

## **Shared norms can lead to the evolution of ethnic markers**

Richard McElreath  
Department of Anthropology  
University of California  
Los Angeles, CA 90095

Robert Boyd  
Department of Anthropology  
University of California  
Los Angeles, CA 90095

and

Peter J. Richerson  
Department of Environmental Science and Policy  
University of California  
Davis, CA 95616

Keywords: Biological anthropology, ethnicity, cooperation, evolutionary game theory

## ***Abstract***

Most human populations are subdivided into ethnic groups which have self-ascribed membership and are marked by seemingly arbitrary traits such as distinctive styles of dress or speech. Existing explanations of ethnicity do not adequately explain the origin and maintenance of group marking. Here we develop a mathematical model which shows that groups distinguished by both differences in social norms and in arbitrary markers can emerge and remain stable despite significant mixing between them, if (1) people preferentially interact in mutually beneficial social interaction with people who have the same marker as they do, and (2) they acquire their markers and social behaviors by imitating successful individuals. We also show that the propensity to interact with people with markers like oneself may be favored by natural selection under plausible conditions.

## ***Introduction***

Unlike other primates, human populations are often divided into ethnic groups which have self-ascribed membership and are marked by seemingly arbitrary traits such as distinctive styles of dress or speech. Significant differences in moral codes and standards of behavior (“norms”) often exist among these groups (Barth, 1969). Members of such groups typically place a higher value on members of their own group compared to other groups (“are ethnocentric”) (LeVine and Campbell, 1972; Tajfel, 1981), and perhaps as a result ethnic groups are sometimes loci of cooperation in war and in commerce, and sometimes exhibit economic specialization (Barth, 1981). Ethnic groups are present in all historical periods, and while groups often split and merge through time, many have substantial historical continuity. Since no other primate forms such groups, and some force opposing mixing is necessary to maintain these groups, it is a puzzle why humans should aggregate in this way (Boyd and Richerson, 1987).

Bound up in this puzzle are two questions: How do groups come to be marked with seemingly neutral diacritica? And how do these differences often remain stable despite frequent interaction between groups, including exchange, intermarriage and warfare (Hodder, 1977; Nettle, 1996)? Students of ethnicity have proposed several distinct answers to these questions, but each has serious flaws.

### ***Lack of interaction among groups***

First, there may be little interaction between members of different geographically or socially isolated groups. In the absence of interaction, cultural changes in different groups

will occur independently, and thus over time groups will diverge. Such divergence should be especially pronounced for symbolic or stylistic characters that may evolve independently of environmental or economic constraints.

While this mechanism is cogent and does account for some cultural variation, it does not provide a very plausible explanation for most observed cases of ethnic marking because most ethnographically known groups are not, nor ever have been, sufficiently isolated to generate their own culture independent of their neighbors (Nettle, 1996). Groups like the Tasmanians, who were isolated for a significant amount of time, would appear marked if put back into contact with other groups. However, such isolation is quite rare in the ethnographic record. Moreover, there are well-documented cases where significant cultural differences are maintained despite frequent social interaction between groups (Hodder, 1977; Nettle, 1996). While mountainous regions and their higher levels of cultural diversity testify to the potential of partial isolation to allow group differences to grow, other peoples like the Efe of the Ituri Forest have interacted and intermarried with the neighboring Lese for generations and still retain a unique set of norms and cultural symbols and institutions (Bailey and DeVore, 1989). All of these data suggest most group differences, including markers, do not result from the failure of peoples to intermingle and thus potentially erase their differences.

### *Signals of intent*

The second possibility, that rational individuals use markers to demonstrate intent to participate in a certain culture or cultural economy (e.g. Barth, 1969), is an important component of a complete understanding of the social dynamics of ethnic markers. Clearly many individuals, especially in some modern settings (Barth, 1981), adopt ethnic markers

strategically in order to gain social benefits. Whenever individuals have access to multiple ethnic identities, the gains from this type of intentional signaling can be great. However, whatever the gains, this sort of strategic use cannot create differences in markers. The markers must already have information value before anyone use them to signal ethnic membership. This hypothesis depends on some other explanation for how informative markers arise and become stable in the first place. Also, people acquire some meaningful ethnic markers unconsciously and find them difficult to fake. Dialect differences and other such markers cannot have much role in social manipulations of ethnic identity, even though they have substantial information content for their groups (Labov, 1982; Van den Berghe, 1981).

### *Signals of ecologically adaptive knowledge*

In previous work, two of us (Boyd and Richerson, 1987) showed how ethnic markers could evolve as an adaptation to spatially varying environments because they allow people to selectively learn from people who live in their own environment and thereby increase the chance of acquiring locally beneficial information. For example, if a group of farmers and a group of pastoralists are neighbors, there may be many elements of their roles that are adaptive in the different environments they inhabit. If individuals can use social markers to increase the likelihood of acquiring the behaviors adaptive in their context, markers and behaviors can become associated, and markers can in fact become exaggerated beyond initial differences between the populations.

This model has three important weaknesses. First, according to this model, ethnic differences arise in response to ecological differences, and while this is sometimes observed (e.g. Barth 1981), it is far from a universal characteristic of ethnic groups.

Second, it does not account for the more common association between ethnic markers and basic norms and values. Third, the model requires that marker traits have much lower rates of migration across groups than behavioral traits. Essentially, markers must be acquired early in childhood and not change during an individual's lifetime. This assumption may capture the nature of some ethnic markers, but it is unlikely to fit many other important examples.

### *Signals of cooperating conspecifics*

A number of authors have suggested that ethnic markers allow individuals to be identified as members of a particular group, and such markers then allow people to selectively cooperate with members of their own group, and behave ethnocentrically towards others (Van den Berghe, 1981; Nettle and Dunbar, 1997; Wiessner, 1983).

For example, Van den Berghe argues that in Pleistocene hunter-gatherer societies members of social groups were more closely related than members of the population as a whole, and this led to evolution of an innate tendency to behave altruistically toward in-group members. Then, because genetic differences between neighboring groups were smaller than cultural differences, selection favored a psychology that used culturally transmitted markers of group membership. Cultural differences were more accurate, or more easily assessed, measures of relatedness than genetic differences. Later when human groups became much larger, this psychology gave rise to culturally marked ethnic groups. Van den Berghe's argument is not very plausible for a number of reasons: first, the measured levels of genetic variation between social groups in small scale societies is typically very low, barely above what would be predicted if they were formed at random (Long, 1986; Smouse and Long, 1988). Thus it is not very plausible that there would have

been selection for generalized altruism toward group members. Second, even if one accepts that people's psychology is such that they attend to culturally transmitted markers, van den Berghe provides no mechanism that explains how markers come to be associated with particular groups, and equally important, what maintains stable differences in the presence of the widely observed movement of people across ethnic boundaries.

Nettle and Dunbar (1997) hypothesized that selection might favor individuals who direct altruistic behavior toward others who have the same marker as themselves, because this would allow altruists to benefit only other altruists, and analyzed a mathematical model to test the logic of this hypothesis. The model suggests that the process can work, but only if ethnic markers are transmitted with an implausibly high error rate. This conclusion is consistent with extensive work in evolutionary biology that suggests that heritable markers cannot function to allow discriminative altruism because cheaters, individuals who display a marker but do not behave altruistically, do better than marked altruists (Grafen 1990).

### ***Ethnic markers as signals of coordination norms***

Here we present a model of the evolution of markers in which individuals use markers to pick individuals with whom to interact. However, rather than assuming that markers allow individuals to selectively direct altruistic behaviors towards co-ethnics, we assume that markers allow people to interact with others who share their social norms. Many social norms are conventions that can be modeled as games of coordination rather than cooperation. Games of coordination (Sugden, 1986, Binmore 1994) occur when interactions between individuals who share beliefs about how people should behave yield higher payoffs than interactions among people with discordant beliefs. If, for example, you

believe that marriage among first cousins is a sin, and believe that people who marry their cousins should be punished, then it is best to interact with people who share your beliefs, and a bad idea to interact with those who believe that such marriages are to be preferred.

We show that if people preferentially interact in coordination games with people who have the same marker as they do, and if they acquire their markers and coordination behaviors by imitating successful individuals, groups distinguished by both norm and marker differences may emerge and remain stable despite significant mixing between them. We also show that the preference to interact with people with markers like oneself may be favored by natural selection under plausible conditions. Next, we return to models of the evolution of ethnic markers based on cooperation and explain why they fail where this model succeeds. Finally we explain several testable predictions of our model.

### *A Simple Model of Ethnic Markers*

For analytical purposes we assume that during each time period the processes of social interaction, imitation, migration, and recombination occur in sequence. While in real life these processes go on in parallel, the assumption of discrete stages facilitates analyzing and understanding the model, and experience with many evolutionary models suggests that it rarely does harm. We assume that there are two discrete culturally transmitted traits, a behavioral trait which directly affects individual well being and an observable marker character which has no direct effect on individual well being, except whatever effects arise as a consequence of others using the marker to infer group membership. Each time period, individuals interact and receive a payoff from the interaction. They then observe the payoffs of another individual, and sometimes copy the behaviors and markers of the other individual if that individual has achieved a higher payoff. Next, some individuals leave

their group and emigrate to the other group. Finally, individuals re-acquire their markers and behaviors from different people and thus recombine behaviors and markers within each group. Our goal is to keep track of how each of these processes causes the cultural composition of the population to change. That is, how they cause some combinations of marker and behavior to become more common and others to become less common. In this section, we formalize each of these phases and present intuitions about the assumptions of the model.

### Social Interaction

Consider a large population divided into  $n$  groups of equal size. Each time period, each individual interacts with another individual from the same group. People's behavior in this interaction depends on culturally acquired beliefs about the proper behavior during this interaction. We will refer to this culturally transmitted belief as the *behavioral trait*. There are two alternative beliefs, labeled (1 or 0). Individuals' payoffs from the social interaction depend on their own behavior and the behavior of their partners in the way given in Table 1.

		II	
		1	0
I	1	$1 + \delta$	1
	0	1	$1 + \delta$

**Table 1.**

Payoffs in the coordination game. Payoffs shown for player I.  $\delta$  is assumed to be positive.

