Cultural Relatedness Under Oblique and Horizontal Transmission Rules

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The concept of genetic relatedness is central to the sociobiological theory of kinship altruism. Genes which code for altruistic acts toward closely related genetic kin can overcome selection pressures favoring self-interested behavior. But genetic relatedness declines rapidly as kinship becomes more distant, thereby restricting genetically-based altruism to very close kin. This paper extends these notions to cultural relatedness, arguing that oblique and horizontal transmission can yield high levels of cultural relatedness in larger groups. A mathematical model of cultural transmission is proposed, and equilibria for several special cases are investigated. For all models, the equilibrium level of relatedness is critically dependent on the influence of exogenous sources. In models with equal influence of nonparents, the level of relatedness varies inversely with group size. On the other hand, when nonparental influence is concentrated on a single individual, the level of relatedness does not vary with group size.

the concept of genetic relatedness is central to the sociobiological theory of kinship altruism. Suppose that there is a gene which says, in effect, "Perform an altruistic act whenever Br > C," where r—the coefficient of relatedness—is the probability that recipient and donor share the same gene by inheritance from a common ancestor, B is the benefit (in reproductive fitness) to the recipient, and C is the cost (also in reproductive fitness) to the donor. It has been shown that such genes will increase in frequency over time and may come to predominate in the population (Hamilton 1964). On the other hand, the probability of sharing altruistic genes decreases geometrically as kinship becomes more distant. Thus, relatedness between first cousins is only .125, requiring that the benefit to the recipient be more than eight times the cost to the donor if the inequality is to be satisfied. Consequently, genetic kinship theory has a hard time accounting for altruistic behavior in large, extended families.

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CULTURAL EVOLUTION

Recently there have been several attempts to apply sociobiological models to the evolution of culture (Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981; Lumsden and Wilson 1981; Pulliam and Dunford 1980). In particular, Werren and Pulliam (1981) have argued that altruistic behavior that is learned from other people may have evolved by processes similar to genetic kinship altruism. Specifically, learned rules that mandate helping behavior toward close "cultural relatives" may be resistant to selection processes that favor strictly self-interested behaviors. For example, suppose that someone has learned a rule which says, in effect, "Be good to those who follow the same customs that you do." While such acts may be costly to the actor, the benefit will go to people who have a high probability of carrying the same rule. This benefit, in turn, can increase the likelihood that the rule will be passed on to others.

But, of course, cultural transmission does not operate exactly like genetic transmission, and it would hardly be surprising if the results were somewhat different. One crucial difference is that genetic transmission only occurs vertically (from parent to child), while cultural transmission can be oblique (from parent to niece, nephew, or unrelated child), horizontal (from adult to adult or from child to child), and even reverse vertical (from child to parent). As a consequence, I have suggested elsewhere that cultural kinship may lead to larger sets of mutual altruists than those produced by genetic kinship (Allison 1991).

For this to work, however, it is necessary that processes of cultural transmission lead to higher levels of cultural relatedness than are produced by genetic transmission. In an unpublished paper, Boyd and Richerson (1978) argued that a combination of oblique cultural transmission and cultural inbreeding is not sufficient to generate significant degrees of cultural relatedness. Specifically, they found that an increase in the number of cultural parents tended to reduce relatedness between siblings, even if those cultural parents were consanguines. In one example, with ten consanguine co-parents accounting for 95 percent of socialization, the relatedness between siblings was only .16.

In this paper, I present more promising results for relatedness between cultural cousins. I begin by formulating a model for cultural relatedness under oblique transmission. Within the framework of this model, I examine the impact of several variables on cultural relatedness: group size, parental vs nonparental influence, variability of nonparental influence, and the influence of exogenous sources. I then extend the model to include horizontal transmission. Although the models are highly simplified, I believe that they capture some of the more important properties of cultural transmission. On the other hand, there are some features of the models that would obviously have to be modified for a fully adequate theory. Thus, I regard this as a preliminary effort at modeling cultural kinship, but one that is sufficient to

(a) show that cultural relatedness can exceed genetic relatedness by substantial degrees and (b) point out some of the key variables that may influence the degree of cultural relatedness.

