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Does Biology Constrain Culture?

Most social scientists would agree that the capacity for human culture was probably fashioned by natural selection, but they disagree about the implications of this supposition. Some believe that natural selection imposes important constraints on the ways in which culture can vary, while others believe that any such constraints must be negligible. This article employs a "thought experiment" to demonstrate that neither of these positions can be justified by appeal to general properties of culture or of evolution. Natural selection can produce mechanisms of cultural transmission that are neither adaptive nor consistent with the predictions of acultural evolutionary models (those ignoring cultural evolution). On the other hand, natural selection can also produce mechanisms of cultural transmission that are highly consistent with acultural models. Thus, neither side of the sociobiology debate is justified in dismissing the arguments of the other. Natural selection may impose significant constraints on some human behaviors, but negligible constraints on others. Models of simultaneous genetic/cultural evolution will be useful in identifying domains in which acultural evolutionary models are, and are not, likely to be useful.

THE TERM *CULTURE* MEANS DIFFERENT THINGS TO DIFFERENT PEOPLE (Kroeber and Kluckhohn 1952). At least within anthropology, however, there is consensus on one point: culture is viewed as something that we learn from each other. When individuals learn from each other, each generation may inherit the knowledge, attitudes, and behaviors of its predecessors even if these are not transmitted genetically. This constitutes a mechanism of *cultural inheritance*. I use a definition of culture that is broad enough to encompass most others; the term will refer here to any pattern of behavior that is influenced by cultural inheritance.

This definition emphasizes that social learning is the basis of culture. Most social scientists would agree that human learning mechanisms were, in all likelihood, crafted by natural selection. They are in profound disagreement, however, about the implications of this supposition. Some scientists believe that the action of natural selection on learning mechanisms constrains culture in important ways, while others are convinced that any such constraints are negligible.

This disagreement is most clearly displayed in the debate over human sociobiology. Critics of sociobiology often argue as follows:

> *Argument for Weak Constraints*
> 1.1 Any biological constraints on culture are too weak to be significant.
> 1.2 Therefore, models of genetic evolution will be of little use in understanding variation in human behavior.

Thus, evolutionary biology has little to offer the social sciences, and further progress in that field will require attention to the dynamics of cultural transmission (Science for the People 1976; Gould and Lewontin 1979; Harris 1979; Gould 1980; Kitcher 1985; Sahlins 1976).

Against this position, sociobiologists offer what Boyd and Richerson (1985) have termed the "argument from natural origins" (Alexander 1979; Irons 1979; Kurland 1979; Durham 1976, 1979; Smith 1987a):

Argument from Natural Origins (i.e., for Strong Constraints)

    2.1   If culturally acquired behaviors tended to reduce Darwinian fitness, then the capacity for culture would be altered or destroyed by natural selection.

    2.2   Therefore, behavior should tend to enhance fitness whether transmission is cultural or not.

This argument implies that biological constraints on culture are so strong that it is reasonable for social scientists to ignore cultural transmission. It provides a rationale for the use of what I shall call *acultural* evolutionary models—those that ignore the dynamics of cultural evolution—even in species where cultural transmission is known to exist. The argument for weak constraints has been strengthened by recent demonstrations (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985) that, under some models of cultural transmission, cultural evolution leads to patterns of behavior that are inconsistent with acultural models. However, neither of these demonstrations is conclusive. Cavalli-Sforza and Feldman do not deal with the simultaneous evolution of genes and culture, and their work therefore tells us little about the extent to which genetic evolution constrains the evolution of culture. Boyd and Richerson do study simultaneous genetic/cultural evolution, but their conclusions concerning the argument from natural origins are based on other models in which genes and culture evolve independently. Thus, the extent to which culture is constrained by the effect of natural selection on mechanisms of learning is still an open question.

A comprehensive theory of behavior, of course, would incorporate both cultural and genetic evolution. The dynamics of cultural evolution, however, are complex, and the comprehensive theory is still beyond our grasp. For the present, all theories of behavior rely on some form of simplification. This article considers the merits of two such simplifications: purely cultural models, which ignore genetic evolution, and purely acultural models, which ignore cultural evolution. The first are justified only when biological constraints on culture are weak, the second only when they are strong.

