

# 23 Models of Cultural Evolution

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As least since the time of Darwin, there has been a tradition of borrowing between evolutionary theory and the social sciences. Darwin himself owed a debt to the Scottish economists who showed him how order can be produced without conscious design. Adam Smith thought that socially beneficial characteristics can emerge in a society as if by an "invisible hand"; though each individual acts only in his or her narrow self-interest, the result, Smith thought, would be a society of order, harmony, and prosperity. The kind of theory Darwin aimed at—in which fitness improves in a population without any conscious guidance—found a suggestive precedent in the social sciences.

The use of game theory by Maynard Smith<sup>1</sup> and others provides a contemporary example in which an idea invented in the social sciences finds application in evolutionary theory. Economists and mathematicians were the first to investigate the payoffs that would accrue to players following different strategies in games of a given structure. Biologists were also to see that game theory does not require that the players be rational or even that they have minds. The behavior of organisms exhibits regularities; this is enough for us to talk of them as pursuing strategies. The payoffs of the behaviors that result from these strategies can be measured in the currency of fitness—i.e., in terms of their consequences for survival and reproduction. This means that the idea of payoffs within games allows us to describe evolution by natural selection. Here again is a case in which a social scientific idea has broader scope than its initial social science applications might have suggested.

At present, there is considerable interest and controversy surrounding borrowings that go in the opposite direction. Rather than apply social science ideas to biological phenomena, sociobiology and related research programs aim to apply evolutionary ideas to problems that have traditionally been thought to be part of the subject matter of the social sciences. Sociobiology is the best known of these enterprises. It has been criticized on a variety of fronts. Although I think that these criticisms differ in their force, I don't want to review them here. My interest is in a somewhat lesser-known movement

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within biology, one that strives to extend evolutionary ideas to social scientific phenomena. I want to discuss the models of cultural evolution put forward by Cavalli-Sforza and Feldman<sup>2</sup> and by Boyd and Richerson.<sup>3</sup> These authors have distanced themselves from the mistakes they see attaching to sociobiology. In particular, they wish to describe how cultural traits can evolve for reasons that have nothing to do with the consequences the traits have for reproductive fitness. In a very real sense, their models describe how it is possible for mind and culture to play an irreducible and autonomous role in cultural change. For this reason, there is at least one standard criticism of sociobiology that does not apply to these models of cultural evolution. They deserve a separate hearing.

In order to clarify how these models differ from some of the ideas put forward in sociobiology, it will be useful to describe some simple ways in which models of natural selection can differ. I focus here on natural selection, even though there is more to evolutionary theory than the theory of natural selection, and in spite of the fact that the two books I am considering sometimes exploit these nonselectionist ideas. Although there are nonselectionist ideas in these two books, the bulk of their models assigns a preeminent role to natural selection and its cultural analogs. So a taxonomy of selection models will help us see how models of cultural evolution are related to arguments put forward in sociobiology.

There are two crucial ingredients in a selection process. Given a set of objects that exhibit variation, what will it take for that ensemble to evolve by natural selection? By evolution, I mean that the frequency of some characteristic in the population changes. The first requirement is that the objects differ with respect to some characteristic that makes a difference in their abilities to survive and reproduce. Second, there must be some way to ensure that offspring resemble their parents. The first of these ingredients is called *differential fitness*; the second is *heritability*.

In standard formulations of the genetical theory of natural selection, different genes or gene complexes in a population encode different phenotypes. The phenotypes confer different capacities to survive and reproduce on the organisms that possess them. As a result, some genes are more successful in finding their way into the next generation than others. In consequence, the frequency of the phenotype in question changes. This is evolution by natural selection with a genetic mode of transmission. Note that traits differ in fitness because some organisms have more babies than others. It may seem odd to say that "having babies"<sup>4</sup> is one way to measure fitness, as if there could be others. My reason for saying this will become clearer later on.

The phenotype treated in such a selection model might be virtually any piece of morphology, physiology, or behavior. Biologists have developed different applications of this Darwinian pattern to characteristics of all three sorts in a variety of species. One way—the most straightforward way—to apply biology to the human sciences is to claim that some psychological or cultural characteristic became common in our species by a selection process of this sort. This is essentially the pattern of explanation that Wilson was using

when he talked about aggression, xenophobia, and behavioral differences between the sexes. An ancestral population is postulated in which phenotypic differences have a genetic basis; then a claim is made about the consequences of those phenotypes for survival and reproduction. This is used to explain why the population changed to the configuration we now observe.

The second form that a selection process can take retains the idea that fitness is measured by how many babies an organism produces, but drops the idea that the relevant phenotypes are genetically transmitted. Strictly speaking, evolution by natural selection does not require genes. It simply requires that offspring resemble their parents. For example, if characteristics were transmitted by parents teaching their children, a selection process could occur without the mediation of genes.

