An Intergenerational Transmission Model
for the Cultural Evolution of Helping Behavior

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The cultural coefficient of similarity, or probability that two individuals learn the same idea from a common ancestor, is offered as an explanation for patterns of helping behavior in human societies. A cultural-transmission model predicts that when maternal influence in offspring learning is predominant, matrilineality will evolve in a culture. Other predictions about the form of matrilineal and palrilineal societies are made from the model and contrasted to a sociobiological explanation of matrilineality.

INTRODUCTION

In recent years sociobiologists have employed the concepts of inclusive fitness (Hamilton, 1964), sexual selection (Darwin, 1871 Trivers, 1972), and reciprocal altruism (Trivers, 1971) to formulate new interpretations of human behavior (Alexander, 1977; Dawkins, 1976; Barash, 1977; Wilson, 1978; Alexander *el al.,* 1979). The central postulate of sociobiological theory is that genes cause individuals to behave in certain ways that increase the likelihood that those genes are replicated in future generations. With this outlook sociobiologists hope to evolutionize the social sciences. The approach is applied to everything from sex roles to human lineage systems and kinship terminologies (Wilson, 1978; Alexander, 1974; Kurland, 1979), and it is quite controversial among social scientists (Sahlins, 1976; Barkow, 1978).

Salient to this controversy, another application of evolutionary theoryv to the study of human behavior is underway (Cloak, 1975; Cavalli-Sforza, 1975; Durham, 1976; Cavalli-Sforza and 1•eldman, 1973a,b; Mav, 1977; Pulliam and Dunford, 1980; Ruyle, 1973; Ruyle *et al.,* 1977). This approach views culture as a population of learned behavioral traits or customs which are transmitted between individuals through social learning. When there is variability in individual behavior within a population, some behavioral traits are more likely than others to be transmitted. Cultural evolution is then viewed as consisting of changes in the frequencies of various socially transmitted behavioral traits, and mathematical models are employed to determine what conditions favor the increase of one behavior over another.

Social transmission of behavior occurs whenever the behavior of one individual enhances the likelihood that a second individual will adopt a behavioral trait characteristic of the first. This may involve either active teaching, including the direction of attention and the selective presentation and withdrawal of reward and punishment, or simply passive observation and imitation. In either case, the learning may take place long before tire fl at occurrence of appropriate circumstances for the actual expression of the learned behavioral trait. Thus, it can be said that what is actually transmitted is an "idea" about the benefits of adopting a particular behavior and that such ideas motivate particular behaviors later in life when appropriate circumstances arise (cf. Pulliam and Dunford, 1980). This is in agreement with Bandura (1977, p. 37), who wrote that "observational learning occurs through symbolic processes during exposure to modeled activitil , before any responses have been performed" and "anticipated benefits can strengthen retention of what has been learned observationally by motivating people to code and rehearse modeled behavior."

An important requisite for developing models of cultural evolution is to define the rules of transmission for the traits being considered. Models of cultural evolution developed so far fall into two general categories.

1. Intergeneration models (Cavalli-Sforza, 1973a,b; Richerson and Boyd, 1978) consider the evolution of ideas that offspring learn early in life from adults. The models presume that certain ideas, once adopted, can motivate their bearers to behave in ways that increase or decrease the likelihood that these ideas are replicated in future generations (Pulliam nd Dunford, 1980). In general, when behaviors are learned solely from biological parents, ideas which increase the survival and reproductive success of their bearers will have increased representation in future generations, though there are important exceptions to this conclusion (see also Richerson and Boyd, 1978).

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2. Models of *intragenerational* transmission (Feldman and Cavalli-Sforza, 1975; Pulliam and Dunford, 1980) apply to ideas which can spread throughout a population within a single generation. Many investigations of the adoption of innovations in human societies (Ammerman and Cavalli-Sforza, 1971; Katz *et* al., 1963; Kim, 1970; Thio, 1971) indicate that intragenerational transmission is a more complex process than intergenerational transmission. For example, intragenerational spread of innovations is strongly influenced by the association between the "new ideas" and previous experience of the potential adopter.