Methods

This article will evaluate the premises of the two arguments above, a much easier task than evaluating the truth of their conclusions. This task is especially easy because these premises (propositions 1.1 and 2.1) have been advanced, not as peculiar features of human culture, but as general properties of culture or of evolution. If they hold in general, then they must also hold in any particular case that we care to examine. If either fails in *any* particular case, then we can conclude that it does not hold in general. Rather than search for particular cases in nature, it will be convenient to conduct a "thought experiment." I shall consider the evolution of a hypothetical species, the "snerdwump," which is characterized by a rudimentary form of culture, described below. By analysis of a graphical and a mathematical model of simultaneous genetic and cultural evolution, it will be shown that neither of the premises above is justified for snerdwumps. I will conclude that, since they fail for snerdwumps, they cannot be general properties of culture or of evolution.

The proposition that species having culture will behave as predicted by acultural models is often confused with another—that such species will behave "adaptively." The latter proposition is not justified by the argument from natural origins since natural selection does not necessarily lead to adaptation. Apparently, this fact is appreciated mainly by population geneticists and behavioral ecologists (Haldane 1932:119; Wright 1969; Smith 1987b), for the distinction between adaptation and agreement with acultural models is often ignored. Thus, it will be useful to evaluate what might be called the strong form of the argument from natural origins—the proposition that, if the capacity for culture evolved by natural selection, culture must then be adaptive.

Culture and Adaptation

Naturalists have long been impressed with the many ways in which plants and animals seem suited to their environments, and refer to the characteristics that make them so as *adaptations*. The importance of Darwin's theory stems in large part from its success in explaining these adaptations. This usage of "adaptation" is widespread in the literature of evolutionary biology (Fisher 1958:41; Haldane 1932), and is also found in standard dictionaries. Unfortunately, another usage is also common. For some evolutionists, natural selection produces adaptation by *definition* (Williams 1966:25; Wilson and Bossert 1972:47–48; Ruyle et al. 1977:49). This, however, confuses what is being explained (adaptation) with the theory used to explain it (natural selection). If adaptation is defined to be the product of natural selection, then some other word is needed to refer to the observation that individuals seem well suited to their environments, and no such word has been suggested. Use of the same word for both purposes is confusing, and has probably contributed to the misconception that Darwin's theory is circular (see Dunbar 1982). To avoid confusion, I use the word "adaptation" only to refer to the observation that organisms are somehow suited to their environments. In any particular case, the relationship of adaptation to natural selection is a matter of hypothesis, not of definition.

Two hypotheses are involved: selection can account for adaptation only when (1) those individuals with highest fitness are also those that are "best adapted," by the criteria being used to recognize adaptation, and (2) selection tends to increase the mean fitness of the population. Fisher's (1958) "fundamental theorem of natural selection" specifies circumstances under which selection will increase mean fitness. This theorem, however, is not nearly as general as was once thought (Wright 1969; Ewens 1979). When selection does not maximize mean fitness, there is no reason to think that it will produce adaptation. Thus, the capacity for culture is expected to be adaptive only if the mean fitness of a population with culture is higher than that of one without. Most of us would agree that human culture is an adaptation (White 1959:8). It is widely assumed that this is to be expected if the capacity for culture evolved through natural selection (Durham 1976). Thus, no special explanation has been sought for the adaptiveness of human culture. As we shall see, however, it is far from obvious that the forms of cultural transmission produced by natural selection will be adaptive.

