Lumsden–Wilson theory of gene–culture coevolution

(human sociobiology/ethnography/epigenetic rules/social development)

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ABSTRACT A critique is presented of the Lumsden–Wilson theory [Lumsden, C. J. & Wilson, E. O. (1980) *Proc. Natl. Acad. Sci. USA* 77, 4382–4386] of the transmission of cultural traits. An analysis of the underlying assumptions and the mathematical nature of the theory clarifies its essentially reductionist and determinist qualities. The mathematical functions governing the transition probability that an individual member of a group of a specified size will switch from one trait to an alternative form of that trait is assumed to be genetically controlled although the single independent variable of this function, the number of individuals characterized by each of the two forms of the trait, is environmentally determined. The model assumes that the cultural properties of a society are simply the sum of the properties of the individuals; that each individual is equally influenced by every other member of the group; and that kinship structures, cultural institutions, and historical factors can be neglected.

Lumsden and Wilson (LW) have proposed a sociobiological theory that treats quantitatively the relationship between genetics and the environment in shaping cultural behavior (1). Rather than assuming the existence of genes determining a particular trait, as is usual in human sociobiology, LW hypothesize that the genes code for the epigenetic rules that determine the probability of changing from one form of a trait to another. Environmental influence is incorporated into the theory by assuming that this probability depends not only on the genes but also on the number of individuals already characterized by each of the forms of the trait. LW then derive a formula for the probability distribution of individuals in the alternative cultural states (the “ethnographic curve”). They find (ref. 1, p. 4382) that “the translation from individual epigenesis to social pattern is amplified, to the extent that differences in [genetic] bias too faint to be detected in ordinary developmental studies can generate conspicuous variation in the ethnographic curves.”

We believe that a critical analysis of the LW paper is important because sociobiologists claim far-reaching implications of the theory as an explanation of human culture. In this critique, we focus our attention on three aspects of the work. First, the mathematical nature of the paper has forced the authors to state in an extremely clear fashion the assumptions underlying their theory of the genetic–environmental interaction. An examination of these assumptions shows that they are not as self-evident as LW imply. Second, the mathematical model illustrates the extreme sensitivity of the predictions of the theory to its assumptions. This sensitivity, rather than signifying the power of the theory to reveal the extreme sensitivity of culture to genetic factors as LW argue, actually undermines it. Third, the LW presentation suggests that, for sociobiology, genetic determinism and environmental determinism are compatible.

ASSUMPTIONS OF THE THEORY

LW propose that we consider one cultural trait (called a “culturgene”) at a time and study the mechanisms by which distributions of alternative forms of the trait in a society are established. The central assumption of the LW theory is that there are genes that code for the rules that determine the probability of changing from one alternative form of the trait to another. There is absolutely no evidence that any genes of this type exist and, as we shall argue more fully below, LW’s claim that there is evidence for the existence of such genes is invalid. The empirical evidence LW cite refers to the observed probabilities that individuals prefer one alternative to another. Quite aside from whether these preferences are genetic, at least one can show that there are differences among individuals with regard to these preferences. No one has ever demonstrated that there are observable differences among people in the probabilities of their *switching* from one cultural trait to another, let alone that such differences might arise from differences in their genes.

Culturgens are assumed to be traits that are possessed and transmitted by individuals, as opposed to behavior that makes sense only in a particular social context. LW have made the reductionist assumption that the characteristics of a society can be understood as simply the sum of the characteristics of the individuals of that society. There are, in this theory, no properties that arise as a consequence of social interactions of the group. Social institutions themselves, such as kinship structures and other groupings, as opposed to membership in these institutions, cannot be included in the theory. It should be noted that all of the examples of what is called culture by LW (e.g., preference for sugar, fear response of strangers, preferred level of visual pattern complexity) are rather rudimentary.

LW then assume that “enculturation is conducted not just by the nuclear family, a common feature of some industrialized Western societies, but by a much broader array of relatives and parent surrogates” (ref. 1, p. 4382). Wilson, in his textbook on sociobiology (2), presented a contrasting view: “The building block of nearly all human societies is the nuclear family. The population of an American industrial city, no less than a band of hunter-gatherers in the Australian desert, is organized around this unit.” The assumption chosen by LW is advantageous for their theory because (i) the mathematical model is easy to realize and solve if every member of the population (15–75, according to LW) exerts equal influence in affecting the cultural state of a given individual and (ii) as we shall see below, the sensitivity of their model is guaranteed by this assumption. There is no hard evidence supporting either the assumption of LW or the one held previously by Wilson.