A postulate of models of cultural transmission is that a "successful" idea is one that leads individuals to behave in ways that maximize the transmission of that idea to other individuals. Ideas may be successful by increasing the survival and reproduction of the idea bearers, so that the ideas are transmitted to offspring, or by increasing the likelihood that other individuals, not necessarily related to the original bearers of the ideas, will adopt the idea from the bearers. The latter may happen when others see that bearers of one idea have greater access to societal rewards than do those with other ideas. This means that ideas may be successful even though they do not necessarily increase fitness in the genetic sense.

The purpose of this paper is to present an intergenerational transmission model for the cultural evolution of helping behavior. To do so we will first discuss the genetic theory of kin selection formulated by Hamilton (1964). Sociobiologists (Alexander, 1977; Greene, 1978) have applied the genetic theory to explain variations in human lineage systems. We contrast the predictions of this model to those of a *cultural-transmission model.* Our analysis indicates that the cultural model is at least equally consistent with the general patterns of lineage systems. Contrasting predictions are offered to separate the cultural-transmission model from the sociobiological model. We conclude by discussing possible general applications of this approach to the study of cultural processes.

GENETIC RELATEDNESS AND MATRILINEALITY

The genetic theory of kin selection (Hamilton, 1964) has stimulated new thought and research into evolution of social behavior in animals (Wilson, 1975). The theory posits that a gene coding for a social behavior can effect its replication success in two ways: first, by its influence upon the reproductive success of the organisms carrying it, and second, by its influence upon the reproductive success of other organisms carrying copies of the same gene. Since genetic kin are likely to have similar genes the

theory has been termed "kin selection." Kin selection allows for the evolution of "altruistic" behavior, which lowers the fitness *of* the individual performing the behavior (the *donor)* and increases the fitness of the *recipient* of the behavior. Hamilton showed that the occurrence of altruism depends on the genetic relatedness of the donor and the recipient. Genetic relatedness (r) is defined as the probability that two individuals share a given gene by descent from a common ancestor. According to genetic kinship theory, altruism is favored in evolution if the decrease in the donor's fitness is less than r times the increase in the recipient's fitness. Charnov (1977) has shown that in populations with random mating the result is unaffected by the frequency of the "altruistic" gene. Recently, Cavalli-Sforza and Feldman (1981) have shown that this result holds only if the fitness effects are additive and that a similar but complicated result holds if the fitness effects are multiplicative.

The genetic coefficient of relatedness is the probability that two individuals share the same gene by descent. It is dictated by the fact that half of an individual's autosomal genes come from the mother and half from the father. Hence the genetic relatedness between a mother and her offspring is $\frac{1}{2}$. Relatedness between full sibs is the probability that both received the same gene from mother plus the probability that both received the same gene from father, or $\frac{1}{4} + \frac{1}{4} = \frac{1}{2}$.

The genetic theory of kin selection makes the important prediction that individuals will prefer to help close kin rather than more distant kin because of the increased genetic returns from such aid. The temptation to apply kinship theory to human societies, where anthropologists have long recognized the important role of kinship, has been overwhelming. Specific patterns of human sociality have been interpreted by Alexander (1977), Wilson (1975, 1978), Dawkins (1976), and Barash (1977) in the light of kin-selection theory (see also Kurland, 1979). We *will* focus upon Alexander's (1977) discussion of matrilineality in human societies.

Matrilineality is a human lineage form in which a man's property is passed to his sister's son instead of to his wife's son (patrilineality). It occurs in approximately 15% of human societies and is associated with (1) matrilocal residence, in which sisters remain together in a household and men live in their wives' households and (2) avunculocal residence, where sisters live in the households of their husbands, but male offspring move into the household of their mother's brothers (the avunculate) upon reaching maturity (Murdock, 1949).

By comparing the genetic relatedness between a male and spouse's offspring with that between a male and sister's offspring, Alexander found an intriguing result. When reliability of paternity (p) is low, a man is genetically more related to his sister's children than to his wife's children

(reliability of paternity is the probability that a husband is the genetic father of an offspring of his wife).

Since maternity is obvious, a woman can be certain of her genetic relatedness to her own children. Paternity is not certain and so a man cannot be sure that he is genetically related to his wife's children. The expected genetic relatedness of a man and his wife's child is p/2. The genetic relatedness of a man to his sister's children is $\frac{1}{z}$ (p=/4 + $\frac{1}{4}$). The man can be certain of sharing some genes with his sister's children since he and his sister were born of the same mother and with probability p' to the same father.

