

Shared norms can lead to the evolution of ethnic markers

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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 (Barth, 1969; Barth, 1981). The modern understanding that ethnic identities are flexible, and ethnic boundaries porous, makes the origin and existence of such groups problematic because the movement of people and ideas between groups will tend to attenuate group differences. Thus, the persistence of existing boundaries and the birth of new ones suggests that there must be social processes which resist the homogenizing effects of migration and the strategic adoption of ethnic identities.

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 persist because they allow people to selectively direct altruistic behavior toward coethnics (Van den Berghe, 1981; Nettle and Dunbar, 1997). On closer analysis, however, this argument turns out not to be cogent. Altruism can evolve only if some cue allows altruists to preferentially interact with each other so that they receive a disproportionate share of the benefits of altruism. One such cue is kinship (Hamilton, 1964). Another cue is previous behavior (Trivers, 1972; Axelrod, 1984). Another idea is that selection might favor altruists who carried an external, visible marker which would allow them to limit their cooperation to others who exhibited the marker. However, evolutionary theorists argue that this mechanism is unlikely to be important (Hamilton, 1964; Grafen 1990). Non-altruists with the marker do best because they get the benefit without paying the cost. Thus, if any

process breaks up the association between the cooperator strategies and the markers, such individuals will rapidly proliferate and altruists will disappear.

Here we argue that markers function to allow individuals to interact with others who share their social norms. We present a simple mathematical model which shows marked groups can arise and persist if three empirically plausible conditions are satisfied: (1) Social behavior in groups is regulated by norms in such a way that interactions between individuals who share beliefs about how people should behave yield higher payoffs than interactions among people with discordant beliefs; (2) People preferentially interact with people with whom they share easily observable traits like dress style or dialect; and (3) People imitate successful people so that behaviors that lead to higher payoffs tend to spread. We also show that the preference to interact with people with markers like oneself may be favored by natural selection under plausible conditions. We conclude the paper by outlining several qualitative, empirically testable predictions of our model.

A Simple Model of the Evolution of Ethnic Markers

Consider a population divided into a number of large groups. Each time period, each individual interacts with another individual from the same group. People's behavior in these interactions depends on culturally acquired beliefs. 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.

(TABLE 1 HERE)

This simple coordination game is meant to capture the intuition that many real social interactions go well if people have the same beliefs about proper behavior. It is likely that human societies face many problems of this kind. An example familiar to many of us is the problems in cross-cultural communication that result from different expectations about interactions and codes for communicating (Gumperz 1982). The parameter δ measures the strength of this effect.

We also assume that it is difficult to determine another individual's beliefs about proper behavior before an interaction occurs. Given the large number of norms and the fact that some of them will only be used a few times in one's lifetime (Nave 2000), people cannot always reliably predict the behavior of everyone they must interact with, or even predict their own behavior, since many such norms are unconsciously held. Much the same argument can be made for rules enforced by third-party 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 (field anthropologists should be familiar with this sort of problem).

Of course, people have many traits, like dialect, clothing style, and cuisine that *can* be observed, and often these traits are the basis of assortative social interaction. 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 . When $e = 1$, individuals interact at random; when $e = 0$, they always interact with somebody with the same marker trait.

There is much evidence that people who do well in life are more likely to be imitated (Henrich and Gil-White 2000). To incorporate this process, we assume that the probability of an individual with behavior i and marker j being imitated is proportional to $\frac{W_{ij}}{\bar{W}}$, where \bar{W} is the average payoff in group. This means that if combinations of behavior and marker that lead to higher than average payoffs will be more likely to be imitated.

