

- chone use of an "abundant" resource. *Yukon Tourism Occasional Papers in Archaeology* 3.
- OSWALT, WENDELL H. 1963. *Mission of change in Alaska*. San Marino: Huntington Library.
- . 1990. *Bashful no longer: An Alaskan Eskimo ethnohistory, 1778–1998*. Norman: University of Oklahoma Press.
- OSWALT, WENDELL H., AND JAMES W. VAN STONE. 1967. *The ethnoarchaeology of Crow Village, Alaska*. Washington, D.C.: U.S. Government Printing Office.
- OWEN, LINDA R., AND MARTIN PORR. Editors. 1999. *Ethno-analogy and the reconstruction of prehistoric artefact use and production*. Tübingen: Mo Vince Verlag.
- ROMANOFF, STEVEN. 1992. "Frasier River Lilloet salmon fishing," in *A complex culture of the British Columbia Plateau: Stl'atl'imx resource use*. Edited by B. Hayden, pp. 222–65. Vancouver: University of British Columbia Press.
- SHAW, ROBERT D. 1998. An archaeology of the central Yupik: A regional overview of the Yukon-Kuskokwim Delta, northern Bristol Bay, and Nunivak Island. *Arctic Anthropology* 35: 234–46.
- STENTON, DOUGLAS R. 1991. The adaptive significance of caribou winter clothing for Arctic hunter-gatherers. *Etudes/Inuit/Studies* 15(1):3–28.
- TESTART, ALAIN. 1982. The significance of food storage among hunter-gatherers: Residence patterns, population densities, and social inequalities. *CURRENT ANTHROPOLOGY* 23: 532–37.
- TORRENCE, ROBIN. 1989. "Tools as optimal solutions," in *Time, energy, and stone tools*. Edited by R. Torrence, pp. 1–6. Cambridge: Cambridge University Press.
- WHITRIDGE, PETER. 2002. "Gender, households, and the material construction of social difference: Metal consumption at a Classic Thule whaling village," in *Many faces of gender: Roles and relationships through time in indigenous northern communities*. Edited by L. Frink, R. S. Shepard, and G. A. Reinhardt, pp. 244–78. Boulder: University Press of Colorado.
- WOODBURY, ANTHONY C. 1992. *Cev'armiut qanemciit qulirait-llu: Eskimo narratives and tales from Chevak, Alaska*. Anchorage: University of Alaska Press.
- WOLFE, ROBERT J. 1984. Commercial fishing in the hunting-gathering economy of a Yukon River Yup'ik society. *Etudes/Inuit/Studies* 8:159–84.
- . 1989a. Myths: What have you heard? *Alaska Fish and Game* 21(6):16–19.
- . 1989b. Tools: A crucial difference. *Alaska Fish and Game* 21(6):20–23.

Shared Norms and the Evolution of Ethnic Markers¹

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Unlike other primates, human populations are often divided into ethnic groups that have self-ascribed membership and are marked by seemingly arbitrary traits such as distinctive styles of dress or speech (Barth 1969, 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 that 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 direct altruistic behavior selectively 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 interact with each other preferentially so that they receive a disproportionate share of the benefits of altruism. One such cue is kinship (Hamilton 1964), and another is previous behavior (Trivers 1972, Axelrod 1984). Another idea is that selection might favor altruists who carried an external, visible marker that 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). Nonaltruists with the marker do best because they get the benefit without paying the cost. Thus, if any process breaks up the association between the co-

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operator 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 showing that 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. (3) People imitate successful people, with the result that behaviors that lead to higher payoffs tend to spread. We also show that the preference to interact with people with markers like one's own may be favored by natural selection under plausible conditions. We conclude 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. In 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 and 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. 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 be used only 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

TABLE 1
Payoffs in the Coordination Game

Player 1's Behavior	Player 2's Behavior	
	1	0
1	1 + δ	1
0	1	1 + δ

NOTE: Payoffs shown for player 1; δ is assumed to be positive.

sort of problem). As long as people are sometimes ignorant in these ways, people with uncommon behaviors will be at a disadvantage, and the model targets these situations, not the entire scope of interaction.

Of course, people have many traits, such as 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 that 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. 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 someone 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 that an individual with behavior i and marker j will be imitated is proportional to W_{ij}/\bar{W} , where \bar{W} is the average payoff in the group. This means that combinations of behavior and marker that lead to higher than average payoffs will be more likely to be imitated (see Gintis 2000 for derivation).

