

Gene–culture coevolutionary theory

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Stone tools appear in the archaeological record approximately two and a half million years ago. The significance of this observation is not simply that *Homo habilis* and later hominid species had the guile to manufacture a lithic technology, but also that these skills were transmitted from one generation to the next. These simple artifacts thus represent the earliest evidence for culture. In fact, comparative evidence for social learning in a variety of vertebrate species suggests that cultural transmission almost certainly preceded *Homo habilis* by a considerable length of time. However, social learning in animals is rarely stable enough to support traditions in which information accumulates from one generation to the next.

The archaeological record documents the fact that for at least the past two million years hominid species have reliably inherited two kinds of information, one encoded by genes, the other by culture. How does dual inheritance affect the evolutionary process? Gene–culture coevolutionary theory is designed to answer this question.

Gene–culture coevolutionary theory is a branch of theoretical population genetics, which, in addition to modeling the differential transmission of genes from one generation to the next, incorporates cultural traits into the analysis. The two transmission systems cannot be treated independently, both because what an individual learns may depend on its genotype, and also because the selection acting on the genetic system may be generated or modified by the spread of a cultural trait. To give a simple example, the frequency of the sickle cell mutant among populations in West Africa depends on their means of subsistence^{1,2}. Populations that chop down trees to cultivate yams create the conditions where heavy rainfall will leave pools of standing water in which mosquitoes thrive, leading to more intense selection. For yam cultivators, there is a correlation between amount of standing water and sickle cell frequency, but not for otherwise identical populations. In this example, the intensity of selection on a gene hangs critically on the frequency of a cultural trait (yam farming) in the population.

Gene–culture models

The quantitative study of gene–culture coevolution began in 1973, when Cavalli-Sforza and Feldman introduced a simple dynamic model of cultural transmission into the nature–nurture debate³. The emerging body of theory has been used in a variety of ways. One class of models is employed to partition the variance in behavioral and personality traits into a variety of components including a transmitted cultural component^{3–5}. Dynamic models address very general questions about the adaptive advantages of complex forms of phenotypic plasticity, such as learning and culture^{6–9}. Other general models explore the forces of cultural change, and the nature of their interaction with

Gene–culture coevolutionary theory is a branch of theoretical population genetics that models the transmission of genes and cultural traits from one generation to the next, exploring how they interact. These models have been employed to examine the adaptive advantages of learning and culture, to investigate the forces of cultural change, to partition the variance in complex human behavioral and personality traits, and to address specific cases in human evolution in which there is an interaction between genes and culture.

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genetics^{8,10,11}. And more recently, these general methods have been applied to address specific cases in which there is an interaction between a cultural trait and some genetic variation that influences its prevalence^{12–17}.

In a gene–culture model, individuals must be described in terms of both their genotype and their cultural trait, a combination known as a 'phenogentotype'. Thus, in addition to the rules of mendelian inheritance, transmission rules for cultural traits must be described¹¹. Typically, it is assumed that the probability of an individual adopting a trait depends on whether its parents have that trait (vertical transmission), but equivalent models have been developed in which learning is from unrelated individuals (horizontal and oblique trans-

mission), key individuals in the social group (indirect transmission), or the majority in the group (frequency-dependent transmission)^{8,11}. In all cases, in the place of a system of recurrence equations that describe how allele or genotype frequencies change over time, gene–culture models use an equivalent system for phenogentotype frequencies.

The methods of gene–culture coevolutionary theory differ from those of sociobiology, human behavioral ecology, and evolutionary psychology in two important respects. First, a population's culture is not regarded as largely dependent on either its genetic constitution or the prevailing pattern of ecological resources. Instead, consistent with the predominant view in the human sciences, culture is treated as shared ideational phenomena (ideas, beliefs, values, knowledge) that are learned and socially transmitted between individuals. Below, we illustrate through examples how this view of culture makes a considerable difference to the evolutionary dynamics of a gene–culture system. Second, although the framework of gene–culture coevolutionary theory does not preclude an adaptationist perspective, and several such models have incorporated the assumption that an individual's genotype influences the probability that a particular cultural trait will be adopted, practitioners are also free to assume that traits may be adopted independent of their fitness consequences. The gene–culture approach is minimalist in that assumptions about the adaptive importance of traits are not an obligatory step in the modeling exercise. Note that although Lumsden and Wilson¹⁸ labeled their theoretical work 'gene–culture coevolution', their approach is in the sociobiological tradition, and should not be confused with contemporary gene–culture coevolutionary theory.