A MODEL OF CULTURAL TRANSMISSION

The general model is for a group of actors which, for concreteness, can be thought of as the male line of a patrilocal group, with one male offspring for each biological father. (The model would also be appropriate for the female line in a matrilocal group.) The requirement of exactly one son for each father avoids the difficult complication of dealing simultaneously with genetic and cultural change. The group practices strict exogamy, so there is no biological or cultural relatedness between husband and wife. Although this assumption greatly simplifies the model, it also biases against high relatedness. Later I shall briefly consider an extended model that allows for some endogamy.

There is a sequence of generations $t = 1, 2, 3, \ldots$ with n males in each generation. Consider a single cultural "locus" for which there are two or more variant traits. By this I mean that there is a certain class of behaviors for which there is a set of well-defined alternatives. For example, there is a set of variants for political party in the U.S. (Democrat, Republican, Independent,) and a set of variants for eating preferences (vegetarian, nonvegetarian). Each male in generation t "selects" his variant by choosing one person in the preceding generation (t - 1) and adopting the variant of that person. Of course, the selection could be unconscious or imposed by members of the prior generation.

The probability that male i in generation t selects his variant from male j in generation t-1 is denoted by a_{ijt} . This probability does not depend on the variant carried by male j. For the moment, it is also assumed that the probability is constant across cultural loci, but we shall later consider the possibility that different loci may have different adoption probabilities and, consequently, different degrees of cultural relatedness. Biological father and son are assigned the same index number, so that a_{iit} is the probability that the son adopts the variant of his father.

If each male always chose his variant from among the members of the preceding generation, the a_{ijt} s would necessarily sum to 1 (over j). But to

¹ This is not an unreasonable restriction since the models considered here apply to any cultural traits without regard to their adaptive implications. Of course, the principal reason for developing these models is to provide support for arguments about altruistic traits, which could be maladaptive at the individual level. Elsewhere, however, I have argued that some culturally transmitted altruistic traits, while leading to actions that reduce an individual's genetic fitness, produce an average increase in fitness for the subgroup of those who carry the trait (Allison 1991).

allow for the possibility that person i does not choose any of the n males, we define

$$e_{it}=1-\sum_{j=1}^n a_{ijt}.$$

This is the probability that person i chooses from the set of variants in such a way that the probability of any particular variant does not depend on the variants chosen by the n males in the preceding generation. In practice, this could mean that he chooses his mother's variant or the variant of someone outside the system. It could also mean that he invents and chooses a new variant (the analog of a mutation). I shall refer to e_{it} as the exogenous component. I also assume that there is no socialization by females other than the mother. This model is a member of the family of additive models proposed by Cavalli-Sforza and Feldman (1981).²

Cultural relatedness r between two persons is the probability that both have adopted the same variant from a common cultural ancestor. Note that this is not the same as the probability that both adopt the same variant, since that variant could have come from entirely different ancestors. If the variant is rare, these two probabilities will be very close. If the variant is common, however, the probability of having adopted the same variant will be much higher than the coefficient of relatedness.³

As an example of the model, consider the four-person, two-generation system in Figure 1. For the first generation, the two curved arrows correspond to relatedness coefficients of $r_{12} = .5$ and $r_{34} = .2$. The absence of curved arrows between several of the pairs means that these individuals are unrelated. The relatedness coefficients for the first generation are treated

$$Pr[A_{it} = 1 \mid A_{1(t-1)}, \ldots, A_{n(t-1)}] = \mu_{Ait} + \sum_{j} a_{ijt} A_{j(t-1)}$$

where μ_{Ait} is the probability that person *i* in generation *t* selects variant A when no one in generation *t*-1 has adopted A. (It can be factored into e_{it} and the conditional probability of choosing A given the nonchoice of any of the persons in generation *t*.)

$$Pr(A_i \mid A_j) = Pr(A_i \mid A_j, C)Pr(C) + Pr(A_i \mid A_j, \overline{C})Pr(\overline{C})$$

= $r + Pr(A_i)(1 - r)$.

Solving for relatedness r yields

$$r = \frac{\Pr(A_i \mid A_j) - \Pr(A_i)}{1 - \Pr(A_i)}.$$

Note that when the two probabilities are equal, r = 0. On the other hand, as $Pr(A_i)$ goes toward 0, r approaches $Pr(A_i \mid A_j)$. Finally, if $Pr(A_i \mid A_j) = 1$, r = 1 and we may say that the two individuals are perfectly related. Although the conditional and unconditional probabilities will usually differ across variants, r will be constant (so long as the a_{ij} , s are constant across variants).