A hypothetical example of how this might happen is afforded by that favorite subject of sociobiological speculation—the incest taboo. Suppose that incest avoidance is advantageous because individuals with the trait have more viable offspring than individuals without it. The reason is that outbreeding diminishes the chance that children will have deleterious recessive genes in double dose. If offspring learn whether to be incest avoiders from their parents, the frequency of the trait in the population may evolve. And this may occur without there being any genetic differences between those who avoid incest and those who do not. Indeed, incest avoidance could evolve in this way in a population of genetically identical individuals, provided that the environmental determinant of the behavior runs in families.<sup>5</sup>

In this second kind of selection model, mind and culture displace one but not the other of the ingredients found in models of the first type. In the first sort of model, a genetic mode of transmission works side by side with a concept of fitness defined in terms of reproductive output—what I have called “having babies.” In the second, reproductive output is retained as the measure of fitness, but the genetic mode of transmission is replaced by a psychological one. Teaching can provide the requisite heritability just as much as genes.

The third pattern for applying the idea of natural selection abandons both of the ingredients present in the first. Genes are abandoned as the mode of transmission. And fitness is not measured by how many babies an organism has. Individuals acquire their ideas because they are exposed to the ideas of their parents, of their peers, and of their parents' generation. So the transmission patterns may be vertical, horizontal, and oblique. An individual exposed to a mix of ideas drawn from these different sources need not give them all equal credence. Some may be more attractive than others. If so, the frequency of ideas in the population may evolve over time. Notice that there is no need for organisms to differ in terms of their survivorship or degree of reproductive success in this case. Some ideas catch on while others become passé. In this third sort of selection model, ideas spread the way a contagion spreads.

It is evident that this way of modeling cultural change is tied to the genetical theory of natural selection no more than it is tied to epidemiology. Rumors and diseases exhibit a similar dynamic. The spread of a novel characteristic in

a population by natural selection, like the spread of an infection or an idea, is a diffusion process.

This third type of selection model has a history that predates sociobiology and the models of cultural evolution that I eventually want to discuss. Consider the economic theory of the firm.<sup>6</sup> Suppose one wishes to explain why businesses of a certain sort in an economy behave as profit maximizers. One hypothesis might be that individual managers are rational and economically well informed; they adjust their behavior so as to cope with market conditions. Call this the learning hypothesis. An alternative hypothesis is that managers are not especially rational or well informed. Rather, firms that are not efficient profit maximizers go bankrupt and thereby disappear from the market. This second hypothesis posits a selection process.

Note that the selection hypothesis involved here is of type III. Individual firms stick to the same market strategies, or convert to new ones, by some process other than genetic transmission. In addition, the biological kind of survival and reproduction (what I have called "having babies") does not play a role. Firms survive differentially, but this does not require any individual organism to die or reproduce.

A different example of type III models, which will be familiar to philosophers of science, is involved in some versions of evolutionary epistemology. Karl Popper suggested that scientific theories compete with each other in a struggle for existence.<sup>7</sup> Better theories spread through the population of inquirers; inferior ones exit from the scene. Popper highlighted the nonbiological definition of fitness used in this view of the scientific process when he said that "our theories die in our stead."<sup>8</sup>

The three possible forms that a selection model can take are summarized in table 23.1. By "learning," I don't want to require anything that is especially cognitive; imitation is a kind of learning. In addition, "having students" should be interpreted broadly, as any sort of successful influence mediated by learning.<sup>9</sup>

The parallelism between type I and type III models is instructive. In the type I case, individuals produce different numbers of babies in virtue of their phenotypic differences (which are transmitted genetically). In the type III case, individuals produce different numbers of students in virtue of their phenotypic differences (which are transmitted by learning).

Selection models of cultural characteristics that are of either pattern I or pattern II can properly be said to provide a "biological" treatment of the

**Table 23.1.** Three types of selection models

	Heritability	Fitness
I	Genes	Having babies
II	Learning	Having babies
III	Learning	Having students

Note: The description of Type III models, in which fitness is measured by "having students," is due to Peter Richerson.

characteristic in question. Models of type III, on the other hand, do not really propose biological explanations at all. A selectional theory of the firm, or a diffusion model that describes the spread in popularity of an idiom in a language, are no more "biological" than their competitors. In type III models, the mode of transmission and the reason for differential survival and replication may have an entirely autonomous cultural basis. Genes and having babies are notable by their absence; the biological concept of natural selection plays the role of a suggestive metaphor, and nothing more.

It is important to recognize that this threefold taxonomy describes the process of natural selection, not the product that process may yield. For example, once a type I process of natural selection has run its course, it is an open question whether the variation that remains is genetic or nongenetic. Consider the work in sociobiology by Richard Alexander.<sup>10</sup> He believes that human beings behave so as to maximize their inclusive fitness. This means that there is an evolutionary explanation for the fact that people in one culture behave differently from those in another. But Alexander does not think that this is due to there being genetic differences between the two cultures. Rather, his idea is that the human genome has evolved so that a person will select the fittest behavior, given the environment he or she occupies. The fact that people behave differently is due to the fact that they occupy different environments. So, in terms of the current variation that we observe, Alexander is, in fact, a radical environmentalist. This is worth contemplating if you think that sociobiology stands or falls with the thesis of genetic determinism.

