MULTILEVEL SELECTION AND THE SOCIAL TRANSMISSION OF BEHAVIOR

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Many evolutionary models assume that behaviors are caused directly by genes. An implication is that behavioral uniformity should be found only in groups that are genetically uniform. Yet, the members of human social groups often behave in a uniform fashion, despite the fact that they are genetically diverse. Behavioral uniformity can occur through a variety of psychological mechanisms and social processes, such as imitation, consensus decision making, or the imposition of social norms. We present a series of models in which genes code for social transmission rules, which in turn govern the behaviors that are adopted. Transmission rules can evolve in randomly formed groups that concentrate phenotypic variation at the between-group level, favoring the evolution of altruistic behaviors and other group-advantageous traits. In addition, a direct bias toward adopting altruistic behaviors can evolve. Our models begin to show how group selection can be a strong force in human evolution, despite the absence of extreme genetic variation among groups.

KEY WORDS: **Altruism; Cooperation; Culture; Gene-culture coevolution; Group selection; Multilevel selection; Social behavior; Social transmission.**

Human social groups often display a degree of coordination and apparent altruism that invites comparison to social insect colonies and single organisms. Nevertheless, evolutionary biologists have been reluctant to make this comparison. The cells of a single organism are genetically iden-

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tical (aside from mutation) and the members of social insect colonies are highly related to each other, which makes it relatively easy to explain the evolution of altruism and other group-advantageous traits. In contrast, the members of human social groups are often only weakly or even completely unrelated to each other. How can human groups evolve into adaptive units when they differ from other adaptive units so greatly in their genetic structure?

This argument is based on a pervasive assumption in evolutionary models that behaviors are coded directly by genes. For example, the standard model for the evolution of altruism assumes a genetic polymorphism for altruism and selfishness at a single locus (Hamilton 1964; Wright 1945). The direct connection between genes and behavior is usually not defended as realistic, but rather as a simplifying assumption that makes mathematical models more tractable without altering the basic results. Real behaviors are caused by complex psychological mechanisms that often rely on individual learning and social transmission.[1] However, if the psychological mechanisms are themselves the product of natural selection, the result can be much the same as if behaviors are coded directly by genes (Alexander 1987; Flinn 1997). We don't have a gene for pulling our hand away from fires, but our psychological mechanisms make us act as if we do, in precisely those situations where such a gene would evolve. Assuming genetic determinism allows behavioral evolution to be explored without worrying about the messy proximate mechanisms that actually separate genes from behavior.

Despite its widespread use, there are reasons to question the validity of the simplifying assumption and the conclusions that issue from it. The evolution of altruism requires the segregation of altruists and nonaltruists into different groups. When behaviors are caused directly by genes, the only way to accomplish this segregation is to increase genetic variation among groups. Yet, people often display extreme behavioral uniformity within groups and variation between groups, despite the absence of corresponding genetic variation. Behavioral variation can be influenced by many psychological mechanisms and social processes, such as imitation, consensus decision making, or the imposition of social norms. These factors may themselves be influenced by genes that have evolved by natural selection, but they do not lead to the same conclusions as simple genetic models, in part because they alter the partitioning of behavioral variation within and among groups.

Boyd and Richerson (1985, 1990) were the first to show how social processes can favor the evolution of altruism by altering the balance between levels of selection. If individuals are guided by the transmission rule "copy the most common behavior in your group," all groups become internally uniform, while groups in which different behaviors are initially in the majority will become different from each other. Group selection becomes the only evolutionary force because the transmission rule concentrates all of the phenotypic variation at the between-group level.

It is important to emphasize that social transmission does not automatically favor group selection. The transmission rule "copy the most successful member of your group" would be disastrous for group selection because it would cause everyone to emulate selfishness. The point is that transmission rules and other proximate psychological mechanisms do not merely evolve to produce the behaviors that would have evolved directly by genes, but themselves change the parameters governing the behaviors that evolve. Since our intuition about the evolution of social behavior is so heavily based on the assumption that genes code directly for behavior, there is an urgent need for models in which genes code for proximate psychological mechanisms, which in turn determine the behaviors that are expressed.

Boyd and Richerson's conformity model is an important step but it leaves at least three issues unresolved. First, copying the majority is only one way to achieve behavioral uniformity within groups. Other possibilities include charismatic individuals who persuade others to copy them, dominant individuals who use force, and decision making processes resulting in a consensus about how to behave (Boehm 1996). Second, the conformity model makes it difficult to understand how new behaviors can become established in the population, since they would first have to achieve a local majority within at least one group. This problem, referred to as the problem of origin in the anthropological literature (e.g., Giddens 1979/1994), may not exist for other mechanisms that create behavioral uniformity within groups. Third, Boyd and Richerson assume that the conformity rule evolves as an adaptation for copying individually advantageous behaviors in a fluctuating environment. The consequences for multilevel selection are treated as a byproduct. It is important to know if transmission rules can evolve directly to alter the balance between levels of selection, rather than for other reasons. We address these issues with a series of models in which genes code for social transmission rules that determine how individuals actually behave.

THE MODEL

We assume that a large population is subdivided into many groups of size *N*. Individuals interact within groups for a period of time before they or their progeny disperse to form a new set of groups (the trait-group model of Wilson 1975, 1998; see Sober and Wilson 1998 for a discussion of how groups are defined in multilevel selection theory). The population is genetically polymorphic for a number of transmission rules. We assume asexual reproduction for simplicity, since diploid sexual reproduction is unlikely to change the basic results. The population is also polymorphic for two behaviors that are not genetically encoded. Thus, each individual can be characterized by a transmission rule that does not change and a behavior that can change, depending on the behaviors and the transmission rules that are present in the group.