² The additive character of the model can be seen from the following equivalent formulation. Let $A_{ii} = 1$ if person i in generation t adopts variant A, otherwise 0. Then

³ Formally, it works like this. Consider $Pr(A_i \mid A_j)$, the probability that person *i* has variant A given that person *j* has variant A. Let C be the event that *i* and *j* both have the same variant by common descent, and let r = Pr(C). By the law of total probability

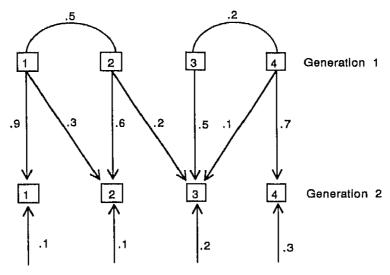


FIGURE 1. Path diagram for two-generation system.

as predetermined although, presumably, they could be derived from the transmission structure of the preceding generation if that were known. The straight arrows from first to second generation correspond to the a_{ijt} s. Person 1 in generation 2 has a probability of .9 of adopting the variant of his parent (person 1) in generation 1, and a probability of .1 of adopting a variant from outside the system. Person 3 in generation 2 adopts his variant from generation 1 with probabilities of .2 from person 2, .5 from person 3, .1 from person 4, and .2 from outside the system.

The diagram in Figure 1 was constructed according to the rules of path analysis (Wright 1968), which also provides convenient methods for calculating relatedness coefficients for any pair of individuals in the model. These methods are described further in the Appendix. If the a_{ijt} s are left completely unconstrained, it is difficult to reach any general conclusions. Therefore, we now consider several special cases in which various restrictions are imposed.

Model 1. Parental Inheritance, Constant Exogenous Component, Equal Nonparent Contributions

In this model, I assume that for each person there is a probability p of adopting the biological father's trait, and a probability e of choosing outside the system. The remaining probability is distributed evenly over other males in the parent generation, so that each nonparent has a probability e that his trait will be adopted. This model bears a close resemblance to the uniparental model of Cavalli-Sforza and Feldman (1981: 193) except that they did not allow for an exogenous component. A two-generation example is shown in Figure 2 in which parental inheritance e is .7, and all other adults have transmission probabilities of e = .05. The exogenous component is e = .15.

For simplicity, I also assume that in the first generation there is a com-

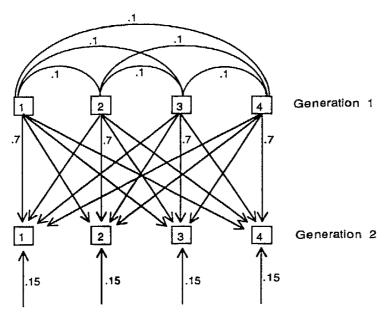


FIGURE 2. Path diagram for an example of Model 1. All oblique paths have a value of .05.

mon level of relatedness for all pairs of individuals, which implies that this will also be true in every subsequent generation. (This is not a restrictive assumption since even if the relatedness coefficients vary within the first generation, they will quickly converge to equality in subsequent generations.) In the Appendix, we obtain the recursion formula

$$r_t = A + Br_{t-1}$$

where

$$A = 2pc + (n - 2)c^{2},$$

$$B = p^{2} + 2(n - 2)pc + (n^{2} - 3n + 3)c^{2}.$$

This equation says that the level of cultural relatedness in generation t is a linear function of the level of cultural relatedness in the previous generation, with the constants dependent on the transmission rules. Thus, if we start out with a given level r_1 in the first generation, the level changes in a determinate way at each new generation.

Suppose, for example, that n = 11, p = .5, c = .04, and $r_1 = .10$. Substituting into the equations above, we get $r_2 = .12$, a slight increase in relatedness. Although such changes could be investigated numerically, it is more efficient to ask whether there comes a point at which the relatedness no longer changes. That is, do there exist points such that $r_{t+1} = r_t$? The equilibrium solution may be found by setting $r_{t+1} = r_t = r$ and solving for r, which yields r = A/(1 - B). This can be written as:

$$r = \frac{2(n-1)p(1-p-e) + (n-2)(1-p-e)^2}{(n-1)^2(1-p^2) - 2(n-2)(n-1)p(1-p-e) - (n^2-3n+3)(1-p-e)^2}$$

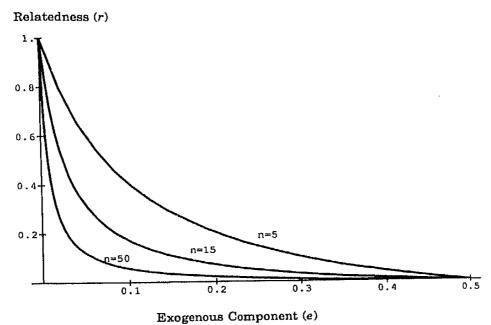


FIGURE 3. Equilibrium relatedness as a function of the exogenous component for Model 1, with p = .5.

