution to binary choices between sociobiological and cultural explanations is bound to fail. The real puzzle is to determine how the genetic and cultural systems interact in a unified evolutionary process.

### Mathematical Appendix

To simplify the notation, we will focus on the changes in the distribution of cultural variants in one of the two habitats. We will refer to this as the "local" habitat, and the other habitat as "foreign." Stages in the life cycle are defined in figure 1. Suppose that the joint distribution of  $A$  and  $M$  among adults has means  $\bar{A}$  and  $\bar{M}$ , variances  $V_a$  and  $V_m$ , and covariance  $C$ .

*The effect of mixing.* Assuming that a proportion  $u$  of models are drawn from the foreign habitat (statistics describing the population from which these individuals are drawn are indicated by an  $f$  superscript), the joint distribution among models has the following moments:

$$\begin{aligned}\bar{M}^* &= (1 - u)\bar{M} + u\bar{M}^f \\ \bar{A}^* &= (1 - u)\bar{A} + u\bar{A}^f \\ V_a^* &= (1 - u)V_a + uV_a^f + u(1 - u)(\bar{A} - \bar{A}^f)^2 \\ V_m^* &= (1 - u)V_m + uV_m^f + u(1 - u)(\bar{M} - \bar{M}^f)^2 \\ C^* &= (1 - u)C + uC^f + u(1 - u)(\bar{M} - \bar{M}^f)(\bar{A} - \bar{A}^f)\end{aligned}$$

The moments of the joint distribution among socializers is given by the same expressions with the mixing rate for socializers,  $m$ , is substituted for  $u$ .

*Transmission of the marker character:* Assume that each naive individual has the opportunity to observe the behavior of  $n$  socializers who have dialects  $M_1 \dots M_n$ . The naive individual then adopts a weighted average of the dialect of  $n$  socializers as his or her own dialect,  $M$ :

$$M = \frac{\sum_{i=1}^n a_i (M_i + e_i)}{\sum_{i=1}^n a_i}$$

The parameter  $a_i$  is the weight of the  $i$ th parent, and  $e_i$  is a normally distributed random variable with mean zero and variance  $E$  that represents the effects of errors.

The mean and variance of  $M$  among offspring is given by:

$$\begin{aligned}\bar{M}'' &= \bar{M}' \\ V_m'' &= \left( \sum_{i=1}^n a_i^2 \right) (V_m' + E)\end{aligned}$$

where  $\bar{M}'$  and  $V_m'$  are the mean and variance of  $M$  among socializers.

*Transmission rule for initial acquisition of adaptive characters:* Assume that individuals initially adopt the following weighted average of the beliefs of  $n$  models, in which a model's weight depends on his or her similarity to the naive individual; individuals who are more similar receive greater weight:

$$A = \frac{\sum_{i=1}^n \alpha_i (1 + S(M, M_i)) (A_i + e_i)}{\sum_{i=1}^n \alpha_i (1 + S(M, M_i))}$$

The parameter  $\alpha_i$  is the weight of the  $i$ th model, and  $S(M, M_i)$  the following function:

$$S(M, M_i) = \exp(- (M - M_i)^2 / 2G)$$

The mean and variance of  $M$  remain unchanged. The remaining moments of the distribution among "teenagers" are given by:

$$\begin{aligned} \bar{A}''' &= \bar{A}^* + (C^*/G) (\bar{M}'' - \bar{M}^*) \\ V_a''' &= (1/n_e) (V_a^* + E) + K (C^*)^2 \\ C''' &= (1 - 1/n_e) (V_m'' C^*/G) \end{aligned}$$

where  $1/n_e = \sum \alpha_i^2$  and  $K$  is a constant.

*Transmission rule for horizontal transmission of both marker and adaptive characters.* Individuals select another individual from their own cohort and from within their own environment and modify their own adaptive and marker characters towards that individual. The weight that they give the selected individual is proportional to his or her success, where the success of an individual with adaptive character  $A$  in habitat  $i$  ( $i = 1, 2$ ) is given by:

$$W(A) = \exp(- (A - \theta)^2 / 2w)$$

The moments of the joint distribution among adults in the next generation are:

$$\begin{aligned} \bar{A}_{t+1} &= \bar{A}''' + (V_a'''/w) (\theta - \bar{A}''') \\ \bar{M}_{t+1} &= \bar{M}''' + (C'''/w) (\theta - \bar{A}''') \\ V_{a,t+1} &= (V_a''' w) / (V_a''' + w) \\ V_{m,t+1} &= (V_m''' + V_m''' V_a''' - (C''')^2) / (V_a''' + w) \\ C_{t+1} &= (C''' w) / (V_a''' + w) \end{aligned}$$

### Notes

*Acknowledgments.* We thank Bruce Knauft, Robert Paul, and Joan Silk for thoughtful comments on the first draft of this paper.

<sup>1</sup>LeVine and Campbell (1972) review evidence suggesting that ethnicity and ethnocentrism are almost universal principles of social organization in traditional societies. During the last decade, work by anthropologists, sociologists, and political scientists has demonstrated that ethnicity is at least as important in modern and modernizing societies as it was in the past (Glazer and Moynihan 1975; Keyes 1981). Recent reviews of the literature on

ethnicity include Cohen (1978), van den Berghe (1981), Bentley (1983), and Horowitz (1985). There has been little discussion of how the capacities that lead to ethnicity might have evolved. The main exception is van den Berghe (1981), who argues that under food-foraging conditions, which typified most of human history, generalized cooperation among members of small, local, culturally similar, groups would be favored by selection. Contemporary ethnic groups result from the action of such predispositions under conditions of much higher population density.

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### <sup>1</sup> **Ethnicity: Problem and Focus in Anthropology**

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