Mathematical analyses suggest that evolution in populations with a dynamic, socially transmitted culture is different from evolution in acultural populations for a number of reasons. First, cultural transmission can modify selection pressures, thereby affecting the course of a population's evolution. For example, below we describe how the cultural tradition of dairy farming may have created the selective

climate in which genes for lactose absorption have been favored. Second, culture can generate new evolutionary mechanisms; for instance, Boyd and Richerson^{8,14,15,19} have developed a series of models of human cooperation, which demonstrate the feasibility of a culturally preserved process of group selection. Third, the interplay between genetic and cultural transmission may produce time lags in the action of any selection that may be operating on a trait¹⁰; the equivalent phenomenon has been seen in recent treatments of maternal transmission of quantitative biological traits²⁰. Fourth, in the same way that there can be non-linear interactions between genes (linkage disequilibrium), nonrandom associations between genes and cultural traits can occur^{21,22} that can significantly affect the genetic response to selection. Fifth, because of its strong, homogenizing influence on behavior, and capacity for rapid diffusion, culture may sometimes generate atypically strong selection pressures, leading to very strong selection. Examples of these last two phenomena are given in the sex-ratio case discussed below.

Lactose absorption

The evolution of lactose absorption represents a good example of gene–culture coevolution. Systematic variation exists in the milk digestive physiology of adult humans. In fact, most adult humans are lactose malabsorbers: that is, their level of enzyme (lactase) activity is insufficient to break down the energy-rich sugar lactose, and milk consumption typically leads to sickness and diarrhea. Genetic differences are largely responsible for the phenotypic difference between absorbers and malabsorbers, with absorption probably inherited as an autosomal dominant trait². A correlation exists between incidence of lactose absorption and history of dairy farming in populations^{23,24}, with absorbers reaching frequencies of over 90% in such populations, but typically less than 20% in populations without dairy traditions. Since milk and milk products have been an important component of the diets of some human populations for over 6000 years, roughly 300 generations, it is conceivable that dairy farming may have created the selective regime under which the allele for absorption was favored.

Feldman and Cavalli-Sforza¹², following work by Aoki^{25,26}, used gene–culture coevolutionary theory to investigate the evolution of lactose absorption. They employed a single-locus, diploid model for lactose absorption, with differential cultural transmission of milk usage. In this model, both darwinian selection based on the nutritional properties of milk and cultural transmission of milk use are influenced by the lactose-absorbing genotype. With three genotypes (*AA*, *Aa* and *aa*) and two culturally influenced behavioral states (milk users and non-users) there are six combinations, or phenogenotypes. However, because the absorption allele (*A*) is dominant, the dynamics can be explored by monitoring the frequency of just four variables, users and non-users in individuals with or without a copy of the *A* allele.

The analysis suggested that whether or not the allele for absorption achieves a high frequency depends critically on the probability that the children of milk users become users themselves. If this probability is very high then a significant viability advantage to absorption will often result in the selection of *A* to high frequency within 300 generations. Typically, however, if a significant proportion of the offspring of users do not exploit milk products, then very strong selection favoring absorbers is required for *A* to spread. As might be expected, given the dependence of cultural transmission on genotype, the system is very sensitive to the initial frequency of allele *A*: Thus the analysis is able to account for both the spread of lactose absorption, and the culturally

related variability in its incidence. There is a broad range of conditions under which the absorption allele does not spread despite a significant fitness advantage. Cultural processes complicate the selection process to the extent that the outcome may differ from that expected under purely genetic transmission. Here, because of interactions between genes and culturally influenced behaviors, the response to selection is typically slowed down.