Cultural transmission occurs when individuals learn from each other as well as from the environment. Thus, to understand the evolution of the capacity for culture, we must study the evolutionary forces that affect mechanisms of learning. The graphical argument presented below is adapted from that of Harpending, Rogers, and Draper (1987), and incorporates ideas developed by Boyd and Richerson (1985). Following Boyd and Richerson, I distinguish *individual learning* (learning directly from the environment) from *social learning* (learning from others). For example, consider the problem of deciding what foods to eat. One way to do this is by experiment—to eat things that you encounter, and wait to see what happens. If you get sick, you would be wise not to try that food again. Otherwise, you might include it in your diet. This is individual learning, and rats are very good at it. Because of their willingness to experiment with novel foods, they have been able to expand over much of the world, occupying many new habitats. However, individual learning entails costs as well as benefits. Rats, for example, undoubtedly ingest poison from time to time. Thus, the value of individual learning reflects a tradeoff between the benefit of a broad diet and the cost of occasional poisoning. A rat that learned his diet socially, by copying an elder, would be less often poisoned, but would be unable to use novel foods. Thus, cultural transmission of diet reduces the risk of being poisoned, at the cost of a narrower diet. Similar remarks have been made by Pulliam and Dunford (1980) and by Boyd and Richerson (1985).

To clarify the implications of these assumptions, let us perform a "thought experiment." Consider the evolution of culture in a hypothetical species, the snerdwump, which inhabits a varying environment. Snerdwumps may adopt various behaviors, and the fit-

ness consequences of each behavior depend on the state of the environment. Some snerd-wumps cope with this situation by individual learning—they obtain, at some cost, information about the environment, and then exhibit the behavior most appropriate to that environment. Flexible responses such as this are often favored by selection in varying environments (Cavalli-Sforza 1974; Via and Lande 1985; Boyd and Richerson 1985). Other snerdwumps employ social learning; they simply adopt the behavior of some individual—their "cultural parent"—of the previous generation. For the moment, it will not matter much whether the cultural parent is also a biological parent or not. The implications of these assumptions are illustrated graphically in Figure 1. The numbers there refer to the numbered paragraphs below.

1. The fitness effect of individual learning depends on its costs and benefits, but not on what others are doing. Thus, fitness is a horizontal line in Figure 1.

2. If social learning is very rare, nearly all cultural parents will be individual learners. Thus, social learners will acquire relatively recent information about the environment. That is, they will acquire behaviors that were appropriate in the immediately preceding generation. Their fitness will therefore exceed that of individual learners, provided that social learning is sufficiently cheap and environmental change sufficiently slow.

3. When all learning is social, no one is monitoring the environment, and the information acquired will eventually be many generations old. Social learning will then have lower fitness than individual learning because, by assumption, information is worthless if sufficiently out of date.

These assumptions imply that the fitness of social learning exceeds that of individual learning when its frequency is low, but falls below as its frequency increases. The shape
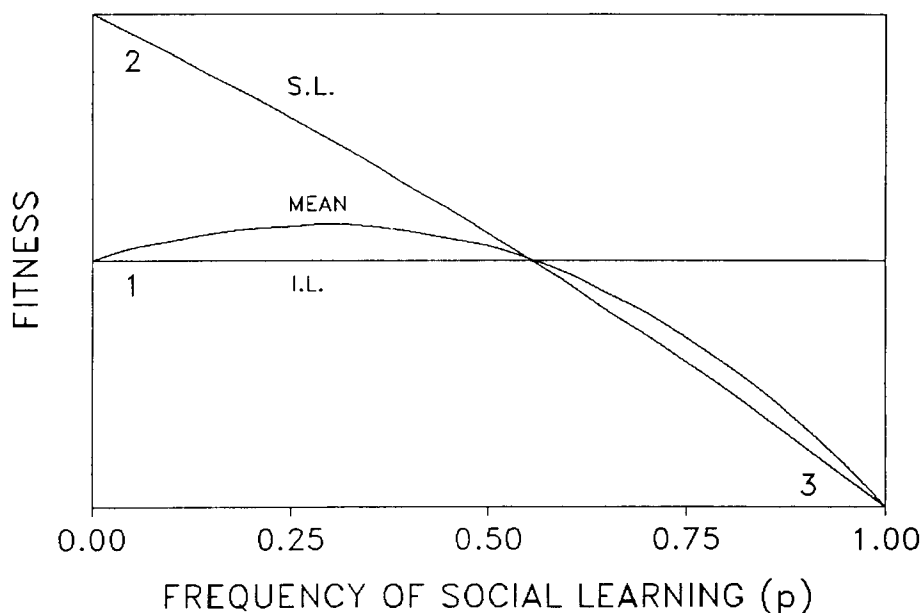