To make the mathematics tractable, LW assume that cultur-

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Abbreviation: LW, Lumsden and Wilson.

gens exist in one of only two possible discrete forms, e.g., preference or lack of preference for sugar. At various decision points, individuals choose between these two alternatives; they either stick or switch. There are no gradual shifts from one alternative to the other. It is assumed that these alternatives are always present in an unchanging form; development of the traits themselves is specifically excluded.

We now come to the assumptions governing cultural decision making. The model adopted by LW has its origins in the models used in the statistical mechanical description of irreversible processes in dilute gases and uses much the same formalism. LW state that, in many cases, decision making is adequately described by a Markov process—i.e., the decision made at any given time either to retain or to switch cultural states depends only on the state of that individual and on the state of all the surrounding individuals at that time. The previous history of the population can be ignored completely. For example, the possibility that the environment was different the previous time a behavioral transition occurred and that this could affect the current transition probability is not considered. In the language of statistical physics, the system has no memory. The social sciences, dedicated to understanding the role of the past in shaping the present, become superfluous.

The Markov approximation is justified only if we possess *complete* relevant knowledge of the state of the system. Only under this condition does the present state determine all future states. It has long been recognized that, even for physical systems, this condition is often not satisfied. In systems far from equilibrium characterized by what is called the “mixing” property, slight changes in the initial state result in drastically different final states. As the initial state for these systems cannot be known with absolute accuracy, the final state cannot be predicted by using the methods of Markov processes (3).

LW circumvent this difficulty by assuming that the state of the system of N individuals is completely determined by the specification of the number of individuals, n_1 and $n_2 = N - n_1$, in each of the alternative culturgens. In mathematical language, at each decision point, a probability transition function, which depends only on n_1 and n_2 , $u_{ij}(n_1, n_2)$, can be defined giving the likelihood that an individual will shift from culturgen 1 to culturgen 2. The Markov approximation dictates that this transition probability does not change with time—i.e., historical circumstances. The key assumption of the paper is that a functional form of u_{ij} and the parameters specifying it, the epigenetic rules of individual behavior, exist and are genetically determined or, in LW's words, are a product of genetic prescription.

Two comments on this use of the Markov approximation are in order. First, in proposing a theory of behavior that depends only on the present overt behavior of individuals in the population, LW adopt an extreme behaviorist view of psychology and culture. Second, LW justify their assumption of the applicability of Markov processes by referring to a textbook in mathematical sociology by Coleman (4). Surprisingly enough, in view of their citation, Coleman sees little merit in the use of the Markov approximation for modeling group behavior. For example, he writes (ref. 4, p. 38), “These models . . . have used the mathematics of the Markov process, and have taken this mathematics about to the limit of its present development. Unfortunately, these limits occur before much substantive complexity has been incorporated, and as a consequence, the models are applicable only to extremely simple experiments.”

LW go on to assume that the frequency of the decision points is described by a first-order rate law—i.e., that the probability that the next decision point will not occur in a time t after the previous one is an exponentially decreasing function of t . This frequency distribution, the same as the one describing radio-

active decay, is characteristic of random processes. LW give no argument justifying this assumption for the frequency of cultural decision points. In fact they do not even mention that their choice of a first-order rate law constitutes an assumption and that other rate laws are conceivable.

As a result of all these assumptions, LW are then able to write a differential equation relating the time rate of change of P , the probability that in a population of N individuals, n_1 and n_2 will possess culturgens 1 and 2, respectively, to the transition probability functions and rate constants:

$$\begin{aligned} \partial_t P(n_1, n_2, t) = & (n_1 + 1) \cdot v_{12}(n_1 + 1, n_2 - 1) \cdot P(n_1 + 1, n_2 - 1, t) \\ & + (n_2 + 1) \cdot v_{21}(n_1 - 1, n_2 + 1) \cdot P(n_1 - 1, n_2 + 1, t) \\ & - [n_1 \cdot v_{12}(n_1, n_2) + n_2 \cdot v_{21}(n_1, n_2)] P(n_1, n_2, t). \end{aligned} \quad [1]$$

In this equation, $v_{ij} = r_i u_{ij}$, where r_i are the first-order rate constants.