The simulation consists of the following stages: (1) One thousand groups of size $N = 10$ are initially formed at random; (2) Individuals in each group change their behaviors, depending on the transmission rules and behaviors initially present in the group; (3) Fitness is determined on the basis of the behaviors expressed after social transmission; (4) Individuals (or their progeny, who initially adopt the behavior of their parent) disperse to a global population from which a new set of one thousand groups is formed at random. The behaviors that were acquired in the old groups are carried into the new groups, to be modified by the next cycle of social transmission, selection and so on.

The two behaviors are "Cooperate" (C, a form of altruism) and "Defect" (D, a form of selfishness) of the standard one-shot prisoner's dilemma model (Axelrod and Hamilton 1981).[2] Fitness within each group is therefore determined by the following equations, where X is the baseline fitness experienced in the absence of the behaviors, q_C is the frequency of C, R is the "reward" (fitness of C playing with C), S is the "sucker's payoff" (fitness of C playing with D), T is the "temptation" (fitness of D playing with C), and P is the "punishment" (fitness of D playing with D):

$$W_C = X + q_C R + (1 - q_C)S \tag{1}$$

$$W_D = X + q_C T + (1 - q_C)P \tag{2}$$

We chose values of $X = 1$, $T = 5$, $R = 3$, $P = 1$, and $S = 0$. These and all other values that qualify as a prisoner's dilemma guarantee that D will increase in frequency within every mixed group. However, groups contribute to the global population in direct proportion to the frequency of C. Thus, D is favored by within-group selection and C is favored by between-group selection.

The following genetically encoded transmission rules are considered, both alone and in competition with each other.

R1. Retain own behavior. If all members of the group follow this rule, the behavioral composition of the group remains unchanged prior to stage 3 outlined above.

R2. Adopt a single behavior, chosen randomly from the initial behaviors in the group. If all members of the group follow this rule, and if q_C is the initial frequency of C in the group, then all group members adopt C with probability q_C and D with probability $(1 - q_C)$. Plausible mechanisms that could lead to this transmission rule will be described in the Discussion section.

R3. Adopt C. If all members of the group follow this rule, they adopt C regardless of its initial frequency.

R4. Adopt D. If all members of the group follow this rule, they adopt D regardless of its initial frequency.

Rules 2–4 promote behavioral uniformity within groups. Rule 2 promotes uniformity in an unbiased manner while rules 3 and 4 are biased toward altruism and selfishness, respectively. So far we have specified what happens when all members of a group follow a single transmission rule. Additional assumptions are required to specify what happens when members of a single group follow different transmission rules. The possibilities are numerous, and those that we have explored will be described along with the results.

RESULTS

We can begin to explore the model by considering a population in which Rule 1 is the only transmission rule. In this case the behaviors remain randomly distributed among the groups. Within-group selection (favoring D) outweighs between-group selection (favoring C), and the selfish behavior evolves to fixation, regardless of its initial frequency in the global population.

Now consider a population in which Rule 2 is the only transmission rule. If Q_C is the average frequency of the altruistic behavior in the newly formed groups, a fraction Q_C of the groups becomes entirely C while a fraction $(1 - Q_C)$ of the groups becomes entirely D. The social transmission process had not changed the frequency of behaviors in the global population, but it has concentrated phenotypic variation at the between-group level. Fitness differences within groups have been eliminated and groups of C are more fit than groups of D, so the C behavior evolves to fixation. This conclusion holds regardless of the frequency of C in the global population (Q_C). Even if C is very rare, the transmission rule guarantees that a very small fraction of groups will be entirely C, allowing the behavior to spread by between-group selection. In short, this population structure is as favorable for the evolution of altruism as interactions among genetically identical clones in standard models that assume a direct connection between genes and behavior.

Now that we have shown how social transmission rules can alter the balance between levels of selection at the phenotypic level, we need to examine the genetic evolution of the transmission rules. The most important question is how rules that create behavioral uniformity within groups (such as R2) can evolve in competition with rules that cause groups to remain behaviorally polymorphic (such as R1). Before we address this issue, it is useful to compete R2 against R3 and R4, which also create behavioral uniformity within groups but bias the behavior that is actually copied.

Consider the group shown in Figure 1, which contains both a mix of transmission rules (R2 and R3) and a mix of behaviors (C and D). Rule 2 specifies that everyone should adopt a randomly chosen behavior. Rule 3 specifies that everyone should adopt an altruistic behavior. We assume that a rule prevails in direct proportion to its frequency in the group. In this group, R2 is at a frequency of $q_{R2} = 0.4$ and the altruistic behavior is at a frequency of $q_C = 0.6$. The probability that all individuals adopt the altruistic behavior is therefore

$$(1 - q_{R2}) + q_{R2}q_C \tag{3}$$

For the group in Figure 1, altruism will be adopted with a probability of 0.84. It is obvious that altruism will evolve in this model. Altruism already evolved when R2 was the only transmission rule, and the inclusion of R3 only makes it evolve faster. However, we are interested in the evolution of the transmission rules in addition to the behaviors that they promote. R2 and R3 always have the same fitness within a single group because all individuals end up behaving the same way. The probability that a group becomes altruistic increases in direct proportion to the frequency of R3 in the group. Even when the transmission rules are randomly distributed among