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

$$\Delta p_1 = \delta U \{ (p_1 - p_0) (1 - |1 - e|) R^2 \}, \tag{1}$$

where $R = D / (UV)^{1/2}$ 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 fewer individuals use it, it decreases. The rate at which this occurs depends on whether the marker allows individuals to interact preferentially 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 ad-

vantage 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 individuals' markers predict little about their 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 shows that this effect decreases as D becomes larger.

Because the effects 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. 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.

We then represent population mixing due to intermarriage, relocation, and other factors with a migration phase which removes a proportion m of each group and replaces it 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 therefore the marker is useless as a predictor of behavior. Now suppose that 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, with the result 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, but it reduces 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.

1. *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 with 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—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 and 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 dif-

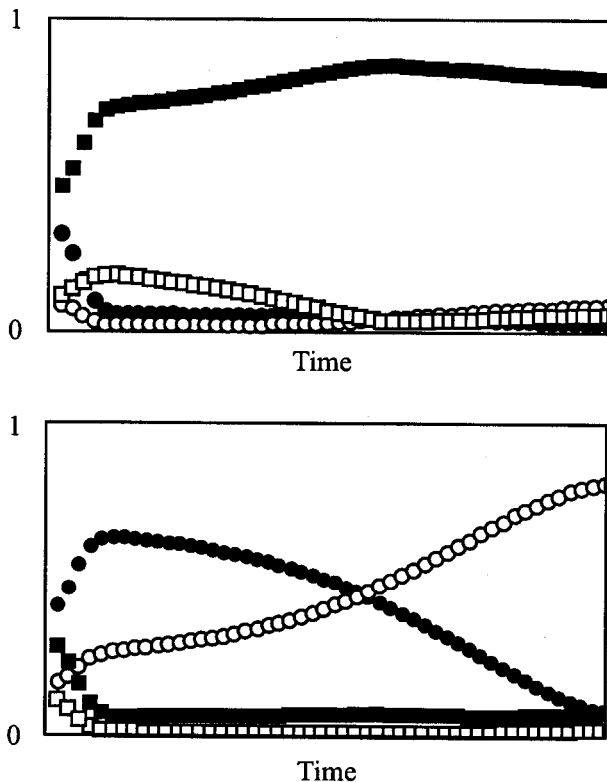


FIG. 1. The frequencies of each the four combinations of behavior and marker over time in each of two populations for $m = 0.025$, $e = 0.25$, and $r = 0.1$. The behaviors are denoted by the shape of the symbol, circle ($= 0$) or square ($= 1$), and the markers are denoted by color, black ($= 0$) or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

ferences between the populations in frequencies of marker and behavior, which then generates greater covariance. This positive feedback process (fig. 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 accurately on the basis of 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 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 3 summarizes these results. When biased imitation can maintain stable behavioral differences in the face of migration, stable marker differences evolve provided that (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 fail to evolve and marker differences manage to become stable.

2. *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 (fig. 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 the evolution of such spatially blended systems more likely. Such situations are an interesting and unexpected outcome of our model.

3. *Increasing the number of populations increases the range of initial conditions that 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 (fig. 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.

4. *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 shows the steady state in ten populations