Individuals achieve the higher payoff when they interact with somebody who shares their belief about proper behavior in the social interaction. This simple coordination game is meant to capture the intuition that many real social interactions go well if people have concordant beliefs. There are alternative ways of organizing the interaction: primogeniture versus ultimogeniture, matrilocality versus patrilocality, and (as modern examples) whether the groom's or bride's family pays for the wedding and whether we should drive on the right or the left side of the road. For all these behaviors, people do best when they agree and worse when they disagree. It is likely that human societies face many problems of this kind. Whenever solving a problem requires coordination among individuals, and individuals interact at random with respect to behavior, people who behave in uncommon ways do worse than those who behave in common ways. We assume that it is not possible to determine another individual's beliefs about proper behavior before an interaction occurs. The intuition behind this assumption is that many important norms are complex multi-faceted rules that specify how people should behave in a wide range of circumstances. Given the large number of these norms and the fact that some of them will only be used a few times in one's lifetime, it is highly unlikely that we can always reliably predict the behavior of everyone we must interact with. Thus when entering into long term social arrangements like marriage or reciprocating partnerships, it will be impossible to discuss what each party to the arrangement considers to be proper behavior for even a small fraction of possible contingencies. Much the same argument can be made for rules enforced by third-party and community punishment. A stranger who moves to a new village cannot guess ahead of time all of the social rules that regulate behavior in his new home. People may be able to tell him some of the things that he needs to know, but it is

still likely that he will make many costly social blunders, perhaps even run afoul of basic moral principles. Finally, individuals are not consciously aware of many social rules, for example those that govern the pragmatics of conversation. Thus, newcomers may be able to determine the right way to behave but not be able to behave accordingly, because their own reactions to the behavior of others are involuntary.

People obviously have many traits, like dialect, clothing style, and cuisine that *can* be observed, and often these traits are the basis of assortative social interaction. People interact with people who look and sound like they do. To formalize this idea, we assume there is also a readily observable *marker trait*. This trait also has variants, labeled 0 and 1, and we assume that individuals tend to interact with others who have the same variant of marker trait as them. The strength of this propensity is given by the parameter  $e$ . In any interaction, there is a probability  $1 - e$  that individuals interact with another individual who shares their marker trait, and a probability  $e$  that they interact at random. Thus, smaller values of  $e$  imply a greater tendency to choose social partners with the same marker. With these assumptions we can write the payoff of each of the four types in population  $k$ . It will be useful to write these expressions in terms of  $D_k$ , the covariance between behavior and marker traits where,  $D_k = x_{11k}x_{00k} - x_{10k}x_{01k}$  and  $x_{ijk}$  is the frequency of individuals with behavior  $i$  and marker  $j$  in group  $k$ . When individuals who have behavior 1 also tend to have marker 1 and individuals with behavior 0 have marker 0, this covariance ( $D_k$ ) is positive. When individuals who have behavior 1 have marker 0, it is negative. And when the two traits are associated randomly,  $D_k$  is zero.

Using the expression for  $D_k$ , the payoffs to each combination of behavior and marker are:

$$\begin{aligned}
W_{11k} &= 1 + \delta(p_{1k} + (1-e)D_k) \\
W_{10k} &= 1 + \delta(p_{1k} - (1-e)D_k) \\
W_{01k} &= 1 + \delta(1 - p_{1k} - (1-e)D_k) \\
W_{00k} &= 1 + \delta(1 - p_{1k} + (1-e)D_k)
\end{aligned} \tag{1}$$

Where  $p_{1k} (= x_{10k} + x_{01k})$  is the frequency of behavior 1 in group  $k$ . When there is no correlation between marker and behavior ( $D_k = 0$ ), these expressions say that the payoff of a particular behavior is proportional to its frequency—the more common the behavior, the higher the payoff. When there is a positive correlation between marker and behavior ( $D_k > 0$ ), individuals with matching marker and behavior (1 and 1 or 0 and 0) receive higher payoffs. When the correlation is negative ( $D_k < 0$ ), the reverse is true: individuals with “mismatched” marker and behavior (1 and 0 or 0 and 1) receive higher payoffs. Since the marker trait is an arbitrary symbol, “mismatched” symbols and behaviors are as effective at creating adaptive interactions as “matched.” What matters is that the absolute value of the covariance be appreciable.

### Imitation

After interaction, individuals assess the relative successes of the members of their group and preferentially imitate those individuals who have done well in past interactions. In particular suppose that the probability of an individual with behavior  $i$  and marker  $j$  being chosen as a model in group  $k$  is  $\frac{W_{ijk}}{\bar{W}_k}$ , where  $\bar{W}_k$  is the average payoff in group  $k$ . This expression results when we assume that individuals can compare their own well-being to a substantial sample of those around them.

It can be shown that the change in the frequency of behavior 1 in population  $k$  due to imitation is given by

$$\Delta p_{1k} = U_k (p_{1k} - p_{0k}) (1 - (1 - e) R_k^2) \quad (2)$$

This equation describes how the difference in the frequencies of the behaviors interacts with the association between behaviors and markers to change the frequency of behavior 1 each time period.  $R_k^2 (= D_k^2 / (U_k V_k))$  is the squared correlation of behavior and marker and  $U_k (= p_{1k} (1 - p_{1k}))$  and  $V_k (= q_{1k} (1 - q_{1k}))$  are the variances of behaviors and markers, respectively.

When there is no association between marker and behavior,  $R_k^2 = 0$ , and this result is the same as simple rare-type disadvantage selection: the common behavior becomes more common. As  $R_k^2$  increases, however, individuals in group  $k$  are more likely to interact with others who have the same behavior, and this restricted interaction reduces the advantage of the common type. To see why, consider the limit when behavior and marker are perfectly correlated ( $R_k^2 = 1$ ), and people only interact with others with whom they share a marker ( $e = 0$ ). Then, individuals never pair with a behavior different from their own. Under those conditions, all behaviors will have the same fitness, as each marker and behavior type is essentially its own isolated population. Thus efficient markers erode rare-type disadvantage as the minority behavior does just as well as the majority behavior, since pairs of individuals can coordinate perfectly using the informative marker.

The expression for the change in the frequency of marker 1 in group  $k$  due to imitation is

$$\Delta q_{1k} = 2\delta D_k (p_{1k} - p_{0k}) \left[ \left(1 - \frac{e}{2}\right) - \frac{D_k}{V_k} \left( \frac{q_{1k} - q_{0k}}{p_{1k} - p_{0k}} \right) (1 - e) \right] \quad (3)$$

This equation describes how the difference in the frequencies of the behaviors interacts with the association between behaviors and markers to change the frequency of marker 1 each time period. To understand what is happening in the evolution of the marker trait, first consider only the situation when  $D_k > 0$  but small. When  $D_k$  is small, the second term in brackets can be ignored, and  $\Delta q_{1k}$  is positive, which occurs whenever  $(p_{1k} - p_{0k}) > 0$ . Since  $D_k > 0$ , individuals with behavior 1 are disproportionately likely to have marker 1. Thus when behavior 1 is more common,  $(p_{1k} - p_{0k}) > 0$ , and the frequency of marker 1 increases. If behavior 0 were more common,  $(p_{1k} - p_{0k})$  would be negative and the frequency of marker 1 would decrease while marker 0 would increase. In summary, when there is a small amount of covariance between behavior and marker, the variant of the marker that is associated with the common behavior will increase.

This result means that, for a given covariance, an individual who possesses a rare marker has a greater chance of interacting with someone with his or her behavior than with someone who possesses a common marker. This then slows the increase of the common marker.

The change in the covariance between marker and behavior,  $D_k$ , is a messy, hard to interpret expression. However when  $D_k$  and  $\delta$  are small enough that terms of order  $D_k^2$  and  $\delta^2$  and higher can be ignored, the change in  $D_k$  due to imitation is approximately

$$\Delta D_k \approx \delta D_k (2U_k (3 - e) - 1) \quad (4)$$

Numerical work suggests that (4) is an excellent approximation. Using expression (4), social interaction will increase  $D_k$  whenever  $2U_k(3-e) > 1$ . To see what this means, notice that when  $e = 0$ ,  $U_k$  must be greater than  $1/6$  for this condition to be satisfied. Since the maximum value of  $U_k$  is  $1/4$ , this means that  $D_k$  increases only when there exists sufficient variance in behavior within the group. Once one behavior becomes the clear majority, in-group dynamics will decrease covariance. Other forces, like migration from other groups may, however, maintain significant covariance at equilibrium.

### Migration

To represent population mixing due to intermarriage, relocation, and between group social learning, we suppose that migration removes a proportion  $m$  of each group and replaces them with migrants drawn from all other groups. When migration is weak, then the changes in the frequencies of behavior, marker, and the covariance between marker and behavior due to migration are:

$$\begin{aligned}\Delta p''_{1k} &= m(\bar{p}'_{1k} - p'_{1k}) \\ \Delta q''_{1k} &= m(\bar{q}'_{1k} - q'_{1k}) \\ \Delta D''_k &= m(\bar{D}' - D'_k + (p'_{1k} - \bar{p}'_{1k})(q'_{1k} - \bar{q}'_{1k})).\end{aligned}\tag{5}$$

where  $\bar{p}'_{1k}$  and  $\bar{q}'_{1k}$  are the average frequencies of behavior 1 and marker 1 in the populations that contribute migrants to population  $k$ . and  $\bar{D}$  is the covariance between behavior and marker across all groups (i.e.  $\bar{x}_{11}\bar{x}_{00} - \bar{x}_{10}\bar{x}_{01}$ , where  $\bar{x}_{ij}$  is the average frequency of behavior  $i$  and marker  $j$  across all populations). Migration reduces the differences in the frequencies of both behavior and marker between neighboring groups. However, as long there is any difference in the frequencies of marker and behavior between

neighboring groups, migration also acts to increase the covariation between marker and behavior within groups. Note that this force is strongest exactly when imitation does not increase covariance—when variance within groups is low but variance between groups is high.

### **Recombination**

It is likely that other learning processes may breakup associations between markers and behaviors created through the imitation of successful individuals. One process that may do this is unbiased vertical transmission, which may result in the acquisition of marker and behavior traits from different individuals (Mom and Dad, for example). This process recombines strategy and marker traits at a rate  $r$ .

Recombination has no effect on the frequencies of behavior and marker. However, it decreases the covariance between marker and behavior a rate proportional to  $r$ .

$$\Delta D_k'' = -rD_k'' \quad (6)$$

### **Summary of effects over one time period**

*Social interaction and imitation.* The tendency to interact with individuals who share the same marker trait when combined with the tendency to imitate the successful:

1. Increases the frequency of the common behavior, but the magnitude of this effect is decreased when marker and behavior are correlated.
2. Increases the frequency of the marker that is correlated with the more common behavior.
3. It increases covariance between marker and behavior when the covariance is small.

*Migration.* The mixing of people or ideas among social groups:

1. Causes the frequencies of both marker and behavioral traits in neighboring populations to become more similar.
2. Increases the covariance between marker trait and behavioral trait within groups.

The magnitude of this increase is proportional to the differences in frequencies of both marker traits and behavioral traits between groups.

*Recombination.* The tendency to acquire marker and behavior from different people always reduces the covariance between behavior and marker.

We have derived composite expressions to compute the net effect of imitation, migration, and recombination on the frequencies of each of the four combinations of behavior and marker in each population ( $x_{11k}$ ,  $x_{10k}$ ,  $x_{01k}$ ,  $x_{00k}$ ). These recursions, however, are very complicated, and they provide little additional insight about the evolution of the system. In the next section we present results achieved by numerical analysis of these recursions. These simulation results show that the processes outlined above produce ethnically marked groups under a wide range of conditions.