	R2	R3
C	1	5
D	3	1

Figure 1. A single group of 10 individuals. Each individual is characterized by a transmission rule (R2 vs. R3) and a behavior (C vs. D).

the groups, some groups have a higher frequency of R3 and these contribute disproportionally to the global population. In sum, the two transmission rules are neutral with respect to within-group selection but R3 is favored by group selection. However, group selection for R3 occurs only while the global population is polymorphic at the behavioral level. As soon as the altruistic behavior evolves to fixation in the global population, there are no fitness differences between the transmission rules at any level. These results are confirmed by our computer simulations. Regardless of the initial frequency of R2 and C in the global population, R3 increases in frequency but only until C evolves to fixation.

At this point it is necessary to consider the relationship between transmission rules and behaviors in more detail. We envision altruism and selfishness as *types* of behavior that exist in many different manifestations. They might take the form of sharing versus hoarding food in the context of hunting, coming to someone's defense versus hanging back in the context of warfare, or helping to till someone's garden versus staying at home in the context of farming. Opportunities to behave altruistically versus selfishly occur in many situations, and in each case the transmission rules determine which behavior is adopted by the whole group. Rule 3 increases the chance that the altruistic behavior will be adopted and therefore is favored by group selection, but only as long as the behavior remains polymorphic in the global population. Each manifestation of altruistic behavior increases the frequency of R3, but only slightly, while the behavior evolves to fixation. Because there are many manifestations, however, this process happens repeatedly and R3 gradually replaces R2 in a rachetlike fashion. Transmission rules that favor the adoption of altruism by everyone in the group therefore can be expected to replace transmission rules that favor uniformity but are unbiased with respect to altruism versus selfishness.

Now consider the interaction between R2 and R4, which favors the adoption of selfishness. As before, the rules are neutral with respect to within-group selection because everyone in a group ends up behaving the same way. R2 increases the chance that the group adopts altruism (compared to R4) and therefore is favored by group selection, but only as long as the global population remains polymorphic at the behavioral level. For the interaction between R2 and R3, the behavioral polymorphism was transient because altruism always evolved to fixation. The situation is more complicated for the interaction between R2 and R4, because R4's bias toward selfishness during transmission opposes the fitness consequences of the behaviors that favor altruism.

To explore this interesting dynamic, let Q_{R2} and Q_C be the frequency of R2 and C in the global population. Using the same reasoning that led to equation 3, social transmission will cause a fraction $Q_{R2}Q_C$ of the groups to become altruistic and the remainder to become selfish. R4's bias towards selfishness during the social transmission stage of the life cycle causes the frequency of altruism to decline in the global population. However, groups of altruists are more fit than groups of selfish individuals (R vs. P), which causes the frequency of altruism to increase again. The net effect of these two opposing forces is given by the following equation, where Q'_C is the frequency of the altruistic behavior in the global population after social transmission and natural selection.

$$Q'_C = \frac{(Q_{R2}Q_C)R}{[(Q_{R2}Q_C)R + (1 - Q_{R2}Q_C)P]} \tag{4}$$

The frequency of altruists remains constant when $Q'_C = Q_C$. Setting equation 4 equal to Q_C and solving for Q_C yields

$$Q_C = \frac{(Q_{R2}R - P)}{[Q_{R2}(R - P)]} \tag{5}$$

When R = 3 and P = 1, this becomes

$$Q_C = \frac{(3Q_{R2} - 1)}{(2Q_{R2})} \tag{6}$$

When $Q_{R2} < 1/3$, the right side of equation 6 is negative, which means that the transmission bias in favor of selfishness overwhelms group selection in favor of altruism and selfishness evolves to fixation. When $Q_{R2} > 1/3$, the right side of the equation is between zero and one, signifying an equilibrium point in which the opposing forces favoring selfishness and altruism exactly balance. This equilibrium is stable, maintaining the altruistic behavior at an intermediate frequency in the global population.

So far our analysis has assumed that the frequencies of R2 and R4 remain constant, but R2 is favored by group selection and will increase in frequency whenever the global population is behaviorally polymorphic. When $Q_{R2} < 1/3$, the behavioral polymorphism is transient and the increase in Q_{R2} is correspondingly small, as is the case for the interaction between R2 and R3. However, it is important to note that R2 is favored over R4, even though the selfish behavior evolves to fixation. When many manifestations of altruism and selfishness are considered, R2 can increase from a low frequency until $Q_{R2} > 1/3$. At this point, the behavioral polymorphism ceases to be transient and is maintained permanently in the global population. R2 is continuously favored by group selection and can replace R4 based on a single manifestation of altruistic and selfish behavior. As the frequency of R2 increases, the equilibrium value of Q_C (determined by equation 6) moves with it until both become fixed in the global population. These results are confirmed by our computer simulations, as shown in Figure 2. When $Q_{R2} = 0.2$ and $Q_C = .9$, the altruistic behavior is quickly eliminated from the population but the frequency of R2 increases slightly

