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Natural Selection and Culture

Peter J. Richerson and Robert Boyd

Natural selection is a general evolutionary mechanism. It can affect cultural evolution indirectly via the genes that affect the invention and imitation of culture. It can also act directly on cultural variation. The behaviors favored by the two modes of selection are not necessarily the same. (*Accepted for publication 14 February 1984*)

Darwin's theory of evolution by natural selection is often portrayed as antithetical to theories invoking the inheritance of acquired variation. Darwin himself, however, maintained that inheritance of acquired variation was important in nature and quite compatible with the action of natural selection. This view continued to be important until the 1930s, when Darwinism became firmly linked with Mendelian genetics.

Recently an interest in human social learning has led theorists from several disciplines to reconsider the consequences of inheritance of acquired variation. Social scientists (Campbell 1965, 1975, Cloak 1975, Durham 1978, Ruyle 1973) have used the analogy between genetic and cultural transmission as the basis for a general theory of culture. Several biologists have considered how culturally transmitted behavior fits into the framework of neo-Darwinism (Boyd and Richerson 1983, Lumsden and Wilson 1981, Pulliam and Dunford 1980). Other biologists and psychologists have used the formal similarities between genetic and cultural transmission to develop theories describing the dynamics of cultural transmission (Cavalli-Sforza and Feldman 1973, 1981, Cloninger et al. 1979, Eaves et al. 1978).

The idea that unifies this work is that social learning or cultural transmission can be modeled as a system of inheritance; to understand cultural change, we must therefore understand the microscopic processes that increase the frequency of some culturally transmitted variants and reduce the frequency of others. Put another way, to understand cultural evolution we must account for all the processes by which cultural variation is transmitted and modified. Because the resulting models resemble

those used in the neo-Darwinian theory of organic evolution, they can be called Darwinian models of cultural evolution.

This article considers the role of natural selection in cultural variation (Boyd and Richerson 1981, Richerson and Boyd 1978). How does natural selection act on a system of culturally transmitted variation when it is also acting on genetic inheritance?

WHAT IS CULTURE?

We define culture as information acquired by imitating or learning from other individuals and able to affect an individual's phenotype, usually behavior. Although our definition emphasizes that culture is a system for the inheritance of acquired variation, it is well within the range of anthropologist's definitions of culture (Keesing 1974, Kroeber and Kluckhohn 1952).

In some respects, cultural transmission and genetic transmission are similar. For example, the skills and dispositions transmitted during the enculturation of children by parents create behavior patterns that are difficult to distinguish empirically from genetically influenced patterns. The great difficulty in allocating the variance in measured IQ to underlying genetic and cultural variation clearly shows this (Cavalli-Sforza and Feldman 1973).

In other respects, cultural and genetic transmission differ sharply. First, culture is transmitted when an individual observes the behavior of others or when a naive individual is taught by an experienced one (the model in social learning theory, Rosenthal and Zimmerman 1978). Thus behavior modified by trial-and-error learning can subsequently be transmitted; culture is a system for the inheritance of acquired variation.

Second, patterns of cultural transmission differ from patterns of genetic transmission. Models other than biological parents, including peers and grandparents, are often involved. The cultural

analogs of generation length and the mating system are different from, and more variable than, their genetic analogs. Such differences in transmission patterns we call the asymmetry between the two systems.

Finally, the naive individual acquiring an item of culture is an active decision-making participant in the transmission process. To some extent, we choose what traits we learn from others, but a zygote cannot choose its genes.

FORCES OF CULTURAL EVOLUTION

The goal of the Darwinian approach to cultural evolution is to understand cultural change in terms of the forces that act on cultural variation as individuals acquire cultural traits, use the acquired information to guide behavior, and act as models for others. Forces are those processes that increase or decrease the proportion of people in a society who hold particular ideas about how to behave. The evolutionary forces that affect culture are divisible into three classes: random forces, decision-making forces, and natural selection acting directly on cultural variation.

The random forces are the cultural analogs of mutation and drift in genetic transmission. Intuitively, it seems likely that random errors, individual idiosyncracies, and chance transmission play a role in behavior and social learning. Linguists, for example, have documented a good deal of individual variation in speech, some of which is probably random individual variation (Labov 1972). Similarly, small populations might well lose rare skills or knowledge by chance from, for example, the premature death of the only individuals who have acquired these skills (Diamond 1978).