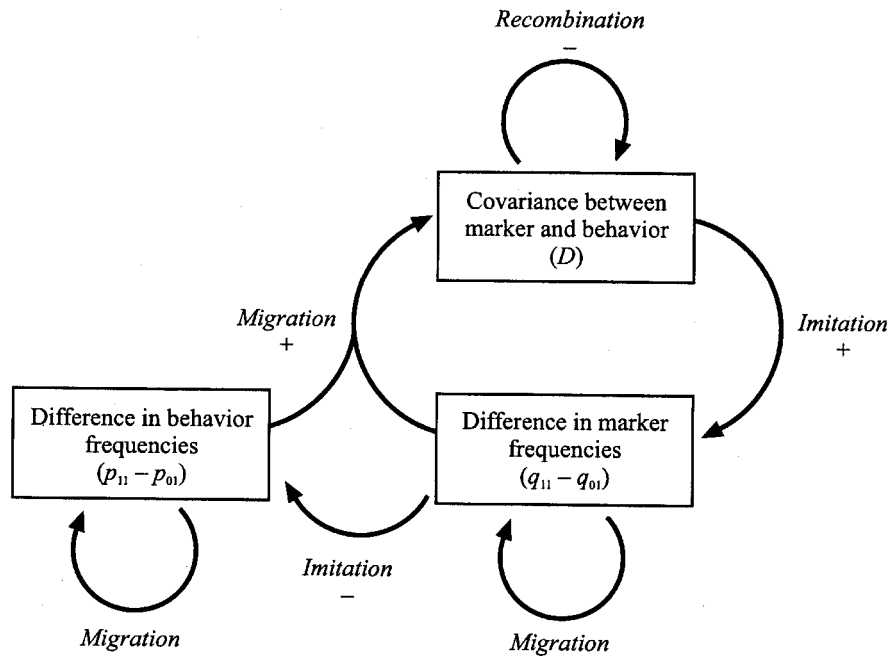


FIG. 2. The feedback process that generates marked groups and the forces that oppose this process.

arranged in a stepping-stone ring. This steady state results from an initial clinal distribution of behavior and marker frequencies with zero correlation between behavior and marker in each population. 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

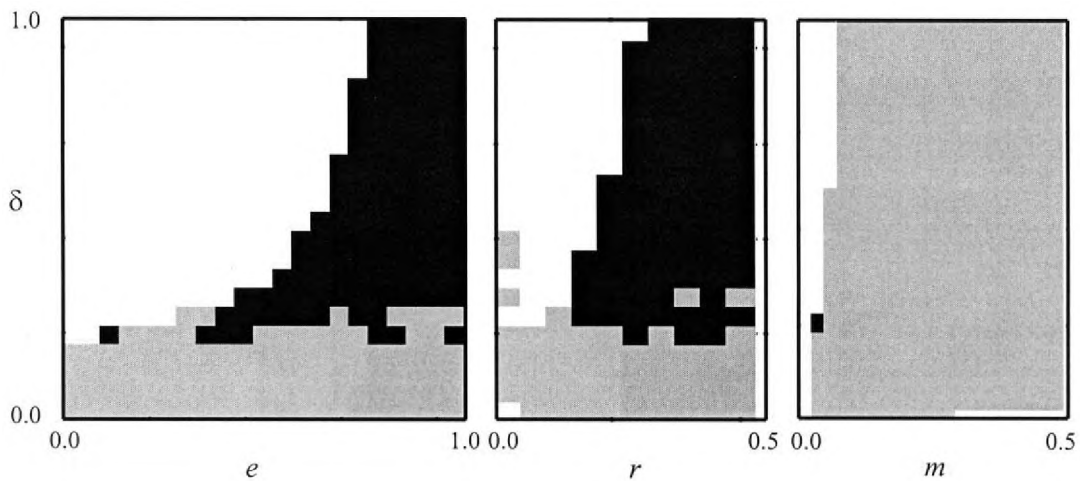


FIG. 3. The evolution of stable marker differences. White regions, combinations of parameter values that produced both stable behavioral and marker differences (that is, these populations became ethnically marked). Black regions, cases in which behavioral differences were stable but marker differences were not (that is, these populations became culturally different but without ethnic markers). Gray regions, cases in which behavioral differences failed to evolve, typically because of strong migration.

