The Evolution of Conformist Transmission and the Emergence of Between-Group Differences

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Unlike other animal species, much of the variation among human groups is cultural: genetically similar people living in similar environments exhibit strikingly different patterns of behavior because they have different, culturally acquired beliefs and values. Such cultural transmission is based on complex, derived psychological mechanisms that are likely to have been shaped by natural selection. It is important to understand the nature of these evolved psychological mechanisms because they determine which beliefs and values spread and persist in human groups. Boyd and Richerson showed that a tendency to acquire the most common behavior exhibited in a society was adaptive in a simple model of evolution in a spatially varying environment, because such a tendency increases the probability of acquiring adaptive beliefs and values. Here, we study the evolution of such "conformist transmission" in a more general model in which environments vary in both time and space. The analysis of this model indicates that conformist transmission is favored under a very broad range of conditions, broader in fact than the range of conditions that favor a substantial reliance on social learning. The analysis also suggests that there is a synergistic relationship between the evolution of imitation and the evolution of conformism. We conclude by examining the role of conformism in explaining the maintenance of cultural differences among groups. © 1998 Elsevier Science Inc.

KEY WORDS: Culture; Evolution; Dual inheritance; Cultural boundaries; Conformism; Conformist transmission.

One of the fundamental tenets of anthropology has always been the notion that most variation between human groups is cultural (Boas 1984: 145). Three ideas form the core of this notion. First, individuals living in the same group tend to behave in similar ways. hold similar moral values,

and believe similar things about the world, whereas people living in different groups tend to think and behave differently. Second, such beliefs and values are transmitted within social groups by various forms of social learning. And third, these differences create boundaries between groups that often persist for long periods of time. Despite the continued prevalence of these assumptions within anthropology, there has been little effort to explain the existence of cultural variation between groups in terms that are consistent with the assumption that the psychological mechanisms that create and maintain such variation are evolved adaptations. In this article, we provide one evolutionary explanation for why people in the same group have similar ideas, values, behaviors and why these endure through time.

Although a vocal minority of anthropologists believe that all important forms of cultural variation can be explained by differences in the physical or biological environment or in technology (Harris 1979), most anthropologists are convinced that these factors are not sufficient to explain most cultural differences. History, linguistic studies, and the ethnographic record furnish evidence that groups possessing entirely different religious systems, social structures, and domestic relations may inhabit similar environments and possess similar technologies. The Amish farmers of Lancaster, Pennsylvania, for example, distinguish themselves as a cultural group in a multiplicity of ways, including their religion, dress, child-rearing strategies, and agricultural practices, despite their proximity to and frequent interaction with their non-Amish neighbors. These Amish differ from their neighbors because they have evolved different sets of ideas, beliefs, and values; they are identifiable as a group because these ideas cause them to behave differently from their non-Amish neighbors even though they live in the same place with access to the same technology.

Moreover, significant differences among groups are maintained through time despite factors such as migration and intermarriage, which constantly mix individuals from different groups. As Barth (1969) points out, cultural "boundaries persist despite the flow of personnel across them." We aim to explain why differences among groups arise and how those differences are maintained despite the fact that such mixing acts to homogenize cultural groups and deplete intergroup variation.

Although most anthropologists agree that cultural variation among groups is real and important, there is little agreement about how such variation arises or why it persists. Often anthropologists simply say these differences are "cultural." Although this is true, it explains little about why differences among groups exist, why similarities within groups are maintained, or why some beliefs are shared and others are not. A complete theory should address these questions at two levels:

1. At a cultural evolutionary level, we want to know how beliefs and values are transmitted among individuals, and why this process generates and maintains differences among groups.
2. At the genetic evolutionary level, we want to understand the conditions under which natural selection could favor the psychological mechanisms posited to explain the cultural evolution of groups.

Previously, Boyd and Richerson (1985) have shown that: (1) a particular form of social learning, termed *conformist transmission*, can maintain similarities within

cultural groups and differences between cultural groups; and (2) natural selection favors genes leading to conformist transmission in a simple model of evolution in a spatially varying environment. Here, we show that selection favors psychological mechanisms that give rise to a conformist transmission under a wider range of conditions, including both spatially and temporally varying environments. We also examine and compare other possible explanations for between-group differences and within-group similarities, and suggest research to delineate and differentiate these hypotheses.