With these assumptions it is possible to derive expressions that describe how imitation and social interaction change the frequency of the behavior and marker traits in each group. The change in the fraction of the people with marker 1 within a group, p_1 , is:

$$\Delta p_1 = \delta U (p_1 - p_0) (1 - (1 - e) R^2) \quad (1)$$

$R (= D/(UV)^{1/2})$ is the correlation of behavior and marker, U , and V , are the variances of behavior and marker, and D is the covariance between marker and behavior. If $R = 1$, everyone who has marker 1 also has behavior 1, if $R = -1$, then everyone who has marker 1 has behavior 0, and if $R = 0$ the traits are randomly associated. Equation (1) says that if more individuals use behavior 1 than behavior 0, it increases; if it is less common, it decreases. The rate at which this occurs depends on whether the marker allows individuals to preferentially interact with people who have the same behavior. When R^2 is near one, most individuals with a given behavior have the same marker, and if e is small, they almost always interact with individuals with the same behavior as themselves, and thus there is little advantage in having the common behavior. When R^2 is near zero, most interactions occur at random and individuals with the most common behavior have an advantage.

The change in frequency of the marker 1, q_1 , is approximately given by:

$$\Delta q_1 \approx 2\delta D(p_1 - p_0) \left(1 - \frac{e}{2}\right) \quad (2)$$

This expression is valid when the covariance between marker and behavior is small—when an individual’s marker predicts little about her behavior. When D is positive, marker 1 is associated with behavior 1, and if behavior 1 increases, so does marker 1. The complete expression for the change in q_1 (given in the electronic enhancements) shows that this effect decreases as D becomes larger.

Because the effect of social interaction and learning depend critically on the covariance between behavior and marker (D), we also need to know how they affect the covariance. In the electronic enhancements we derive an expression which shows that social interaction and imitation increase covariance between marker and behavior when the covariance is small. The reason is simple: individuals with the most common combinations of behavior and marker are more likely to interact with others with the same behavior, and thus achieve a higher payoff.

To represent population mixing due to intermarriage, relocation, and other reasons, migration then removes a proportion m of each group and replaces them with migrants drawn from neighboring groups. Clearly, such mixing will reduce the differences in the frequencies of both behavior and marker between neighboring groups. However, migration also has a less obvious and very important effect: as long there is any difference in the frequencies of marker and behavior between neighboring groups, migration increases the covariance between marker and behavior within groups.

$$\Delta D = m(\bar{D} - D + (p_1 - \bar{p}_1)(q_1 - \bar{q}_1)) \quad (3)$$

where \bar{p}_1, \bar{q}_1 , and \bar{D} are the average frequencies of behavior and marker and the covariance between behavior and marker in neighboring groups that provide immigrants. To understand why mixing increases the covariance within groups consider the case in which the frequency of marker and behavior is 0.9 in one group and 0.1 in a second group. Further suppose that the covariance between marker and behavior within both groups is zero, and so the marker is useless as a predictor of behavior. Now suppose we mix the two groups completely. Most of the individuals coming into the first group will carry both marker and behavior 0, while those coming into the second will carry both marker and behavior 1. The frequency of both markers and both behaviors will be 0.5, but most (82%) of the individuals in the population will be either 1,1 or 0,0, so that markers are now good predictors of behavior within groups.

Finally, suppose that individuals sometimes acquire marker and behavior traits from different individuals, which leads to the randomization of behavior and marker, a process we term *recombination*. Recombination has no effect on the frequencies of behavior and marker. However, it decreases the covariance between marker and behavior at a rate proportional to r .

Simulation Results

We have derived recursions that give the net effect of imitation, migration, and recombination on the frequencies of behavior and marker, and the covariance between them. However, these recursions are too complex to solve analytically, and we have, therefore, relied on numerical simulation. We begin by describing simulations of the model when there are only two interacting populations. This system provides an intuition for the

processes that sometimes give rise to marked groups. We then explore the parameter space of the model, varying e (the chance of interacting at random), m (migration), δ (the effects of social behavior on individual welfare) and r (the rate of recombination) to map the range of conditions under which marked groups arise. Finally, we generalize the model, allowing larger numbers of populations and a general coordination game structure. These analyses suggest 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. 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. 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 rate of mixing 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. Initially behavior 1 is more common in population 1, and less common in population 2. Marker 0 is initially more common than marker 1 in *both* populations, but

relatively more common in population 2 than in population 1. 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 negative covariance between marker behavior so that behavior 1 tends to co-occur with marker 0, and marker 0 with behavior 1. This in turn, strengthens the forces increasing the differences between the population in frequencies of marker and behavior, which then generates greater covariance. 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.