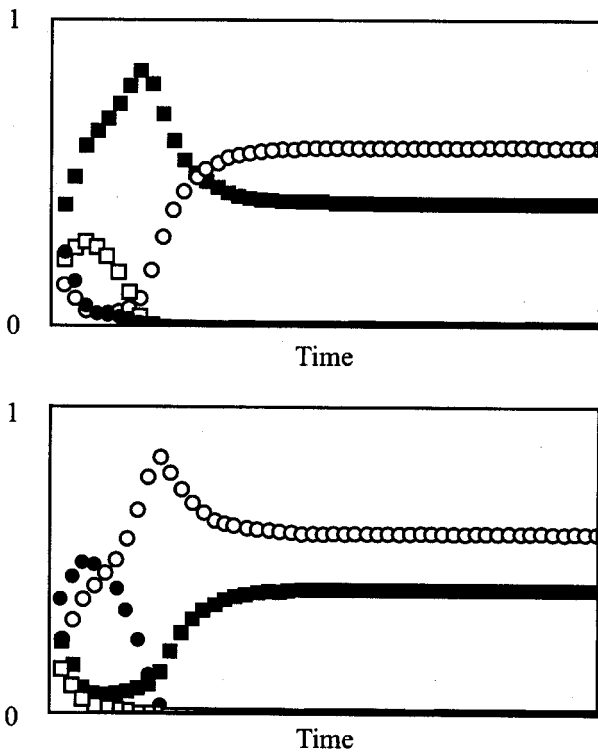


FIG. 4. The frequencies of each the four combinations of behavior and marker over time in each of two populations. The behaviors are denoted by the shape of the symbol, circle ($= 0$) or square ($= 1$), and the markers are denoted by color, black ($= 0$) or white ($= 1$). The initial conditions and value 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 (equation 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 increases more rapidly in population 1, the marker-behavior variant in population 2 experiences a transient advantage that is preserved at equilibrium.

are intermediate and there is substantial correlation between marker and behavior.

5. 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 the two 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.

The results 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.

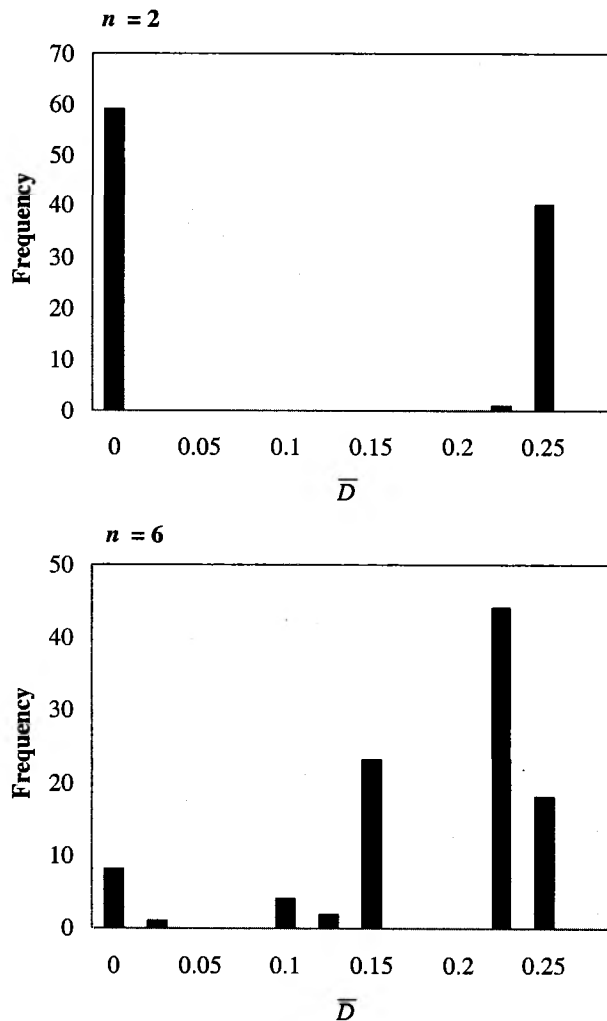


FIG. 5. Equilibrium absolute values of \bar{D} (covariance in the population as a whole) for simulations involving two groups (top, 100 simulations) and six groups (bottom, 100 simulations). Starting conditions were random with parameter values $m = 0.025$, $r = 0.10$, $e = 0.30$, $\delta = 0.50$. High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

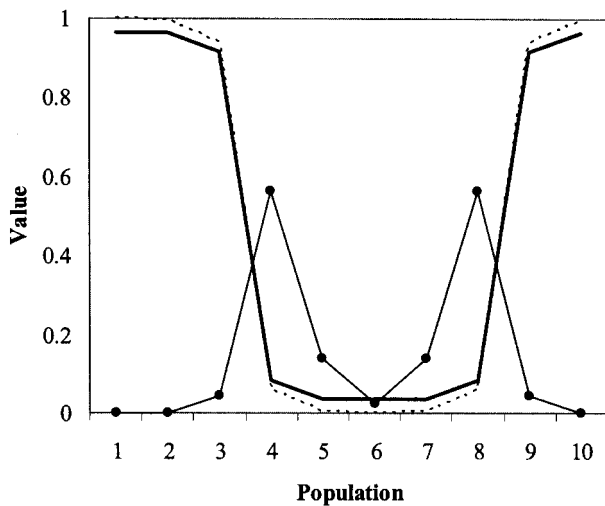


FIG. 6. The steady state that arises from slightly clinal initial distributions of the frequencies of marker 1 and behavior 1 in ten populations arranged in a ring. Broken line, p_1 ; heavy solid line, q_1 ; light solid line, R .