Figure 1
The fitnesses of both learning strategies and also the mean fitness of the population are plotted against the frequency of social learning, assuming that $w = b = 1.$, $c = 0.9$, $s = 0$, and $u = 0.8$. The numbers refer to the following assumptions: (1) the costs and benefits of individual learning are independent of its frequency; (2) when social learning is rare, its fitness value exceeds that of individual learning because it provides relatively up-to-date information at low cost; and (3) when social learning is very common, its fitness value falls below that of individual learning because the information it provides is out of date.

of the curve connecting points 2 and 3 will depend on the structure of the cultural inheritance system, that is, on the tendency of social learners to learn more from some individuals than from others. The curve in Figure 1 was drawn using the mathematical formulation presented below, but any monotonic curve connecting these points will produce a graph of the same general form. The conclusions that follow hold regardless of the structure of the cultural inheritance system.

This representation is consistent with a variety of assumptions about the genetics of social learning. It applies equally when social learning is inherited as a single Mendelian character, and when what is inherited is merely a propensity to learn socially, affected by genes at many loci. Under most (but not all) forms of genetic inheritance, natural selection will tend to increase the frequency of the learning mechanism with the highest fitness, and I assume this to be the case. From this assumption several conclusions follow. The frequency of social learning among snerdwumps will increase under natural selection until it reaches an equilibrium at the point where the curves for individual and social learning cross, and I assume this equilibrium to be stable. At this equilibrium the fitness of social learning (and the mean fitness of the population as a whole) is exactly the same as that of individual learning; a population (or individual) with social learning has no higher mean fitness than one without. The evolution of culture among snerdwumps, therefore, does not maximize mean fitness. Selection often fails to maximize mean fitness when, as here, the fitness of a morph decreases with its frequency. This result is hardly new (Haldane 1932; Wright 1969). The novelty here is the insight that the evolutionary process that produced culture is likely to have been characterized by this form of frequency dependence.

Recall that natural selection is expected to produce adaptation only if mean fitness is increased. Since mean fitness is not increased in the present model, there is no reason to expect that snerdwump culture will be adaptive. This does not, of course, mean that human culture is not adaptive. It does show, however, that if human culture is adaptive, it must be so because of some feature not included in the present model. Adaptation is neither an inevitable consequence of evolution nor of culture. Rindos (1986) agrees that evolution can produce forms of culture that are not adaptive. He also claims (1986:316), however, that the evolution of culture *is* an adaptive process when fitness depends on the relationship of behavior to the physical, rather than on the social environment. The snerdwump example shows that this is not necessarily so.

These results also contradict the widely held belief that, if the capacity for culture evolved through natural selection, then culture must, on average, enhance fitness (Durham 1979:43). However, it is a mistake to assume, as does Schwartz (1986), that sociobiology must stand or fall on this issue, for maximization of fitness is not a general feature of evolutionary models. The relevance of acultural evolutionary models depends on how well they predict human behavior, not on whether culture maximizes fitness. It is important to ask, then, how well such models can be expected to predict behavior in species with cultural transmission.

How Much Does Biology Constrain Culture?

To answer a quantitative question, a quantitative model is needed, and the one offered here is a simple formulation of the assumptions just discussed. Suppose that there are two environmental states, labeled 0 and 1, two behaviors labeled in the same way, and that individual fitness depends on behavior and environment as follows:

		Environmental State	
		0	1
	0	$w + b$	$w - b$
Behavior			
	1	$w - b$	$w + b$

Note that the fitness effect of each behavior is independent of the frequency with which it is exhibited. Thus, although the fitness effects of snerdwump learning mechanisms are frequency-dependent, the effects of the behaviors learned are not. Further suppose that, in each generation, the environment is perturbed with probability u, and that after perturbations it is equally likely to be in either state.