While this equation may appear forbidding, it is easily shown that when e=0, r=1. In other words, if people always choose their cultural variants from among the members of the preceding generation, the degree of relatedness eventually converges to unity—everyone is perfectly related to everyone else. Conversely, e=1 implies p=0 and, hence, r=0. Since r is a continuous function of e, it follows that any degree of equilibrium relatedness can be obtained by appropriate choice of the exogenous component e. On the other hand, for this statement to be true, it is necessary that the total influence of nonparents (1-p-e) be positive; if it is zero, the equilibrium relatedness is also zero.

Figure 3 illustrates this dependence of r on e, and also shows the inverse relationship between relatedness and group size. For groups larger than 50, the exogenous component must be quite small to get appreciable levels of relatedness. Figure 4 shows that when both the exogenous component and group size are held constant, relatedness varies directly with the oblique component—the total influence of nonparents—which is equal to 1 - p - e. Relatedness increases rapidly from zero, but at a diminishing rate. The initial rate of increase and eventual level of r depends greatly on e, the exogenous component.

Of course, these are just equilibrium values. To see how rapidly the equilibria are attained, I ran computer simulations for several different sets of parameter values. Regardless of the parameter values or the initial value of r, equilibrium was reached fairly rapidly, typically in about 15 generations.

The importance of e in determining the equilibrium level of relatedness suggests some plausible "strategies" for ensuring high relatedness within a group. For groups that are strictly exogamous, one possibility is to create

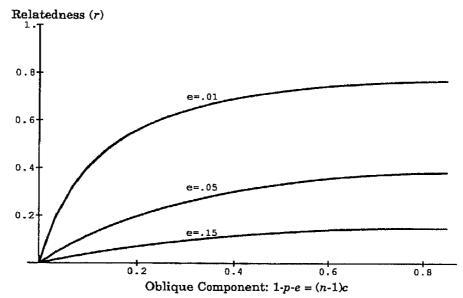


FIGURE 4. Equilibrium relatedness as a function of the oblique component for Model 1, with n = 15.

social structures and practices that reduce the cultural influence of the extralinear parent. While it may not be practical to reduce the absolute importance of the mother, it may be possible to restrict her influence in the following way. To this point I have assumed that the a_{ijt} s are constant across cultural loci. Suppose, however, that loci can be divided into two or more domains, with different values of e and the a_{ijt} s in each domain. Then the influence of the extralinear parent could be restricted to certain domains. For example, while mothers could be given free rein in socializing personality characteristics, males could handle all socialization regarding religious beliefs and practices (some of which may mandate altruistic behavior). Consequently, cultural relatedness for personality variants would be rather low while relatedness for religious variants would be quite high.

Alternatively, a strategy of cultural endogamy can greatly reduce e, although it also complicates the model considerably. To get some idea of the effect of endogamy, let us extend the present model by supposing that all wives are taken from a neighboring clan. Instead of being completely unrelated, the women from this clan have a coefficient of relatedness d with each man in the focal group. They also have a common relatedness d with each other. Finally, let d0 be the probability that the son will adopt the variant of his mother. For simplicity, I assume that all these values are constant across individuals and across generations, and I retain the assumption that mothers are the only females who may influence their sons.

It can be shown that the equilibrium solution for this expanded model is given by

$$r = \frac{2pc + (n-2)c^2 + m^2s + 2(n-1)dmc + 2dmp}{1 - [p^2 + 2(n-2)pc + (n^2 - 3n + 3)c^2]}.$$

If mothers have no influence on their sons (i.e., m=0), we are effectively back to the case with no endogamy. If we assume that any increase in the mother's influence is exactly offset by a reduction in e, then we can increase m while leaving p and c constant. This can substantially increase the equilibrium relatedness. For example, if we suppose that n=5, p=.5, c=.0625, and m=0 (no effect of mother on son), equilibrium relatedness is .14. If we now set m=.2, s=.3, and d=.2 (which reduces e from .25 to .05), the equilibrium relatedness rises to .29. Of course, higher levels of relatedness between spouses e0 and between females e1 would produce even higher equilibrium relatedness. Even higher values could be obtained by allowing these values to increase with successive generations.