Figure la shows graphically how genetic relatedness depends on the reliability of paternity. When p is less than $\frac{1}{4}$, a man is more closely related to his sister's children and, according to kinship theory, should therefore be more willing to aid his sister's children than to aid his wife's children.

Matrilineality is often associated with matrilocal residence, where sisters remain together in a household and men live in their wives' households. Kurland (1979) argues that this residence pattern leads to loose marriage bonds and therefore, a low reliability of paternity. There are two ways that genes might "cause" the evolution of matrilinear societies. First, societies could contain both "matrilineal genes" and "patrilineal genes," with the former increasing in frequency when reliability of paternity is low. This view represents an extreme form of biological determinism and would find few supporters even among sociobiologists. Alternatively, genes for "behavioral scaling" (Wilson, 1978) could specify that when paternity reliability is low, males should preferentially help their sisters' offspring. Such genes might be fixed in all human populations.

CULTURAL SIMILARITY AND MATRILINEARITY

In contrast to the genetic theory of kin selection, which explains patterns of human sociality in terms of the genetic similarity between individuals, we posit that patterns of human cooperation and aid-giving may best be explained in terms of the cultural similarity between individuals. We use the term "cultural coefficient of similarity" or just "cultural similarity" to indicate the probability that two individuals share the same idea by descent (i.e., by social transmission) from a common ancestor. A population model justifying the use of cultural similarity by *descent* and deriving a cost/beneficial threshold for helping is presented in Appendix 1.

Consider the following simple model of cultural inheritance. Suppose there arc two alternative "ideas" which are learned early and uncritically in life by offspring from parents. One is that "a man should help his spouse's offspring" and the other is that "a man should help his sister's offspring."
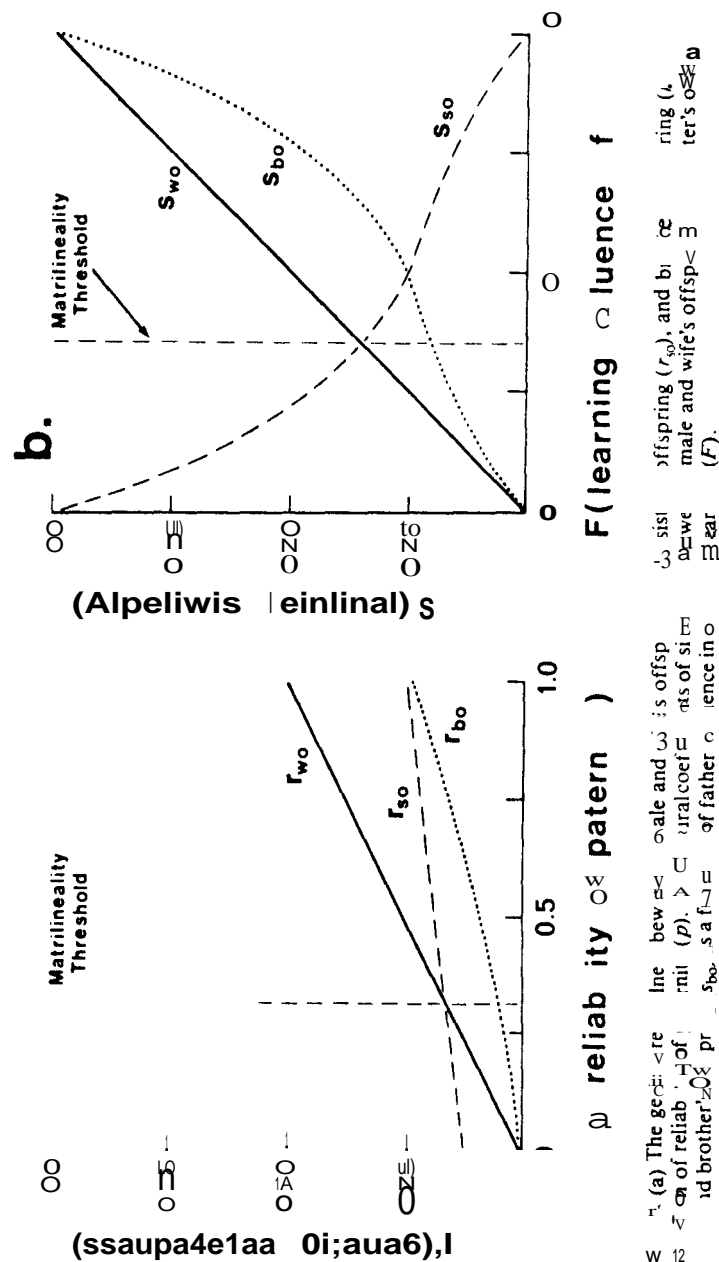