However, 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. 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.

These qualitative arguments are supported by systematic sensitivity analysis. We determined the range of parameters under which groups become marked by performing a

large number of simulations. For each simulation we calculated the value of \bar{D} , the population average covariance between behavior and marker, averaged over the 100 simulations. We held parameter values constant at $m = 0.01$, $e = 0.3$, $r = 0.01$, $\delta = 0.5$, for parameters not varied in a run of simulations. Figure 4 summarizes these results. When biased imitation can maintain stable behavioral differences in the face of migration, 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). There are no cases in which behavioral differences failed to evolve and marker differences managed to become stable.

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, if individuals are able to use markers to assort accurately ($e \approx 1$) spatial structure is no longer necessary to maintain ethnic markers once such covariance arises (Figure 4), and groups end up mixed together in space, but high covariance between markers and behaviors remains. This configuration can only be a stable equilibrium if r and e are very small. However, for somewhat larger values of r and e , there is a long transition period during which two ethnically marked types are present without spatial variation. 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. Such situations are an interesting and unexpected outcome of our model.

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 5). 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.

Group differences are strongest at boundaries

When more than two groups are arrayed in space, the correlation between marker and behavior ($R = D_k / \sqrt{U_k V_k}$) is greatest at the boundaries between culture areas. Figure 6, Part A shows the initial distributions of the frequencies of marker 1 and behavior 1 in 10 populations arranged in a stepping-stone 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 boundary areas in which frequencies are intermediate, and there is substantial correlation between marker and behavior.

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

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. To test whether our results were sensitive to this assumption, we ran a number of simulations in which we varied the parameters of the completely general two person coordination game shown in Table 2.

[Table 2 about here]

These results (see electronic enhancements) indicate that the system regularly evolves toward marked, behaviorally distinct groups even when there are large deviations from the perfect coordination structure. Thus our results do not depend in a sensitive way on the perfect nature of the game structure we have chosen. This 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 , δ , r , and e . The first two formalize assumptions about the ecology of the evolving populations. The second pair of parameters represents assumptions about human psychology. 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, or, 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. In the electronic enhancements, 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 .

However, selection on other aspects of social learning and demands on interaction may restrict the extent to which selection can reduce these parameters.

Discussion

In the introduction, we argued that ethnic markers do not function to allow individuals to direct altruism to others like themselves because such a system cannot resist invasion by cheaters who signal altruistic intent, but who then do not deliver. In contrast, ethnic markers can signal one's behavioral type when social interactions have a coordination structure because in such situations there is nothing to be gained from cheating. Both parties in the coordination setting gain the most when they honestly advertise their strategy, and as a result, both the behavior, and its advertisement spread when the successful are imitated. Axtell et al. (1999) have analyzed another model which is quite different structurally, yet which works for similar reasons.

However, we do not think that the intuition that ethnic markers and cooperation are related is without merit. Humans are peculiar because we often cooperate with large numbers of unrelated individuals. As we have argued, the existence of ethnic markers alone cannot explain the scale of human cooperation. Yet we have shown that markers may evolve when individuals interact in a two person coordination game, and we believe that any process which leads groups to occupy multiple stable equilibria may produce the same result. Two of us 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 1998, 1999). 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, some of which create group beneficial cooperation, should come to be marked by ethnic markers by the process described above. Punishment transforms the Prisoner's Dilemma structure of a cooperation problem into a coordination structure. The process we describe in this paper can then lead to individuals selecting individuals with whom to cooperate based upon markers, but the markers themselves do not stabilize the cooperation.

Corollaries and predictions

The goal of this kind of modeling study is to demonstrate the cogency of a deductive argument linking assumptions about the micro-level social interactions, to empirically observable macro-level social patterns that result. Accordingly, we conclude by describing several testable predictions of the model. First, we describe predictions about features of human psychology that lead to the evolution of ethnic markers, and then predictions about the population-level distribution of behaviors and markers that result from the processes assumed in the model.

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 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. If this is not true, the process we describe here is unlikely to work.