Excess female mortality

That the nature of a genetic response to selection may depend on the characteristics of cultural transmission is illustrated even more clearly in a gene–culture coevolutionary analysis of the evolutionary and demographic consequences of excess female mortality. In many regions of the world (China, India, Pakistan), parents exhibit a preference for sons over daughters and act on this bias to change the natural sex ratio among their offspring^{27,28}. Such behavior includes direct female infanticide, the neglect and abandonment of daughters, differential allocation of resources toward sons, and female-biased abortion following sex determination by amniocentesis or ultrasound. The aggregate effect of these activities over vast continents may generate significant distortion of the adult sex ratio. For instance, in India, the adult sex ratio has shown a consistent trend toward increasing male bias over the past century^{29,30}, while in China, the reported sex ratio at birth is 1.14 sons for every daughter³¹. Locally, such ratios can be as extreme as five males for every female, which represents the killing, abandonment, or premature death of nearly 80% of female children. As genetic variation distorting the human sex ratio has now been identified^{32,33}, Kumm, Laland and Feldman^{17,34} used a gene–culture model to investigate how this culturally generated glut of males might influence the selection of distorter genes.

Kumm *et al.* found that whether or not parentally mediated excess female mortality generates selection for a male- or female-biased primary sex ratio hangs critically on the psychological rules that parents employ when they manifest their preference for sons. If parents act so as to increase the proportion of sons irrespective of the natural sex ratio among their offspring, and if they compensate for any daughters they lose by having further children, the sex ratio will evolve a female bias. This is because any parents who express genes that make them more likely to conceive daughters will end up having proportionally more grandchildren, since not all sons will mate. At equilibrium, the female bias in the primary sex ratio exactly compensates for the parental preference for sons, leaving the adult sex ratio unbiased. In contrast, if parents try to achieve a desired sex ratio among their offspring, and if they have fewer children than impartial parents as a consequence, the primary sex ratio becomes male-biased. This is because under such circumstances parents who express genes that make them more likely to conceive daughters would have to destroy more daughters in order to achieve their male-biased desired sex ratio. In comparison, parents with genes that distort the primary sex ratio toward sons will have to kill fewer of their offspring to achieve their desired sex ratio, and will have more children in total. At equilibrium, the primary sex ratio equals the average parental desired sex ratio, leaving the adult sex ratio permanently distorted. Darwin³⁵ may have been correct when he suggested that the universally male-biased birth sex ratio may reflect a history of female infanticide.

Kumm *et al.*'s study also illustrates the profound effect that cultural processes can have on evolutionary rates.

Figure 1a shows sweeping oscillations in the frequency of the bias against females among parents, coupled with oscillations in the genetic variation that distorts the proportion of sons born. This interaction between genetic and cultural processes significantly slows down the response to selection of the allele; several thousand generations are needed to reach equilibrium. In Fig. 1b, the entire population is biased toward sons, with the initial sex ratio maintained by a genetic polymorphism. Here, substantial genetic change occurs within just a handful of generations. This strong selection results exclusively from the culturally transmitted parental activities. For illustration, consider a population where prejudicial parents act to achieve a sex ratio of three sons for every daughter, and where biased parents have no more children to compensate for those they kill. Under such circumstances, relative to impartial parents, biased parents would have a fitness of 0.667, which represents unusually strong selection. This capacity for culture to generate strong selection has been reported in other gene-culture analyses. For instance, Laland¹⁶ found that cultural influences on human mating preferences could generate strong sexual selection for anatomical and personality traits, such as small feet or macho male behavior.

Transmission effects and group selection

Much gene-culture coevolutionary modeling has explored the adaptive advantages and disadvantages of different modes of social transmission under a variety of environmental conditions. In spite of a plurality of approaches, a consensus is emerging regarding the adaptive advantages of social learning in changing environments: when environments are constant, social learning has no adaptive value relative to genetic transmission, and cannot invade^{8,36}. When environments change very fast relative to the lifetime of an organism, vertical cultural transmission is of little advantage, since through social learning, individuals would acquire outdated information about previous or distant states of the environment. Under such circumstances, learning about the environment just by trial-and-error or pavlovian conditioning is a better strategy^{8,9}. However, there are circumstances when horizontally or obliquely transmitted culture may be advantageous in a variable environment, for example, when individuals cannot find or exploit distantly located resources alone³⁷, or when scrounging and scavenging interfere with the individual learning of a food-producing technique³⁸. It is in slowly changing environments that learning from parents is advantageous; when changes are not so fast that parents and offspring experience different environments, but not so slow that appropriate genetically transmitted behavior could evolve^{8,9}.