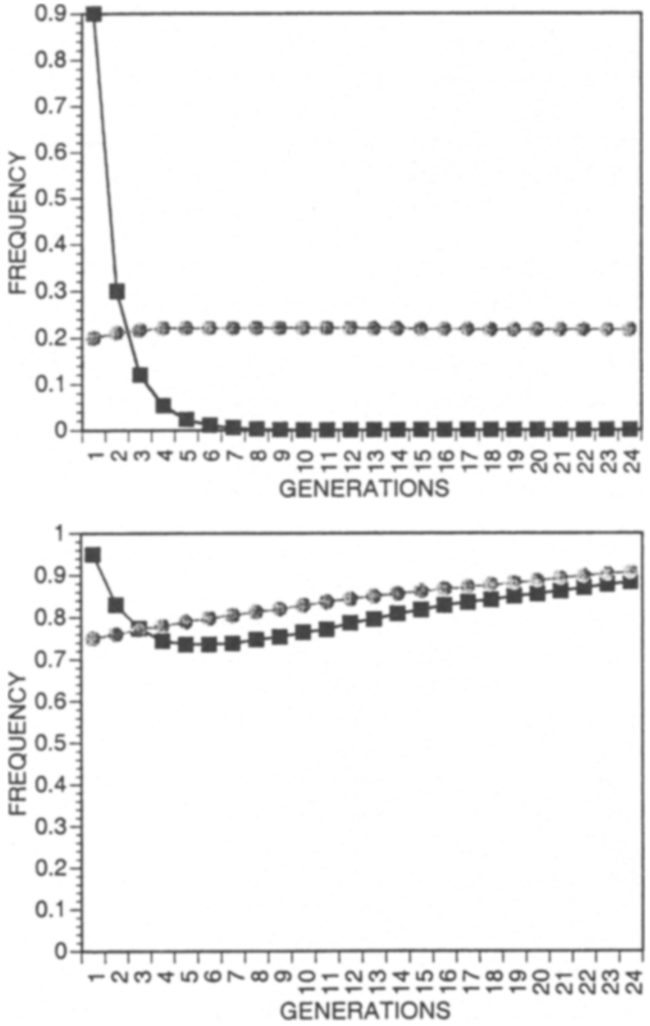


Figure 2. Two outcomes of interactions between R2 (randomly adopts behaviors) and R4 (biased toward selfishness). In the top graph, the frequency of R2 begins at $Q_{R2} = 0.2$ (circles) and the frequency of the altruistic behavior (squares) begins at $Q_C = 0.9$. Q_{R2} increases in frequency, but only as long as the altruistic behavior remains in the population. Altruism is driven extinct because R4's bias toward selfishness overwhelms group selection in favor of altruism. In the bottom graph, Q_{R2} begins at 0.75 and Q_C begins at 0.95. For these initial values, R4's bias toward selfishness and group selection in favor of altruism lead to a stable equilibrium. Q_C first descends to this equilibrium and then increases to fixation as R2 increases to fixation.

during the process. When $Q_{R2} = 0.7$ and $Q_C = .95$, the altruistic behavior initially decreases to the equilibrium value determined by equation 6 after which Q_{R2} and Q_C increase together to fixation.

Our results so far can be summarized as follows. Transmission rules R2, R3, and R4 all create behavioral uniformity within groups but differ in the type of behavior that is favored. R2 adopts a behavior at random, R3 is biased toward altruism, and R4 is biased toward selfishness. All of the rules eliminate phenotypic variation within groups and therefore are neutral with respect to within-group selection. However, group selection favors transmission rules that cause the group to become altruistic, which promotes R2 over R4 and R3 over R2. A transmission rule can be favored by group selection only while the global population is behaviorally polymorphic. When either altruism or selfishness evolves to fixation, the behavioral polymorphism is transient and produces only a slight change in the frequency of the transmission rules. In this case, many manifestations of altruistic and selfish behaviors are required to eliminate rules that are biased toward selfishness and evolve rules that are biased toward altruism. However, in some cases, the interaction between the transmission rules and behaviors can result in a stable behavioral polymorphism in the global population, allowing the selfish transmission bias to be quickly eliminated. In either case, evolution over the long term should produce genetically encoded transmission rules such as R3, which create behavioral uniformity within groups and are biased toward adopting altruistic behavior.

The next step is to see how rules that create behavioral uniformity within groups can evolve in competition with rules that cause groups to remain behaviorally polymorphic. This involves making additional assumptions about how the rules interact when they occur together in the same group. Consider a group that initially contains the mix of transmission rules (R1 and R2) and behaviors (C and D), shown in the left box of Figure 3. R2 specifies that everyone should adopt a randomly chosen behavior. We assume that all R2 individuals follow this rule, changing the composition of the group to one of the middle boxes in Figure 3. In addition, even though R1 individuals do not change their behavior on their own, we assume that they potentially can be influenced by the presence of R2 individuals in the group. In particular, each R2 individual is able to "convert" a number (V) of R1 individuals.[3] R2 has no influence on R1 when $V = 0$, but a single R2 can convert a group otherwise composed entirely of R1s when $V = 9$. We assume that $V = 1$ in Figure 3, leading to the final behavioral compositions of the groups in the boxes on the right. Notice that the group remains behaviorally mixed, unlike the previous examples in which groups always became uniform. The question is how this particular linkage between genes and behavior influences the evolution of altruism and the evolution of the transmission rules that create the linkage.