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Each trait is learned from parents only and then retained for life. We assume that if both parents have the same ideas about inheritance the children will learn this idea with probability 1, but if the parents differ, the children will learn their father's idea with probability F and learn their mother's idea with probability M $(F + M = 1)$. We refer to the probabilities F and M, respectively, as paternal influence and maternal influence. Our model is a special case of the additive, vertical-transmission model of cultural inheritance developed by Cavalli-Sforza and Feldman (1981).

In one respect the mode of learning modeled here is similar to genetic inheritance: in general, the learned traits of those individuals with greater survival and reproductive success will be represented with greater frequency in future generations. Still, there are significant differences. In genetic inheritance a child inherits half its genes from its father and half from its mother, whereas in the cultural inheritance described above, mother and father influence can vary between zero and 1. This differences has an important effect upon the probability that kin share the same ideas (i.e., on cultural relatedness). Richerson and Boyd (1978) appreciated the significant effect of this asymmetry of learning upon the evolution of matrilineality.

Whenever children learn ideas only from parents, coefficients of similarity are calculated in a manner similar to genetic coefficients of relationship. For example, the similarity between two full sibs is the probability that both learn the particular trait from father plus the probability that both learn from mother, or $P + Mz$. Table I represents the formula for genetic relatedness and cultural similarity for various relatives (assuming that sibs always have the same cultural father).

As is shown in Appendix 1, for a particular additive model of cultural inheritance, cultural coefficients of similarity can be used to make exact predictions about the evolution of helping behavior in general and patterns of inheritance in particular. Based on the simplifying assumptions of the model, a quantitative criterion is derived for the spread of particular helping behaviors based on the benefits to recipients and the costs to donors. One of the simplifying assumptions necessary to establish such quantitative criteria is that mating is at random with respect to the behavior in question. As discussed in Appendix 1, when this and other assumptions arc violated, the quantitative results do not hold exactly. Nevertheless, the qualitative prediction can still be made that the greater the cultural similarity between individuals, the more likely they are to help one another.

The critical conceptual difference between the genetic model and the cultural model is in the mode of transmission of behaviors from parents to offspring. The genetic model assumes that the behavioral differences between matrilineal and patrilineal societies are genetically determined. Thus, the relevant measure of relatedness between parents and their offspring is

Table 1. Formulas for Genetic Relatedness and Cultural Similarity for Various Relatives

Relation	Genetic relatedness	Cultural similarity
Mother	$\frac{1}{2}$	M
Father	$\frac{1}{2}$	F
Sibs	$\frac{1}{4} + p4/4$	$M' + F4$
Wife's children	$p/2$	F
Sister's children	$14(\frac{1}{4} + p4/4)$	$M(M' + F4)$
Brother's children	$(p/2)(\frac{1}{4} + p4/4)$	$F(M= + F4)$

genetic similarity, and the genetic similarity between a man and his wife's children depends on paternal uncertainty over who is the genetic father of the children. The cultural model, on the other hand, assumes that the differences between societies are perpetuated by social transmission of learned behavioral differences. Thus, the relevant measure of relatedness between parents and offspring is cultural similarity, and the cultural similarity of a man and his wife's children depends on paternal influence on what children learn.

Figures la and lb contrast the genetic and cultural relatedness of a man and his (1) wife's chiildren, (2) sister's children, and (3) brother's children. In genetic relatedness is shown as a function of the reliability of paternity (p). Figure 1 b presents cultural relatedness as a function of F, the influence of the father on his children's learning. These two parameters, p and F, are contrasted because both reflect the "influence of a male on the transmission of a trait to his wife's offspring

Although and lb differ in detail, they have striking similarities. First, there is a region (low p in the genetic model, low F in the cultural model) where a male is genetically more related or culturally more similar to his sister's children than to his wife's children. Second, in both models a male is never more related (or similar) to offspring of his brother's spouse than he is to offspring of his own spouse.