### *Simulation Results*

Numerical simulation of the model indicates that social interaction, migration and recombination generate a rich variety of behavior. We begin by describing simulations of the model when there are only two interacting populations. This exercise provides insight about how the processes described above often give rise to ethnic markers, and also why they sometimes do not. Next, we explore the parameter space of the model, varying  $e$  (the chance of interacting at random),  $m$  (migration),  $\delta$  (the effects of social behavior on individual welfare) and  $r$  (the rate of recombination). Finally, we consider more general

models with larger numbers of populations and a general coordination game structure.

This analysis suggests that the simple model is relatively robust.

### **Stable behavioral differences between groups usually become ethnically marked**

Social interaction alone can lead to the evolution of stable differences in behavior between two groups. From equation (3) we know that imitation will increase the more common behavior in each of the two populations. People with more common behaviors achieve higher payoffs in the coordination game, and are more likely to be imitated. Thus if one behavior is initially common in one group, and the alternative behavior is initially common in the other group, payoffs from social behavior coupled with imitation of the successful will cause the groups to become more different. For example, if initially  $p_{11} = 0.55$  and  $p_{12} = 0.45$ , imitation will increase  $p_{11}$ , and decrease  $p_{12}$ . Migration will oppose this change. If the diversifying effect of payoff biased imitation is sufficiently strong compared to the homogenizing effect of migration, the two populations will reach an equilibrium at which behavior 1 is common in group 1 and behavior 2 in group 2. In contrast, if the migration rate is too high, or if initially the same behavior is common in both populations, only one behavior will be present in both populations at equilibrium.

If stable behavioral differences between groups exist, each behavior can become associated with a different marker variant—individuals with behavior 1 will, for example, be associated with marker 0 and behavior 0 with marker 1. Figure 1 illustrates this dynamic. Here, we plot the frequencies of each the four combinations of behavior and marker over time. The top pair of graphs give the frequencies of each the four combinations of behavior and marker over time in each of two populations for  $m = 0.025$ ,  $e = 0.25$ , and  $r = 0.1$ . The behaviors are denoted by the shape of the symbol, circle (= 0) or

square (= 1), and the markers are denoted by color, black (= 0) or white (= 1). The bottom pair of graphs gives the frequency of behavior 0 (gray circles), marker 0 (black diamonds), and the covariance between them (white ovals). Initially behavior 1 (squares) has frequency 0.55 in population 1, and 0.45 in population 2. Marker 0 (black) is initially more common than marker 1 in both populations, but relatively more common in population 2 ( $q_{11} = 0.8$ ) than in population 1 ( $q_{12} = 0.7$ ). There is no initial covariance within populations. At first, rare type disadvantage causes behavior 1 to become more common in population 1 and behavior 0 in population 2. At the same time, migration generates a positive covariance between marker 1 and behavior 0, which increases the frequency of marker associated with the more common behavior in each population, marker 1 in population 1 and marker 0 in population 2 (eqn. 6). Differences between populations generate covariances within populations, which amplify the differences between populations. This positive feedback process (diagrammed in Figure 2) continues until a symmetrical equilibrium is reached at which a different behavior is common in each population and each behavior is associated with a different marker. The adaptive behaviors have become symbolically marked, even though the same marker was initially common in both groups.

But markers will evolve only if migration and recombination are not too strong. Migration and recombination oppose the positive feedback process described above. Migration tends to make the two populations the same, equalizing the frequency of the markers in each population, and recombination destroys the covariance between marker and behavior. If recombination is strong, it dissipates the covariance between marker and behavior more rapidly than migration and imitation can create it. Also, the force causing

the markers' frequencies in the two populations to diverge may not be sufficiently strong to prevent migration from homogenizing the two populations. Figure 3 illustrates this dynamic, plotting the frequencies of each of the four combinations of marker and behavior for the same parameter combinations as before, except that recombination has increased ( $r = 0.2$ ). Even though the payoff advantage of being in the majority is sufficient to maintain behavioral differences between the two populations, these differences do not become ethnically marked. When individuals are unable to assort well based on markers ( $e$  is large), the pattern is similar: stable group differences in behavior may emerge and persist, but selection on markers is too weak to generate covariance between marker and behavior.

The argument above suggests there are three kinds of outcomes: 1) behavioral differences and marker differences both evolve; 2) behavioral differences evolve, but marker differences do not; 3) neither behavioral nor marker differences evolve. It would be useful to know the ranges of parameter values under which each of these three outcomes is likely.

We determined the range of parameters under which these processes give rise to a high correlation between marker and behavior by performing a large number of simulations at different parameter values. In each simulation the initial conditions were  $p_{11} = q_{11} = 0.55 + \varepsilon$  and  $p_{12} = q_{12} = .45 + \varepsilon$ , where  $\varepsilon$  is a uniformly distributed random number between  $-0.016$  and  $0.016$  independently chosen for each frequency. For each combination of parameters we iterated the complete recursions until a steady state had been reached for 100 different randomly perturbed initial conditions. We used such perturbed initial conditions because we found they were a good way to satisfy two competing desiderata.

Simply using random starting conditions over the entire range of possibilities generates a large amount of variance among simulations, and thus requires a large number of simulations for each parameter combination. On the other hand, symmetric initial conditions lead to “knife-edge” trajectories that are both uninteresting and numerically unstable. The use of slightly perturbed symmetric initial conditions allows for a reasonable number of simulations and avoids knife-edge trajectories.

For each simulation we calculated the value of  $\bar{D}$ , the population average covariance between behavior and marker, averaged over the 100 simulations. Notice that this measure includes covariance due to association of marker and behavior within each population as well as associations between populations. So, for parameter combinations like that shown in Figure 1, the within population covariance is small because the frequency of one behavior-marker combination is high in each population, but over the population as a whole, there is a strong association between marker and behavior. Thus such a result has a high  $\bar{D}$ . We held parameter values constant at  $m = 0.01$ ,  $e = 0.3$ ,  $r = 0.01$ ,  $d = 0.5$ , for parameters not varied in a run of simulations.

In the results which follow, we summarize the evolution of the system by dividing the outcomes into the three categories mentioned above: 1) behavioral differences and marker differences both evolve (white regions in the figures); 2) behavioral differences evolve, but marker differences do not (gray regions in the figures); 3) neither behavioral nor marker differences evolve (black regions in the figures). We considered marker differences to have evolved whenever the average of 100  $\bar{D}$ ’s for a set of parameter values was non-zero.

Figure 4 summarizes these results, which support the argument above. When selection on behavior is strong enough to produce stable behavioral differences in the face of migration (white and black regions), stable marker differences evolve (white regions) provided (1) recombination ( $r$ ) is not too strong and (2) individuals interact sufficiently often with individuals like themselves ( $e$  is not too high). Thus white regions above are combinations of parameter values that produced both stable behavioral and marker differences. That is, these populations became ethnically marked. Black regions are cases in which behavioral differences were stable, yet marker differences were not. That is, these populations became culturally different but without ethnic markers. Gray regions are cases in which behavioral differences failed to evolve, typically due to strong migration. There are no cases in which behavioral differences failed to evolve and marker differences managed to become stable, because marker evolution requires behavioral differences.

**Spatial structure is needed to generate ethnic markers, but not to maintain them**

Migration between groups generates the initial covariance essential for the evolution of ethnic markers. However, under the right conditions, once such covariance arises, spatial structure is no longer necessary to maintain ethnic markers. When individuals rarely interact with anyone without similar markers ( $e$  is small) and  $r$  is small such that traits do not often recombine, a set of equilibria are possible where the groups collapse together in space but high covariance between markers and behaviors remain.

Figure 5 plots the frequencies of each four combinations of behavior and marker for the same parameters and initial conditions as above except that now there is no recombination, ( $r = 0$ ) and people interact only with others who share their marker ( $e = 0$ ). Because there is no recombination, the covariance between marker and behavior builds

very rapidly, and initially this causes the marker frequencies in the two groups to diverge. However, as the covariance increases, the advantage of being the common type decreases because individuals are able to use the marker to interact with people who share the same behavior. As the rare-type disadvantage decreases, migration increasingly acts to homogenize the groups. At the eventual equilibrium, each behavior is associated with a unique marker, but there is no difference between the two populations; both contain the same frequency of individuals with behavior 1 and marker 0 and behavior 0 and marker 1, but none of the other two possible types. This configuration can only be a stable equilibrium if  $r$  and  $e$  are very small. However, for somewhat larger values  $r$  and  $e$ , there is a long transient period at which two ethnically marked types are present without spatial variation. Eventually, however, even a small amount of rare-type disadvantage leads to the elimination of the rarer combination of behavior and marker. A more complex model in which groups occupied different niches would likely be able to sustain spatially mixed ethnically marked groups in a wider range of circumstances. Also, we will demonstrate later that natural selection would reduce values of  $r$  and  $e$  if at all possible. This makes the possibility of evolving such spatially-blended systems more likely.

**Increasing the number of populations increases the range of initial conditions which give rise to ethnic markers.**

Random starting conditions (random frequencies of behavior and marker in each group) often lead to the evolution of behaviorally different and marked groups, and this result becomes more likely as more groups are added to the system (see Figure 6). The two group system is most sensitive to starting conditions, as this case has the highest chance of randomly generating all groups with similar initial behavior frequencies. Recall that stable

behavioral differences quite often evolve stable marker differences, regardless of the initial frequencies of the marker traits. However, the initial frequencies of the behavioral traits have a large impact on whether or not stable behavioral differences emerge. When there are only two groups, it is common for both to begin with the same common behavior, which precludes the possibility of any stable behavioral differences emerging. When there are more groups, more stable differences emerge, and these differences bootstrap the evolution of ethnically marked regions.

### **Group differences are strongest at boundaries**

When populations are arrayed in space, groups of adjacent populations have high frequencies of the same marker and behavior. The correlation between marker and behavior ( $R = D_k / \sqrt{U_k V_k}$ ) is greatest at the boundaries between such regions. Figure 7, Part A shows the initial distributions of the frequencies of marker 1 and behavior 1 in 10 populations arranged in a ring. The correlation between marker and behavior is initially zero everywhere. Part B shows the configuration of the populations at steady state. There is a region of three populations in the middle in which the frequency of marker 1 and behavior 1 is low, and a region of three populations at the edges in which these frequencies are high (remember that the populations wrap around so that population 1 exchanges migrants with population 10). In both of these regions there is little or no correlation between marker and behavior. In between these regions are boundaries areas in which frequencies are intermediate, and there is substantial correlation between marker and behavior.

This result is not surprising, given that markers serve no function in behaviorally uniform regions. At the boundaries between regions of different behaviors, markers allow individuals to avoid costly mistakes in interaction, and at these boundaries high correlations between behaviors and markers are more likely to evolve and become stable.