One decision-making force, biased transmission, results when naive individuals exposed to a variety of models preferentially imitate some rather than others. A second decision-making force results when individuals modify existing behaviors or invent new ones by individual learning. If the modified behavior is then transmitted, the resulting force is much like the guided, nonrandom variation of classical "Lamarckian" transmission.

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Decision-making forces are derived forces (Campbell 1965). Decisions require rules for making them, and ultimately the rules must derive from the action of other forces. These decision-making rules may be acquired during an earlier episode of cultural transmission, or they may be genetically transmitted traits that control the neurological machinery for acquiring and retaining cultural traits. The latter possibility forms the basis of the various sociobiological hypotheses about cultural evolution (Alexander 1979, Lumsden and Wilson 1981). These authors, among others, argue that the course of cultural evolution is determined by natural selection operating indirectly on cultural variation via the decision-making forces.

Natural selection may also operate directly on cultural variation, for it is an extremely general evolutionary process (Campbell 1965). Darwin was able to formulate a clear statement of natural selection without correctly understanding genetic inheritance because natural selection will operate on any system of inheritance with a few key properties: There must be heritable variation, the variants must affect phenotype, and the phenotypic differences must affect individuals' chances of transmitting the variants they carry. That variants are transmitted by imitation rather than sexual or asexual reproduction does not affect the basic argument, nor does the possibility that some of the variants are acquired under the guidance of individual decisions. Darwin had no problem in imagining that random variation, acquired variation, and natural selection all acted together as forces in organic evolution. For cultural evolution, we see none either.

How selection on cultural variation differs from random and decision-making forces can be illustrated by the causes for change in religious preference over time. A young person might choose among one of many similar liberal Protestant denominations according to random factors, such as the church's location, the pastor's personality, or recruitment by a chance acquaintance. Such drift-like effects might determine which churches prosper and which disappear, especially in small communities. Alternatively, people may select a denomination on the basis of strong preferences. In rural Peru, substantial numbers of peasants have converted from Catholicism to Seventh Day Adventism because Adventist missionaries gave literacy classes, and many peasants wanted to

learn to read (Lewellen 1979). The spread of Adventism in rural Peru seems to have resulted from the decision-making force of biased transmission.

Natural selection may also play an appreciable role in changes in the frequency of religious beliefs. Religious preference is highly variable in countries like the United States, and this variation is heritable in the sense that children acquire the religious preferences of models, usually their parents (Cavalli-Sforza and Feldman 1981, Kirkpatrick 1936). Religious belief systems include variation for norms that affect fecundity and mortality, the basic elements of Darwinian fitness. For example, in one carefully analyzed sample, Catholics had about .5 more children per family than non-Catholics (Janssen and Hauser 1981). Similarly, members of the abstemious Reformed Latter Day Saints Church of Missouri showed sharply lower age-adjusted mortalities compared to a control population (McEvoy and Land 1981). These are strong effects on important components of Darwinian fitness, so it is quite possible that natural selection may increase the frequency of some religious beliefs relative to others. Whether selection on cultural traits is strong or weak relative to the effects of random and decision-making forces is an empirical question.

The direct action of natural selection on cultural variation can greatly complicate the adaptive interpretation of human behavior. To see why, consider the following thought experiment: First imagine a system of social learning in which children are constrained to imitate only their genetic parents and in which both parents have equal probabilities of being imitated. Selection will act on cultural variation transmitted in this way, much as it would act on genes, to increase the fitness of individuals (Durham 1978).

Now imagine a social system in which teachers, as well as parents, play roles as models. Selection in this case will favor

cultural variants that make individuals effective teachers, even at some cost to success at having children. Selection will tend to optimize an individual's total ability to transmit cultural variants to others as a teacher *and* a parent, rather than optimizing only the genetic fitness.

A MODEL OF SELECTION ON CULTURE

The following simple model shows in more detail the effects of natural selection on nonparentally transmitted culture. Consider the evolution of a dichotomous cultural trait with two variants, labeled *c* and *d*. Each naive offspring is enculturated by two models, one of his genetic parents and a teacher. Suppose that cultural transmission follows the linear rule given in Table 1, i.e., the parent has weight *A* and the teacher $1-A$.