CULTURAL EVOLUTION AS A PROBLEM IN POPULATION DYNAMICS

In humans, social learning gives rise to cumulative cultural change not seen in other animals, and, as a result, understanding human evolution requires new principles not relevant to the study of other species (Boyd and Richerson 1996). This does not mean that humans have somehow transcended biology. Quite to the contrary, we can construct a foundation for emergent cultural phenomena by understanding the evolution of complex cognitive adaptations. Evolutionary psychology proposes that all brains, including human brains, consist of numerous domain-specific mental processors designed by natural selection to solve problems that were recurrent in the evolutionary past. Cultural transmission mechanisms represent a kind of special purpose adaptation constructed to selectively acquire information and behavior by observing other humans and inferring the mental states that give rise to their behavior. Our effort here is to show the evolutionary plausibility of one such mechanism and its implication for higher level processes related to cultural group formation and cultural change.

Before beginning our discussion of conformist transmission and its consequences for the population-level dynamics of cultural change, it is important to understand why we distinguish cultural transmission from other forms of learning. In all forms of phenotypic plasticity, organisms modify their behavior based on cues available from their environment. As a consequence, genetically similar individuals behave differently in different environments. The psychological mechanisms that determine which environmental cues are salient, and how organisms respond to these cues, can often be understood as adaptations. In many group-living organisms, social cues are important—individuals adjust their behavior in response to the behavior of others in their group. In many species, the use of social cues can lead to the development of local "traditions" (Lefebvre and Palmeta 1988; McGrew 1992; Wrangham et al. 1994); however, there is no evidence that nonhuman traditions change cumulatively over time or allow the development of behaviors that individuals could not learn on their own. In contrast to these types of phenotypic plasticity, cultural transmission in humans arises because people are able to acquire novel behaviors, which they could not learn on their own, by observing or being taught by others. In other animals, the ability to acquire novel behaviors by observational learning is absent, as is the case in most species, limited to a narrow range of behav-

iors, as in the case of song learning in song birds, or very rudimentary, as seems to be the case in apes (Galef 1992; Tomasello et al. 1993; Whiten and Ham 1992).

One of us has argued at length (Boyd and Richerson 1996; see also Tomasello 1994) that the human ability to acquire novel behaviors by observation is the reason that human cultural change is cumulative. The following example illustrates the essence of the argument. Suppose an early hominid learned, through independent, trial-and-error experimentation, to strike rocks together in order to make flakes useful for food processing. Her companions, because they spent time near her and would thereby be exposed to the same kinds of learning conditions, might learn to make flakes too—entirely on their own. This behavior could be preserved through socially mediated learning (termed "local enhancement" by students of animal social learning) because, for example, groups in which tools were used would spend more time in proximity to the appropriate stones and food, thereby increasing an individuals' probability of acquiring a flaking technique. (This mechanism is similar to that thought to preserve chimpanzee nut-cracking or termiting behaviors [Tomasello 1994]). However, that is, as far as it would go. If an especially talented individual found a way to improve the flakes, this innovation would not spread to other members of the groups because each individual acquired the information necessary to manufacture the tool by interacting with the environment. In contrast, if the early hominid had the ability to acquire the knowledge of how to make the tools by observing other tool makers, then innovations could persist as long as younger individuals were able to acquire the modified behavior by observing the actions of others. As a result, observational learning can lead to the cumulative evolution of behaviors that no single individual could invent on her own.

Because human culture is cumulative, understanding human behavior requires us to link the population dynamics of cultural variation to the psychological mechanisms that shape social learning. To understand why a group of people speak the way they do, you have to know the linguistic environment in which they grew up and the psychological mechanisms that shape the language acquisition in that linguistic environment. Thus, the linguistic environment of this generation is determined jointly by the linguistic environment during the last generation and the action of the learning mechanisms that control language acquisition. Therefore, to understand the evolution of the psychological mechanisms that shape culture, it is necessary to simultaneously account for how individual psychology shapes the cultural environment and how that environment conditions the behavior that people acquire.

In an effort to link individual psychology to the population-level dynamics of cultural evolution, Boyd and Richerson (1985) have conceptualized cultural transmission as the product of a series of analytically separable cognitive learning processes or transmission biases—here learning refers to both passive (e.g., observational learning, imitation) and active (e.g., teaching) processes. Because it is highly unlikely that biological evolution produced a generalized problem-solving capacity (Boyd and Richerson 1985; Cosmides and Tooby 1994; Lumsden and Wilson 1981; Tooby and Cosmides 1992; Fodor 1983 for an opposing view; and see Sperber 1994 for a refutation of Fodor), it makes sense to propose a complex of learning mechanisms or "transmission biases" that allow humans to effectively and efficiently ac-

quire beliefs, ideas, and behaviors from the immense amount of confusing and often contradictory information presented by the external world. Evolutionary considerations suggest that our cognitive abilities consist of learning rules that preferentially select and evaluate sensory data from prescribed subsets of externally produced information. These learning mechanisms provide "rules of thumb" that bias humans towards acquiring certain beliefs and behaviors without exhaustively examining and processing the immense amount of available social and environmental information.