Model 1.a. Constant exogenous component, no special inheritance. Returning to the strict exogamy of Model 1, we now examine a special case in which the biological father plays no special role and all males are equally important in socialization. Thus, we have Model 1 plus p=c. In this case, the equilibrium solution simplifies to

$$r = \frac{1}{1 + n\left(\frac{e(2 - e)}{(1 - e)^2}\right)}.$$

Again, r decreases with n, but the rate is critically dependent on e.

Model 1.a.1. p = c = e. In this model, the exogenous component is constrained to be equal to the contribution of each adult, all of which are constrained equal. The equilibrium solution is r = n/(3n + 1), which equals .31 when n = 5 and converges to $\frac{1}{3}$ as n gets large.

Model 2. Inherited Headman

With Model 1, we established that an increase in nonparental transmission resulted in an increase in equilibrium relatedness, but that model assumed an equal role in socialization for all nonfathers. I now consider the opposite extreme where there is only one male in each generation who has a cultural influence on nonbiological offspring in next generation, and this influence is distributed equally across the members of that generation. In the current model, this special role (which I call the headman) is passed on from father to son, an assumption that will be relaxed in Model 3. There continues to be a special influence of the biological father.

Model 2 has two parameters. Let h represent the influence of the headman on each member of the next generation, and let p be the influence of each nonheadman on his son. Then p + h is the influence of the headman on his own son. Once p and h are determined, so is the exogenous component e. In the Appendix, I show how this model may be obtained by imposing restrictions on the general model. An example is diagrammed in Figure 5.

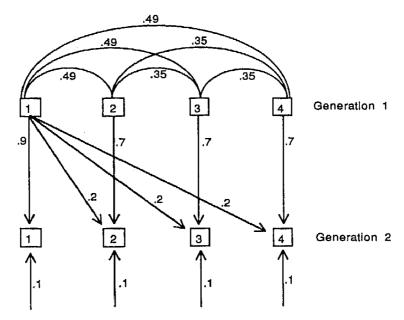


FIGURE 5. Path diagram for an example of Model 2.

For this model, it is necessary to define two different relatedness coefficients: r_t is the common relatedness between any two individuals in generation t, neither of whom is the headman, and r_{ht} is the relatedness between the headman and any other person in the same generation. In the Appendix, the equilibrium levels of relatedness are shown to be:

$$r = \frac{(1 - e - p)^2}{(1 - p^2)} \left(\frac{1 + p(1 - e)}{1 - p(1 - e)} \right),$$

$$r_h = \frac{(1 - e - p)(1 - e)}{1 - p(1 - e)}.$$

It can be shown that r_h is always higher than r; that is, the headman is more closely related to other members of the same generation than they are to each other. The most striking feature of this model, however, is that unlike Model 1, neither r nor r_h depend on n; that is, the level of relatedness is independent of group size. As with Model 1, if e = 0, both r and r_h are 1. Consequently, even a relatively small influence of the headman can yield high levels of relatedness if the influence of exogenous sources is also small. For example, e = .05, p = .80, and h = .15 gives r = .46. Table 1A displays equilibrium relatedness values for several other combinations of e and e.

Figure 6 shows the dependence of r on e for three different values of h. The curves are quite similar to those in Figure 3. In Figure 7, we see the dependence of r on h. While this is similar in form to Figure 4, both the rate of increase and the maximal value of relatedness are substantially higher.

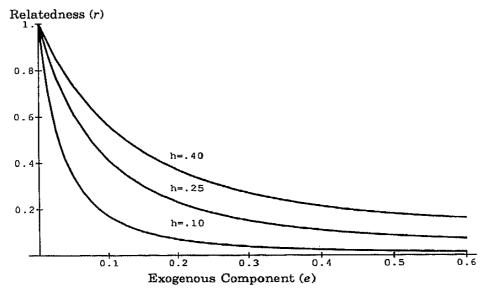
Model 3. Random Headman

One might suspect that the high levels of relatedness found for Model 2 are at least partly a consequence of the fact that the headman's son inherits his

