

# A SIMPLE DUAL INHERITANCE MODEL OF THE CONFLICT BETWEEN SOCIAL AND BIOLOGICAL EVOLUTION

by Robert Boyd and Peter J. Richerson

Donald T. Campbell's address is an important contribution to the understanding of human behavior because it takes seriously the problem of understanding how cultural and genetic processes jointly determine human behavior.<sup>1</sup> It is difficult to see how any useful theoretical approach to the human condition can evade specifying important roles for both genes and culture and for the mechanisms by which they interact. His approach is the intelligent middle ground between complete genetic determinism and complete cultural determinism, either of which simply ignores the real problem.

Furthermore, we applaud the extension of natural selection explicitly to cultural modes of inheritance. Even if rational strategizing or other processes play roles in shaping human culture, limitations on the calculating ability and the availability of information ensure that "chance variation and selective retention" will play a role in cultural as well as genetic evolution. It is interesting to note in this connection that Darwin, in chapter 5 of *Descent of Man*, was perfectly willing to posit selection of "mental and moral faculties" which he treated as inherited in a Lamarckian fashion.<sup>2</sup> The triumph of genetical theory in this century has caused biologists to overlook the peculiar importance of a non-Mendelian form of inheritance in humans, much as the reaction to Social Darwinism has caused most social scientists to ignore the importance of both genes and natural selection. Campbell's raising of these issues in so prestigious a forum as the presidential address of a major social scientific society, we hope, signals the end to the neglect of the problem and of the possible contribution of the natural selection mechanism to its solution.

While agreeing with Campbell that human behavior is shaped chiefly by natural selection acting on both culture and genes, we be-

Robert Boyd is a lecturer in environmental studies, and Peter J. Richerson is assistant professor of environmental studies, both at the University of California, Davis.

[*Zygon*, vol. 11, no. 3 (September 1976).]

© 1976 by The University of Chicago. All rights reserved.

lieve that the detailed nature of the interaction between these codes is so complex and difficult as to preclude any immediately definitive generalizations about the resulting system. Our own approach has been to consider the simplest possible mathematical models of the interaction of culture and genes in the hope of obtaining at least a clear, if rudimentary, picture of the mechanisms involved.<sup>3</sup>

#### SIMULTANEOUS EVOLUTION OF CULTURE AND GENES

These models will be described briefly below, but first we must admit that they are at least oversimplified and perhaps wrong in their description of human cultural behavior. Our aim is to start with a set of simple assumptions so that our ideas may be understood clearly and their consequences deduced. We do not suppose that the models are sufficiently complicated to correspond accurately to any real system. Robert Solow has likened models of this kind to parables—simple stories that make certain relationships more transparent.<sup>4</sup> The lessons drawn from a parable may be inapplicable or, worse, misleading, but they at least have the virtue of being clearly understood. Nor is this a trivial virtue. It is an illuminating experience indeed to translate some verbal hypothesis that one thinks is well understood even into the simplest mathematical model. All too frequently, the vagueness and confusion of one's own ideas become embarrassingly apparent.

We enter this realm through the same portal as Campbell—Darwin's three necessary conditions for the existence of natural selection. The trait in question must be heritable, it must be variable, and different traits potentially must be represented in subsequent generations in different relative numbers. If these postulates hold true, then the frequency of those traits that reproduce themselves most efficiently will increase with time. This conclusion, often called the central dogma of evolutionary biology, can be restated: Let fitness be defined as the efficacy with which a trait propagates itself. For genes, fitness then is the number of offspring, and the central dogma is that selection acts to maximize fitness.

Like Campbell, we see no reason why traits acquired through cultural processes and coded in memory rather than genes should escape the analog of the central dogma—selection will act to maximize cultural fitness. Indeed, from physical principles alone it is difficult to conceive of any code which is not under the influence of some mechanism like natural selection. Random entropic changes in the physiochemical basis of a code (DNA strands for genetic codes) rapidly will destroy a message during storage and replication unless such a mechanism intervenes to cull errors as they arise, much less adapt

the message to changing circumstances. Surely, cultural traits are also subject to these very general problems of code systems.

Our basic postulate is that the action of natural selection on cultural traits tends to adjust phenotype so as to maximize cultural fitness. Similarly, the action of natural selection on genes alters phenotype so as to maximize genetic fitness. These two postulates taken together carry the seeds of a paradox; selection cannot act simultaneously to maximize genetic and cultural fitness if those fitnesses are different. It is easy to see the reason for this purely logical difficulty. Suppose there is some behavioral trait that is controlled by both culture and genes. In figure 1 hypothetical cultural and genetic fitnesses are shown as a function of this trait. It is impossible, in general, to find a value of the behavioral trait that maximizes both fitnesses. It can be done only in the case where both happen to have the same maxima. It will be argued later that there are circumstances in which one would not expect this to be true.