In the absence of any information about present or past environmental states, the environment is equally likely to be in either state. Therefore, the unconditional fitness of either behavior is $w + (\frac{1}{2})b - (\frac{1}{2})b = w$. Fitness can be enhanced by obtaining information about the environment. Suppose that the state of the environment can be determined accurately by individual learning, but that this effort reduces fitness by bc units due to risk of predation or expenditure of time and energy. Then the fitness of a snerdwump adopting individual learning is

$$w_I = w + b(1 - c) \tag{1}$$

How does this compare to the fitness of a snerdwump who learns socially? The fitness, w_s, of a social learner depends on the probability that social learning will provide accurate information, and this probability changes as culture evolves. Let p denote the frequency after selection of individuals adopting social learning in the current generation. If cultural evolution is fast compared with genetic evolution, then p can be treated as a constant for the purpose of finding what I shall call the *cultural equilibrium*, $\tilde{w}_s$. This is the equilibrium value of w_s under the action of cultural evolution only. Through social learning, an individual acquires behavior that was originally acquired by individual learning in some previous generation. The probability that this occurred τ generations ago is $p^{\tau-1}(1-p)$, if cultural parents are random members of the previous generation. The expected benefit obtained by adopting such behavior is zero if the environment has been perturbed in the past τ generations, and b if no perturbation has occurred. The probability of no perturbation is $(1-u)^\tau$. Putting this together, we can write

$$\tilde{w}_S = w + b\sum_{\tau=1}^{\infty} p^{\tau-1}(1-p)(1-u)^\tau$$

$$= w + b(1-p)(1-u)\sum_{\tau=1}^{\infty} p^{\tau-1}(1-u)^{\tau-1}$$

By the formula for the sum of a geometric series, this is

$$\tilde{w}_S = w + \frac{b(1-p)(1-u)}{1-p(1-u)}$$

This expression ignores the possibility that social learning may entail costs of its own. These could be introduced in several ways, but the simplest results are obtained by assuming that they produce a proportional reduction in b, that is, that

$$\tilde{w}_S = w + \frac{b(1-s)(1-p)(1-u)}{1-p(1-u)} \tag{2}$$

where s measures the cost of social learning. The qualitative conclusions drawn below are unchanged if the costs in this model are made additive instead of multiplicative. It can be shown that w_s is a stable equilibrium and that convergence toward it is rapid unless $(1-u)p \approx 1$. As shown in Figure 1, $\tilde{w}_s$ is a monotonically decreasing function of p that exceeds w_I when p is small, but falls below it as p increases.

Changes in p, the frequency of social learning, are produced by genetic evolution, which is assumed to be much slower than cultural evolution. In studying the evolution of p, therefore, it is reasonable to assume that convergence toward (2) is effectively instantaneous. Equation 2 implies that $\tilde{w}_s = w_I$ when p is equal to

$$\hat{p} = 1 - \frac{(1-c)u}{(1-u)(c-s)}$$

This is the *evolutionary equilibrium* of p (i.e., the equilibrium under the combined effects of cultural and genetic evolution). It is between zero and one, provided that $(1-u)(1-s)>(1-c)$.

We are interested in measuring the consistency of behavior under this model with the behavior that would be predicted by a model ignoring cultural transmission. Because the fitness effects of the two behaviors are frequency independent, an acultural model would predict that natural selection would maximize fitness. It would, in other words, predict appropriate behavior in each environment. Thus, the consistency between behavior and the predictions of the acultural model can be measured by the correlation between behavior and environment. To define such a correlation, we must first define two random variables. Let B equal zero or unity depending on the behavior exhibited by a random member of the population, and let S take the same values depending on the state of the environment. These variables have the same means and variances: $E(S) = E(B) = 1/2$, and $Var(S) = Var(B) = 1/4$. The correlation of S and B is

$$r = \frac{E\{SB\} - E\{S\}E\{B\}}{\sqrt{(Var\{S\}Var\{B\})}} = 4E\{SB\} - 1 \tag{3}$$

and it measures the tendency of individuals to behave appropriately. The acultural model would predict that $r=1$.