Matters change when we consider not the present situation, but the evolutionary past that generated it. The genome that Alexander postulates, which gives current humans their ability to modify behavior in the light of ecological conditions, evolved because it was fitter than the alternatives against which it competed. That is, the process of natural selection that led to the present configuration is one in which genetic differences account for differences in behavior.

So Alexander sees genetic differences as being crucial to the process of evolution, but environmental differences as characterizing the product of that evolution. He is a type I theorist, since these types pertain to the process of natural selection, not its product.

The distinction between process and product is perhaps a bit harder to grasp when we think of the evolution of some behavioral or psychological trait, but it really applies to any evolutionary event. For the fact of the matter is that evolution driven by a type I selection process feeds on (additive) genetic variation, and uses it up. A morphological character can display the same double aspect. The opposable thumb evolved because there was a genetic difference between those with the thumb and those without it. But once that trait has finished evolving, the difference between those with and those without a thumb may owe more to industrial accidents and harmful drugs taken prenatally than to genetic oddities.

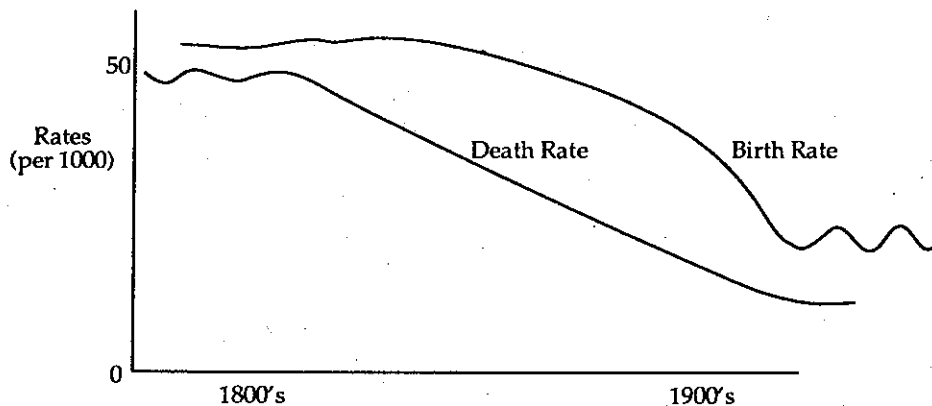
This threefold division among selection models is of course consistent with there being models that combine two or more of these sorts of process. My

taxonomy describes "pure types," so to speak, whereas it is often interesting to consider models in which various pure types are mixed. This is frequently the case in the examples worked out by Cavalli-Sforza and Feldman and by Boyd and Richerson. I want to describe one example from each of these books. The point is to discern the way in which quite different selection processes interact.

In the nineteenth century, Western societies exhibited an interesting demographic change, one that had three stages. First, oscillations in death rates due to epidemics and famines became both less frequent and less extreme. Second, overall mortality steadily declined. This latter change had a multiplicity of causes; improved nutrition, sanitation, and (if the more recent past is also considered) medical advances played a role. The third part of this demographic transition was a dramatic decline in birth rates. Typically, there was a time lag; birth rates began to decline only after death rates were already on the way down. Cavalli-Sforza and Feldman (p. 181) give the somewhat idealized rendition of this pattern shown in figure 23.1.

Cavalli-Sforza and Feldman consider the question of how fertility could have declined in Europe. From the point of view of a narrowly Darwinian outlook, this change is puzzling. A characteristic that increases the number of viable and fertile offspring will spread under natural selection, at least when that process is conceptualized from the point of view of a type I model. Cavalli-Sforza and Feldman are not tempted to appeal to the theory of optimal clutch size due to Lack, according to which a parent can sometimes augment the number of offspring surviving to adulthood by having fewer babies.<sup>11</sup> Presumably, this Darwinian option is not even worth exploring, because women in nineteenth-century Europe easily could have had more viable fertile offspring than they in fact did. People were not caught in the bind that Lack attributed to his birds.