This equation is the master equation of irreversible statistical mechanics (5). It can be solved numerically on a computer and can even be solved exactly in the steady state for certain choices of u_{ij} . However, LW make the further assumption that $(n_2 - n_1)/N$ can be treated as a continuous parameter, an assumption true only for large values of N . Recall that N is the number of individuals in the population, all of whom have equal influence in determining the probability that a given person will switch from one culturgen to another.

CONCLUSIONS OF THE THEORY

In their discussion, LW present two conclusions. First, “even small differences in the epigenetic rules, reflected in the assimilation functions (the u_{ij} s), are magnified during social interactions into the dependent ethnographic patterns.” Second, “[e]ven when the underlying epigenetic rules and assimilation functions are rigidly constrained, they can generate wide cultural diversity” (ref. 1, p. 4384). LW's major point is that imperceivable genetic differences can lead to widely varying social behavior.

To support their contention of the specificity of the epigenetic rules, LW summarize in their table 1 approximate values of the relative assimilation probabilities for such traits as sugar preference and color classification, which they estimate from experimental data. Their table 1, however, is labeled “Estimate of innate preferences” and the footnote to it states that “[t]he preferred culturgen is arbitrarily designated as c_2 , and the estimated probability of choice of this culturgen as opposed to c_1 is denoted as u_{12} .” This definition of u_{12} is inconsistent with the definition of u_{ij} given in the body of the paper, where u_{12} is defined as the probability of making a switch from c_1 to c_2 . For example, although 80% of the individuals may prefer c_2 and so, according to table 1, $u_{12} - u_{21} = 0.8 - 0.2 = 0.6$, it may be the case that each individual is satisfied with his or her choice and so the probabilities of a switch from c_1 to c_2 or from c_2 to c_1 are both zero.

This ambiguity in the meaning of the epigenetic rules appears throughout the paper. In table 1 and in the introduction, the epigenetic rules are described as those that “affect the probability of acquiring one culturgen as opposed to another (ref. 1, p. 4382), while, in the methods section, they are described as “transition probabilities u_{ij} from culturgen i to culturgen j ” (ref. 1, p. 4383). To make contact with experiment, the definition of epigenetic rules as it appears in table 1 is necessary because, as LW point out, cultural “responses have not been investigated with reference to their dependence on the behavior of the rest of society” (ref. 1, p. 4385), as would be required in evaluating $u_{12}(n_1, n_2)$ as defined in the body of the paper. The LW theory

cannot be related to experiment, as least at present, because the *transition* probability function, which is needed to quantify the master equation, is a totally unknown quantity and cannot, as LW imply, be estimated from the experimental data of table 1. It can only be concluded that the data of table 1 and the examples of biologically determined traits offered in the introduction of the LW paper are irrelevant to the mathematical model for gene-culture coevolution.

Let us now examine LW's conclusion that small changes in the assimilation function are magnified during social interactions. Their figure 3 displays the ethnographic curve P as a function of $\xi = (n_2 - n_1)/N$, based on the transition probability functions $u_{12} = a_1 \exp(a_2 \xi)$ and $u_{21} = a_3 \exp(-a_2 \xi)$, where a_1 , a_2 , and a_3 are arbitrary parameters. For this particular choice of u_{ij} , there is no need to assume the continuity of ξ because the master equation can be solved exactly in the steady state. We find

$$P(\xi) = \left[P(0, N) \binom{N}{n_1} \right] \left[\left(\frac{a_3}{a_1} \right)^{n_1} \right] \left\{ \exp \left[-\frac{1}{2} a_2 N (1 - \xi^2) \right] \right\}. \quad [2]$$

The three curves of LW's figure 3 correspond to three choices of a_2 . The uppermost curve, which arises on setting $a_2 = 0$, is not simply a slight adjustment of a parameter. Instead it changes the transition probability function u_{ij} , which varies exponentially with ξ (the "trend watcher"), into one that is independent of ξ —i.e., independent of all influences from the other members of the society (we might call it the loner). The term in braces in Eq. 2 reduces to 1, and the expression becomes that of a random walk (first bracket) that has a bias term (second bracket) (5). For $a_2 > 0$, the term in braces, which varies exponentially with group size (25 in LW's example), is no longer equal to 1. This exponential term totally dominates the random-walk term as a_2 increases. As a result, the lower two curves of LW's figure 3, characterized by $a_2 = 1.2$ and 2.0, respectively, show qualitatively different behavior from the uppermost one.