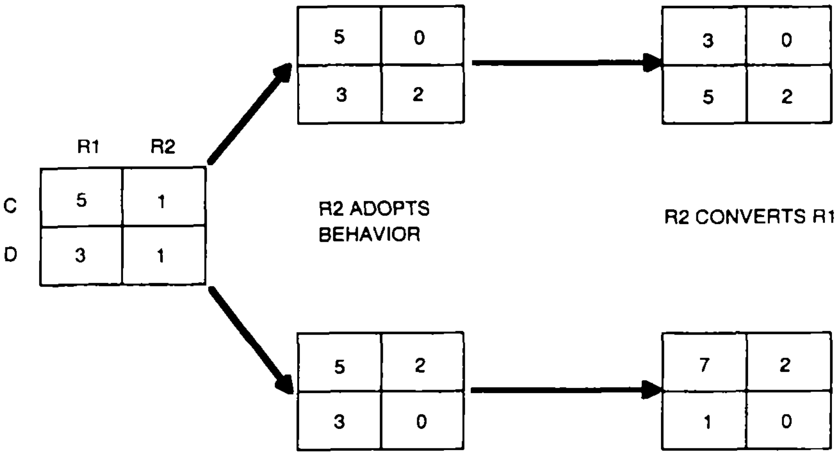


Figure 3. The interaction between R1 (retains own behavior in absence of other transmission rules) and R2 (randomly adopts behaviors) in a single group. First the R2 individuals randomly adopt a behavior among themselves, which can be D (top branch) or C (bottom branch). Then each R2 individual converts a number (V) of R1 individuals who are behaving differently. V = 1 for this example.

The simplest case to consider is when R2 is at mutation frequency and completely converts its group to one phenotype or the other (V = 9). If Q_C is the frequency of the altruistic behavior in the global population, the average fitness of the mutant R2 type (and the R1s in its group) is

$$W_{R2} = Q_C R + (1 - Q_C)P \tag{7}$$

The temptation (T) and sucker's (S) payoffs do not appear in this equation because R2 has caused its group to be either entirely altruistic or entirely selfish. The vast majority of R1s are in groups without R2 and have an average fitness of

$$W_{R1} = Q_C[Q_C R + (1 - Q_C)S] + (1 - Q_C)[Q_C T + (1 - Q_C)P] \tag{8}$$

The temptation and sucker's payoffs do appear in this equation because groups of R1 are behaviorally mixed. R2 has a higher fitness than R1 in the global population when $W_{R2} > W_{R1}$, which simplifies to

$$R + P > T + S \tag{9}$$

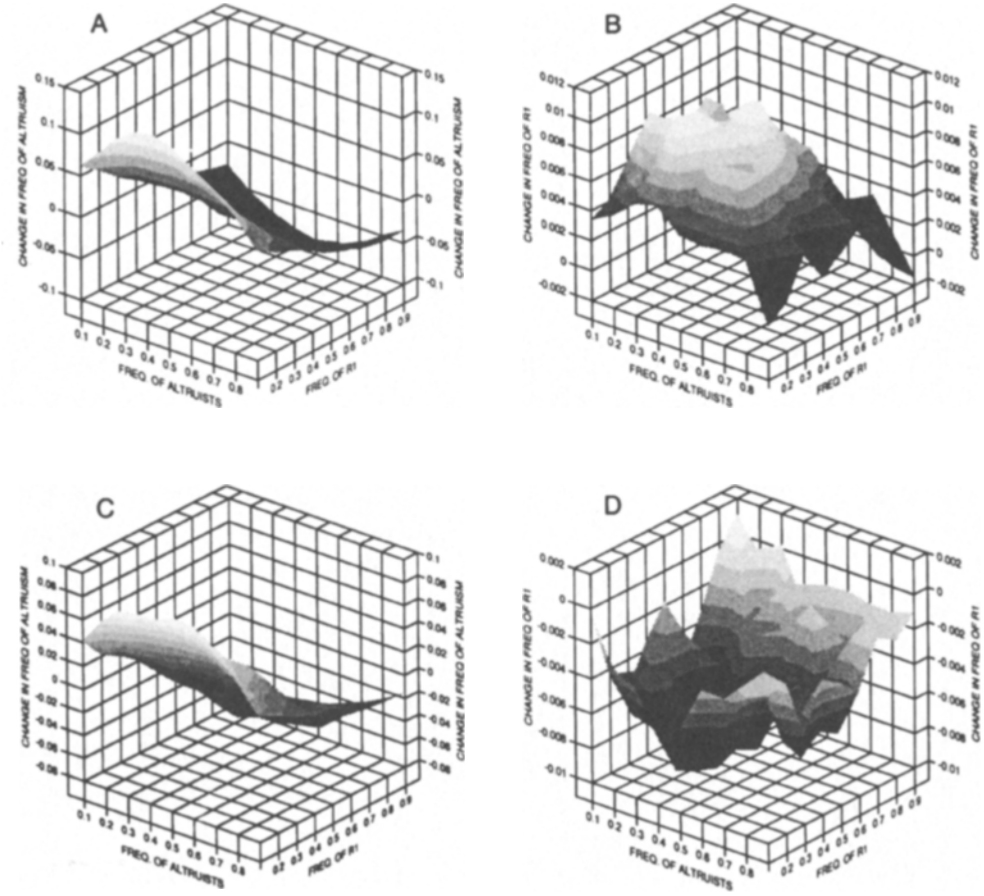
R2's effect on its group includes both R and P because it merely makes the group more variable, rather than more altruistic. R2 is favored by group selection only when there is a net positive effect of increasing C-C and D-D interactions at the expense of C-D interactions. Inequality 9 is satisfied for some values of the prisoner's dilemma game (e.g., R = 4, T = 5, S = 0, and P

= 2) but not others (e.g., R = 3, T = 5, S = 0, and P = 1).Thus, the transmission rule that promotes the evolution of altruism by increasing phenotypic variation among groups can only sometimes invade the population.