The trait that increased in the modern demographic transition was one of reduced biological fitness. The trait spread *in spite of* its biological fitness, not *because of* it. In Italy, women changed from having about five children on



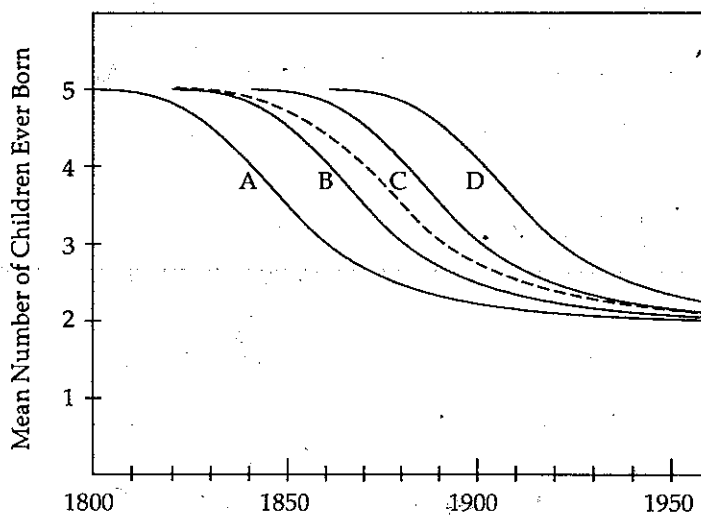
**Figure 23.1** Cavalli-Sforza and Feldman's (p. 181) idealized representation of the demographic time lag in Europe. Mortality rates decline; then, after a time lag, the birth rate declines also. (Reprinted by permission of Princeton University Press.)

average to having about two. The trait of having two children, therefore, has a biological fitness of  $2/5$ , when compared with the older trait it displaced.

Cavalli-Sforza and Feldman focus on the problem of explaining how the new custom spread. One possible explanation is that women in all social strata gradually and simultaneously reduced their fertilities. A second possibility is that two dramatically different traits were in play and that the displacement of one by another cascaded from one social class down to the next. The first hypothesis, which posits a gradual spread of innovation, says that fertilities declined from 5 to 4.8 to 4.5 and so on, with this process occurring simultaneously across all classes. The second hypothesis says that having five children competed with having two, and that the novel character was well on its way to displacing the more traditional one among educated people before the same process began among less educated people. This second hypothesis is illustrated in figure 23.2. There is some statistical evidence that the second pattern is more correct, at least in some parts of Europe.

Cavalli-Sforza and Feldman emphasize that this demographic change could not have taken place if traits were passed down solely from mothers to daughters. The Darwinian disadvantage of reduced fertility is so great that purely vertical transmission is not enough to offset it. This point holds true whether fertility is genetically transmitted or learned. A woman with the new trait will pass it along to fewer offspring than a woman with the old pattern, if a daughter is influenced only by her mother.

What is required for the process is some mixture of horizontal and oblique transmission. That is, a woman's reproductive behavior must be influenced by her peers and by her mother's contemporaries. However, it will not do for a woman to adopt the behavior that she finds represented on average in the group that influences her. What is required is that a woman find small family size more attractive than large family size even when very few of her peers



**Figure 23.2** Cavalli-Sforza and Feldman's (p. 185) idealized picture of the demographic transition in Italy. A is the most educated class; B, C and D are progressively less educated. (Reprinted by permission of Princeton University Press.)

possess the novel characteristic. There must be a "transmission bias" in favor of the new trait.

Having a small family was more attractive than having a large one, even though the former trait had a lower Darwinian fitness than the latter. Cavalli-Sforza and Feldman show how the greater attractiveness of small family size can be modeled by using ideas drawn from population genetics. However, when these genetic ideas are transposed into a cultural setting, one is talking about cultural fitness, not biological fitness. So the model they end up with for the demographic transition combines two selection processes. When fitness is defined in terms of having babies, having a small family is selected against. When fitness is defined in terms of the attractiveness of an idea ("having students"), there is selection favoring a reduction in family size. Cavalli-Sforza and Feldman show how the cultural process can overwhelm the biological one; given that the trait is sufficiently attractive (and their models have the virtue of giving this idea quantitative meaning), the trait can evolve in spite of its Darwinian disutility.

The example I want to describe from Boyd and Richerson's book is developed in a chapter that begins with a discussion of Japanese kamikaze pilots during World War II. Self-sacrificial behavior—altruism—has been an important problem for recent evolutionary theory. Indeed, Wilson called it "the central problem of sociobiology."<sup>12</sup> Although some apparently altruistic behaviors can be unmasked—shown to be predicated on the selfish expectation of reciprocity, for example—Boyd and Richerson are not inclined to say this about the kamikazes. They died for their country. Nor can one explain their self-sacrifice by saying that it was coerced by leaders; kamikaze pilots volunteered. Nor is it arguable that the pilots volunteered in ignorance of the consequences; suicide missions were common knowledge in the Japanese air force.

So why did kamikaze pilots volunteer? Boyd and Richerson (pp. 204–5) refer to one historian who "argues that the complex of beliefs that gave rise to the kamikaze tactic can be traced back to the Samurai military code of feudal Japan which called for heroic self-sacrifice and put death before dishonour. When the Japanese military modernized in the nineteenth century, the officer corps was drawn from the Samurai class. These men brought their values and transmitted them to subsequent generations of officers who in turn inculcated these values in their men."