**A more general model of social interaction leads to similar results.**

Generalizing the model of social interaction to a general coordination game does not change the qualitative behavior of the model. So far we have assumed that social interaction can be modeled by a game of pure coordination with equal average payoffs for both equilibria. Symmetric, pure coordination games are very special because the basins of attraction of both equilibria are the same size. A completely general two person, two strategy coordination game is given in Table 2.

		II	
		1	0
I	1	$1 + \delta + g$	$1 - h$
	0	1	$1 + \delta$

**Table 2. General game with two stable equilibria.**

Payoffs shown for player I.  $\delta$ ,  $g$  and  $h$  are assumed to be positive.

This payoff structure leads to an unstable equilibrium at

$$\tilde{p} = \frac{\delta + h}{2\delta + g + h} \tag{7}$$

Increasing  $g$  increases the domain of attraction of behavior 1, while increasing  $h$  decreases its domain of attraction (see Figure 8). If  $h > g$ , then a population in which behavior 1 is common has a higher average payoff than one in which behavior 0 is common, but behavior 1 has a smaller domain of attraction.

Altering the coordination payoffs has predictable effects on the equilibria the system typically reaches. Higher values of  $g$  causes more groups to evolve behavior 1, and those groups will also typically evolve that behavior's covarying marker (see Figure 9, below). Even when behavior one has twice the fitness at internal equilibrium than the alternative behavior, groups practicing behavior 2 and possessing the alternative marker may evolve. We ran 100 simulations with  $d = 0.5$ ,  $g = 0.5$ ,  $h = 0$  for a ten group system with random starting conditions. The results (Figure 10) show that even under such extreme advantage for behavior 1, almost a quarter of all simulations evolve an equilibrium absolute value of  $\bar{D}$  greater than zero. Increasing  $h$  tells a similar story.

In sum, even extreme deviations from the perfect coordination structure allow the system to evolve ethnic-like groups much of the time. Thus our results do not depend in a sensitive way on the perfect nature of the game structure we have chosen. This means the alternative behaviors need not be arbitrary variants, like driving on the left or right side of the road. It also suggests that any stable behavioral equilibria, regardless of their relative consequences for group or individual welfare, may become marked. This is a point we will return to later in discussing the link between markers and cooperation.

### *Evolutionary stability of the parameters*

This model depends on four parameters:  $m$ ,  $\delta$ ,  $r$ , and  $e$ . The first two formalize assumptions about the ecology of the evolving populations. The migration parameter,  $m$ , tells us how much contact there is between adjoining populations, and the selection parameter,  $\delta$ , tells us how strongly the social interaction effects individual well-being. The second pair of parameters represents assumptions about human psychology. The interaction bias,  $e$ , measures the strength of the propensity to interact with others who share the same marker (as well as how able they are to choose), and the recombination rate measures the extent to which people tend to acquire behavior and marker from the same individual. The simulation results indicate that social interactions in which common behaviors have high payoff will lead to the evolution of ethnic markers if both  $e$  and  $r$  are small. In other words, if people have a psychology that predisposes them to interact with individuals with the same marker as themselves, and to acquire some markers and behaviors as a package, then ethnic markers are liable to arise. In this section we show that natural selection will, all other things being equal, favor such a psychology. That is, we show that selection will favor mutations which reduce the values of  $e$  and  $r$ .

### **Natural selection favors smaller values of $e$**

We have already assumed that cultural transmission is not vertical—people acquire their behavior and marker by imitating successful people, not their parents. When cultural transmission is not vertical, there is a high degree of recombination between culture and genes, and therefore “gene-culture covariation” (Cavalli-Sforza and Feldman, 1981) can be ignored. This means that we can calculate the fitness of genes that affect social interaction

and cultural transmission by assuming that they are randomly associated with the cultural variants in the population.

Suppose that an individual's propensity to interact with others who have the same marker,  $e$ , is affected by heritable genetic variation. The fitness of an individual in group  $k$  with a particular value of  $e$ , say  $e'$ , is:

$$W_k(e') = 1 + \delta \left( p_{1k}^2 + p_{0k}^2 + (1 - e') \frac{D_k^2}{U_k} \right) \quad (8)$$

Thus individuals with smaller values of  $e$  will have higher fitness as long as the covariance between marker and behavior is not exactly zero. As we saw before, migration will generate covariance between behavior and marker, and any random variation in the frequency of the marker in space will tend to generate non-zero values of  $D_k$ . Thus it seems in coordination games a preference for individuals with a marker similar to one's own is quite easy to evolve genetically.

### **Natural selection favors smaller values of $r$**

Since the strength of other learning processes,  $r$ , has such a strong effect on the system's outcome, it would be useful to know how selection would affect a gene that increases or decreases the rate of recombination between marker and behavior loci.

Events here occur in the following sequence. Again ignoring gene-culture covariation, imagine first that, in each time period, recombination occurs before individuals interact. This change does not alter the characteristic behavior of the model, and it allows us to easily calculate how accumulated recombination affects fitness. That is, individuals imitate to acquire markers and behaviors, other learning processes may then break up those associations, and finally individuals pair-up and interact. If different individuals have

different rates of recombination, then markers will be more informative in some classes of individuals than in others, once all actors reach the interaction phase.

Now imagine an allele that causes individuals on average to recombine marker and behavior traits at a rate  $r$ . The fitness of this allele is

$$W(r) = rD_k [(W_{10k} + W_{01k}) - (W_{11k} + W_{00k})] + \bar{W}_k \quad (9)$$

Genes that decrease  $r$  by an amount  $s$  will be favored by selection as long as

$$W(r - s) - W(r) = sD_k \left[ \underbrace{(W_{10k} + W_{01k})}_A - \underbrace{(W_{11k} + W_{00k})}_B \right] < 0 \quad (10)$$

Suppose  $D_k$  is positive. Then term  $B$  in expression (10),  $(W_{11k} + W_{00k})$ , is greater than term  $A$ ,  $(W_{10k} + W_{01k})$ , and so the contents of the brackets are negative and (10) is satisfied. The reason term  $B$  is greater when  $D_k$  is positive is because matched behavior and marker combinations do well when there is positive covariance between behavior and marker. This means the fitnesses in term  $B$  are greater than those in term  $A$ , because individuals receiving term  $B$  payoffs are avoiding costly errors in interaction, while those receiving term  $A$  payoffs are not.

Similarly, when  $D_k$  is negative,  $(W_{11k} + W_{00k})$  is less than  $(W_{10k} + W_{01k})$ , and so the terms in brackets are positive, resulting in the same reversed inequality and result. Smaller values of  $r$  lead to higher average payoffs, higher values lead to lower payoffs. This is not a surprising result, as the covariance of behavior and marker traits establishes a coadaptation, and any allele that reduces that covariation is therefore less fit. This analysis suggests that, to the extent that it is not constrained to higher values, selection will reduce  $r$  zero.

### ***Why Coordination But Not Cooperation Causes the Evolution of Markers***

As we suggested in the introduction, one recurring intuition in the social sciences is that, since ethnic markers signal ethnic group membership and ethnic groups are often loci of cooperation, markers must allow people to selectively direct altruistic behavior toward coethnics (Van den Berghe, 1981; Nettle and Dunbar, 1997). We argue that these models fail. However, we do not think the relationship between cooperation and social markers to be entirely spurious. In this section, we briefly explain why markers cannot function to regulate cooperation. We then discuss what we understand to be the more likely relationship between ethnic-like markers and cooperation in large groups.

Within evolutionary and rational choice theory, “cooperation” refers to behaviors that are beneficial to the group but costly to the individual. Table 3 gives the payoff structure for the famous “the prisoners’ dilemma,” the game that defines cooperation in pairs. Individuals receive the highest average payoff when both cooperate. However, each is better off defecting, regardless of what the opponent does. If individuals interact at random, cooperation cannot evolve because, although cooperation increase average fitness of both strategies, it reduces the fitness of cooperators *relative* to defectors.

		II	
		C	D
I	C	$1 + b - c$	$1 - c$
	D	$1 + b$	1

**Table 3.**

Payoffs in a Prisoner’s Dilemma game.  
Payoffs shown for player I. C is cooperation.  
D is defection. The parameters  $b$  and  $c$  are positive.

Cooperation can evolve only if some cue allows cooperators to preferentially interact with other cooperators. One such cue is kinship. If behaviors are genetically transmitted, then the kin of cooperators will be more likely to be cooperators than the average member of the population. Another cue is previous behavior (Axelrod, 1984). When people interact repeatedly, individuals can limit cooperation to those who have cooperated in the past. These models work because past behavior serves as an honest signal of genotype (or behavior, in the cultural case).

At first blush, it would seem that selection might favor cooperators who carried an external, visible marker of their cooperative nature. Cooperators could then limit their cooperation to others who exhibited the marker. However, evolutionary theorists do not think this mechanism is likely to be important in nature (Hamilton, 1964; Grafen 1990). If any process breaks up the association between the cooperator strategies and the markers this will create individuals who do not cooperate but nevertheless carry the marker. Biased imitation favors these individuals and their behavior spreads at the expense of all other behavior. In terms of our model, if  $r$  is greater than zero, the model will never produce stable cooperation in a variable population. Our model with a cooperation structure is essentially a two-trait green beard model (Hamilton, 1964; Dawkins, 1976). Whenever the marker may recombine with the behavior, cheaters invade and destroy any information value of the marker.

This means that it is unlikely that ethnic markers serve to regulate cooperation among strangers. In a kin-recognition model like Nettle and Dunbar (1997), it is too difficult to keep defectors from imitating the marker. When imitation is possible, the rate of change must be unrealistically high. In a formulation like our own, unless the rate of

recombination is absolutely zero and groups start out with a perfect association between marker and behavior, the system cannot evolve ethnic-like groups.

However, the model allows the evolution of markers when the payoffs have a coordination structure because in such interactions there is nothing to be gained from cheating. Both parties in the coordination setting gain the most when they honestly advertise their strategy. Under those conditions, markers may readily evolve in one-shot interactions.

*Another coordination model of social markers works for the same reasons*

Axtell et al. (1999) have analyzed another model of the evolution of ethnic markers. Their model also rests upon a coordination game structure, the Nash demand game (Nash, 1950). In this game, two individuals must divide a resource between them. Each demands a certain share of the total, and if their summed demands do not exceed the total, they each receive their demand. If the sum of their demands exceeds the total, however, neither individual receives any share of the resource. Like in our model, individuals in their model also have hidden strategies and visible markers, but instead of acquiring strategies by imitation, they play the “best response” strategy based upon their limited recall of interactions from the last time period. For example, if an individual encountered only individuals who demanded 75%, her best response in the next time period would be to always demand 25%. Marker traits categorize the individual’s memory so it is possible to have separate “best responses” for differently marked individuals. For example, if all “blue” individuals demand 75% and all “red” individuals 50%, the best responses are 25% and 50%, respectively. The strength of this formulation is that it allows for individuals to have different responses for in-group and out-group interactions.