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. Natural selection will, all other things being equal, favor such a psychology (that is, selection will favor mutations that 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

We have 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 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, Epstein, and Young (1999) have ana-

TABLE 2
Payoffs in a General Two-Person Game with Two Stable Equilibria

Player 1's Behavior	Player 2's Behavior	
	1	0
1	$1 + \delta + g$	$1 - h$
0	1	$1 + \delta$

NOTE: Payoffs shown for player 1; δ , g , and h are assumed to be positive.

lyzed another model that is quite different structurally but works for similar reasons.

The intuition that ethnic markers and cooperation are related is not, however, without merit. Humans are peculiar in that 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 that 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, Boyd, and Richerson 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 have described here can then lead to individuals' selecting individuals with whom to cooperate on the basis of 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 microlevel social interactions to the empirically observable macrolevel social patterns that result. Accordingly, we conclude by describing several testable predictions of the model.

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

1. *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 toward 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.

2. *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 noncoordination 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 life spans. If this is not true, the process we describe here is unlikely to work.

The model makes three clear predictions about the nature of the distributions of marker traits and their relations to ethnic groups and their histories:

1. *Ethnic differences should be stronger at boundary regions than deep within ethnic territories.* Hodder (1977) suggests that this is true for some ethno-archeological data from the Lake Baringo region of Kenya, but the data 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 that holds promise for testing this prediction is fragmentary migration that 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 may be able to conclude that interaction with the other ethnic groups has increased selection on markers and magnified initial differences in those settings.

2. *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 in which there are multiple coordinated solutions to the same problem—should correspond to the distributions of marker differences.

3. *Potential marker traits with the greatest initial differences should become marked first.* One test of this prediction would be to examine ethnographic settings in which two isolated source populations have contributed migrant groups that 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 that might have grown from

those initial differences. This prediction will earn support if the traits with greater differences between source populations appear to have led to marked traits in the contact groups.

References Cited

- 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: Santa Fe Institute.
- BARTH, F. 1969. "Introduction," in *Ethnic groups and boundaries*. Edited by F. Barth. Boston: Little, Brown.
- . 1981. *Features of person and society in Swat: Collected essays on Pathans*. London and Boston: Routledge and Kegan Paul.
- BOYD, R., AND P. J. RICHESON. 1990. Group selection among alternative evolutionarily stable strategies. *Journal of Theoretical Biology* 145:331–42.
- . 1992. Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethology and Sociobiology* 13: 171–95.
- GINTIS, H. 2000. *Game theory evolving*. Princeton: Princeton University Press.
- GRAFEN, A. 1990. Do animals really recognize kin? *Animal Behaviour* 39:42–54.
- GUMPERZ, J. J. 1982. *Discourse strategies*. Cambridge: Cambridge University Press.
- HAMILTON, W. D. 1964. The genetical evolution of social behaviour. *Journal of Theoretical Biology* 7:17–52.
- HENRICH, J., AND F. GIL-WHITE. 2001. The evolution of prestige: Freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human Behavior* 22:165–96.
- HODDER, I. R. 1977. The distribution of material culture items in Baringo District, western Kenya. *Man* 12:239–69.
- NAVE, A. 2000. Marriage and the maintenance of ethnic group boundaries: The case of Mauritius. *Ethnic and Racial Studies* 23:329–52.
- NETTLE, D., AND R. J. M. DUNBAR. 1997. Social markers and the evolution of reciprocal exchange. *CURRENT ANTHROPOLOGY* 38:93–99.
- RICHESON, P. J., AND R. BOYD. 1998. "The evolution of human ultra-sociality," *Indoctrinability, ideology, and warfare*. Edited by I. Eibl-Eibesfeldt and F. Salter, pp. 71–95. New York: Berghahn Books.
- . 1999. The evolutionary dynamics of a crude super organism. *Human Nature* 10:253–89.
- SOLTIS, J., R. BOYD, AND P. J. RICHESON, 1995. Can group functional behaviors evolve by cultural group selection? An empirical test. *CURRENT ANTHROPOLOGY* 36:473–94.
- TRIVERS, R. L. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology* 46:35–57.
- VAN DEN BERGHE, P. L. 1981. *The ethnic phenomenon*. Westport, Conn.: Praeger.