The value of r is easy to find if $(1-u)(1-s)<(1-c)$, since that condition implies that social learning will not evolve. Thus, all snerdwumps are individual learners, and $r = 1$. In the Appendix it is shown that

$$r = \frac{1-c}{(1-u)(1-s)} \tag{4}$$

in the more interesting case when $(1-u)(1-s)>(1-c)$. Comparison with equation 1 reveals that the numerator here, $1-c$, is the proportion of the potential benefit of individual learning that is actually realized. It is, if you will, the efficiency of individual learning. Similarly, the denominator is the efficiency of social learning. Thus, the agreement between behavior and acultural models is measured by the ratio of the efficiencies of the two learning mechanisms. Since both efficiencies are positive fractions, it is clear that $r>0$ for any set of parameter values under which learning can evolve at all. This means that natural selection does constrain culture in the model considered here. An acultural model would explain a fraction r^2 of the variance in culturally acquired behavior. Where the efficiency of individual learning is much lower than that of social learning, however, this fraction may be very small, and the constraints on culture very weak.

Equation 4 can be re-expressed in terms of p as follows:

$$r = \frac{1-\hat{p}}{1-\hat{p}(1-u)} \tag{5}$$

This shows that r is at least as large as $1-\hat{p}$, the frequency of individual learning. Thus, behaviors that are acquired primarily through individual learning should track the environment well. Furthermore, if environmental change is slow enough (i.e., if $u \approx 0$), then r will be large even if most learning is social.

However, this may require that environmental change be unrealistically slow. In each generation, the probability of an environmental change is $u/2$, and this implies that the time between environmental changes is a geometric random variable with mean $2/u$. Using (5), this quantity can be expressed as

$$2/u = \frac{2r\hat{p}}{(1-r)(1-\hat{p})} \tag{6}$$

Note that r and $\hat{p}$ can both be near unity only if $2/u$ is large, that is, if environmental change is very slow. For example, if $r=\hat{p}=0.9$, then the average time between environmental changes is $2/u = 162$ generations—nearly 4,700 years for humans. If environmental change is sufficiently slow, selection will favor obligate behavior over any form of learning (Cavalli-Sforza and Feldman 1983), so the model analyzed here would be irrelevant. Social learning cannot evolve if $2/u$ is too large, and that implies that r and $\hat{p}$ cannot both be near unity. We should not expect, therefore, to find a close match between behavior and environment when the frequency of social learning is high.

Discussion

The study of culture is in a position similar to that of biology before Darwin. Most of us would agree that human culture is adaptive: culturally acquired behaviors are essential to humans, and have enabled them to colonize habitats far outside the ecological niche of their primate ancestors. Yet we have no satisfactory explanation for this adaptation. It is possible to devise models in which natural selection produces adaptive forms of culture (Robert Boyd, personal communication, 1987). As we have seen, however, selection can also produce forms of culture that are not adaptive. This leaves us with an important unanswered question: What accounts for the adaptiveness of human culture?

In answering this question, some theoretical work will be necessary. We must identify ways in which adaptive mechanisms of cultural inheritance can evolve. The model studied here ignores a variety of factors that may tend to make culture adaptive. For example,

1. There is no cultural selection—individuals with high fitness are no more likely than others to serve as cultural parents.

2. There are no learning biases favoring transmission of behaviors that enhance fitness.

3. Individual learning does not modify or improve behaviors acquired culturally. Therefore, the value of culturally transmitted information does not accumulate; it decays.

4. Decisions about which form of learning to adopt are not contingent on the quality of available environmental information.

Departures from any or all of these assumptions may contribute toward the apparently adaptive nature of human culture, but their relative importance is unclear. Models of simultaneous genetic and cultural evolution should help clarify this question, and useful starts in this direction have already been made by several authors (Lumsden and Wilson 1981; Boyd and Richerson 1985, 1988).

Many of us believe that acultural evolutionary models (those that ignore cultural evolution) provide useful insights into the evolution of behavior—even that of species in which cultural transmission is important. One way to justify this position is what Boyd and Richerson (1985) have called the argument from natural origins. In its simplest form, this argument rests on the premise that a mechanism of cultural inheritance can evolve by natural selection only if it is adaptive. As we have seen, this premise is false. However, this simple form of the argument from natural origins has few supporters and is of no great importance. Most modern evolutionists are well aware that natural selection can be maladaptive, especially where interactions between individuals are involved.