Certain predictions can be derived from these characteristics. Both models predict that matrilineality **will** be associated with extended male absence from the household because both genetic paternity (p) and male influence on learning (F) are likely to be low in human societies when the male is away from home for extended periods of time (see Kurland, 1979). This accords well with the observed patterns. For example, matrilineality is also common in Micronesia, where men participate in long-distance trading, and in Melanesia it occurs more frequently along the coast and on islands where long-distance trading occurs, but is uncommon in the interior where men participate less in long-distance trading. Harris (1975: 347) recognized that "matrilocal cases may be due to subsistence activities
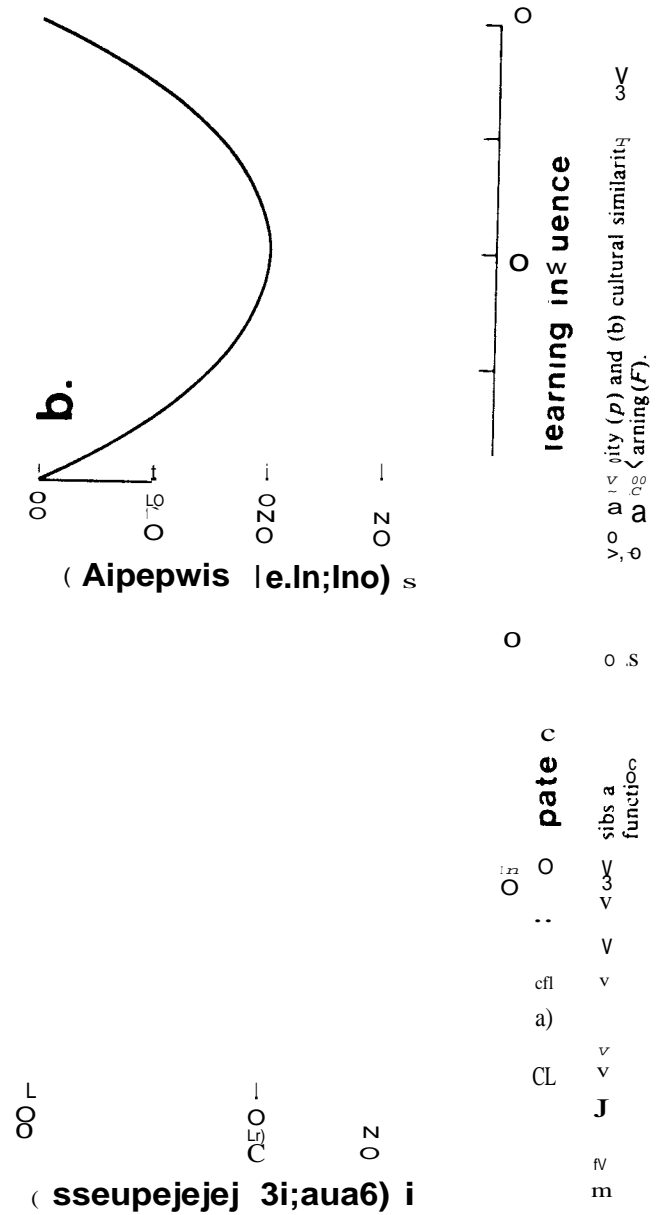
that require males to be absent on long expeditions." Similar reasoning can apply to matrilineality since it is strongly correlated with matrilocality (see Murdock, 1967).

A second prediction of both models is that there should be no societies in which the standard form of inheritance is from a male to his brother's offspring (the logical analog of matrilineality). Although such a lineage system is possible, no such arrangement is known (Murdock, 1949).

The general patterns discussed so far are consistent with both cultural and genetic models of inheritance. This illustrates an important point often overlooked by sociobiologists anxious to apply genetic theory to human be havior: namely, that behaviors that increase genetic fitness need not be genetically determined (Durham, 1978). In what follows, we present predictions of a cultural model that are quite distinct from predictions of a genetic model. In drawing this distinction we are not denying that all learning depends ultimately on genetic inheritance of learning structures (Pulliam and Dunford, 1980). Rather, we are arguing only that different individuals with identical learning structures may learn different traits, depending on differences in their social environments. Since social environ- ments change with accumulated cultural experiences, cultural evolution of behavioral traits may proceed independently of any further genetic evolution of learning structures.