Table 1. Equilibrium Relatedness for Selected Values of Parameters in Models 2, 3, and 4

A. Relatedness among Nonheadmen in Model 2 Parental Influence (p) .90 .80 .70 .60 .40 .50 e.74 .91 .86 .96 .95 .93 .01 .17 .61 .46 .76 .70 .80 .05 0.0.17 .47 .35 .56 .10 .63 † .17 .04 .30 .49 .40 .15 t 0.0 .28 .07 .37 .18 .20 † † .02 .09 .25 .27 .18 B. Relatedness in Model 3 .70 .80 .90 .50 .60 .67 .89 .83 .94 .93 .01 .96 .17 .58 .42 .74 .68 .80 .05 0.0 .18 .56 .46 .34 .10 .63 † .06 .42 .30 .19 .15 .50 † .20 0.0 .29 .10 .20 .38 † .12 .04 † .21 .25 .29 C. Relatedness in Model 4 .80 .90 .70 .50 .60 .40 .81 .90 .93 .97 .96 .95 .01 .25 .77 .69 .56 .84 .81 .05 0.0 .25 .56 .44 .69 .10 .64 † .25 .06 .39 .49 .56 .15 0.0† .11 .25 .36 .20 .44 † † .14 .03 .25 .34 .25

FIGURE 6. Equilibrium relatedness as a function of the exogenous component for Model 2.



 $[\]dagger$ Impossible combinations of e and p.

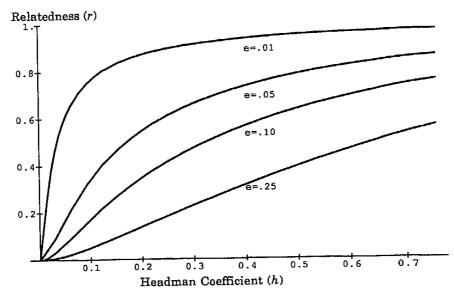


FIGURE 7. Equilibrium relatedness as a function of the headman coefficient for Model 2.

capacity to influence the next generation. To examine this possibility, we consider Model 3, which is the same as Model 2 except that the headman status is randomly reassigned within each new generation. I investigated this model by simulation. After approximately 20 generations, the levels of average relatedness appear to vary randomly within a narrow range. Mean values of equilibrium relatedness for several pairs of parameter values are shown in Table 1B. The rs in this table are averages over all possible pairs for n = 5, which means that they combine pairs with and without the headman. Comparing these with the values of those in Table 1A for Model 2, it is apparent that the levels of average relatedness are very close to those for the inherited headman model. Thus, random allocation of the headman status does not appear to have any substantial effect on levels of relatedness.

Model 4. Textual Transmission

Suppose our hypothetical group has a sacred text that (a) mandates one of the variants on the cultural locus, (b) is faithfully copied and transmitted across generations, and (c) is read by (or to) each person in the group. This notion can be modeled as a minor variation of Model 2. Each person has a probability h of adopting a variant as a result of exposure to the text, and a probability p of adopting his father's variant. The exogenous component e is equal to 1 - p - h. As shown in the Appendix, this model has the equilibrium solution

$$r = \left(\frac{h}{1-p}\right)^2 = \left(\frac{h}{h+e}\right)^2.$$

Values of r for several values of e and p are presented in Table 1C. Comparing

these results with those in Table 1A, we find that textual transmission produces relatedness values that are somewhat but not enormously higher than the headman model, the largest difference being about .10.

HORIZONTAL TRANSMISSION

The preceding models can easily be extended to allow for horizontal transmission by inserting an intragenerational stage after each of the intergenerational stages. Models for the horizontal stage have the same form as the vertical-oblique models, except that the two sets of nodes represent the same people at two different points in time. Influence on the self is treated as a vertical path while peer influence is treated as an oblique path.

Specifically, let us suppose that there is a fixed interval between the time that a generation selects its variants from the preceding generation and the time that it passes on its variants to the next generation, and suppose further that people can switch variants during that interval. They may switch more than once, but we are only concerned with the initial and final choices. Let b_{ijt} be the probability that person i in generation t adopts his final variant by choosing the variant initially selected by person j in generation t. Of course b_{jit} is the probability that person i does not switch variants during the interval. Note also that this setup allows for i to switch to j's initial variant while j switches to i's initial variant. As before, a_{ijt} is the probability that person i in generation t selects his variant from person t in the preceding generation, but we now add that this selection occurs only after the horizontal changes have occurred in the preceding generation.