The weak form of the argument from natural origins assumes that mechanisms of cultural transmission can evolve only if the behaviors produced tend to be consistent with the predictions of acultural evolutionary models. The consistency between behavior and acultural models is measured here by r, a coefficient of correlation. Equation 4 shows that, at least within our hypothetical species, the snerdwump, there is some tendency for behavior to accord with acultural models. However, if the efficiency of social learning is high, then $r=0$, and this tendency will be negligible. There is therefore no basis for the

claim that, if the capacity for culture evolved by natural selection, then culture must be explicable in terms of ordinary, acultural evolutionary models.

On the other hand, equation 4 also shows that, if the efficiency of individual learning rivals that of social learning, then $r = 1$, which implies that culture will be highly consistent with the predictions of acultural models. Thus, there are circumstances under which biological constraints on culture are important. There is, therefore, no basis for the claim that since humans have culture, models of genetic evolution are necessarily irrelevant to contemporary variation in human behavior. Thus, neither extreme position in the sociobiology debate can be justified by appeal to general properties of evolution or of culture. It is possible for biological constraints on culture to be negligible; it is also possible for them to be of fundamental importance. If either extreme position is correct, it must be because of some peculiar feature of human culture that has yet to be identified.

The advantages of theories of simultaneous genetic/cultural evolution are obvious, but such theories are difficult to construct, and it seems likely that both purely cultural and purely acultural approaches to social science will continue in importance. These approaches, however, need not arise from contradictory philosophical positions about the causes of human behavior. The past two decades of psychological research have undermined the old notion that there are general laws of learning that apply universally to all behaviors and all species (Lumsden and Wilson 1981; Roper 1983). Learning abilities are species-specific, and are constrained and biased in many ways. It is likely that each mammalian species possesses a constellation of learning abilities, each evolved for a specific purpose. Within a single species, biological constraints may be strong for some behaviors, but negligible for others. Purely acultural explanations would be needed for the former behaviors, and purely cultural explanations for the latter. To reconcile the two approaches to social science, what is needed is a way to distinguish behaviors whose evolutionary dynamics are primarily genetic ($r \approx 1$) from those whose dynamics are primarily cultural ($r \approx 0$). This will be possible if appropriate models of simultaneous genetic/cultural evolution can be developed.

The present model is far too simple to be advanced as a realistic description of human culture. The conclusions drawn so far, however, do not depend on the model's realism but only on its consistency with what is known about the process of natural selection. This cannot be said of the conclusions I am about to draw, and they should be regarded with some skepticism. However, experience has shown that simplistic models are often successful in capturing the main features of phenomena that are too complex to model in detail. For example, the premises of the Hardy-Weinberg theorem of population genetics almost never hold in nature, yet its predictions are approximately correct more often than not. Consequently, this theorem is fundamental both to empirical and theoretical studies in population genetics. Only experience will tell whether the model advanced here is similarly robust. In the meantime, the model's broader implications seem worthy of discussion.

The model assumes that the fitness effects of particular behaviors are independent of their frequency. This may be true of behaviors, such as techniques of farming or foraging, with which resources are extracted from the environment, but it is unlikely to be true of social behavior: the success of particular social behaviors ordinarily does depend on what others are doing. As we have seen, such frequency dependence can profoundly alter the outcome of evolution. Thus, the model developed here is probably a poor guide to the evolutionary dynamics of social behavior.

The model's main result is equation 4, which relates the correlation between behavior and the environment to the efficiencies of individual and social learning. As these undoubtedly vary from behavior to behavior, it follows that some behaviors should track the environment well, others poorly. Consequently, ecology should be more useful in understanding some behaviors than others, a fact that cultural ecologists have long understood (Oliver 1962: Steward 1955). This equation also implies that acultural evolutionary

models are unlikely to be helpful in understanding behaviors that are usually learned socially.