The model produces what the authors call “economic classes” rather than ethnic groups, however they are formally like the ethnic groups of our model. At equilibrium, their model is unlikely to produce differently marked and behaving groups of individuals, yet for long periods of time on the way to equilibrium, the model can maintain such groups. One such outcome is two differently labeled groups sharing 50%-50% internally but demanding unequal shares in between-group interactions (one of the groups always winning the larger share). The markers individuals carry evolve to become honest and informative signals of their behaviors, even though these markers start off absent of social information.

Axtell et al.’s model produces informative markers for the same basic reason ours does: in a coordination game, there exists no advantage in cheating and wearing someone else’s marker. Everyone in the population wants to know how everyone else will behave, but behavior is hidden. Also, all individuals would like everyone else to know how they will behave, but communication is restricted. Thus if markers exist at all, they will likely be honest signals of behavior, since wearing the wrong signal can hurt the wearer as much as the receiver.

We have argued for an association between norms, or matters of coordination, and social markers. Axtell et al.’s independent result, relying upon the same basic intuition but using rather different population assumptions and quite different analytical methods, suggests our results are robust.

### *Markers facilitate cooperation in repeated interactions*

Humans are peculiar because we often cooperate with large numbers of unrelated individuals. As we have seen, the existence of ethnic markers cannot explain the scale of

human cooperation. However, we do not think that the intuition that ethnic markers and cooperation are related is entirely without merit. We have shown that markers may evolve when individuals interact in a two person coordination game. We believe that the same conclusion will apply whenever groups occupy multiple stable equilibria. As long as some adaptive force maintains different equilibria in the groups, individuals imitate the successful, and there exists some mixing between groups, markers may evolve which allow individuals to preferentially interact with others who share the same norms and values. We have argued at length elsewhere that human cooperation results from norms enforced by socially created *rewards* and punishments (Boyd and Richerson 1990, 1992; Soltis et. al 1995, Richerson and Boyd 1999, in press). Culturally transmitted rules specify which behaviors are morally correct, and that people who deviate from such behaviors are to be punished. If punishment is sufficiently costly, such systems can stabilize a very wide range of behavior. Then, competition between groups will lead to the spread of moral systems that enhance group survival, welfare, and expansion, including norms that lead to enhanced cooperation in economic and military activities. As a result, we expect that systems of moral norms, many of which create group beneficial cooperation, should come to be marked by ethnic markers by the process described above.

### ***Corollaries and predictions***

In this final section we comment on corollary observations about our model and the evolution of ethnic markers, as well as provide some obvious predictions. These predictions divide logically into two types: 1) predictions about the population-level distribution of behaviors and markers and 2) predictions about features of human psychology that lead to the evolution of ethnic markers.

### *Non-ethnic social markers*

The model Axtell et al. (1999) analyze stimulates another important observation: there is no reason that these models, ours or theirs, must refer to ethnic groups or social classes alone. The models are general in specifying the nature of the groups, and similar mechanisms could explain the emergence of social markers at other levels of social organization, including moieties, clubs, trade guilds, or religious orders. Wherever relevant norm differences occur in the presence of limited interaction, social markers like those in our model could evolve to carry social information. Some American class markers, such as BMW's and designer clothing, do not fall into this category: expensive signals are not neutral diacritica, since not everyone is able to acquire or display the signal. Yet we might say that some groups can be "ethnic-like," in that they sometimes organize cooperative behaviors and are often marked by neutral diacritica like flags, badges, or jerseys (Van den Berghe, 1981).

We do not think that our model is relevant to all sorts of groups. Norm differences among clubs or trade guilds are sometimes well known, even to non-members. This removes the principle advantage of markers in our model, where we assume many norm differences are often hidden, unknown or unobservable. In other cases, such groups may have all the necessary characteristics: academic disciplines, for example, have norms that are quite cryptic and may not be apparent to insiders or outsiders. Also, where organizations like these possess many arbitrary norms, pertaining to initiation or procedure, for example, there is little risk of interacting with non-members using these cultural rules. In these cases, our model has little to offer. Another case where our model seems less relevant are situations like those common in North American football rivalries, for

example, where the signals themselves carry all the information. That is, a Bruin fan wearing a UCLA sweatshirt, face-painted in blue and gold, is communicating who they support. These signals might provide some information about how the fan will behave in some interactions, but they are more like messages than signals. The information in these cases is clear, where it is cryptic in our model. Finally, many of these markers do not evolve, but rather come to represent groups by decision of their members. This does mean such markers do not serve the same function, but it does suggest they evolve through another, and probably important, mechanism.

Recall that for marker differences to emerge, all that our model requires is any initial difference in marker frequencies. Migration creates covariance between marker and behavior from this initial difference, and then selection increases the frequency of the marker associated with the common behavior in each group. The size of the initial difference in marker frequencies,  $q_{11} - q_{12}$ , is proportional to the magnitude of the initial covariance migration will create. Therefore, if we were to alter the model to include a number of marker traits, each with varying frequencies, the markers with the greatest initial difference between groups would acquire the greatest covariance and evolve to mark behavior faster than other marker traits with smaller initial differences between groups.

It is not easy for our model to predict whether other markers will then cease evolving or whether each additional marker will evolve to carry even more information about behavior. The recursions we have developed will select for additional markers, but these recursions do not include any cost of the mental apparatus or cognitive effort needed to use increasing numbers of markers. It may turn out that using one or two markers is a better strategy than gaining small amounts of information from more than a few markers.

In short, our intuition is that the model as it stands now will accumulate many markers, if we were to extend it to a multiple marker system.

A related issue is whether a model with many behavioral traits will evolve many markers, one for each behavior, or whether it will maintain only one or a few markers for a larger number of behaviors. Empirically, it is clear that people sometimes use several markers, although it is unclear how many behaviors, if any, these markers index.

### *The evolution of ethnic markers does not usually protect ethnic groups from dissolution*

In many modern settings ethnic groups are brought together in urban settings, increasing rates of interaction and migration far beyond what existed when the groups emerged. We have shown that marked ethnic groups will evolve as long as rates of migration is low enough. Can groups that arise in this way survive if rates of migration or recombination are increased?

To answer this question we performed a number of simulations in which initially migration was low enough that ethnic groups could emerge, and then once an equilibrium was reached in which there were marked groups, we increased in migration rate to a level that would have prevented the emergence of groups. Even after strong behavior and marker differences had evolved, increasing mixing between groups quickly eroded those differences. Ethnic groups under suddenly increased rates of mixing move to the equilibrium they would have reached had we begun a new simulation with the changed parameters. These results suggest the processes we model do not necessarily maintain ethnic markers once differences have emerged any more readily than it would if beginning with a population of undifferentiated groups. This result, combined with the previous

result that ethnic groups coming to occupy the same space persist only when  $e$  and  $r$  are near zero, suggests ethnic markers do a poor job of protecting group differences unless other forces, which degrade the quality of information in the markers, are quite weak.

### *Two psychological predictions of the model*

Our analysis of the evolutionary stability of  $e$  and  $r$  makes two predictions about the psychological tendencies of human beings.

*Individuals in marked communities should prefer interaction with similarly marked individuals.* Our analysis of the evolution of  $e$ , the rate at which individuals interact at random with respect to markers suggests that natural selection or an analogous process operating on cultural rules for interaction should reduce  $e$  to zero, if possible. Thus to the extent that  $e$  represents a psychological bias towards interacting with those who *look* like oneself, rather than the ability or freedom to interact with ones that *behave?* like oneself, we expect members of marked communities to prefer individuals marked like themselves, at least when it comes to coordination interactions.

*Individuals in marked communities should acquire bundles of at least some norm and marker traits.* While the model does not suggest anything about the social learning of non-coordination behaviors and social markers, our analysis of the evolution of  $r$ , the rate of recombination of behavior and marker traits, predicts that, for our model to be relevant, individuals should acquire norm and marker traits as a bundle. They should also preserve these associations throughout substantial portions of their lifespan.

### *Three predictions about patterns of cultural variation*

Our model makes three clear predictions about the nature of the distributions of marker traits and their relations to ethnic groups and their histories. We present these predictions here, spelling out the kind of data appropriate to test them, although we do not undertake such tests in this paper.

*Ethnic differences should be stronger at boundary regions rather than deep within ethnic territories.* Hodder (1977) suggests this is true for some ethno-archeological data from the Lake Baringo region of Kenya, but the data themselves are inadequate to test this prediction. The appropriate test would be examination of a large ethnic group, such as the Kikuyu of Kenya, which interacted at many border areas with a number of different ethnic groups. The model predicts that markers should be most pronounced at those contact areas on the borders of ethnic territories rather than deep within Kikuyu territory, where almost all interactions would have been among Kikuyu individuals. Another setting which holds promise in testing this prediction is fragmentary migration which brings smaller units of a larger ethnic population into contact with other ethnic groups. For example, throughout the last hundred years, herders in East Africa have migrated, often over great distances, moving into the territories of other ethnic groups. These splinter groups, most famously the Parakuyu Maasai (Rigby, 1992), are often surrounded by other ethnic groups, and therefore have the opportunity to interact with members of other groups much more than Maasai individuals still living in north Tanzania, for example. If these groups are more marked than their source populations, we might be able to conclude that interaction with the other ethnic groups has increased selection on markers and magnified initial differences in those settings.

*Norm and marker boundaries should coincide, while the distributions of other culture items may map onto one another differently.* Our model makes no predictions about the nature of other cultural traits and the distribution of ethnic markers. While the field currently lacks much data at all on within-group variation in cultural items, those data which do exist, on material culture from archaeology (Hodder, 1977; Wiessner, 1983) and on medical beliefs and a few other categories, show that patterns of ethnic interaction or ascription do not always well predict trait distributions. However, if this model is correct, a number of norm differences—on beliefs in inheritance, child rearing, household labor, and other categories of human life where multiple coordinated solutions exist to the same problem—should correspond to the distributions of marker differences.

*Potential marker traits with the greatest initial differences should become marked first.* While we have not yet simulated a system with multiple potential marker traits, our understanding of the model leads us to predict there should exist a noticeable difference in importance between those markers with initially large differences and those with initially small differences between groups. One test of this prediction would be to examine ethnographic settings where two isolated source populations have contributed migrant groups that have been in contact for some time. The source populations provide estimates of the initial differences present in the migrant groups when they came into contact. The migrant groups provide estimates of the differences that might have grown from those initial differences. This prediction will earn support if the greater differences between source populations appear to have lead to marked traits in the contact groups.