Similar conditions apply when R2 has no effect on R1 (V = 0), as shown by computer simulations in Figure 4. The payoff values for R, T, S, and P are 3,5,0,1 in the top row and 4,5,0,2 in the bottom row. In both cases, the altruistic behavior evolves only when R2 is common. However, the R2 transmission rule evolves only for the second set of parameter values.

Figure 4d shows that R2 can evolve even when it has no influence on R1 (V = 0). The ability of R2 to influence the behavior of R1 can be regarded as a form of dominance—not social dominance, in which some individuals obtain more resources than others, but genetic dominance, in which some individuals mask the phenotypes of others.[4] Just as a dominant gene masks the expression of recessive genes in heterozygotes, R2 tends to mask the expression of R1 in mixed groups when V > 0. In the extreme case of V = 9, a group with 9 R1 and 1 R2 individuals is phenotypically identical to a group of 10 R2 individuals. This masking effect has important consequences for rates of evolution. When V = 9, there is no within-group selection for transmission rules and between-group selection occurs only when at least some groups have no R2 individuals. If Q_{R2} is the frequency of R2 in the global population and N is the size of the group, the proportion of groups without R2 individuals is $(1 - Q_{R2})^N$, which quickly becomes very small as Q_{R2} and N increase (e.g., less than 1 in 1,000 groups when $Q_{R2} = .5$ and $N = 10$). At this point, selection against R1 becomes so weak that it is essentially neutral and R1 can be expected to persist in the population indefinitely for the same reason that deleterious recessive alleles persist at low frequencies. In short, the stronger the influence of R2 on R1, the more R1 can be expected to persist in the population for the simple reason that its phenotype is seldom expressed.

Figure 4. (On facing page.) The coevolution of behaviors and transmission rules for the interaction between R1 (retains own behavior in the absence of other transmission rules) and R2 (randomly adopts behaviors). In all cases the x and y axes are the initial frequency of altruists (Q_C) and R1 (Q_{R1}) in the global population and the z axis is the change in frequency of either altruism (4A,4C) or R1 (4B,4D) after a single episode of selection. In 4A and 4B, R = 3, T = 5, S = 0, P = 1, and V = 0 (R2 has no influence on R1). In 4C and 4D, R = 4, T = 5, S = 0, P = 2, and V = 0. Both sets of parameter values qualify as a prisoner's dilemma but differ with respect to equation 9. In both cases, selfishness evolves at high frequencies of R1 and altruism evolves at high frequencies of R2 (compare 4A with 4C). However, R1 evolves for the first set of parameter values and R2 evolves for the second set (compare 4B with 4D).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So far we have considered the interaction between R1 (which does not change its behavior on its own) and R2 (which randomly adopts a behavior). However, we have already shown that R2 can be replaced by R3, which is predisposed to adopt the altruistic behavior. We might therefore expect the evolutionary progression R1 → R2 → R3. Another possible evolutionary progression is R1 →R3, without R2 as an intermediate step. If R3 is at mutation frequency and completely converts its group to altruism (V = 9), its fitness (and the fitness of the R1s in its group) is R. The vast majority of R1 individuals are in groups without R3 and have an average fitness given by equation 8. R3 has a higher fitness than R1 in the global population when

$$R > \frac{[Q_C(S + T) + (1 - Q_C)P]}{(1 + Q_C)} \tag{10}$$

This inequality becomes $R > P$ when $Q_C = 0$ and $R > (S + T) / 2$ when $Q_C = 1$. Both of these inequalities must be satisfied for the payoffs to qualify as a prisoner's dilemma game, so R3 can always invade a population of R1 when V = 9. However, R3 cannot invade for low values of V, as shown in Figure 5 . Recall from Figure 4d that R2 can replace R1 when V = 0 for at least some values of the prisoner's dilemma (e.g., R = 4, T = 5, S = 0, and P = 2). Thus at least four outcomes are possible for the parameter space that we have explored: (1) R1 can resist invasion by both R2 and R3 (low values of V and R = 3, T = 5, S = 0, and P = 1); (2) R1 can be invaded by both R2 and R3 (high values of V and R = 4, T = 5, S = 0, and P = 2); (3) R1 can be invaded by R3 but not R2 (high values of V and R = 3, T = 5, S = 0, and P = 1); and (4) R1 can be invaded by R2 but not R3 (low values of V and R = 4, T = 5, S = 0, and P = 2). In the last case, R3 can replace R2 after R2 has replaced R1. Thus, for some but not all of the parameter space, it is reasonable to expect the evolution of transmission rules such as R3 that are biased toward altruism and promote uniformity within groups.