Boyd and Richerson (pp. 204–5) say that this historical explanation is "unsatisfactory for two reasons. First, it is incomplete. It tells us why a particular generation of Japanese came to believe in heroic self-sacrifice for the common good; it does not tell us how these beliefs came to predominate in the warrior class of feudal Japan. Second, it is not general enough. The beliefs that led the kamikazes to die for their country are just an especially stark example of a much more general tendency of humans to behave altruistically toward members of various groups of which they are members." They then impose two conditions of adequacy on any proposed explanation: (1) it must show how the "tendency to acquire self-sacrificial beliefs and values could have



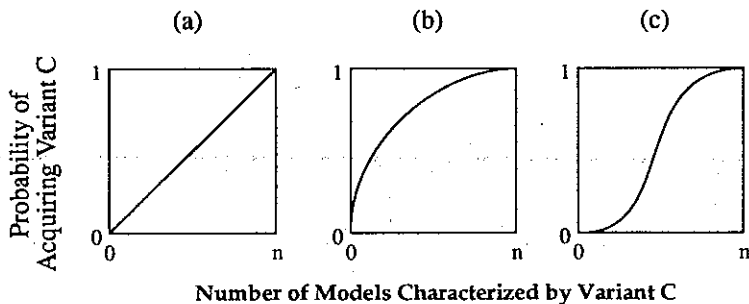
evolved"; (2) it must show "why altruistic cooperation is directed toward some individuals and not others" (p. 205).

In answer to these requirements, Boyd and Richerson then construct a group selection model that incorporates a certain form of learning. Altruists and selfish individuals exist in each of several groups. Within each group, altruists do less well than selfish people. However, groups of altruists go extinct less often and found more colonies than groups of selfish individuals. These ideas are standard fare in the models of group selection that evolutionary biologists have considered.<sup>13</sup> A type I selection model of the evolution of altruism will require a between-group process favoring altruism that offsets the within-group process that acts to eliminate the trait.

The new wrinkle introduced by the idea of cultural transmission is as follows. Boyd and Richerson postulate that cultural transmission favors common characteristics and works against rare ones. Within a group, individuals are especially biased toward adopting altruism if most individuals are altruists and toward becoming selfish if most people are selfish. What I mean by "especially" biased is illustrated in figure 23.3. In all cases of cultural transmission, the state that a naive individual acquires is influenced by the frequency of traits in the population. Boyd and Richerson impose a more extreme demand. They require that the probability of acquiring a common trait be higher than its population frequency; this is what they call "frequency-dependent biased transmission" (depicted in figure 23.3c).

The process of cultural transmission can work within the time frame of a single biological generation. The effect is to augment the amount of variation there is among groups. Whereas traditional genetic models of group selection allow for a continuum of local frequencies of altruism, the result of this biased transmission rule is to push each local population toward 100 percent altruism or 100 percent selfishness. This has the effect of raising the probability that altruism will evolve and be maintained.

Boyd and Richerson also raise the question of how this biased "conformist" transmission rule could have evolved in the first place. They speculate that if



**Figure 23.3** Boyd and Richerson's (p. 207) characterization of three patterns of cultural transmission. In all three cases, the probability that a naive individual will acquire a trait depends on the frequency of the trait among the individual's models. (a) represents unbiased transmission, (b) directly based transmission, and (c) frequency-dependent biased transmission. (Reprinted by permission of University of Chicago Press.)

a species is composed of a set of local populations, and if these populations inhabit qualitatively different micro habitats, an individual moving into a new habitat may do best by imitating the traits that are common there. Their proposal is a Darwinian explanation for acting Roman in Rome, so to speak. Once this transmission bias has evolved, it may have various spin-off consequences that have the effect of harming organisms rather than helping them. If you find yourself living with altruists, the transmission bias will lead you to become altruistic yourself, even though you would be better off remaining selfish. Boyd and Richerson admit that there is little or no psychological evidence that people deploy the extreme form of transmission bias that their model postulates.

Just as in the example discussed from Cavalli-Sforza and Feldman, this model of Boyd and Richerson's mixes together the concepts of biological and cultural fitness. Altruism is deleterious to individuals, when fitness is calibrated in terms of the survival and reproduction of organisms. But common characteristics are more contagious than rare ones, when the individuals use a conformist transmission rule. This means that when altruism is common, it is more catching than selfishness. In such cases, the cultural fitness of altruism is greater than the cultural fitness of selfishness, when one considers a group in which altruism is common. The net result is that the special cultural transmission rule can allow a characteristic to evolve that could not evolve without it. Within purely biological models, altruism is eliminated in a large range of parameter values. The prospects for altruism to evolve are enhanced when culture is included in the model. Just as in Cavalli-Sforza and Feldman's discussion of the demographic transition, assumptions about cultural transmission lead to predictions that would not be true if a purely biological and non-cultural process were postulated.