Three predictions about patterns of cultural variation

The 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 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. 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. If these groups are on average 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 all cultural traits and the distribution of ethnic markers. 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. The model predicts that those markers with initially large differences will become marked more quickly than 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 which have since 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 which might have grown from those initial differences. This prediction will

earn support if the traits with greater differences between source populations appear to have lead to marked traits in the contact groups.

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		Player II's Behavior	
		1	0
Player I's Behavior	1	$1 + \delta$	1
	0	1	$1 + \delta$

Table 1.

Payoffs in the coordination game. Payoffs shown for player I.

δ is assumed to be positive.

		Player II's Behavior	
		1	0
Player I's Behavior	1	$1 + \delta + g$	$1 - h$
	0	1	$1 + \delta$

Table 2. General game with two stable equilibria.

Payoffs for a general two person game with two equilibria.

Payoffs shown for player I. δ , g , and h are assumed to be positive.

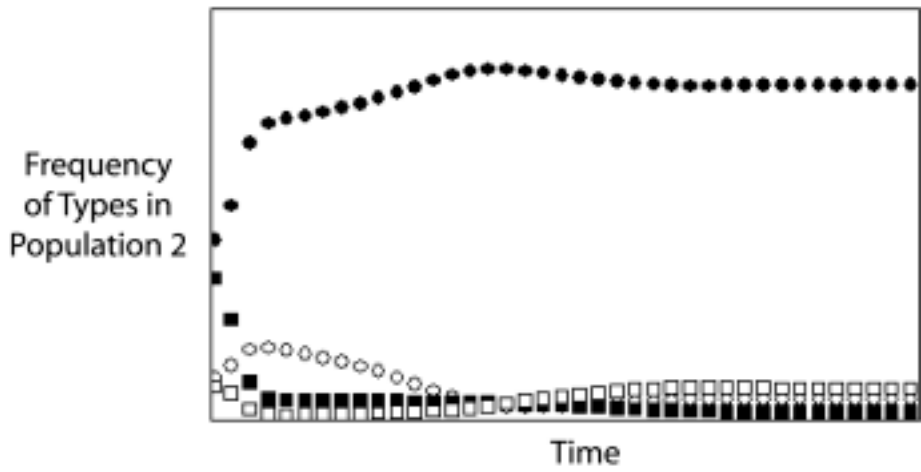
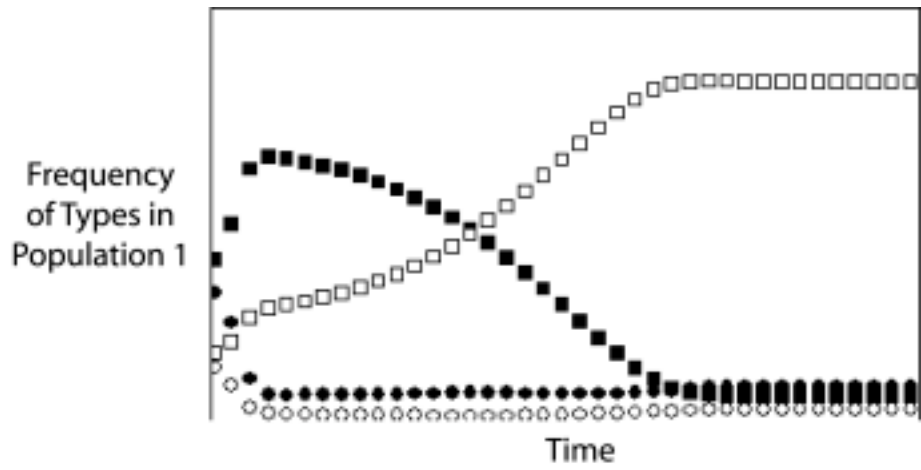


Figure 1. The frequencies of each the four combinations of behavior and marker over time in each of two populations for $m = 0.025$, $e = 0.25$, and $r = 0.1$. The behaviors are denoted by the shape of the symbol, circle (= 0) or square (= 1), and the markers are denoted by color, black (= 0) or white (= 1). 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 1 ($q_{11} = 0.8$) than in population 2 ($q_{12} = 0.7$). 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. 4), 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. 1). This process 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.