In effect, we have simply inserted another "generation" between each of the original generations, but we alternate between possibly different transmission rules, one set for intergenerational transmission and another set for intragenerational transmission. The outcome, of course, depends on how different the two sets of transmission probabilities are. Two special cases can be easily examined. One case is to assume that the two sets are identical, i.e., that $b_{ijt} = a_{ijt}$ for all i, j and t. In that event, the outcomes described in the previous sections are unchanged, except that equilibrium is reached in half the number of generations. At the other extreme, let us suppose that there is no horizontal transmission, i.e., that $b_{iit} = 1$ and $b_{ijt} = 0$ for all $i \neq j$. Since this leaves the original models unchanged, we again have identical outcomes.

Although both of these special cases are implausible, I believe that the plausible cases are likely to lie within their range. In particular, I would expect that the father's influence on the son would be less than the son's influence on himself at a later point in time, i.e., that $b_{iit} > a_{iit}$. I would also expect the influence of exogenous sources to be greater in intergenerational transmission than in intragenerational transmission. Less obvious is what

happens to the oblique paths. Are people more influenced by their peers or by nonparental adults?

Leaving aside this last question, I have investigated what happens to Models 1 and 2 when $b_{iit} > a_{iit}$ but $b_{ijt} = a_{ijt}$ for all $i \neq j$. That is, the increase in self influence over parental influence is exactly compensated by a decrease in the exogenous component, leaving nonparental contributions unchanged. The two-step recursion equation for the relatedness coefficients are found by two applications of Appendix Eq. (3) or Appendix Eqs. (6) and (7) using different values of p at each step. It can be shown that the resulting equilibrium values are always higher than those for models without the horizontal stage (proof available on request).

In general, I hypothesize that the equilibrium values for two-stage models will be somewhere between the equilibrium values for each stage iterated separately. Computer simulations are consistent with this hypothesis, but so far I have only investigated a few possibilities.

DISCUSSION

The following general conclusions seem warranted from these results. First, for all models, the level of relatedness that is attainable under oblique or horizontal transmission is critically dependent (inversely) on the influence of exogenous sources. This influence could be reduced either by reducing the socialization role of the extralineal parent, by partitioning the socialization process, or by endogamy. Second, in models where nonparents are equally influential, the level of relatedness varies inversely with group size. Third, the level of relatedness does not depend on group size when nonparental influence is concentrated on one individual.

The lack of dependence on group size for the headman models may be somewhat misleading because, in real life, the parameter h measuring the influence of the headman is likely to decline with group size. Surely, the larger the group, the harder it is for a single individual to influence everyone in that group. On the other hand, progress in communication and transportation technologies has tended to increase the potential influence of single individuals (as well as single institutions) over large groups of people.

Real-life situations are undoubtedly somewhere between the equal influence models and the headman models, suggesting that the level of relatedness for a given group size should also be somewhere in between. Indeed, simulation results suggest that the level of relatedness for a given group size is an increasing function of the coefficient of variation for the a_{ij} s.

All the models considered are ostensibly for the transmission of discrete characters, but they readily allow for quantitative characters so long as the quantitative scale is treated as discrete. In other words, the theory is not at all dependent on the number of possible variants for a given cultural locus. On the other hand, while it is plausible that the adoption of one variant from

only two possibilities could be made without error, it seems a little farfetched to assume the error-free adoption of a quantitative variant. Boyd and Richerson (1985) have formulated models for the inheritance of quantitative characters with error, but it is not obvious how relatedness could be defined for such models.

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APPENDIX

For the general model, cultural relatedness between males i and j in generation t+1 is given by the following recursion formula:

$$r_{ijt} = \sum_{k=1}^{n} a_{ikt} a_{jkt} + \sum_{k=1}^{n} \sum_{m \neq k}^{n} a_{ikt} a_{jmt} r_{km(t-1)}.$$
 (1)

If we apply this equation to the example in Figure 1, we get the following coefficients of relatedness among the second generation:

$$r_{12} = (.9)(.3) + (.9)(.6)(.5) = .54,$$

 $r_{13} = (.9)(.2)(.5) = .09, r_{14} = 0,$
 $r_{23} = (.6)(.2) = .12,$
 $r_{24} = 0,$
 $r_{34} = (.5)(.7)(.2) + (.1)(.7) = .14.$