Figure 2 shows the genetic relatedness and the cultural similarity be- tween sibs as a function of reliability of paternity (p) and paternal influence on learning (F), respectively. For the cultural model sib similarity is lowest when mother and father influence are equal ($M = F = \frac{1}{2}$), but it rises rapidly when either parent predominates in offspring learning. When only one parent contributes, sibs are culturally identical for the behaviors in question. Genetic relatedness, on the other hand, never exceeds "/z. Using the principle of kin-selection theory that high relatedness favors greater helping between individuals, the genetic model predicts that sibs will show greater cooperation in patrilineal societies and more conflict in matrilineal societies because sibs are less related in matrilineal societies. For the cultural model, if we assume that paternal influence on learning (F) never exceeds $\frac{1}{2}$, then the model makes the precisely *opposite prediction* that sibs should be much more cooperative in matrilineal societies than in patrilineal societies because their coefficient of similarity is greater.

Other predictions also follow. When maternal influence on learning (M) is significantly greater than paternal influence (F), male offspring have a lower ability to transmit learned behaviors. Therefore learned behaviors will be favored which deemphasize male reproductive success and emphasize male ability to invest in sister's offspring, because the ideas them- selves are more likely to be propagated through the sister's offspring. This could be reflected in a decrease in the bride price that maternal uncles are

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Figure 2. ... sibs as a function of (a) reliability of paternity (p) and (b) cultural similarity ... learning (F).

willing to pay for their sister's sons. We also expect male prestige to be associated with the fathering of children to a lesser extent in matrilineal societies than in patrilineal societies. Among matrilineal Trobrianders of Melanesia, the association between fornication and parentage is not even recognized (Malinowski, 1922). Also, we would expect less female infanticide in matrilineal cultures (if one controls for the prevalence of warfare) because of the greater transmission success of female offspring.

According to the genetic model, we always expect women to favor their own children over the children of their sisters, because women always share more genes with their own children than they do with their sisters' children. However, according to the cultural model, if M is very close to 1, women are equally related culturally to their sisters' children and to their own children. This may be true even if children do not learn solely from their parents. For example, when children learn certain ideas solely from their mothers and their mothers' maternal aunts, the cultural coefficient converges to 1. This can be shown by defining A as the influence of maternal aunts in learning. Then the cultural coefficient of similarity between full sibs is given by:

$$S_{,;63} = A (A + M \cdot SS_{;b3}) + M(M + A \cdot Sib_,).$$

Solving for $S_{,;,,,}$, we find a cultural coefficient of similarity for full sibs of 1.

Therefore, in matrilineages, high internal similarity is most likely to occur with matrilocal residence when offspring are reared in association with mothers and mothers' sisters. The high cultural relatedness in matrilineages could result in the communal rearing of children, with mothers decreasing the distinctions between their own and their sisters' children.

In summary, the contrasting predictions between the two models are:

1. The cultural model predicts greater sib cooperation in matrilineal societies than in patrilineal societies. The genetic model predicts the reverse.

2. The cultural model predicts a deemphasis upon genetic fitness in males and an emphasis upon their lineage obligations in matrilineal societies. The genetic model predicts an equal emphasis on male reproductive success in both matrilineal and patrilineal societies.

3. The cultural model predicts that the cultural similarity in matrilocal-matrilineal groups will result in a great deal of cooperation between sibs and a lowering of distinctions that females make between their own and their sisters' offspring. The genetic model predicts that, if anything, those distinctions should increase because of lower sib relatedness.

At present, data are insufficient to quantitatively test these predictions. Furthermore, a reliable test requires a detailed knowledge of lineage systems because of the multiple factors which covary with lineage. We urge anthro-pologists with this expertise to consider the contrasting predictions of the models.

Some societies exhibit both patrilineal-descent and matrilineal-descent patterns. We make the general prediction that the lines of learning will determine descent. Those behaviors which are learned predominantly from the mother will tend to favor the matrilineage. Behaviors which have a significant paternal influence (greater than about $1/4$ in the simple model above) will favor the patrilineage. This is not a battle between the sexes since both fathers and mothers are favored to teach patrilineal ideas when paternal influence is high and to teach matrilineal ideas when paternal influence is low. The patterns of learning merely determine whether the ideas favoring patrilineality or those favoring matrilineality will increase in frequency.