The general situation is portrayed in figure 2. The genotype and the culturetype or cultural message interact to determine the behavior of the organism. The behavior (a sort of generalized phenotype) in turn determines the genetic and cultural fitnesses of each individual. Contours of equal fitnesses are plotted in this figure.

In each figure the "culture" or "gene" line is plotted. To find the culture line, first fix the genotype and then find the cultural

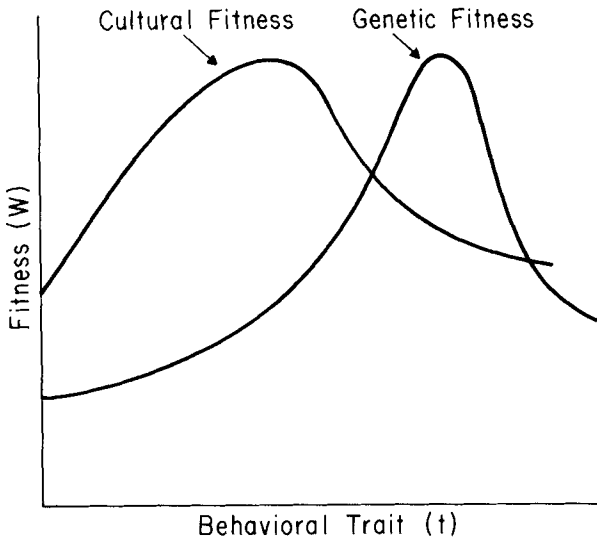


FIG. 1.—Hypothetical genetic and cultural fitnesses as a function of values of the same quantitative trait, controlled jointly by genes and culture.

type that maximizes cultural fitness. This point represents the results of natural selection on culture if genotype was fixed at that value. Then repeat this process for all possible genotypes. The culture line then is the set of cultural outcomes associated with each genotype. The gene line is found in the same way except that genetic fitness is maximized over genotype for each value of culturetype.

We picture selection as causing genotype and culturetype to change slowly, but always in the direction of increasing the relevant fitness.

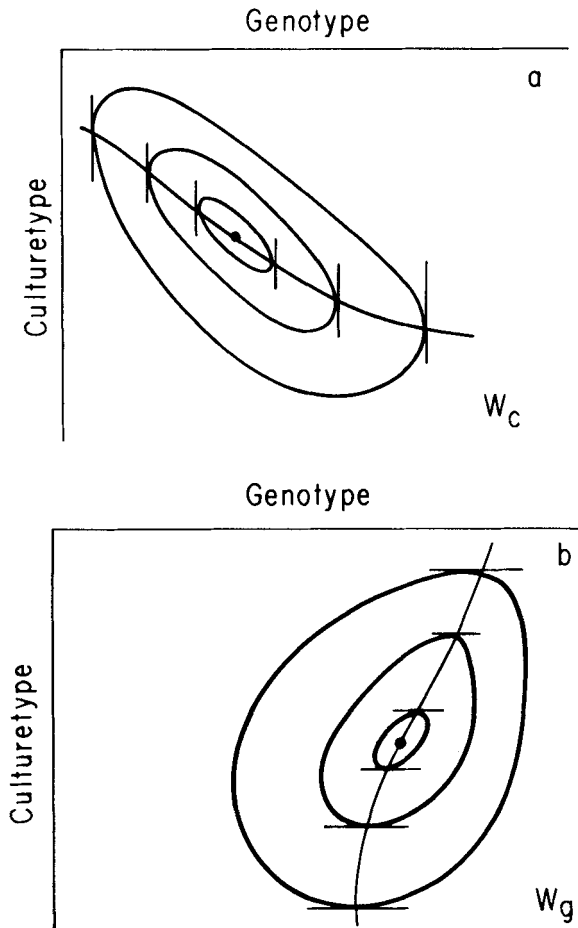


FIG. 2.—*a*, Cultural fitness ( $W_c$ ) topography as a function of genotype and culturetype. The culture line is the set of points for which, given a value of genotype, cultural fitness is a maximum. *b*, Genetic fitness ( $W_g$ ) as a function of genotype and culturetype. The gene line is the set of points for which, given a value of culturetype, genetic fitness is a maximum.

## ZYGON

Such a process will come to equilibrium only when any change decreases fitness. For both genotype and culturetype to be in equilibrium this must be true for both of them. Thus the equilibrium can be only the intersection of the culture line and the gene line. This is the only point where neither fitness can be increased.