The two examples I have described are typical of the models discussed in the two books. The models aim to show how different patterns of cultural transmission make a difference for how a psychological or social characteristic will evolve. Although most of the emphasis is placed on identifying cultural analogs of natural selection, the authors do develop nonselective models of cultural change. For example, population geneticists have described how genes of nearly identical fitness can change frequency in a population by doing a random walk. The models developed for random genetic drift, as it is called, can be used to describe the process by which family names disappear. This helps explain why the descendants of the *Bounty* mutineers have come to share the same surname. A reduction in variation is the expected consequence of random walks, both genetic and cultural.<sup>14</sup>

What are we to make of the research program embodied in these books? Biologists interested in culture are often struck by the absence of viable general theories in the social sciences. All of biology is united by the theory of biological evolution. Perhaps progress in the social sciences is impeded because there is no general theory of cultural evolution. The analogies between cultural and genetic change are palpable. And at least some of the disanalogies can be taken into account when the biological models are transposed.

For example, the Weismann doctrine tells us that variation is "undirected"; mutations do not occur because they would be beneficial. But ideas are not invented at random. Individuals often create new ideas—in science, for example—precisely because they would be useful.<sup>15</sup> Another and related disanalogy concerns the genotype/phenotype distinction. An organism's genotype is a cause of the phenotype it develops; that same genotype also causally contributes to the genotype of the organism's offspring. But there is no further pathway by which a parental phenotype can causally shape the genotype of its offspring. This is one way of describing the idea that there is no "inheritance of acquired characteristics." No such constraints seems to apply to the learning that occurs in cultural transmission.

These disanalogies between genetic and cultural change do not show that it is pointless or impossible to write models of cultural evolution that draw on the mathematical resources provided by evolutionary theory. In a sense, it is precisely because of such differences that there is a point to seeing the consequences of models that take these differences into account. These structural differences between genetic and cultural evolution do not undermine the idea that models of cultural evolution have a point.

Another reservation that has been voiced about models of cultural evolution is that they atomize cultural characteristics. Having two children rather than five, or being a kamikaze pilot, are characteristics that are abstracted from a rich and interconnected network of traits. The worry is that by singling out these traits for treatment, we are losing sight of the context that gives them cultural meaning.

It is worth mentioning that precisely the same question has been raised about various models in genetic evolution itself. If you wish to understand the population frequency of sickle cell anemia, for example, you cannot ignore the fact that the trait is correlated with resistance to malaria. In both cultural and genetic evolution it is a mistake to think that each trait evolved independently of all the others. Of course, the lesson to be drawn from this is not that one should not atomize characteristics, but rather that the atoms one identifies should be understood in terms of their relationship to other atoms.

In fact, this emphasis on context is one of the virtues that Boyd and Richerson think their approach has over the approach taken by sociobiology. According to the models under review, genetic selection has given our species the ability to engage in social learning. Once in place, this cultural transmission system allows characteristics to evolve that could not have evolved without it. In other words, it is only because the traits in question evolve in the context of a cultural transmission system that they are able to evolve at all.

We need to recognize that the descriptors singled out for treatment in science always abstract from complexities. If there is an objection to the descriptors used in models of cultural evolution, it must concern the details of how these models are constructed, not the mere fact that they impose a descriptive framework of some sort or other.<sup>16</sup>

Although the criticisms I have reviewed so far do not seem very powerful, there is a rather simple fact about these models that does suggest that they may be of limited utility in the social sciences. Insofar as these models describe culture, they describe systems of cultural transmission and the evolutionary consequences of such systems. Given that the idea of having two children was more attractive than the idea of having five, and given the horizontal and oblique transmission systems thought to be in place, we can see why the demographic transition took place. But as Cavalli-Sforza and Feldman recognize, their model does not begin to describe why educated women in nineteenth-century Italy came to prefer having smaller families, or why patterns adopted in higher classes cascaded down to lower ones. The model describes the consequences of an idea's being attractive, not the causes of its being attractive.

This distinction between the consequences of fitness differences and the causes of fitness differences also applies to theories of biological evolution.<sup>17</sup> A population geneticist can tell you what the evolutionary consequences for a population will be, if the genes in the population bear various fitness relationships to each other. It is a separate question to say why a given gene in fact is fitter than the alternatives. For example, consider the simplest of one-locus two-allele models for a diploid population. There are three genotypes possible at the locus in question, which we might label AA, Aa, and aa. If the heterozygote genotype is fitter than the two homozygote forms, the population will evolve to a stable polymorphism. Neither allele will be eliminated by the selection process. This is a simple algebraic fact, one having nothing to do with the biological details of any living population. Models such as this one can be thought of as intellectual resources that biologists interested in some particular population might find reason to use.