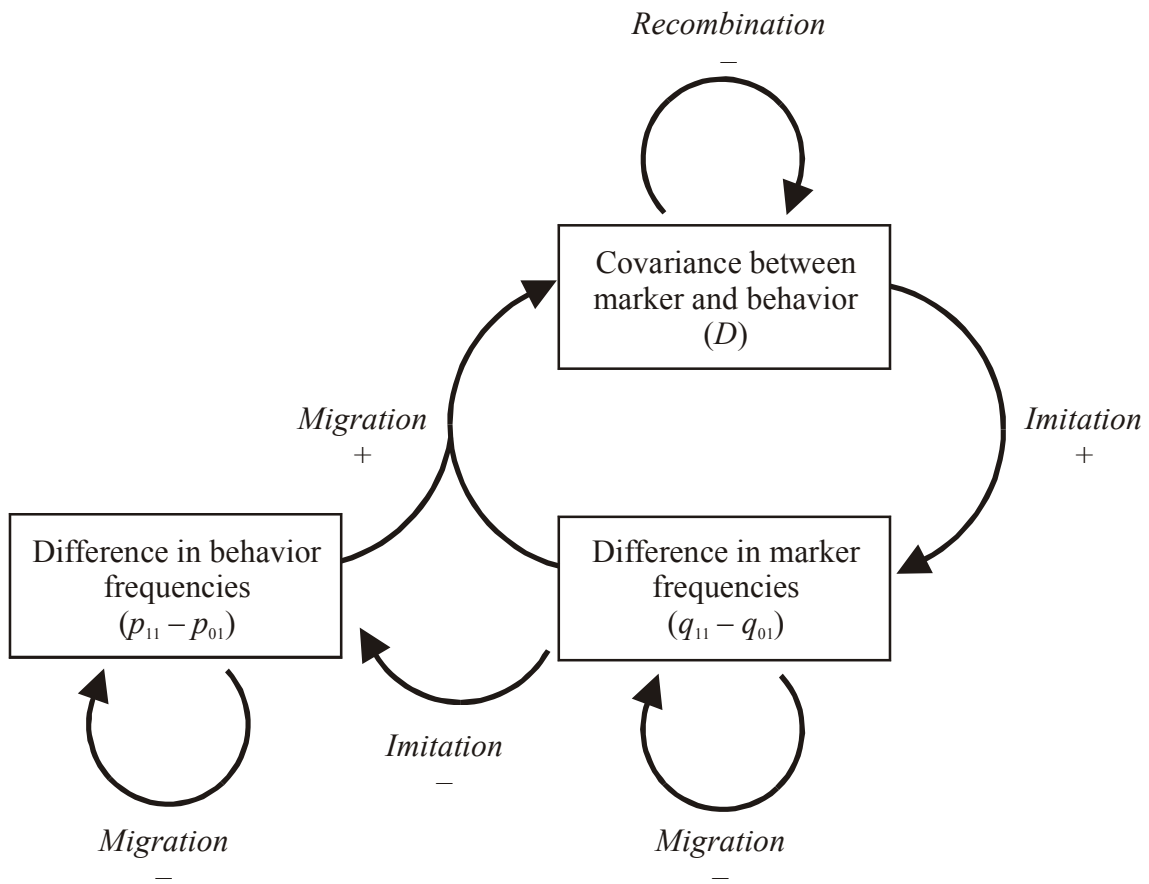


Figure 2. Diagram of the feedback process which generates marked groups, as well as the forces which oppose this process. At first, rare type disadvantage causes behavior 1 to become more common in population 1 and behavior 0 in population 2. At the same time, migration generates a positive covariance 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.