Also suppose that individuals characterized by the two different cultural variants have different probabilities of becoming parents. The probability for variant *c* is W_c and for variant *d*, W_d . Finally, suppose that individuals with different cultural variants have different probabilities of becoming teachers. Let V_c be the probability that an individual with the variant *c* becomes a teacher and V_d the probability for individuals characterized by variant *d*. This means that there are two different and potentially conflicting selective processes acting on the cultural variants. One process selects among individuals, allowing some to become parents and thereby enculturate children, while a second process selects individuals who will become teachers and also be in a position to enculturate children.

To determine the kinds of phenotypes that result from this kind of selection process, let us derive a recursion for the frequency of the cultural variant *c*. Let P_0 be the frequency of *c* among children just after cultural transmission. First, we want to compute the frequency of *c*

Table 1. The probability that naive individuals (children) acquire cultural trait *c* or *d* as a function of two available models, one parent and one teacher.

Trait of		Probability that child acquires trait	
Parent	Teacher	<i>c</i>	<i>d</i>
<i>c</i>	<i>c</i>	1	0
<i>c</i>	<i>d</i>	<i>A</i>	$1-A$
<i>d</i>	<i>c</i>	$1-A$	<i>A</i>
<i>d</i>	<i>d</i>	0	1

among parents and teachers. The frequency of *c* among parents, P_p , is

$$P_p = \frac{P_o W_c}{(1 - P_o)W_d + P_o W_c} \quad (1)$$

By analogy, the frequency of the cultural variant *c* among teachers, P_t , is

$$P_t = \frac{P_o V_c}{(1 - P_o)V_d + P_o V_c} \quad (2)$$

The frequency of *c* after transmission in the next generation, P'_o , is given by the equation: $P'_o = P_p P_t \times$ (Probability child acquires *c* given both teacher and parent are *c*) + $P_p(1 - P_t) \times$ (Probability child acquires *c* given parent is *c* and teacher is *d*) + $(1 - P_p)P_t \times$ (Probability child acquires *c* given parent is *d* and teacher is *c*).

Assuming that sets of models are formed at random and that transmission follows Table 1, this equation becomes

$$P'_o = P_p P_t [1] + P_p(1 - P_t)[A] + (1 - P_p)P_t [1 - A] \quad (3)$$

By writing the [1] in the first term as $[A + (1 - A)]$, equation (3) can be simplified to

$$P'_o = AP_p + (1 - A)P_t \quad (4)$$

Equation (4) says that the frequency of the cultural variant *c* after transmission is the weighted average of the frequencies of *c* among parents and teachers, where the weights are the relative importances of parents and teachers in the transmission of the cultural trait in question.

Now suppose that individuals with cultural variant *c* are more likely to become teachers, and those with the cultural variant *d* are more likely to become parents. Thus the frequency of *c* individuals will be higher among the pool of teachers, and the frequency of *d* individuals will be higher among parents. Given equation (4), *c* could increase in the population if teachers were important enough, even though *d* individuals are assumed to have higher genetic fitness.

This intuitive argument becomes more precise by using equations (1) and (2) in combination with equation (4) to derive a recursion for the frequency of the variant *c*. For a dichotomous trait, this means that $W_d > W_c$ and $V_c > V_d$. To simplify this process, suppose that selection is weak. The weak selection assumption is expressed mathematically as follows: Let

$$W_c/W_d = 1 + w \text{ and } V_c/V_d = 1 + v \quad (5)$$

where *w* and *v* are small enough that w^2 and v^2 are much smaller than *w* and *v*. The parameters *w* and *v* measure the selection advantage (or disadvantage) of *c* in the two selection processes. So, for instance, if $v > 0$ and $w < 0$, individuals with variant *c* are more likely to become teachers but less likely to become parents than individuals characterized by variant *d*. With this assumption the recursion for *p* is

$$P'_o = P_o + P_o(1 - P_o)[Aw + (1 - A)v] \quad (6)$$

This recursion has a simple interpretation. The term $[Aw + (1 - A)v]$ can be thought of as "effective total selective advantage." It is the advantage of variant *c* in the selective processes that cull potential parents and teachers, weighted by the importance of parents and teacher in enculturation. If this term is positive, the variant *c* always increases; if it is negative, the reverse occurs. For example, if the "teacher behavior," *c*, is a relatively small handicap in becoming a parent but a relatively big advantage in becoming a teacher, the frequency of behavior *c* can increase, even if parents have considerably more influence on children than do teachers (*A* is well above 1/2).