It is evident, as even LW state, that the sensitivity of their results is due to this exponential variation with group size, which obtains for many choices of u_{ij} . At least one of the supposed genetically determined parameters is multiplied by the large number N . Because this product appears as an exponent, the sensitivity of the results to small changes in the parameter is guaranteed. LW maintain that this sensitivity is a strength of the theory because it shows how small changes in the genetic rules, the u_{ij} s can result in large changes in the cultural patterns. This sensitivity can also be regarded as arising from the extreme sensitivity of the model to its fundamental assumptions. The magnification property arises because each individual is affected to an equal extent by every other member of the population and this population is fairly large (15–75). This model is similar to that for a dilute gas. A model based on, for example, that of a liquid would assume that an individual is influenced to a great degree by its nearest neighbors (approximately six or eight for a liquid), to a much lesser degree by its next-nearest neighbors, and so on. Why should cultural influences be modeled better by a gas, as LW propose, than, say, by a liquid?

APPLICATION OF THE THEORY

Recently, Lumsden and Wilson (6) have applied their theory to a discussion of "the relationship between the epigenetic rules of brother-sister incest avoidance which operate during individual development, and the frequency of occurrence of this form of incest among cultures" (ref. 6, p. 6248). LW chose to study this particular behavioral pattern because of their belief

that it represents the "simplest conceivable relationship" that can be found to test their theory. This putative simplicity arises as a result of three assumptions: (i) incestuous behavior is governed by rules influencing individual development; (ii) the transition probability function describing the propensity of an individual to change behavior with respect to incest is independent of the behavior of the other members of the society; and (iii) incestuous behavior can be subjected to a simple binary classification, either its most extreme manifestation or its complete absence. We will not discuss these assumptions here.

To implement their theory, LW need a means of determining u_{ij} s (transition probabilities) from existing anthropological studies. These studies, however, can provide only average frequencies of incest avoidance, $\bar{n}_1$. By solving, in the steady state, the simple kinetic equation for the rate of change of n_1 ,

$$\dot{n}_1 = v_{21} \cdot (N - n_1) - v_{12} \cdot n_1,$$

they find,

$$\bar{n}_1 = N(1 + u_{12}/u_{21})^{-1},$$

where they assume, without justification, that the average time between decision points for outbreeders and inbreeders, τ_1 and τ_2 , are equal.

Because this equation provides $\bar{n}_1$ as a function of the ratio of u_{21} and u_{12} (but not of u_{21} and u_{12} themselves), a further assumption is required. LW therefore make the additional assumption, again without justification, that $u_{12} = u_{22}$ and $u_{21} = u_{11}$. The first equality states that the probability of making a transition into the inbreeding state from the outbreeding state is the same as the probability of staying in the inbreeding state if the individual is already in that state. The second equality is the analogous statement for the opposite case. Thus, the probability of making a transition to a particular state in the future does not even depend on the *present* state of the individual! By using this assumption, LW can then determine that $u_{21} = \bar{n}_1 N^{-1}$.

LW next set up the master equation and solve it. Because the u_{ij} s are constants, the steady-state solution is given by Eq. 2 with $a_2 = 0$, namely, a random walk that has a bias term. This simple *exact* solution is true for all n_1 and N . There is no need for making, as LW do, the continuous ξ approximation, which results in a much more cumbersome and complicated formula.

LW conclude that their theory "yields a correspondingly clear and unsurprising relation between the degree of bias in the epigenetic rules and the mode of the ethnographic curve" and that "even fixed epigenetic rules, provided they do not favor one culturgen absolutely, can be expected to yield substantial cultural diversity" (ref. 6, p. 6250). These conclusions, however, are vacuous. They arise from the fact that, as a consequence of LW's assumptions, $\bar{n}_1 = u_{21}N$. Consequently, the average number of outbreeders is directly proportional to the transition probability of switching from inbreeding to outbreeding behavior. Because the transition probability is assumed to be < 1 , $\bar{n}_1$ is less than N —i.e., not everybody is an outbreeder. In nonmathematical terms, this paper states that if people are more likely to switch from incestuous to nonincestuous behavior than they are to make the reverse switch, then the society will be characterized by a high proportion of incest-avoiding individuals.