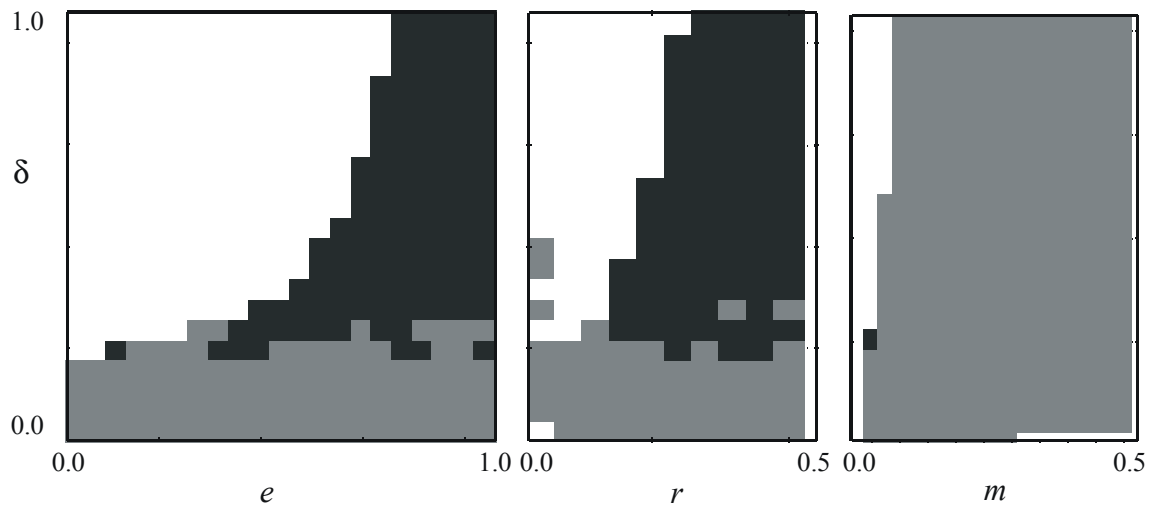
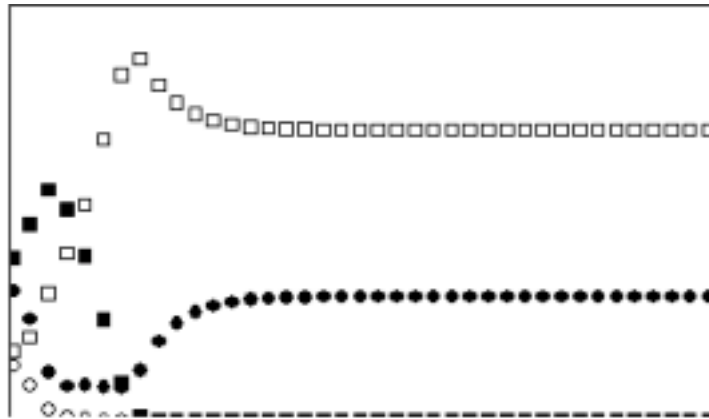


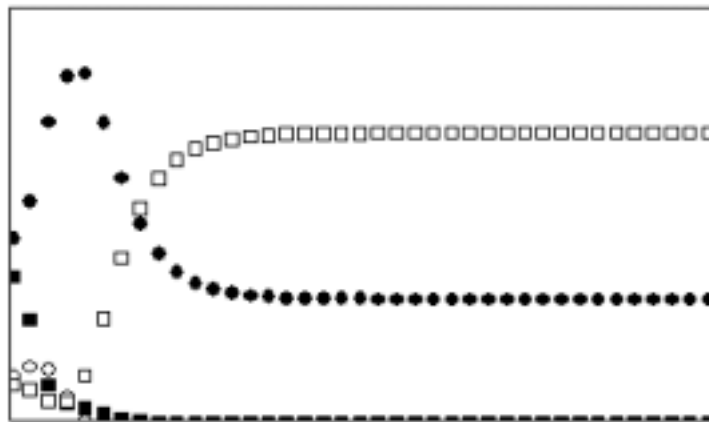
Figure 3. When selection on behavior is strong enough to produce stable behavioral differences in the face of migration (white and black regions above), stable marker differences evolve (white regions) provided 1) recombination (r) is not too strong and 2) individuals interact sufficiently often with 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.

Frequency
of Types in
Population 1



Time

Frequency
of Types in
Population 2



Time

Figure 4. 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 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. 4). 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.