DISCUSSION

The evolution of altruism requires the segregation of altruists and nonaltruists into different groups. The greater the cost of the altruistic behavior, the more segregation is required to offset the advantages of selfishness within groups. Assuming a direct connection between genes and behavior leads to a relatively simple theory in which genetic similarity is exactly proportional to behavioral similarity and therefore to the degree of altruism that can evolve. Complicating the relationship between genes and behaviors leads to an expanded set of possibilities in which groups can become behaviorally uniform despite being genetically diverse. The complexity

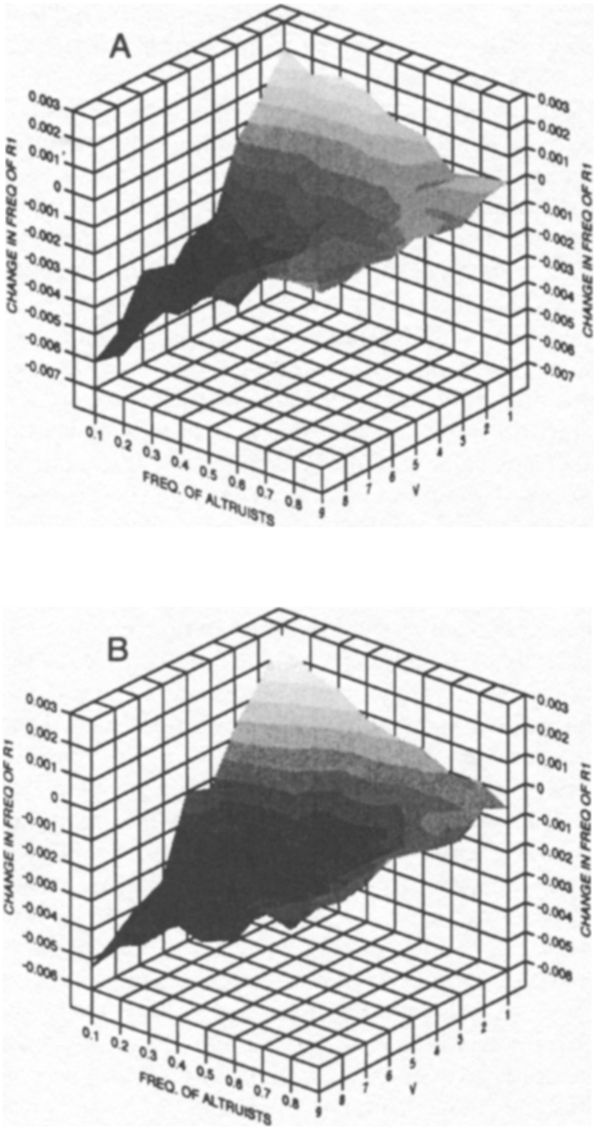

Figure 5. The coevolution of behaviors and transmission rules for the interaction between R1 (retains own behavior in the absence of other transmission rules) and R3 (biased toward altruism). The *x* and *y* axes are the initial frequency of altruists (Q_C) and the ability of R3 to convert R1 (V). The frequency of R1 is assumed to be very high ($Q_{R1} = 0.99$), as when R3 is invading the population. Values for R, T, S, and P are 3,5,0,1 in 5A and 5,4,0,2 in 5B. These two sets of parameters make a difference in the interaction between R1 and R2 (see Figure 4), but they have the same qualitative effect for the interaction between R1 and R3. In both cases, R3 is favored by high values of V and Q_C.

can be disorienting compared to the elegant simplicity of Hamilton's rule, but it also has greater potential to explain the forms of altruism that have evolved in humans and other species.

When we focus on the partitioning of phenotypic variation rather than genetic relatedness per se, the comparison among human social groups, social insect colonies, and single organisms begins to look more appropriate (Boehm 1997, this issue; Sober and Wilson 1998). According to Boehm, an "egalitarian syndrome" has governed the expression of behavior in human groups for much of our evolutionary history. The egalitarian syndrome promotes sharing and other activities that benefit the whole group, encourages decision making as a public process that leads to a single outcome for the whole group, discourages overt striving for dominance within groups, and punishes free riders who try to share social benefits without paying the costs. Egalitarianism reduces behavioral variation within groups (especially when it is likely to result in fitness differences) and concentrates behavioral variation at the between-group level.[5] Boehm's analysis is supported by ethnographic accounts of human societies around the world. In a survey of cultures randomly chosen from the Human Relations Area Files (Murdock 1967), Sober and Wilson (1998: ch. 5) found statements such as the following to be common: "Any infringement of the socially accepted way or value of life may be a crime . . . , however small it may be. . . . They have a large body of civil laws, a system of rights and obligations in all spheres of life, economic, social and religious, which are fulfilled very scrupulously" (referring to the Bhil; Naik 1956: 223). "All more or less important acts of social life, even including sacrificing one's life in a battle of vengeance for one's clansman, are categorical imperatives of a religious world-outlook which neither allow hesitation or require compulsion" (the Gilyak; Shternberg 1933:116). "Even the most insignificant and routine action in the daily life of the family is potentially of major concern to the band as a whole. . . . It is important that there should be a pattern of behavior that is generally accepted, and which covers every conceivable activity" (Mbuti; Turnbull 1965:118). "There are almost no conventionalized variations from the normal behavior pattern; the guiding principles apply to everyone. No man can ignore them because of his wealth, position as village leader, or special skill. . . . The facts that failure to perform in a socially approved manner will inevitably become common knowledge and that general censure is sure to follow constitute a powerful deterrent to breaking the mores" (Papago; Joseph et al. 1949:166).