Conformist transmission implies that individuals possess a propensity to preferentially adopt the cultural traits that are most frequent in the population. Under conformist transmission, the frequency of a trait among the individuals within the population provides information about the trait's adaptiveness. This psychological bias makes individuals more likely to adopt the more common traits than they would under unbiased cultural transmission. Unbiased transmission may be conceptualized in several ways. For example, if an individual copies a randomly selected individual from the population, then the transmission is unbiased. If individuals copy their parents or just their mother, then transmission also is unbiased.

At the population level, conformist transmission causes more common traits to increase in frequency. If cultural transmission is unbiased, then, barring the action of other forces, transmission will leave the frequency of the traits unchanged from one generation to the next. For example, if 60% of a population is performing a certain behavior, barring other forces, 60% of the population in the next generation also will perform that behavior. In contrast, conformist transmission would increase the frequency of the trait from 60% in one generation to, say, 65% in the next generation. All other factors being equal, the frequency of the most prevalent trait will continually increase from one generation to the next. If it were the only transmission bias, conformist transmission would rapidly cause the most frequent cultural traits to become the only cultural traits. Operating among other learning mechanisms (mechanisms that select, prioritize, and evaluate different kinds of social and environmental information) and under constraining external conditions, conformist transmission creates a directional force that tends to establish and maintain cultural norms.

The unbiased transmission (or faithful imitation) of beliefs and values from one generation to the next is *not* sufficient to maintain cultural variation or cultural boundaries unless cultures are perfectly isolated from each other. When transmission is unbiased, any amount of cultural mixing will rapidly obliterate cultural differences between groups. To see why, consider the following example: suppose people living in two neighboring cultures have different ideas about the appropriate level of bride price. Further, suppose that in each culture, 95% of the groups' members acquire their beliefs about the appropriate levels of bride price by accurately internalizing the values of their local community, whereas 5% acquire their beliefs from individuals in the other culture. Such mixing could be due to intermarriage, other forms of migration, or simply contact with members of the other group. With these assumptions, the average difference between the two groups will decrease at 5% per generation. Given that intermarriage and other forms of cultural influence are common along cultural boundaries and that cultural boundaries often persist for

many generations, unbiased transmission by itself cannot explain the maintenance of cultural boundaries.

Boyd and Richerson (1985) analyzed a model that showed that natural selection favors conformist transmission relative to unbiased transmission in spatially varying environments. In each of two habitats, learning processes cause the locally favored cultural traits to be more common than less favored variants. At the same time, however, migration among habitats introduces and maintains less favored variants in each habitat. Individuals predisposed to imitate the common type have a greater chance of acquiring the favored variant, and thus genes leading to this psychological mechanisms are favored by natural selection. Tooby (1996, personal communication) pointed out a possible weakness in this model by arguing that conformist transmission would likely be deleterious in a temporally varying environment. If the conformist effect was strong enough to preserve cultural differences among groups, Tooby argued, it would also be strong enough to prevent the spread of newly beneficial beliefs and practices following a change in the environment. Immediately after a rapid environmental change, beliefs that are beneficial in the new environment would be rare, whereas beliefs that were beneficial in the old environment would be common; therefore, a strong conformist effect wold preserve deleterious beliefs and prevent the spread of beneficial ones. If this argument were correct, then it would be much less obvious how conformist transmission could evolve.

To understand the conditions under which conformist transmission is adaptive, we constructed a model of the evolution of conformist transmission in an environment that varies in both space and time. We also allowed an individuals' reliance on social learning to coevolve with conformist transmission and compete with individual learning. Because conformist transmission produces nonlinear dynamics, analytical results are difficult to achieve when environments change stochastically. Accordingly, we performed a number of computer simulations intended to explore the parameter space and illuminate the evolutionary dynamics of both conformist and unbiased transmission. The results of these simulations indicate that conformist transmission is favored in temporally varying environments under a broad range of conditions. In fact, the present results indicate that a strong conformist effect in social learning evolves under a wider range of conditions than does a heavy reliance on social learning—whatever the equilibrium reliance on social learning, it always contains a strong conformist effect.