It is of interest to note that the model described above is formally identical with a two-person, non-zero-sum game played between culture and genes. The intersection of the culture line and the gene line is the Nash equilibrium solution to this game. In the ordinary theory of natural selection it is often said that organisms behave as if they were maximizing individuals, choosing genotypes to attain the maximum fitness. Here we offer a similar notion: Organisms carrying two codes behave as if each code were a strategizing individual, playing a game against the other code in which the payoffs are fitnesses. The outcome of this game is the Nash equilibrium solution.

At this point the question arises, Why should the cultural and genetic fitnesses be different? This question can be put another way. Most organisms carry many chromosomes; each chromosome is a code; and yet we need not speak of chromosomes playing a game against one another. How is the addition of culture different from the addition of a chromosome?

The answer to these questions lies in the fact that the rules of transmission of genes and culture are most probably quite different, while the rules of transmission for two chromosomes of the same organism have identical rules. Among the differences are:

1. The timing of transmission: One transmits genes to one's offspring only once, at conception, while socialization is spread over a longer period. This implies that cultural fitness might favor a different life cycle than genetic fitness. For example it might imply a greater importance in the human case for postreproductive individuals.
2. Differential contribution of mother and father: Unlike genetic inheritance, with culture it is no longer automatic that the mother and father contribute equally to the child's cultural parentage.
3. Nonphyletic transmission: Cultural information may be transmitted to totally unrelated individuals. It might enhance cultural fitness to devote resources to increasing the number of cultural "offspring" by reducing the investment in genetic offspring. A possible example of this is the existence of celibate priesthoods.
4. The serial nature of cultural transmission: Parents transmit genes to their offspring in parallel, the whole message simultaneously. Cultural transmission on the other hand occurs serially, some messages transmitted after others. This allows the rate of transmission of various kinds of cultural messages at some time to be influenced by the nature of the messages received at earlier times. This phenomenon makes possible a complicated interaction between culturetype and cultural parentage.

These are undoubtedly but a few of the many differences between the transmission of culture and genes. However, they seem sufficient to show that the kinds of behavior that maximize genetic fitness are not necessarily the same as those that maximize cultural fitness. Thus fitness has the form suggested in figure 2, and the game analysis is correct.

In contrast, let us consider the fitness of two different chromosomes. Figure 3 shows an evolutionary game between two chromosomes. Since probabilistically both chromosomes are transmitted identically to every offspring, the fitnesses are identical for each chromosome. Let us now see what this implies for the outcome of selection. Because the fitnesses are identical, only one diagram is necessary. Note that the analogs of the gene line and culture lines intersect at the maximum. This follows easily from the definitions of the lines (the partial derivatives of fitness with respect to message equal zero) and necessary conditions for a maximum (both partials simultaneously equal zero). Thus, when the fitnesses are the same, the game reduces to a simple problem, maximizing fitness, consistent with the general rule for genetic inheritance cited earlier.

Thus we have proposed a rule for the simultaneous evolution of culture and genes analogous to the usual survival of the fittest applied to genes alone. In a manuscript in press we have developed two kinds of analyses to examine the adequacy of the dual-inheritance, natural-selection hypothesis.<sup>5</sup> First, a series of very simple game theoretic models are developed in order to investigate the properties of such an evolutionary system. The intention of these models is to

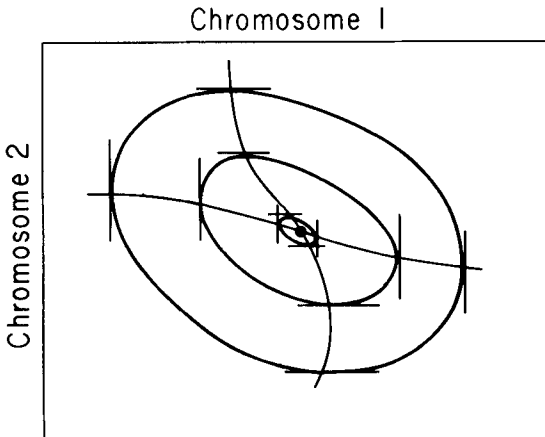


FIG. 3.—Fitness as a function of a message on two different chromosomes

## ZYGON

show that "two-channel" theory is formally plausible and that simple models based on it yield interesting, intuitively reasonable results. Second, an attempt is made to use empirical evidence drawn from the study of human kinship behavior to test the adequacy of the dual-inheritance, natural-selection hypothesis relative to other approaches to the interaction of gene and culture in humans.