The theoretical argument against group selection is based on models that assume genetic inheritance, and the criticisms may not hold for culturally transmitted traits. When individuals adopt the behavior of the majority, a conformist transmission is generated. As a result of its frequency-dependence, conformist transmission can act to amplify differences in the frequency of cultural traits in different sub-populations. Boyd and Richerson^{8,14,15,19} have shown that one of the by-products of a conformist frequency-dependent bias is an increase in the strength of the group selection of cultural variation so that it may be a strong force relative to forces acting within groups, such as natural selection. Since selection between groups may favor beliefs and attitudes that benefit the group at the expense of the individual, this provides a new explanation for human cooperation. Conformist transmission may be favored by natural selection even though it has this deleterious effect for individuals,

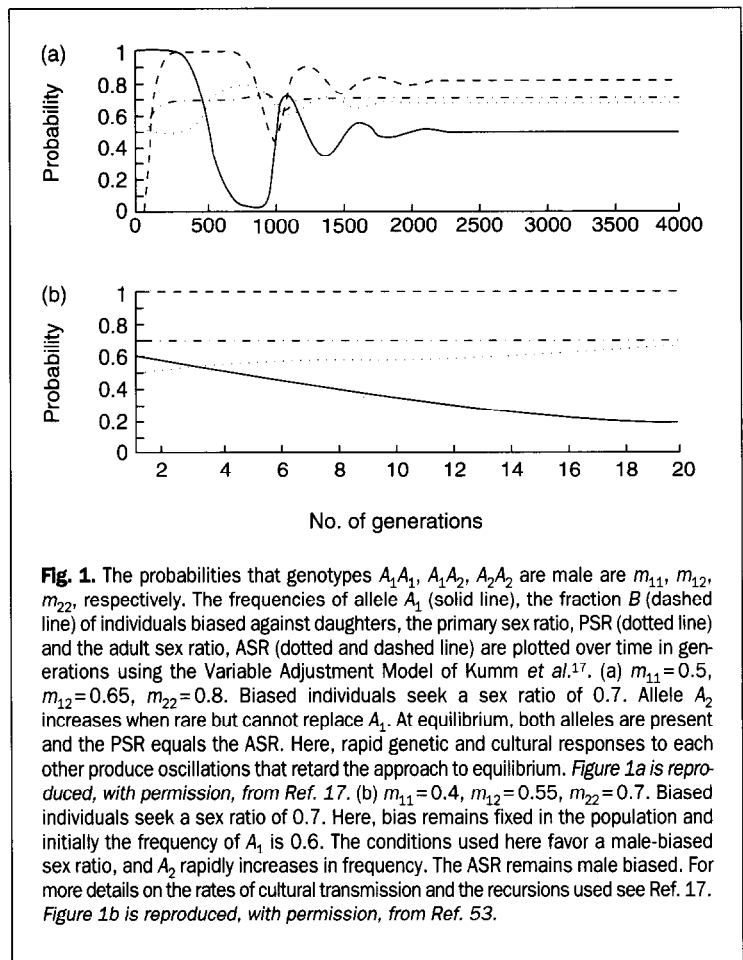


Fig. 1. The probabilities that genotypes A_1A_1 , A_1A_2 , A_2A_2 are male are m_{11} , m_{12} , m_{22} , respectively. The frequencies of allele A_1 (solid line), the fraction B (dashed line) of individuals biased against daughters, the primary sex ratio, PSR (dotted line) and the adult sex ratio, ASR (dotted and dashed line) are plotted over time in generations using the Variable Adjustment Model of Kumm *et al.*¹⁷. (a) $m_{11}=0.5$, $m_{12}=0.65$, $m_{22}=0.8$. Biased individuals seek a sex ratio of 0.7. Allele A_2 increases when rare but cannot replace A_1 . At equilibrium, both alleles are present and the PSR equals the ASR. Here, rapid genetic and cultural responses to each other produce oscillations that retard the approach to equilibrium. Figure 1a is reproduced, with permission, from Ref. 17. (b) $m_{11}=0.4$, $m_{12}=0.55$, $m_{22}=0.7$. Biased individuals seek a sex ratio of 0.7. Here, bias remains fixed in the population and initially the frequency of A_1 is 0.6. The conditions used here favor a male-biased sex ratio, and A_2 rapidly increases in frequency. The ASR remains male biased. For more details on the rates of cultural transmission and the recursions used see Ref. 17. Figure 1b is reproduced, with permission, from Ref. 53.

because it increases the chances of acquiring locally adaptive variants in a heterogeneous environment. Boyd and Richerson found that when there is conformist transmission, interdemographic group selection can be a strong force in determining the eventual equilibrium of the population, even when sub-populations are arbitrarily large, extinction rates are small, and migration rates are substantial. These authors also suggest that cultural group selection may have driven the evolution of an unlearned predisposition for in-group favoritism¹⁹. This analysis demonstrates that when the rules of cultural transmission are different from those of genetic transmission, similar selective regimes may result in very different equilibria.

The spread of agriculture