SELECTION AND COSTLY INFORMATION

The model shows that selection acting on nonparentally transmitted cultural variation can lead to the evolution of behaviors that reduce Darwinian fitness. One could argue that this effect is unlikely to be important because a system of cultural inheritance with such properties would not be favored by selection and thus could have evolved only by chance. Selection, the argument would run, ought to have acted to prevent such distorted cultural adaptations either by the creation of decision-making forces that counteract the effect of selection on nonparentally transmitted cultural variation or by preventing nonparental individuals from becoming important in cultural transmission.

We believe that this argument is incomplete because it ignores the fact that individual decision making may be costly compared with social learning. If the costs of individual decision making are high, selection may not favor decision-making forces that completely compensate for the maladaptive effects of nonparental transmission. Similarly, if nonparental patterns of cultural trans-

mission offer advantages to individuals of economy in information acquisition, selection on the genes that underlie a capacity for asymmetric transmission may be favored.

All organisms rely to some degree upon various modes of phenotypic flexibility (Bonner 1980). Phenotypic flexibility can be exemplified by trial-and-error learning: Individuals perform "experiments" to determine the nature of the local environment and then, based on the results and on inherited learning rules, modify their behavior. Both the experiments and the cognitive machinery necessary to evaluate them consume time and resources that could be devoted to other components of fitness. Thus we expect phenotypic flexibility to be more useful in variable environments than in constant environments.

Many authors have argued that cultural inheritance is adaptive because it can reduce the cost of acquiring useful information about how to behave (e.g., Bandura 1977, Pulliam and Dunford 1980). In simple models in which culturally transmitted characters can be modified by individual learning, selection (acting on genes) can reduce the importance of individual learning and therefore the strength of the resulting decision-making force. This is most likely to occur when individual learning is costly or error prone and environmental variability is not too great (Boyd and Richerson 1983, 1984). Under such conditions, a combination of very weak decision-making forces and accurate cultural transmission may be the best way to acquire adaptive information.

Nonparental individuals may also be more useful models than parents because they may be more skilled or knowledgeable. The effort in decision making required to discriminate exactly among adaptive skills and maladaptive inclinations of teachers and other nonparental models may demand extensive and costly empirical checks of each element of the teacher's behavior. In contrast, using relatively simple, low-cost decision-making rules to bias the choice of models, or behaviors to imitate, may substantially increase a naive person's skills at a tolerable cost of imitating some maladaptive behaviors.

Analyzing the evolutionary consequences of a variety of simple bias rules suggests that nonparental transmission may often be adaptive, despite the cost of selection, especially in variable environments (Boyd and Richerson 1982, 1984).

CULTURE AND DARWINIAN EXPLANATIONS

The foregoing arguments lead to the following hypothesis about the interaction between genes and culture in human evolution:

- Culture acts as an inheritance system.
- Various evolutionary forces will act on culturally transmitted variants. The directional forces include decision-making forces and natural selection.
- If the pattern of cultural inheritance includes nonparental or otherwise asymmetric transmission, natural selection on cultural variation can increase cultural variants that are not favored by selection on genes.
- Selection on genes can, however, favor nonparental transmission because this mode of transmission has its own advantages.
- The capacity for a particular form of cultural transmission will be favored by selection on genes whenever the net fitness advantages exceed the costs. Information costs will frequently favor weakly biased imitation of models, even nonparental models, because the effort needed to accurately separate adaptive from maladaptive behaviors is high.

If this hypothesis is correct, there is no reason to expect that any particular human trait in any particular society should conform to the predictions of ordinary Darwinian theory. To understand why humans behave the way they do, we must first understand how the existing cultural transmission system interacts with social and environmental contingencies to create a behavior pattern. To understand the evolution of human behavior, we must further understand why the system of cultural transmission has taken the form that it has; we must understand why selection on the genes that affect cultural transmission favored or permitted that form.

The demographic transitions in the industrial nations during the last century may be an example of the genetically maladaptive effects of selection acting on nonparentally transmitted variation. In terms of simple genetic fitness, this phenomenon is paradoxical. People in the wealthier nations and classes, with ample resources to devote to raising children, are typically those that most severely restrict family size. Poorer people tend to convert their smaller share in the benefits of industrial production to larger

families. The wealthy groups that reduce family size are exposed to many nonparental models through formal education and participation in large-scale bureaucracies and economic enterprises. And professionals and managers often feel that competition for the important roles in such organizations conflicts with raising large families. At the same time, children who compete for such roles need considerable parental investment (Terhune 1974). Nonparental transmission may well play an important part in the spread of norms for small families in today's developing countries (Caldwell 1976, Freedman 1979).