### COMPLICATIONS IN THE ANALYSIS OF HUMAN EVOLUTION

The most important conclusion which can be deduced from the models is that if a second code such as culture arises, and permits the achievement of genetically advantageous phenotypes which could not be produced by genes alone, many resulting traits may not be the genetic optimum. Contrariwise, when the phenotype could be achieved by genes alone, cultural behaviors will be permitted only insofar as they result in the genetic optimum. Presumably, humans are an example of the former situation and, in an important but limited sense, culture has escaped the control of natural selection acting on genes. Protocultural traits, like the necessity of some birds to learn their songs from their parents, are probably examples of the latter case. Natural selection acting on genes might favor the evolution of protocultural systems of inheritance when the cultural mechanism for some reason allows phenotypes of slightly higher genetic fitness than are possible by genes alone.

We should emphasize that the models we have examined so far are fundamentally Mendelian since natural selection acting on genes can optimize genetic fitness by controlling the capacity for culture. Even though some traits may not be at the genetic optimum, the average of all culturally determined traits must be. The capacity for culture is thus like a pleiotropic gene whose positive effects must exceed its negative ones if it is to persist in the population. There is no "eugenic" possibility in the sense that the models do not permit culture as a whole to reduce individual genetic fitness in order to increase cultural fitness. Such a model may be possible, but additional mechanisms would have to be postulated. It is not clear at this point that further assumptions of this type are required since considerable independent cultural evolution of the type observed in human societies is permitted by the models.

Even in these very simple models the addition of culture greatly complicates the analysis of human evolution. And this is only a beginning; a more nearly complete consideration will have to deal with even greater complications. For example, different cultural traits may be transmitted in different contexts to different individuals or at different times of life. Thus the selective situation of different traits well

may be different; some may be group selected, others selected at the subindividual level. Certainly, their fitness will be different, and this will lead not to a selective game between genes and culture but to a far more complex interaction of many different cultural traits and genes.

Campbell suggests that the main conflict between culture and genes results from individual selection for genes and group selection favoring more altruism for cultural traits. Before coming to any conclusions about whether cooperative human behaviors are group or individually selected, we will need to consider an intermediate case: the extent to which complex interactive behavior is controlled by frequency-dependent selection. For example, the existence of mating rituals, warning signals, threat displays, and other forms of communication among animals results from such selection. A similar mechanism could act on culturally controlled human behaviors. Language would seem a plausible candidate.

Other complex processes may be important. The existence of complicated, seemingly integrated, multispecies ecosystems is usually not explained through the use of group selection. Rather, ecologists assume that the coevolution and other higher-order (and poorly understood) mechanisms are responsible. In complex human societies occupational, ethnic, and class distinctions may provide units upon which cultural evolution acts analogously to species, and the integrated nature of such societies may require evolutionary explanations similar to that used to explain ecosystemic integration.<sup>6</sup>

We mention these complexities for two reasons. First, we believe that, given our primitive level of understanding of cultural evolutionary mechanisms, it is premature to attempt to explain the broad features of human society or to assign the major elements of human behavior to any one evolutionary cause. Detailed models of specific evolutionary processes need to be developed and tested empirically where possible. Second, we want to suggest that the basic dual-inheritance model underlies a rich series of formal models based upon adding realistically complicated features. There is the obvious possibility of using these models to develop a rigorous theory of human behavior on a par with population genetics in evolutionary biology.

We believe that there will be substantial rewards in pursuing this approach. It should not be thought that progress will constitute merely the application of genetic and ecological dogmas to culture with a shade of difference. Many of these problems are still very much unresolved in biology. Perhaps it is not too much to hope that Campbell's long interest in natural-selection models will be vindicated, even to the extent that both social and biological scientists will contribute to



## ZYGON

their solution, thus ending three-quarters of a century of near-total estrangement of these branches of human knowledge.

### NOTES

1. Donald T. Campbell, "On the Conflicts between Biological and Social Evolution and between Psychology and Moral Tradition," in this issue.
2. Charles Darwin, *The Descent of Man and Selection in Relation to Sex*, 2d ed. (London: Murray, 1886).
3. Peter J. Richerson and Robert Boyd, "A Dual Inheritance Model of the Human Evolutionary Process," *Journal of Human and Social Biology* (in press).
4. Robert Solow, *Growth Processes* (Oxford: Clarendon Press, 1970).
5. Richerson and Boyd.
6. See Peter J. Richerson, "Ecology and Human Ecology: A Comparison of Theories in the Biological and Social Sciences," *American Ethnologist* (in press).