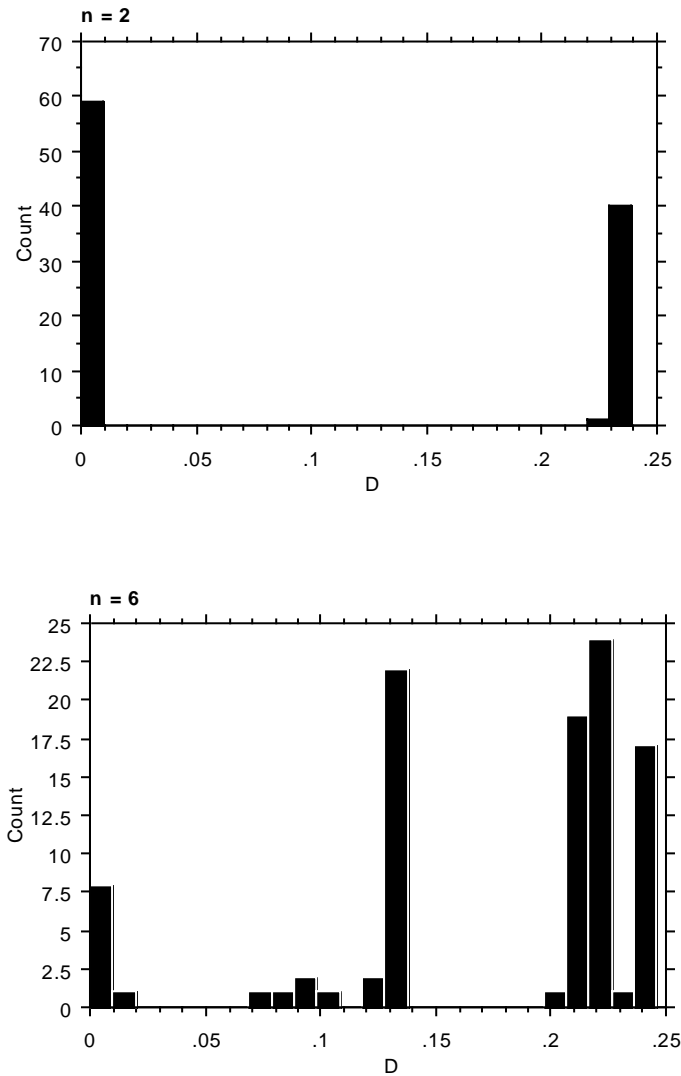


Figure 5. Histograms of equilibrium absolute values of \bar{D} (covariance in the population as a whole) for simulations involving two groups (top, 100 simulations) and six groups (bottom, 100 simulations). Starting conditions were random with parameter values $m = 0.025$, $r = 0.10$, $e = 0.30$, $\delta = 0.50$. High \bar{D} becomes more likely as the number of groups increases.

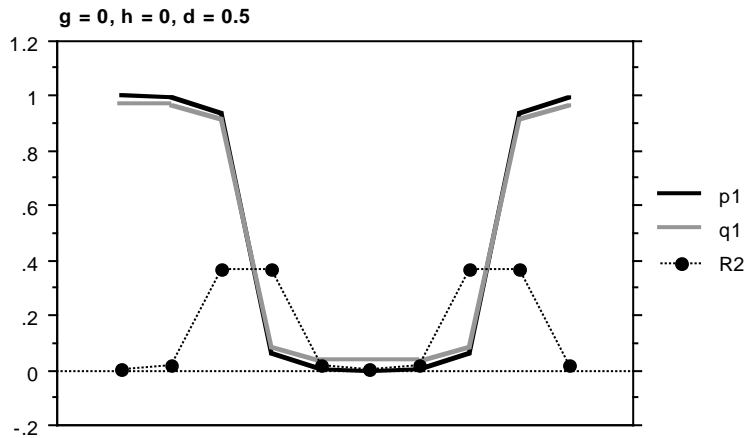


Figure 6: When populations are arrayed in space, groups of adjacent populations have high frequencies of the same marker and behavior. The correlation between marker and behavior ($R = \frac{D_k}{\sqrt{U_k V_k}}$) is greatest at the boundaries between such regions. The figure shows the steady state which arises from slightly clinal 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. 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.