Behavioral ecologists have had considerable success in using acultural models to explain aspects of human foraging. For example, Hawkes, Hill, and O'Connell (1982) showed that the resource species chosen by Aché foragers were consistent with the predictions of a simple evolutionary model. The availability of various food items may change so rapidly that tradition would be a poor source of information about the optimal choice of diet. Thus, we might expect a reliance on individual learning, leading to a strong correlation between behavior and environment. This conclusion can be obtained from equation 4 by noting that a high rate of environmental change (large u) tends to increase r. It may explain the predictive success of the acultural model used by Hawkes, Hill, and O'Connell (1982). Hunting techniques, on the other hand, may be much easier to learn socially than by trial and error ($s \ll c$), and should not rapidly become obsolete ($u \ll 1$). If so, equation 4 indicates that $r \approx 0$, and acultural models should do a poor job of explaining variation in hunting techniques.

The results of this study are broadly consistent with the conventional assumption that evolutionary models will best predict those behaviors with large effects on fitness. Such behaviors would be identified as those with large values of $b(1 - c)$, since b is the fitness benefit of appropriate behavior and $1 - c$ the efficiency of individual learning. The conventional assumption is partially consistent with the present model, since r is also an increasing function of $1 - c$. On the other hand, r depends also on the efficiency of social learning, but does not depend on b. Does this mean that acultural models may sometimes be useful even for behaviors whose effect on fitness is small? Perhaps, but we have ignored the fact that each learning mechanism may affect several behaviors. In a more realistic model, it is likely that evolution of the learning mechanism would be most sensitive to those behaviors with large values of b. Thus, the present results are broadly consistent with the conventional assumption.

Conclusions

Natural selection can produce mechanisms of cultural transmission that are not adaptive and that may be only weakly consistent with the predictions of *acultural* evolutionary models (those that ignore cultural evolution). This refutes what Boyd and Richerson have called "the argument from natural origins" as a general principle, and raises the question: Why is culture adaptive? On the other hand, natural selection can also produce mechanisms of cultural transmission that are highly consistent with acultural evolutionary models. This refutes the claim that, since humans have culture, acultural models are necessarily irrelevant to human behavior. It seems likely that both purely cultural and purely acultural theories of behavior will continue in importance. These conclusions do not depend on the realism of the model studied here.

To the extent that the model is accurate in spite of its simplicity, several additional conclusions can be drawn. The correlation between behavior and the predictions of acultural models should be better for some behaviors than others. It should be greatest where the efficiency of individual learning rivals that of social learning or, equivalently, where the frequency of social learning is low. Thus, in field studies it may be useful to ask (1) what are the relative efficiencies of social and individual learning in the acquisition of particular behaviors, and (2) what are the relative frequencies of the two modes of learning? The dynamics of cultural evolution are likely to be most important where the efficiency and frequency of social learning are high.

Appendix

To evaluate r when $(1-u)(1-s) > (1-c)$, note that the term $E(SB)$ in (3) is

$$E\{SB\} = Prob\{\, S = 1 \text{ and } B = 1\,\} = 0.5x_T$$

where x_T is the probability that a random individual in the population is behaving appropriately with respect to the current environment. Since all individual learners adopt appropriate behavior, x_T is

$$x_T = 1 - \hat{p}(1 - x_S) \tag{7}$$

where x_S is the probability that a social learner behaves appropriately. Now the fitness of a social learner is $w + (1-s)b$ with probability x_S, and $w - (1-s)b$ with probability $1 - x_S$. Thus,

$$\hat{w}_S = w + (1-s)b(2x_S - 1)$$

At equilibrium, we also have

$$\hat{w}_S = w_I = w + b(1 - c)$$

since both strategies have equal fitnesses at equilibrium. Equating these expressions leads to

$$1 - x_S = \frac{c - s}{2(1 - s)}$$

and substituting this into equation 7 produces

$$x_T = 1 - \frac{(c - s)(1 - u) - (1 - c)u}{2(1 - s)(1 - u)}$$

Finally, substituting into the expressions for and $E(SB)$ and then into equation 3 produces equation 4.

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