MODELING THE EVOLUTION OF SOCIAL LEARNING AND CONFORMIST TRANSMISSION

We assume that the central adaptive problem facing individuals is how to best use environmental cues to choose behavior when the environment changes in space and time. For the purpose of modeling this situation, we have divided environmental cues into two kinds: nonsocial and social. Nonsocial cues predict the current environmental state, but these cues are imperfect. Relying on the nonsocial cues alone will allow individuals to do better than random, but will sometimes lead to errors.

Individuals also can observe the behavior of other individuals in the population, and to the extent that individuals in the population are doing better than random, their behavior also provides a cue about the best behavior in the current local environment. The question is: How should psychology evolve to best use these two sources of information? It is important to keep in mind that the usefulness of social cues depends on how people have utilized both social and nonsocial information in the past; therefore, this question cannot be answered without taking into account how evolving psychology shapes observable behavior in the population over time.

To investigate this question, we constructed a simple mathematical model. Here we provide only an informal description of the model. A complete description may be found in the Appendix. In our model, a population is subdivided into a number of large subpopulations. Each subpopulation experiences one of two environmental states, labeled 1 and 2. Each individual also can acquire one of two behaviors, similarly labeled 1 and 2. Behavior 1 is favored (meaning it gives the individual a better chance of surviving) in environment 1 and behavior 2 is favored in environment 2. Thus, selection will favor learning mechanisms that make individuals more likely to acquire the favored behavior in the current environment.

The model is divided into four stages: cultural transmission (which includes conformist transmission), individual learning, migration, and natural selection. First, individuals acquire their initial behavior by imitating members of the previous generation. Genetic variation among individuals affects both the extent to which individuals rely on social learning and the degree of conformism in that social learning. The probability that an individual without any propensity for conformism (which we term unbiased transmission) acquires a behavior is the same as the frequency of that behavior in the previous generation. For example, if 73% of the previous generation exhibits behavior 1, an individual using unbiased transmission has a 73% chance of acquiring behavior 1. Those with a conformist psychology will have a probability higher than 0.73 (in this example) of acquiring behavior 1—their particular probabilities depend on the strength of the conformist effect in their particular genotype.

Next, all individuals try to learn the best behavior for the current environment. Each individual acquires information from the environment that allows her to infer which trait is currently adaptive. We refer to this process as individual learning. Because environmental information is imperfect, individual learning does not always produce the correct behavior for the current environment. The average quality of environmental information is measured by the parameter ρ, which ranges from 0.50 to 1.0. This parameter represents the probability of selecting the currently adaptive behavior given that the individual relies entirely on individual learning. When $\rho = 0.50$, the environment provides no information to the learner; each behavior seems equally likely to be best. As ρ increases, the environment yields more accurate information (on average) and the probability of acquiring the best behavior using environmental cues approaches one. Individuals within a population may acquire different behaviors through individual learning, because the ambiguity of the environmental information leads some to select the correct (currently adaptive) behavior and others to acquire the incorrect behavior. The higher the value of ρ, the more likely it is that individuals will accurately infer the correct behavior from the available environmen-

tal information. We believe that real world cases of learning span this range—from very difficult to quite easy. For example, avoiding prolonged exposure to the sun in order to prevent skin cancer 20 or 30 years later would be extremely difficult to learn on the basis of an individual's experience in the environment (ρ would be close to 0.50). On the other hand, an individual will quickly, if painfully, learn to avoid touching the radiator cap on an overheated engine without ever being told not to touch it.

In the above-described stages, we assume that in order to avoid errors, individuals adopt a particular behavior only if the probability that it is correct is *sufficiently* better than its alternative, meaning these individuals have acquired sufficiently accurate environmental information through trial-and-error learning, for example, to allow them to select the adaptive behavior with an acceptable degree of certainty. When environmental cues are not of sufficiently high quality, individuals imitate. Of course, raising the standards of evidence will also cause more trials to be indecisive (because there often is insufficient information available to make the choice with an acceptable degree of certainty), and more individuals will rely on imitation. Thus, there is a tradeoff: selection can increase the accuracy of individual learning, but only by also increasing the probability that environmental cues will be indecisive and thereby causing individuals to increase their reliance on imitation.

The structure of social learning is described by two parameters, L and Δ. L measures the relative reliance on social learning versus individual learning. For example, if $L = 0.60$, an individual learns socially 60% of the time and from the environment 40% of the time. Small values of L mean that an individual is wiling to depend on even low-quality environmental cues; larger values of L mean that individuals only rely on individual learning when environmental cues provide a clear indication that one trait is better than the other. In this model, social learning may be more or less influenced by conformist transmission. The strength of the conformist effect is measured by the parameter Δ, which ranges from 0 to 1. If $\Delta = 0$, individuals simple perform unbiased imitation; the frequency of a trait does not affect their propensity to acquire that trait. When $\Delta = 1$, individuals are much more likely to select the more frequent of the two behaviors. See the Appendix for the functional form of this relationship.