## References

- AXELROD, R. M. 1984. *The evolution of cooperation*. New York: Basic Books.
- AXTELL, R. L., J. M. EPSTEIN, AND H. P. YOUNG. 1999. The emergence of economic classes in an agent-based bargaining model," in *Social Dynamics* edited by S. Durlauf and P. Young. Santa Fe, NM: Santa Fe Institute,.
- BAILEY, R. C., AND I. DEVORE. 1989. Research on the Efe and Lese populations of the Ituri Forest, Zaire. *American Journal of Physical Anthropology* 78:459-471.
- BARKOW, J. H., L. COSMIDES, AND J. TOOBY. 1992. *The adapted mind: evolutionary psychology and the generation of culture*. New York: Oxford University Press.
- BARTH, F. 1969. "Introduction," in *Ethnic groups and boundaries*. Edited by F. Barth. Boston: Little Brown & Co.
- BARTH, F. 1981. Features of person and society in Swat : collected essays on Pathans. International library of anthropology. London ; Boston: Routledge & K. Paul.
- BARTH, F. 1990. Ethnic processes on the Pathan-Baluchi boundary. *Newsletter of Baluchistan Studies Naples* 7:71-77.
- BINMORE, K. 1994. *Game theory and the social contract*. MIT Press, Cambridge.
- BOYD, R. AND P. J. RICHERSON. 1987. Evolution of ethnic markers. *Cultural Anthropology* 2:65-79.
- BOYD, R., AND P. J. RICHERSON. 1990. Group selection among alternative evolutionarily stable strategies. *Journal of Theoretical Biology* 145:331-342.
- BOYD, R., AND P. J. RICHERSON. 1992. Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethology and Sociobiology* 13:171-195.
- CAVALLI-SFORZA, L. L., AND M. FELDMAN. 1981. *Cultural transmission and evolution: A quantitative approach*. Princeton: Princeton University Press.
- COSMIDES, L., AND J. TOOBY. 1994. "Origins of domain specificity: The evolution of functional organization," in *Mapping the mind: Domain specificity in cognition and culture*. Edited by L. A. Hirschfeld, and S. A. Gelman, pp. 85-116. New York: Cambridge University Press.
- DAWKINS, R. 1976. *The selfish gene*. New York: Cambridge University Press.
- Gadgil, Madhav and Romila Thapar. 1990. Human ecology in India: Some historical perspectives. *Interdisciplinary Science Reviews* 15: 209-223.

- GRAFEN, A. 1990. Do animals really recognize kin? *Animal Behaviour*, 39: 42-54
- HAMILTON, W. D. 1964. The genetical evolution of social behaviour. *J. Theoretical Biology* 7:17-52.
- HODDER, I. R. 1977. The distribution of material culture items in Baringo district, western Kenya. *Man* 12:239-269.
- LABOV, W. 1982. *The social stratification of English in New York City*. Washington, D.C.: Center for Applied Linguistics.
- LEVINE, R. A., AND D. T. CAMPBELL. 1972. *Ethnocentrism: Theories of conflict, ethnic attitudes, and group behavior*. New York, N.Y.: John Wiley & Sons.
- LONG, J. C. 1986. The allelic correlation structure of Gainj and Kalam speaking people. I Estimation and interpretation of Wright's F statistics. *Genetics* 112: 629-647.
- NASH, J. 1950. The bargaining problem. *Econometrica* 21:128-140.
- NETTLE, D. 1996. Language diversity in West Africa: An ecological approach. *Journal of Anthropological Archaeology* 15:403-438.
- NETTLE, D., AND R. I. M. DUNBAR. 1997. Social markers and the evolution of reciprocal exchange. *Current Anthropology* 38:93-99.
- RICHERSON, P. J. AND R. BOYD. 1998. The evolution of human ultra-sociality, in: *Indoctrinability, Ideology, and Warfare: Evolutionary Perspectives*, edited by I. Eibl-Eibesfeldt and F. Salter,. NY: Berghahn Books, Pp. 71-96.
- RICHERSON, P. J AND R. BOYD. 1999. The evolutionary dynamics of a crude super organism. *Human Nature*. 10: 253-289
- RIGBY, P. 1992. Cattle, capitalism, and class : Ilparakuyo Maasai transformations. Philadelphia: Temple University Press.
- SUGDEN, R. 1986. *The economics of rights, co-operation, and welfare*, Oxford, B. Blackwell.
- SMOUSE, P. AND J. C. LONG. 1988. "A comparative F-statistic analysis of the genetic structure of human populations from lowland South America and highland New Guinea," in: *Proceedings of the Second International Conference on Quantitative Genetics*. Edited by B. S. Weir, G. Eisen, M. M. Goodman, and G. Namkoong, pp. 32-47, Sunderland MA, Sinauer and Associates.
- TAJFEL, H. 1981. *Human groups and social categories: Studies in social psychology*, Cambridge: Cambridge University Press.
- TOOBY, J., AND L. COSMIDES. 1992. "The psychological foundations of culture," in *The adapted mind: Evolutionary psychology and the generation of culture*. Edited by

J.H. BARKOW, L. COSMIDES, AND J. TOOBY, pp. 19-136. New York: Oxford University Press. New York, NY, USA.

VAN DEN BERGHE, P. L. 1981. *The ethnic phenomenon*. Westport, CT: Praeger Publishers.

WIESSNER, P. 1983. Style and social information in Kalahari San projectile points. *American Antiquity* 48:253-276.

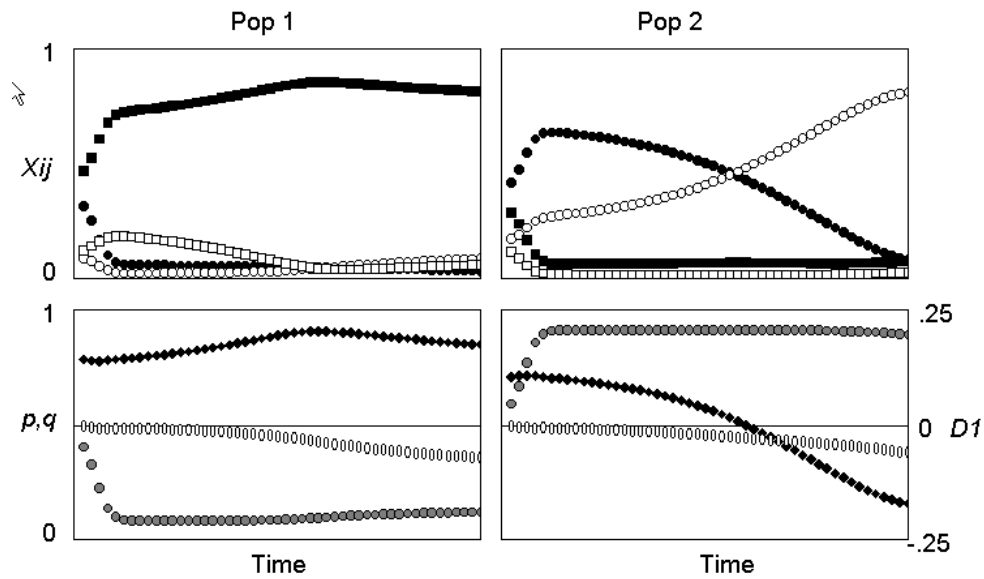


Figure 1. The top pair of graphs give the frequencies of each the four combinations of behavior and marker over time in each of two populations for  $m = 0.025$ ,  $e = 0.25$ , and  $r = 0.1$ . The behaviors are denoted by the shape of the symbol, circle (= 0) or square (= 1), and the markers are denoted by color, black (= 0) or white (= 1). The bottom pair of graphs give the frequency of behavior 0 (gray circles), marker 0 (black diamonds), and the covariance between them (white ovals). Initially behavior 1 (squares) has frequency 0.55 in population 1, and 0.45 in population 2. Marker 0 (black) is initially more common than marker 1 in both populations, but relatively more common in population 2 ( $q_{11} = 0.8$ ) than in population 1 ( $q_{12} = 0.7$ ). There is no initial covariance within populations. At first, rare type disadvantage causes the behavior 1 to become more common in population 1 and behavior 0 in population 2. At the same time, migration generates a positive covariance between marker 1 and behavior 1 (eqn. 9), which increases the frequency of marker associated with the more common behavior in each population, marker 1 in population 1 and marker 0 in population 2. (eqn. 6). This process continues until an symmetrical equilibrium is reached at which a different behavior is common in each population and each behavior is associated with a different marker.