The cultural model presented above assumes that individual children learn a behavior either from the mother (with probability M) or from the father (with probability F), but not from both parents. A more accurate representation of social transmission might be a form of "blending" inheritance, in which the degree of matrilineality adopted by a child could be intermediate between that of its parents. This would allow for an intermediate expression of matrilineal inheritance with a portion of wealth going to each parental line. A preliminary investigation of such a model suggests that the same basic principle holds that increased paternal influence over learning favors increased patrilineality.

We believe that our model complements traditional anthropological explanations for matrilineality. Anthropology has, of course, developed functional explanations for many cultural characteristics, such as lineage systems and kinship terminology; however, the underlying mechanisms responsible for cultural change are usually not explicitly defined. Explanations are often oriented towards group or societal benefits, which suggests either an underlying process of "efficient" cultures replacing "inefficient" cultures or a process of cultures evolving toward greater internal consistency.

An ecologically or technologically induced shift in the division of labor that enhances the role of women in subsistence has been invoked to explain matrilineality (Murdock, 1949; Aberele, 1961; Keesing, 1975). It is suggested that the shift favors matrilocal residence, which in turn promotes the formation of local groups related through women. This eventually leads to matrilineal descent. Harris (1977; 61) argues that "shifts from patrilineal to matrilineal organization originate as an attempt on the part of absentee males to turn over the care of jointly owned houses, lands and property to sisters." Absentee males rely on their sisters rather than their wives because wives are drawn from someone else's paternal interest group and have divided loyalties. Absentee brothers therefore discourage marriage

which would remove their sisters from the household, resulting in matri-locality. This can be accomplished by the simple expedient of changing bride price to bride service-for example, by requiring the husband to pay for his wife by working at the wife's locality.

These theories rely heavily upon "common sense," i.e., intuitive assumptions about the way humans should behave. The underlying mechanism is psychological in that individuals are presumed to behave so as to maximize their "perceived interests." This explanation would be more satisfying if it included an explanation of how environmental and social factors determine perceived interests.

Our cultural explanation of matrilineality can be viewed as consistent with the anthropological explanation just discussed. Ecological circumstances which result in prolonged male absence from home lead to both an increased female role in what children learn and to an increased likelihood that some individuals will perceive that matrilocal residence is in their own best interest. Once females predominate in the teaching of children, ideas favoring matrilineality can increase in frequency regardless of whether or not they are perceived to favor self-interest. Though this process requires no perception of self-interest, such awareness would necessarily speed the acceptance of the ideas favoring matrilineality. Whereas the blind process is slow and results in the gradual accumulation of matrilineal ideas between generations, awareness of the benefits of matrilocal residence and matrilineal inheritance could lead to rapid acceptance within a few generations.

We believe that the value of cultural-transmission theory is that it provides a mechanism for the evolution of ideas within a culture. Even when the mode of transmission is most similar to that of genes, i.e., early parent-offspring learning, the predictions of cultural transmission can be quite different.

The more we relax the assumption of learning only from parents and allow other adults to have an influence, the more dramatically the "success" of ideas can diverge from that which enhances genetic fitness (Feldman and Cavalli-Sforza, 1975). In general, those ideas which either (1) increase an individual's chance of becoming a "cultural parent" or (2) increase the chances of other individuals with the same idea of being cultural parents, will be favored. In other words, "cultural fitness" is not necessarily the same as "genetic fitness."

Cultural-transmission theory is complicated by the fact that there are many possible modes of learning; however, testable predictions can be derived using certain assumptions about the form of transmission. The model presented in this paper produces predictions about human lineage systems which can be tested as we learn more about the patterns of learning

and helping in human societies. Research into learning patterns will also help to determine the kinds of cultural transmission models which should be pursued.

ACKNOWLEDGMENTS

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APPENDIX 1

Here we derive conditions for the increase in frequency of altruistic behavior in a mixed population of altruists ("A") and nonaltruists ("a") assuming intergenerational parent-offspring transmission by social learning.