DISCUSSION

Critiques of the type presented in this paper are often open to the rejoinder that the assumptions made in the model are not crucial to the success of the theory, that the assumptions are made for ease in computation, and that relaxing them will not alter the results. For example, in their paper on incest, LW state

that the assumption that the u_{ij} s are constants can be relaxed to the assumption that the transition probabilities can be written in the form $u_{ij}(\xi) = a_{ij} + b_{ij}\xi$, where $a_{ij} = u_{ij}(0)$ and $b_{ij} = du_{ij}(0)/d\xi$. This, however, is a trivial modification. Because it is stated that $|b_{ij}| \ll |a_{ij}|$, the u_{ij} are essentially constants and so it is not surprising that this relaxation does not affect the predictions of the theory.

It is impossible to *prove* that a more realistic mathematical theory of culture cannot be constructed. Nevertheless, we regard such a possibility as highly unlikely. For example, for the Markov approximation to be relaxed, it would be necessary to incorporate memory effects into the theory. Since, as we have seen, even within the Markov framework, the empirical data do not provide enough information to calculate the u_{ij} s, it is difficult to imagine how the additional data needed for memory terms could be generated. The basic difficulties lie in the unjustified assumptions concerning the existence of genes governing transitions from one trait to another and in the reductionist belief that culture can be explained by a mathematical theory incorporating a few behaviorist empirical parameters. It is our belief that the simplifications inherent in any such mathematical treatment are irremediable.

We conclude with some remarks about the determinism of the theory. Aspects of both genetic and environmental determinism play an important role. The epigenetic rules—i.e., the functional forms of the transition probabilities—are genetically determined subject to alteration only by processes of natural selection. These rules are functions of the numbers of people in the relevant cultural states, an environmentally determined quantity. This description of the distribution of various cultural behaviors is thus reduced to a genetically determined function of a single behaviorist parameter. We have seen that the model is extremely sensitive to assumptions concerning the precise nature of the functional form of the u_{ij} s. It seems likely that corrections of the failings of the theory resulting from the extreme behaviorist assumptions that are necessary for its con-

struction would result in even greater changes in the ethnographic curves. These factors, such as the inclusion of memory effects, of internal states of the individuals, and of the influence of groups of individuals and cultural institutions, to name just a few, could be incorporated as parameters to manifest themselves as changes in what LW consider to be the genetic functional forms and parameters. Furthermore, as mentioned above, the increased complexity could lead to instabilities, so that small changes in the relative importance of these factors could result in major changes in the curves. Such instabilities would result in a complete breakdown of the LW model; the initial states cannot be determined with arbitrary precision, so that the final curves cannot be predicted at all.

LW constructed their theory in an attempt to overcome the current limitations of sociobiology. Instead of the biological determinism of postulating genes that code directly for various human behavioral traits, LW propose that genes code for transition probability functions that depend on environmental parameters. However, because the assumptions of the theory are so severe and because the environmental parameters are limited to a single one (the number of individuals in a particular cultural state), the LW theory does not appear to offer any new understanding of the coevolution of genes and culture.

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1. Lumsden, C. J. & Wilson, E. O. (1980) *Proc. Natl. Acad. Sci. USA* 77, 4382–4386.
2. Wilson, E. O. (1975) *Sociobiology: The New Synthesis* (Harvard Univ. Press, Cambridge, MA), p. 553.
3. Balescu, R. (1975) *Equilibrium and Nonequilibrium Statistical Mechanics* (Wiley, New York), pp. 695–729.
4. Coleman, J. S. (1964) *Introduction to Mathematical Sociology* (Free Press, New York), pp. 38; 460; 528.
5. Reif, F. (1965) *Fundamentals of Statistical and Thermal Physics* (McGraw-Hill, New York), pp. 7–11; 548–550.
6. Lumsden, C. J. & Wilson, E. O. (1980) *Proc. Natl. Acad. Sci. USA* 77, 6248–6250.