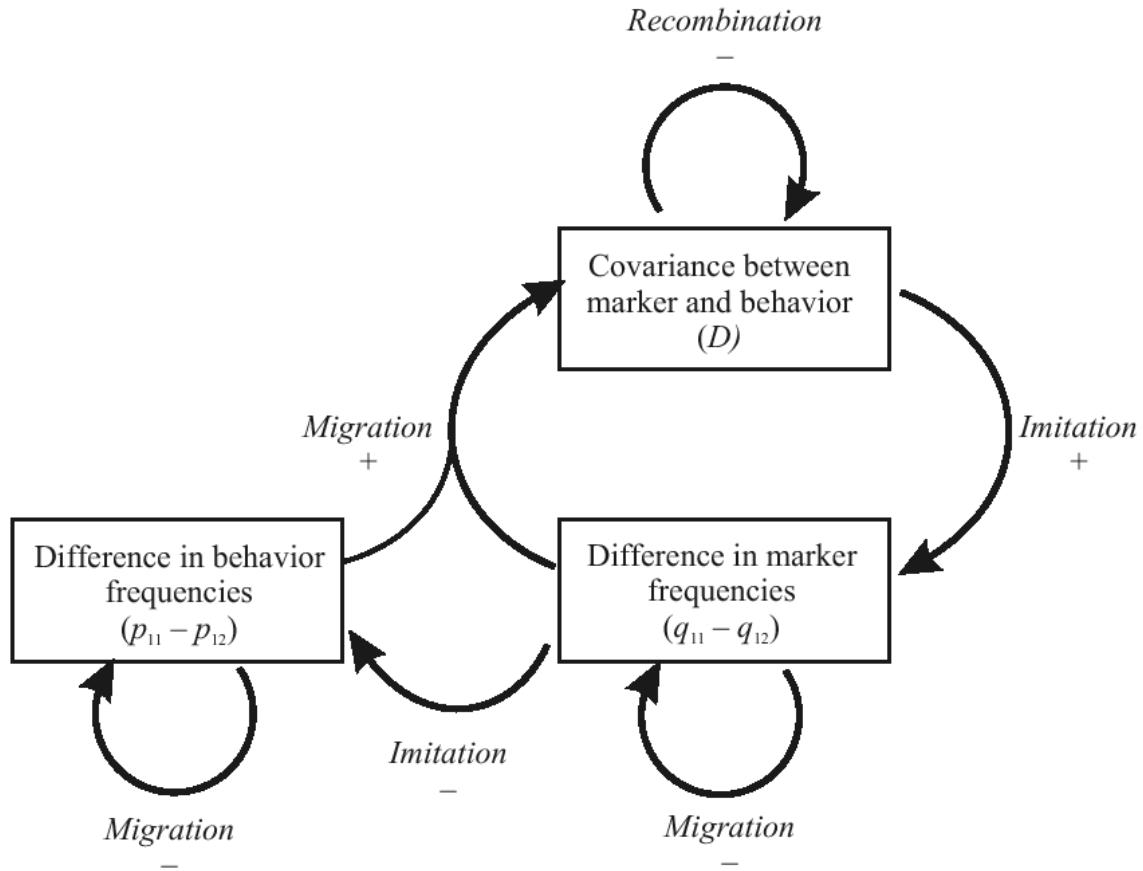


Figure 2. Diagram of the feedback process which generates marked groups, as well as the forces which oppose this process. At first, rare type disadvantage causes behavior 1 to become more common in population 1 and behavior 0 in population 2. At the same time, migration generates a positive covariance between marker 1 and behavior 0 (eqn. 9), which increases the frequency of marker associated with the more common behavior in each population. Differences between populations generate covariances within populations which amplify the differences between populations. This positive feedback process continues until an symmetrical equilibrium is reached at which a different behavior is common in each population and each behavior is associated with a different marker. The behaviors have become marked. However, migration and recombination oppose this positive feedback process. Migration tends to make the two populations the same, equalizing the frequency of the markers in each population, and recombination destroys the covariance between marker and behavior. If recombination is strong, it dissipates the covariance between marker and behavior more rapidly than it can be created by migration and imitation. Also, the force causing the markers frequencies in the two populations to diverge may not be sufficiently strong to prevent migration from homogenizing the two populations.

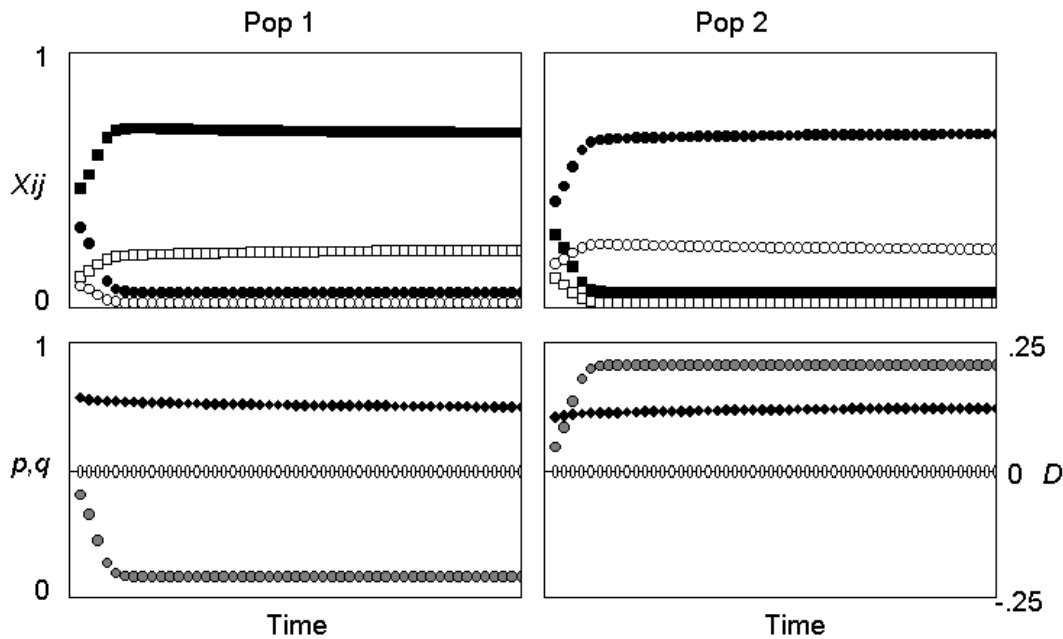


Figure 3. The top pair of graphs give the frequencies of each the four combinations of behavior and marker over time in each of two populations. The behaviors are denoted by the shape of the symbol, circle (= 0) or square (= 1), and the markers are denoted by color, black (= 0) or white (= 1). The bottom pair of graphs give the frequency of behavior 0 (gray circles), marker 1 (black diamonds), and the covariance between them (white ovals). The initial conditions and value of  $m$  are the same as in Figure 1 except that the rate of recombination,  $r$ , has been increased to 0.2. As before, at first, rare type disadvantage causes the behavior 1 to become more common in population 1 and behavior 0 in population 2, and migration generates a positive covariance between marker 1 and behavior 1 (eqn. 9). However, because the rate of recombination is higher, there is no accumulation of covariance between marker and behavior. This in turn, reduces the force causing the marker traits to diverge, and migration rapidly causes the frequency of the markers in the two populations to converge to the same value. Even though there are behavioral differences between the populations, the initial difference in markers disappears.

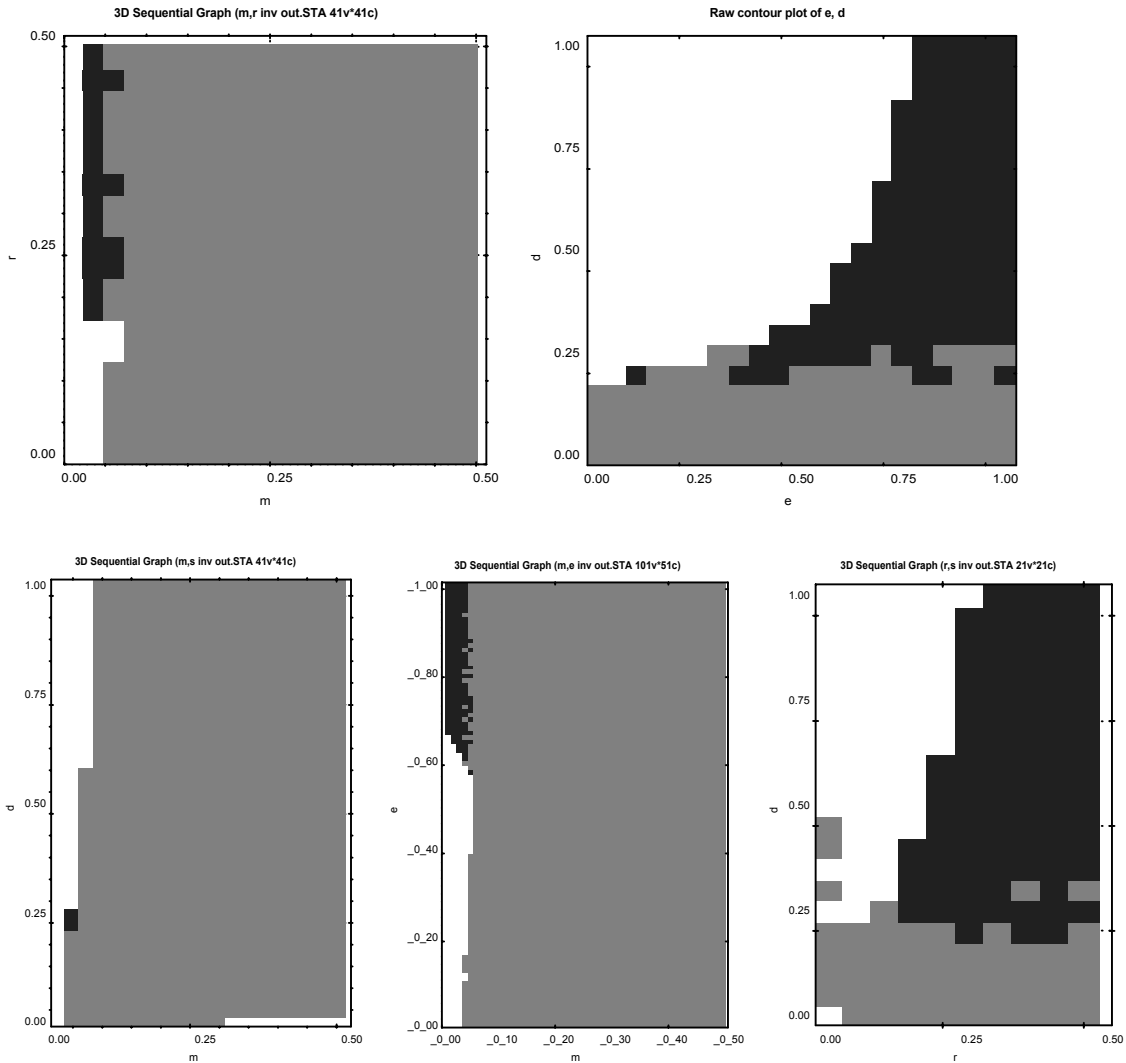


Figure 4. When selection on behavior is strong enough to produce stable behavioral differences in the face of migration (white and black regions above), stable marker differences evolve (white regions) provided 1) recombination ( $r$ ) is not too strong and 2) individuals interact sufficiently often with individuals like themselves ( $e$  is not too high). Thus white regions above are combinations of parameter values which produced both stable behavioral and marker differences. That is, these populations became ethnically marked. Black regions are cases in which behavioral differences were stable, yet marker differences were not. That is, these populations became culturally different, but without ethnic markers. Gray regions are cases in which behavioral differences failed to evolve, typically due to strong migration. There are no cases in which behavioral differences failed to evolve and marker differences managed to become stable, as marker evolution requires behavioral differences.