Aoki, Shida and Shigesada³⁹ used gene-culture coevolutionary methods to investigate the spread of agriculture into a region previously occupied by hunter-gatherers. Since farming allows human populations to attain a higher density than hunter-gathering⁴⁰, a population that adopts farming may increase in number and expand geographically. But farming may also spread through the conversion of hunter-gatherers by social learning. In Aoki *et al.*'s model, there are no genes influencing which behavior (farming or hunting and gathering) is adopted. However, there are two kinds of selection operating, darwinian selection and cultural selection, the latter representing the conversion of hunter-gatherers to farmers. The model monitors the dynamics of initial farmers, converted farmers and hunter-gatherers, and yields the conditions under which wave fronts of initial or converted farmers advance. Aoki *et al.* found that the composition of the expanding wave of farmers depends on the relative magnitude of r_f versus $r_c + eL$, where r_f and r_c represent intrinsic

growth rates of initial and converted farmers, L is the carrying capacity of environments containing hunter-gatherers, and e is the rate at which hunter-gatherers are converted to farmers. If $r_f < r_c + eL$, an advancing wave of converted farmers may be generated, provided the conversion rate is not too small. However, if $r_f > r_c + eL$, an advancing wave of initial farmers is generated. In the former case, in the wake of the advancing wave, initial farmers and converted farmers may mix through diffusion or interbreeding. If there are genetic differences between initial and converted farmers, this process should generate gene frequency clines in the region occupied by the farmers. Aoki *et al.* also compute expressions that give the rate of spread of farming. This analysis provides a theoretical framework that can aid the reconstruction of major demographic changes associated with the dispersal of human populations.

Behavioral traits

An additional application of gene-culture methods is to aid understanding of the inheritance of complex behavioral and personality traits. Following the early work by Cavalli-Sforza and Feldman³, Otto, Christiansen and Feldman⁵ have combined gene-culture models and path analysis methods to specify how the phenotype of an individual is determined and how genetic and cultural effects are transmitted between generations. They consider the effects of a variety of different mechanisms of cultural inheritance, deviations from random mating, and non-transmitted environmental components, and develop models applicable to data for different patterns of relatedness between individuals. Despite their complexity relative to other linear models of heritability^{41,42}, Otto *et al.*'s models are nonetheless forced to make extremely simple assumptions about the etiology of behavior. The significance of this analysis is not that the results can tell us how to manipulate environmental factors to enhance a person's intelligence or scholastic achievement. Rather, the analysis illustrates the sensitivity of heritability estimates to the model assumptions. Otto *et al.* illustrate how a variety of simple models may fit the observed data, irrespective of whether or not they capture the paths of influence on a trait, leading to quite different estimates for genetic and cultural heritability.