Norms for small families could spread by selection based on competition for prestigious roles that are likely to be effective for nonparental transmission. Children (or their parents) might, however, have difficulty evaluating exactly how heavily to rely on nonparental teachers and which of their traits to imitate. Choosing such models well could increase income, health, and ability to cope with environmental variation. Determining which traits modeled by teachers yield these benefits and which decrease fitness is a task in evolutionary calculus that even scientific students of the problem would find daunting. More likely, actual human decisions depend upon simple rules, such as choosing to imitate apparently happy and successful people. Although such simple rules may capture many of the benefits of the nonparental transmission of culture, they also expose individuals to significant costs if selection acts directly on nonparentally transmitted cultural variation.

The hypothesis that selection on nonparentally transmitted cultural variation can sometimes reduce genetic fitness is logically consistent. Whether it is correct is an empirical matter.

At least two important empirical objections can be raised: Perhaps culture does not actually have the properties of an inheritance system, and so there is little heritable cultural variation on which selection could work. The decision-making forces may be so strong that imitators are never so naive or so limited in their choice of models that cultural variants could replicate themselves (Alexander 1979, Daly 1982). Or perhaps every member of a society knows all of its cultural variants, and cultural evolution reduces to environmentally and genetically influenced decisions about which of the known behaviors an individual comes to use (Lumsden and Wilson 1981). If all individuals make up their

own minds about what and whom to imitate based on a wide range of alternatives, their cultural traits cannot depend on exposure to particular models. Individuals in this case would not exhibit patterns of heritable variation for selection to act on (although cultures themselves might be subject to group selection).

Several lines of evidence suggest, however, that cultural variation is actually maintained in every society because the decision-making forces are too weak to eliminate it. Classical studies of parent-offspring and other familial correlations for such traits as political and religious beliefs (Roff 1950) have long suggested that substantial heritable cultural variation exists. Modern psychometric analyses of various behavioral traits (e.g., Cloninger et al. 1979, Eaves et al. 1978, Henderson 1982) appear to confirm this result, even for IQ.

In addition, behavioral decision theory provides evidence that human decision-making powers are weak relative to the amount and complexity of culturally acquired behavior (Einhorn and Hogarth 1981, Nisbett and Ross 1980, Slovic et al. 1977). If heritable cultural variation exists, and if the decision-making forces are not too strong, natural selection acting directly on cultural variation could be an important force in cultural evolution. Indeed, if information is costly to acquire by individual learning but cheap to imitate, social learning may be adaptive because natural selection usually maintains roughly appropriate cultural traits in high frequency (Boyd and Richerson 1983).

A second objection is that most cultural variation may be transmitted by parents, and even if the decision-making forces are weak, natural selection on a small amount of nonparental variation might be weaker still. In this way, most differences between individuals and between groups could stem from cultural history; at the same time, human behavior could be well predicted from considering which cultural traits optimize genetic fitness (Durham 1978, 1982).

The evidence bearing on this question is circumstantial and inconclusive. Some aspects of human behavior, such as demographic transition, seem consistent with a hypothesis based on the effects of selection on nonparentally transmitted cultural traits. Several authors (Pulliam 1982, Richerson and Boyd 1978, Werren and Pulliam 1981) have argued that the predominance of unilineally organized kinship systems in human societies re-

sults from this effect. Another possible example is the existence of celibate religious orders. It seems plausible that, by avoiding the costs of bearing or supporting children, celibates could devote more resources to spreading their beliefs by nonparental transmission.

Because these hypotheses are plausible does not mean they are correct. In virtually every case, one can construct a hypothesis indicating that the seemingly maladaptive behaviors in question are, in fact, genetically adaptive. Others have argued that low confidence in paternity can make matrilineal social organization adaptive (Alexander 1979, Green 1978, Kurland 1979). Celibate priests may be second or third sons who may increase their inclusive fitness by not reproducing (Alexander 1979).

Determining which of these hypotheses is correct in any particular circumstance requires much more information than is typically available. There is no reason to accept either hypothesis a priori. Both sociobiological models and models based on the effect described here are consistent with conventional Darwinism. Which hypothesis is correct in any given situation is an empirical question. For some behaviors, those involving sexual jealousy, for example, the sociobiological hypothesis may well be correct. For others, like celibate religious orders and the limitation of family size among the modern middle class, other mechanisms are more likely at work.

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