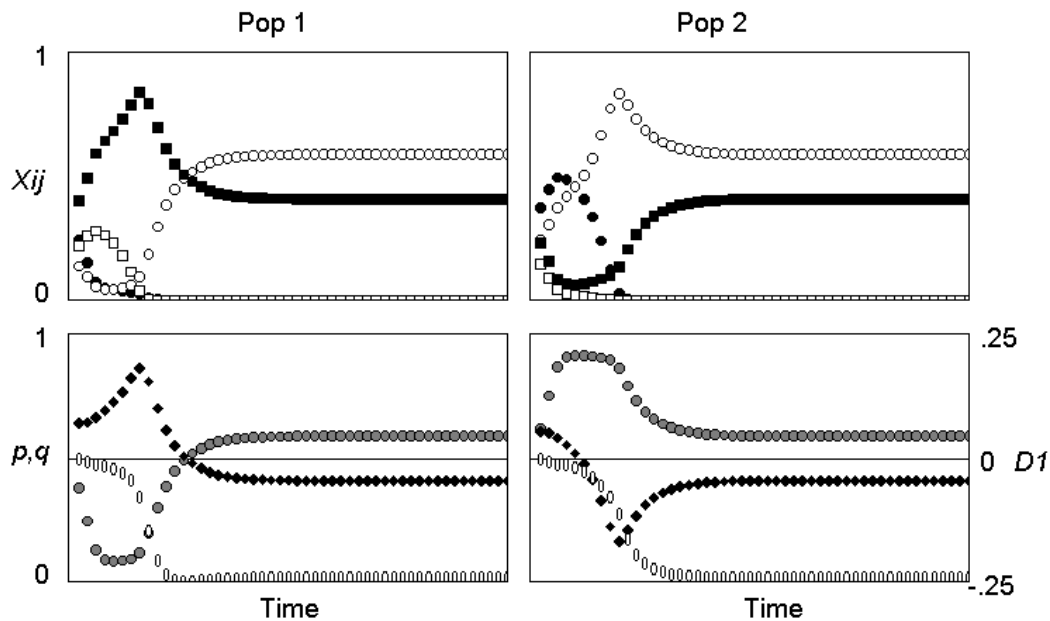


Figure 5. The top pair of graphs give the frequencies of each the four combinations of behavior and marker over time in each of two populations. The behaviors are denoted by the shape of the symbol, circle (= 0) or square (= 1), and the markers are denoted by color, black (= 0) or white (= 1). The bottom pair of graphs give the frequency of behavior 0 (gray circles), marker 1 (black diamonds), and the covariance between them (white ovals). The initial conditions and value of  $m$  are the same as in Figure 1, but now assortment is perfect,  $e = 0.0$ , and there is no recombination,  $r = 0.0$ . As before, at first, rare type disadvantage causes the behavior 1 to become more common in population 1 and behavior 0 in population 2, and migration generates a positive covariance between marker 1 and behavior 1 (eqn. 9). However, because there is no recombination, this covariance builds up much more rapidly, especially in population 1 in which the initially relatively more common marker was also absolutely more common. The high correlation between marker and behavior combined with the accurate assortment eliminates rare type disadvantage, and migration mixes the two groups until they are identical. Because the covariance increased more rapidly in population 1, the marker-behavior variant in population 2 experienced a transient advantage that is preserved at equilibrium.

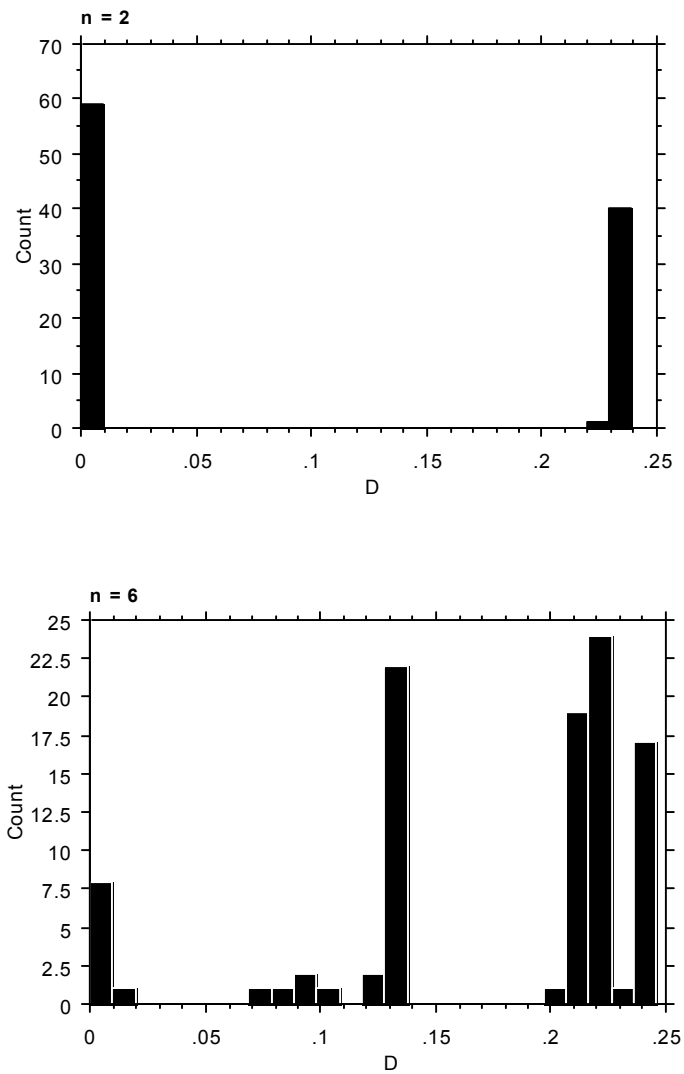


Figure 6. Histograms of equilibrium absolute values of  $\bar{D}$  (covariance in the population as a whole) for simulations involving two groups (top, 100 simulations) and six groups (bottom, 100 simulations). Starting conditions were random with parameter values  $m = 0.025$ ,  $r = 0.10$ ,  $e = 0.30$ ,  $\delta = 0.50$ . High  $\bar{D}$  becomes more likely as the number of groups increases.

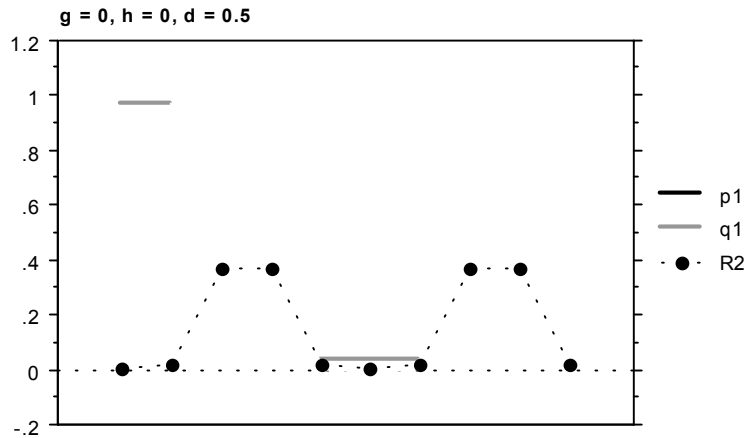


Figure 7: When populations are arrayed in space, groups of adjacent populations have high frequencies of the same marker and behavior. The correlation between marker and behavior ( $R = \frac{D_k}{\sqrt{U_k V_k}}$ ) is greatest at the boundaries between such regions. Part A.

shows the initial distributions of the frequencies of marker 1 and behavior one in 10 populations arranged in a ring. The correlation between marker and behavior is initially zero everywhere. Part b shows the configuration of the populations at steady state. There is a region of three populations in the middle in which the frequency of marker 1 and behavior 1 is low, and a region of three populations at the edges in which these frequencies are high (remember that the populations wrap around so that population 1 exchanges migrants with population 10). In both of these regions there is little or no correlation between marker and behavior. In between these regions are boundaries areas in which frequencies are intermediate, and there is substantial correlation between marker and behavior.

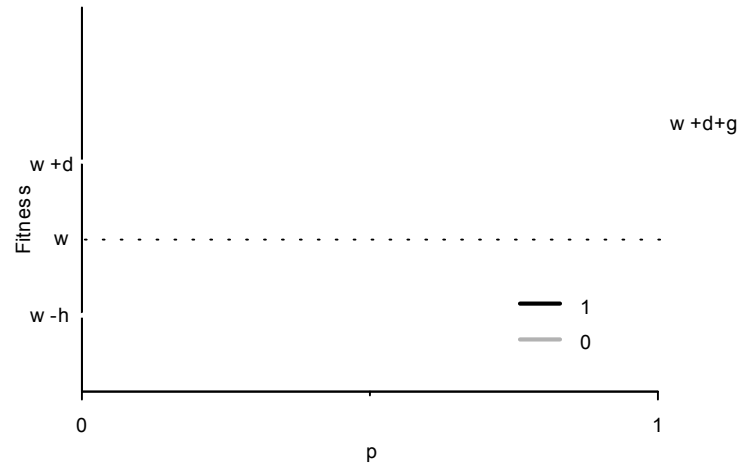


Figure 8. Fitnesses based on general coordination game structure in Table 2. The black line corresponds to behavior 1, the gray line to behavior 0.  $p$  is the frequency of behavior 1 ( $p_{1k}$ ). Adjusting the values of  $g$  and  $h$  allows us to change to domains of attraction of the two behaviors, as well as make one behavioral equilibrium more fit.

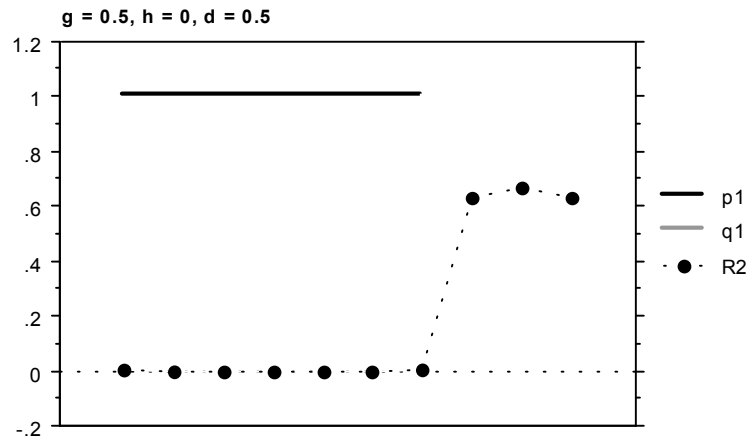


Figure 9. Spatial plot of the equilibrium state of a simulation of a circular ring of groups. The horizontal axis is space, with the far right group connecting back to the far left group. R2 (the dotted line) is the squared correlation between marker and behavior. In settings where  $g = 0.0$ , we normally see a more equal distribution of groups practicing behaviors 1 and 0. With  $g = 0.5$  here, the domain of attraction for the first behavior is larger, and more groups arrive at that equilibrium.

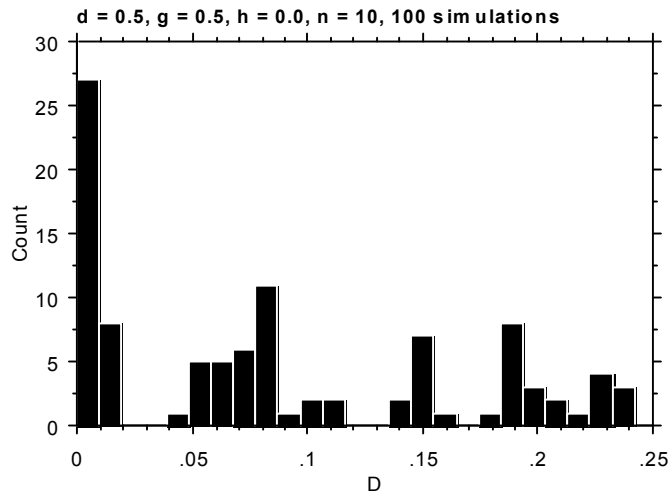


Figure 10. Histogram results of 100 simulations with parameter values found in Figure E. Even under such extreme advantage for behavior 1, almost a quarter of all simulations evolve informative ethnic markers at equilibrium, showing that the model is not delicately sensitive to the perfect symmetry of our original coordination game.