Following Cavalli-Sforza and Feldman (1980), the structure of vertical transmission for a two-state trait is given in Table 11. We, present a special case of what Cavalli-Sforza and Feldman call the additive model of vertical transmission. As in the text, we assume the special case in which offspring of two altruistic parents are always altruist as adults (i.e., b = 0, see Table

11). When b = 0, mating is at random, and there is no natural selection for the trait involved, the frequency (U) of altruists in the population at generation 1 is given by:

$$U,,_{1} - U^2 + U(1-U,)M + U,(1-U,)F = U,. \qquad (1)$$

That is, in the absence of selection, there is no change in the frequency of altruists.

Selection can be added to the model by letting $W_A(1)$ be the average reproductive success of altruistic individuals and $W,(t)$ be the average reproductive success of nonaltruistic individuals. Then, if U, is the frequency of altruists before selection, the frequency after selection is given by:

$$U\pm = U_r F_A(1)I[U_1 W_A(1) + (1- U)W. (1)],$$

from which it is seen that the frequency of altruists increases under selection so long as $W_A(t) > W,(t)$. If this inequality holds for all time, the altruistic behavior eventually spreads to all of the population.

The criterion $W_A(t) > W,(t)$ can be expressed in terms of the cultural coefficient of relationship by defining the following:

N = the total population size;

n = the average number of altruistic acts per generation;

x = the proportion of altruistic acts directed towards other altruistic individuals;

B = the incremental increase in reproductive success of a recipient per altruistic act;

C = the incremental decrease in reproductive success of a donor (altruist) per altruistic act.

From these definitions it follows directly that:

$$W_A(1) = 1 + (nBx-nCINU, \qquad (3)$$

and

$$W,(1) = 1 + [nB(1-x)]1N(1-U,)]. \qquad (4)$$

Thus, the condition $W_A(1) > W,(t)$ can be expressed as:

$$BIC > (1- U,)I(x- U,) . \qquad (S)$$

The proportion x of altruistic acts directed towards altruistic individuals depends on (1) the mating structure of the population, (2) the frequency of altruists in the population, and (3) the "helping rules" that

altruists use when deciding whom to help and whom not to help. For example, assuming random mating, the value of x for the rule "help sibs" is given by

$$x = M(M + UF) + F(F + U,M) = M1 + F^l + 2 U,MF. \qquad (6)$$

Now substituting this value of x into Eq. (S), we find that the criterion for $W_A(t) > W,(t)$ is

$$BIC > (1- U,)l[M2 + F^l + U,(1- 2 MF)J \qquad (7)$$

and since $M^l + F^l = 1-2MF,$ this simplifies to

$$BIC > 1 /(M^l + F1). \qquad (8)$$

That is, the altruistic behavior between sibs will increase in frequency so long as the ratio of benefits (B) to costs (C) exceeds the reciprocal of the cultural coefficient of relationship between full sibs $(M2 + F1)$.

This result can be generalized for a randomly mating population by noting that the proportion x of altruistic acts directed towards other altruists is

$$x = r + U, (1-r), \qquad (9)$$

where r is the cultural coefficient of relationship. Substituting Eq. (9) into Eq. (S) gives the criterion

$$BIC > (I-U,)l[r + U,(1-r)-U] \qquad (10)$$

or

$$BIC > 1/r.$$

Thus, for an additive model of intergenerational transmission with b = 0 and random mating, an exact criterion for the spread of altruism is that the benefits to the recipient multiplied by the cultural coefficient of relationship between the altruist and the recipient exceed the cost to the altruist.

When b is not zero, the criterion $W_A(t) > Wft)$, and therefore the criterion $B/C > 1/r$, does not assure that the altruistic trait *will be* fixed in the population. Rather the condition $B/C > 1 /r$ increases the likelihood for altruism as a stable equilibrium. In other words, the criterion $BIC > 1/r$ increases the likelihood that the altruistic trait is fixed in the population but does not assure that it is.

Similarly, Eq. (10) does not hold when mating is nonrandom or when a multiplicative rather than an additive model of inheritance is employed. Nonetheless, the criterion is a good approximation for the initial spread of altruistic behavior, because when the trait is rare, mating is approximately random with respect to the trait. Also, the criterion is a good approximation when there are small multiplicative effects during transmission. Even for large deviations from random mating or large multiplicative effects, the general results seems to hold that *for altruistic behavior to evolve, the smaller the cultural coefficient* of *relationship, the larger the required ratio* of *benefits to costs.*

We are currently exploring the generality of our result to situations in which individuals other than parents play some role in intergenerational cultural transmission.