The behavioral uniformity resulting from these and other social processes rivals the uniformity of groups of highly related individuals whose behaviors are determined directly by genes. However, this does not mean that we can ignore genes in our analysis of human social behavior. Many social processes can be imagined, only some of which concentrate phenotypic variation at the between-group level. We must therefore build models that reflect what is already known to be biologically realistic, in which genes code for traits that influence social processes rather than coding directly for behaviors.

Our models explore the evolution of transmission rules that promote behavioral uniformity, concentrating behavioral variation at the between-group level. In addition, the rules can be biased or unbiased with respect to the actual behaviors that are adopted. A variety of specific mechanisms can have these effects. For example, a group of people might discuss how to behave, resulting in a decision that applies to the whole group (Boehm 1996). Alternatively, the group may form a strong dominance hierarchy in which the behavior is imposed by the top-ranked individual or coalition of individuals. Or, we might imagine a charismatic religious leader who manages to convince a group to follow a certain creed. Witte and Davis (ed., 1996) review a large social science literature on the complicated and dynamic ways that members of groups influence each others' opinions. All of these processes can result in groups that behave in a uniform fashion and may or may not be biased with respect to the actual behavior that is adopted.[6]

In general, our results lead us to expect the frequent evolution of transmission rules that cause everyone in the group to behave altruistically. It is important to realize that two processes of multilevel selection are occurring in parallel. The behaviors evolve on the basis of their fitness consequences within and among groups. Extreme variation among groups is required for altruism to evolve because altruists have such a large fitness disadvantage within groups. The transmission rules also evolve on the basis of their fitness consequences within and among groups. If two transmission rules exist in a single group, and the group ends up behaving in a uniform fashion, then no fitness differences exist between the transmission rules within that group. However, group selection still favors rules that increase the fitness of their group, relative to other groups. Random variation among groups is sufficient for these rules to evolve because within-group selection is neutral. In this fashion, weak forms of group selection operating at the level of the transmission rules enable a strong form of group selection to operate at the level of behaviors. Sober and Wilson (1998) discuss a similar process for the evolution of rewards and punishments, which they call "the amplification of altruism" (also see Boyd and Richerson 1992).

It might seem that our models are "rigged" to favor the evolution of altruism. After all, if it is possible to cause everyone in a group to behave uniformly at little cost, then *of course* altruism should evolve! However, it is an important fact of human social life that groups often *can* effectively regulate the behavior of their members at little cost. The cost is low because the capacity of the group to punish deviant members is so great that it rarely needs to be employed. In addition, other aspects of our model are "rigged" conservatively in ways that do not favor the evolution of altruism. In particular, our models assume only random variation among ephemeral groups, which is a very weak form of group selection. Groups of genetic relatives or groups that persist indefinitely and transmit their social traditions intact to descendant groups are probably much more favorable for the evolution of transmission rules that benefit the whole group (Boyd and Richerson 1990). The important point is that we must go beyond models that assume a direct connection between genes and behavior, on which so much of our evolutionary intuition is based. Clearly, a very large family of models (sensu Boyd and Richerson 1987) will be required to fully explore the evolution of proximate mechanisms that separate genes from behavior.

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NOTES

1. The vocabulary for describing how individuals acquire their behaviors from others leaves much to be desired (Lakoff and Johnson 1980). The term "cultural transmission" invokes a mechanical, agent-recipient process that is not necessarily required for our model. We use the term "social transmission" to avoid the connotations associated with the word "cultural," while realizing that we have not escaped the connotations associated with the word "transmission." Some of the many specific ways that individuals modify each other's behavior are discussed in the body of the article.
2. Altruism and cooperation are often discussed as if they were different concepts but mathematically they are virtually identical. For example, Hamilton's

(1964) model of altruism which forms the basis of inclusive fitness theory involves a benefit *(b)* to a recipient and a cost *(c)* to the altruistic donor. If individuals interact in groups of size 2, then altruists in AA groups serve as both donor and recipient, receiving a payoff of $b - c$. Altruists in AS groups serve only as donor and get a payoff of $-c$. Selfish individuals get a payoff of b in AS groups and zero in SS groups. These payoffs conform to the standard prisoner's dilemma in game theory, which is the standard model for the evolution of cooperation. See Wilson and Sober (1994), Wilson (1998), and Sober and Wilson (1998) for more detailed discussion of altruism, cooperation, and the relationships among major theoretical frameworks.

3. R1 individuals could be called "docile" in the sense that they remain the same unless influenced by others. The evolution of docility and the relationship between docility and altruism have been discussed by Boyd and Richerson (1985), Simon (1990), and Boehm (1997).

4. Social dominance is one of numerous mechanisms that might cause R2 to influence the phenotype of R1, but the masking effect is similar to the phenomenon of genetic dominance.

5. Group selection promotes behavioral uniformity in the case of altruistic behaviors, but a mixture of behaviors might be favored by group selection in other contexts. In addition, group selection can favor the evolution of incentive systems that create fitness differences within groups, rewarding group-beneficial behaviors and punishing group-detrimental behaviors. Thus, only *some* forms of fitness differences within groups can be interpreted as evidence against group selection. See Sober and Wilson (1998) for a discussion of these topics.

6. Boyd and Richerson's (1985) concept of "indirect bias" provides one possible mechanism for convergence upon a randomly chosen behavior. If one member of the group is chosen as a model on the basis of one trait (e.g., hunting ability), but also is copied with respect to a second trait (e.g., tendency to share), then selection of the second trait is random if the two traits are randomly associated with each other in the population.

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