When human geneticists apply this model to the sickle cell system, they say that Aa is the fittest genotype because heterozygotes at the locus in question have enhanced resistance to malaria and little or no anemia. The two homozygotes have lesser fitnesses because they are either anemic or lack the malaria resistance. These specific remarks about the locus in the relevant human population describe the sources of fitness differences. Alternatively, a fruitfly geneticist may take the same population genetics model and apply it to a locus in some *Drosophila* population by saying that the heterozygote has enhanced temperature tolerance over the two homozygotes. The population consequences of heterozygote superiority are the same in the two cases; a stable polymorphism evolves. It is the sources of the fitness differences that distinguish the human application from the application to fruitflies.

This, I think, is the main shortcoming of the models of cultural evolution I am considering. The illumination they offer of culture concerns the consequences of cultural transmission systems. But there is far more to culture than the consequences of the rules that describe who learns what from whom. Social scientists have not wholly ignored the way that patterns of influence are structured in specific cases. A historian of nineteenth-century Italy might attempt to explain why some traits found among educated people were trans-

mitted to lower social strata, while others were not. Again, it is the sources of the transmission system that will interest the social scientist. The social scientist will take it for granted that the consequences of this influence will be that ideas cascade from one class to another.

Models of transmission systems describe the quantitative consequences of systems of cultural influence. Social scientists inevitably make qualitative assumptions about the consequences of these systems. If it could be shown that these qualitative assumptions were wrong in important cases, and that these mistakes actually undermine the plausibility of various historical explanations, that would be a reason or social scientists to take a greater interest in these models of cultural evolution. But if the qualitative assumptions turn out to be correct, it is perhaps understandable that historians should not accord much importance to these investigations.<sup>18</sup>

Population genetics really is a unifying framework within evolutionary theory. Fruitflies and human beings differ in many ways, but if a one-locus system exhibits heterozygote superiority, the population consequences will be the same, regardless of whether we are talking about people or *Drosophila*. Evolutionary theory is much less unified when we consider what it has to say about the sources of fitness differences. There are many, many models that treat a multiplicity of life-history characteristics and ecological relationships. Evolutionary theory achieves its greatest generality when it ignores sources and focuses on consequences.

The transposition of evolutionary models to the social sciences is a transposition of the most unified and complete part of evolutionary theory, one that leaves behind less unified theoretical ideas. This is not a criticism of the models of cultural evolution that result, but a fact about the price one pays for very general theorizing of this type. Cultural learning is a cultural universal. And patterns of cultural learning conveniently divide into vertical, horizontal, and oblique subcases. When ideas differ in their attractiveness, the system of transmission will determine the rate of change and the end-state that the population achieves. Only because they develop theories *within* this narrow compass do these models of cultural evolution have the generality they do.

Many of the examples discussed in the two books I have been considering describe evolution within a culture, not the evolution of the cultural transmission system itself. However, Boyd and Richerson, especially, also concern themselves with the way a system of cultural learning could have evolved by straightforward Darwinian means. Here the authors are not giving a model of how human cultures work, once they exist, but are trying to show how cultural learning became a possibility in the first place. This project obviously is a very important one, but not one that applies to many social scientific research programs. A correct genetic explanation of this important feature of the human phenotype would not provide a unifying framework within which social scientists would then do their work. They would not use this theory at all. It is one thing to explain the demographic transition in nineteenth-century Italy, something else to explain why human beings are able to learn from individuals who are not their biological parents.

In spite of these shortcomings, there is a basic achievement of these models of cultural evolution that deserves emphasis. A persistent theme in debates about sociobiology, about the nature/nurture controversy, and in other contexts as well is the relative "importance" that should be accorded to biology and culture. I place the term "importance" in quotation marks to indicate that it is a vague idea crying out for explication. Nonetheless, it has been a fundamental problem in these controversies to assess the relative "strength" or "power" of biological and cultural influences.

One virtue of these models of cultural evolution is that they place culture and biology into a common framework, so that the relative contributions to an outcome are rendered commensurable. What becomes clear in these models is that in assessing their relative importance of biology and culture, *time is of the essence*. Culture is often a more powerful determiner of change than biological evolution because cultural changes occur faster. When biological fitness is calibrated in terms of having babies, its basic temporal unit is the span of a human generation. Think how many replication events can occur in that temporal interval when the reproducing entities are ideas that jump from head to head. Ideas spread so fast that they can swamp the slower (and hence weaker) impact of biological natural selection.

There is a vague idea about the relation of biology and culture that these models help lay to rest. This is the idea that biology is "deeper" than the social sciences, not just in the sense that it has developed further, but in the sense that it investigates more fundamental causes. A social scientist will explain incest avoidance by describing the spread of a custom; the evolutionary biologist goes deeper by showing us why the behavior evolved. The mind-set expressed here is predisposed to think that culture is always a weak influence when it opposes biology. The works described here deserve credit for showing why this common opinion rests on a confusion.