Otto *et al.* fitted their models to familial correlations for IQ collated by Bouchard and McGue⁴³ from 111 studies and found that no models gave a good fit to all the data without a parameter that measured the degree of common environment in monozygotic twins raised apart (see also Cloninger *et al.*⁴⁴). This finding, which strongly implies that monozygotic twins raised apart share common cultural and non-transmitted experiences, questions the validity and applicability of heritability estimates based solely on twin data^{41,45}. In general, the best-fitting models to the IQ data include a large influence of common environment parameters, and ignoring these parameters, as is common in the behavior genetics literature, leads to a significant drop in the goodness of fit, and a marked increase in heritability estimates. The obtained heritability estimates for IQ are around 0.3, which contrast starkly with the inflated estimates generated using twin data alone, which range from 0.5 to 0.8. Similar findings surrounded estimates of heritability when the models were applied to personality traits. Inclusion of common environment parameters uniformly lowered estimates of heritability, sometimes increasing the estimated influence of cultural transmission, and for psychoticism and neuroticism data, significantly improved the fit of the model. Once again, heritability estimates relying exclusively on twin or parent-offspring correlations were inflated. In the case of

the neuroticism data, the narrow heritability was close to zero. Otto *et al.*'s findings strongly repudiate the claim that personality variables are not influenced by social learning⁴⁶.

One of the important findings to emerge from gene-culture coevolutionary theory is that there are a variety of mechanisms by which culture can lead to the transmission of behavior, which confers a fitness cost relative to behavioral alternatives. Cavalli-Sforza and Feldman¹¹ provided theoretical confirmation of the intuitive notion that a maladaptive behavior may increase in frequency in a population if it is adopted with sufficient regularity through social learning. Boyd and Richerson's model of indirect bias⁸, where individuals adopt the behavior of influential or successful members of their society, also found that maladaptive cultural variants can spread, even if associated with a substantial viability disadvantage. Other gene-culture models reach the same conclusion^{9,10,16,47}. Moreover, if social transmission may result in the spread of maladaptive behavior in human populations, the same processes may operate among those animals capable of social learning. This has incited some controversy⁴⁸, since most instances of animal social learning appear to enhance fitness. The criticism is misguided, since the findings of the models are consistent with the observation that most social learning will be adaptive; indeed the analyses conclude that social learning would not be favored if it were not generally adaptive. What the theoretical work implies is that, in a spatially or temporally variable environment, individuals that adopt the behavior of others may acquire information that is inappropriate or sub-optimal. Such individuals might be expected to adjust their behavior to the contingencies of their immediate surroundings, but they might pay a fitness cost in the mean time. Experimental studies are required to investigate the conditions under which social learning increases or decreases an animal's ability to track changing environmental resources, so that the predictions of the models can be put to the test.

Several other studies that employ gene-culture coevolutionary methods deserve mention: Aoki and Feldman¹³ have investigated the coevolution of recessive hereditary deafness and the transgenerational inheritance of sign language. Laland *et al.*⁴ develop a gene-culture model of handedness, which gives a better fit to familial and twin data than established genetic models. This review is necessarily incomplete, since the body of gene-culture coevolutionary theory represents over 20 years research, by practitioners in a variety of disciplines, addressing numerous different questions. More-comprehensive descriptions of gene-culture methods and related approaches can be found elsewhere⁴⁹⁻⁵¹.

The models make a variety of testable predictions: Aoki *et al.*³⁹ detail the conditions under which the spread of farming will generate gene frequency clines. Laland's¹⁶ model of sexual selection implies that there should be society-specific correlations for anatomical traits and learned preferences for such traits in the opposite sex. Soltis, Boyd and Richerson⁵² have used data on rates of population extinction among New Guinea communities to test Boyd and Richerson's group selection hypothesis. The models also generate insights of relevance to other bodies of theory. For instance, Feldman and Cavalli-Sforza¹⁰ developed models of uniparental cultural transmission, which anticipated many of the findings of quantitative genetics models of maternal inheritance²⁰. The clear conclusion of gene-culture coevolutionary analyses is that cultural transmission can transform evolutionary dynamics in numerous ways, implying that, for many questions related to human evolution or human behavior genetics, traditional methods and models are no longer appropriate.

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