In spite of this achievement, I doubt that these models of cultural evolution provide a general framework within which social scientific investigations may proceed. My main reason for skepticism is that these models concern themselves with the consequences of transmission systems and fitness differences, not with their sources. Social scientists interested in cultural change generally focus on sources and make do with intuitive and qualitative assessments of what the consequences will be. It isn't that the biologists and the social scientists are in conflict; rather, they are talking past each other.

Dobzhansky is famous for having said that "nothing in biology can be understood except in the light of evolution." His idea was not the modest one that evolution is necessary for full understanding; that would be true even if evolution's contribution were minor, though ineliminable. Rather, Dobzhansky had in mind the stronger claim that evolutionary considerations should be assigned pride of place in our understanding of the living world. A transposition of Dobzhansky's slogan to the topic of this chapter would say that "nothing in the social sciences can be understood except in the light of models

of cultural evolution." My suspicion is that only the weaker reading of this pronouncement is defensible.

## NOTES

I worked on this chapter while a William Evans Fellow at the University of Otago during parts of July and August 1990; my thanks to the university and to the members of the Philosophy Department for inviting me and for making my stay such an enjoyable one. This work expands upon a talk I gave in December 1985 at the University of Palma de Mallorca, "Natural Selection and the Social Sciences." I'm grateful to Robert Boyd, Dan Hausman, Peter Richerson, and David S. Wilson for comments on an earlier draft.

1. John Maynard Smith (1982), *Evolution and the Theory of Games*, Cambridge University Press.
2. L. Cavalli-Sforza and M. Feldman (1981), *Cultural Transmission and Evolution: A Quantitative Approach*, Princeton University Press.
3. R. Boyd and P. Richerson (1985), *Culture and the Evolutionary Process*, University of Chicago Press.
4. "Having babies" should be interpreted broadly, so as to include "having grandbabies," "having greatgrandbabies," and so forth. In some selection models (e.g., Fisher's sex ratio argument), fitness differences require that one consider expected numbers of descendants beyond the first generation.
5. See R. Colwell and M. King (1983), "Disentangling Genetic and Cultural Influences on Human Behavior: Problems and Prospects," in D. Rajecki (ed.), *Comparing Behavior: Studying Man Studying Animals*, Lawrence Erlbaum Publishers.
6. These are reviewed in J. Hirshliefer (1977), "Economics from a Biological Viewpoint," *Journal of Law and Economics* 1: 1-52.
7. See K. Popper (1973), *Objective Knowledge*, Oxford University Press.
8. A variety of "selective-retention" models of learning and of scientific change are reviewed in Donald Campbell (1974), "Evolutionary Epistemology," in P. Schilpp (ed.), *The Philosophy of Karl Popper*, Open Court Publishing. David Hull's *Science as a Process* (University of Chicago Press, 1988) develops some interesting ideas about how evolutionary ideas can be used to explain scientific change.
9. I do not claim that this taxonomy is exhaustive. For example, the spread of an infectious disease may be thought of as a selection process, in which the two states of an individual ("infected" and "not infected") differ in how catching they are. Clearly, this is not a type I process. Arguably, the concept of learning does not permit this process to be placed in type II. Perhaps the taxonomy would be exhaustive, if "learning" were replaced by "phenotypic resemblance not mediated by genetic resemblance."
10. See, for example, Richard Alexander (1979), *Darwinism and Human Affairs*, University of Washington Press.
11. See D. Lack (1954), *The Optimal Regulation of Animal Numbers*, Oxford University Press.
12. E. Wilson (1975), *Sociobiology: The New Synthesis*, Harvard University Press.
13. See E. Sober (1988), "What is Evolutionary Altruism?" *New Essays on Philosophy and Biology* (*Canadian Journal of Philosophy Supplementary Volume 14*), University of Calgary Press.
14. See Cavalli-Sforza and Feldman, pp. 255-66.

15. The difference between directed and undirected variation is conceptually different from the difference between biased and unbiased transmission. The former concerns the probability that a mutation will arise; the latter has to do with whether it will be passed along.

Directed variation (mutation) can be described as follows. Let  $u$  be the probability of mutating from  $A$  to  $a$  and  $v$  be the probability of mutating from  $a$  to  $A$ . Mutation is directed if (i)  $u > v$  and (ii)  $u > v$  because  $w(a) > w(A)$ , where  $w(X)$  is the fitness of  $X$ .

16. See J. M. Smith (1989), *Did Darwin Get it Right?* Chapman and Hall.

17. See Elliott Sober (1984), *The Nature of Selection*, MIT Press.

18. So the question about the usefulness of these models of cultural evolution to the day-to-day research of social scientists comes to this: Are social scientists good at intuitive population thinking? If they are, then their explanations will not be undermined by precise models of cultural evolution. If they are not, then social scientists should correct their explanations (and the intuitions on which they rely) by studying these models.