To model the genetic evolution of social learning and conformist transmission, we assume that an individuals' propensity to imitate and the importance of the conformist bias in imitation are genetically variable. In particular, we assume a haploid genetic system with 400 alleles (at a single locus) that vary in both the degree of reliance on social learning and the strength of conformist transmission that they produce. The first component, the degree of reliance on social learning of each allele, determines an individuals' overall reliance on imitation relative to individual learning (i.e., her L value); 20 allelic values range uniformly from total imitation ($L = 1$) to complete reliance on individual learning ($L = 0$). The conformist transmission component determines the degree to which an individual uses the prevalence of a behavior in the previous generation to bias the acquisition of that behavior (i.e., her Δ value); again, 20 allelic values range uniformly from unbiased imitation ($\Delta = 0$) to a very strong conformist effect ($\Delta = 1$). Initially, populations consist mostly

(99.99%) of individuals possessing the genotype for 100% individual learning ($L = 0$) and no conformist effect ($\Delta = 0$). The remaining portion (0.01%) of the population is uniformly distributed over all the remaining genotypes; thus, all 400 possible combinations of the 20 possible values of L and the 20 possible values of Δ are present in the population.

After the cultural transmission and individual learning, each subpopulation experiences migration and selection. These events affect the frequencies of behaviors 1 and 2, and the allelic frequencies in each subpopulation. During the migration phase, individuals move between subpopulations. In each generation, some immigrants enter a given subpopulation from other subpopulations that have experienced a different history of recent environmental fluctuations. Immigrants with a heavy reliance on social learning (high L) and a strong conformist effect ($\Delta \approx 1$) can more rapidly learn the common behavior in their new environment through imitation. However, increasing the number of immigrants affects the extent to which the current subpopulation can be used as an accurate indicator of the recently adaptive behavior. The parameter m, the rate of migration among subpopulations, represents the proportion of each subpopulation that has moved to a new subpopulation. Each population receives an equivalent number of immigrants who possess a distribution of genotypes drawn at random from the overall population.

Finally, selection influences the process because individuals with the nonadaptive behaviors are less likely to survive than those with the adaptive behavior. This differential mortality increases the frequency of individuals with the adaptive behavior. This, in turn, leads to natural selection favoring genetically transmitted learning mechanisms that increase an individual's chance of acquiring the locally adaptive behavior.

During each generation, a subpopulation may experience a sudden shift in the environment from the current state to the alternative state. When the environment switches, say from state 2 back to state 1, behavior 2, which may have been the adaptive behavior for the last 100 generations, is no longer adaptive. Individuals seeking to survive must find a way to learn behavior 1, the new adaptive behavior. The probability that the environment does not shift is given by the parameter ϵ. If $\epsilon = 0.98$, for example, then the environment remains unchanged 98% of the time, meaning that there is a 98% chance that the current environment matches the environment of the preceding generation. Hence, $1 - \epsilon$ (0.02 in our example) is the probability that the environment switches during any given generation.

This model makes a number of unrealistic simplifying assumptions in order to focus clearly on the effects of a temporally varying environment on the evolution of conformist transmission. The effects of relaxing some of these assumptions have been studied elsewhere (Boyd and Richerson 1985, 1989). Increasing the number of individuals available to imitate or increasing the number of traits increases the strength of the conformist effect at evolutionary equilibrium. Allowing nonrandom sampling or continuously varying trait values has little qualitative effect on the results. Multiple learning events within a generation can be accommodated by reinterpreting the time scale—the evolutionary time step becomes a month or year rather than a generation. All the same results hold, the only thing that changes is the rate at

which things happen. Other assumptions are essential to the structure of the model. For example, if individuals can learn, and facultatively use, the optimal behavior in each possible environment, then the central adaptive problem disappears, and there is no need for social learning.

RESULTS

By systematically varying ρ, the accuracy of environmental information, m, the migration rate, ϵ, the degree of environmental stability, and n, the number of sub-populations, we have learned several important things about the evolution of social learning and conformist transmission. First, the degree of reliance on social learning (L) depends on strongly on the accuracy of environmental information (ρ) and the frequency of environmental fluctuations ($1 - \epsilon$). The evolution of high values of L requires low-accuracy environmental information ($\rho \approx 0.5$) and infrequent environmental shifts ($\epsilon \approx 1.0$). In contrast, conformist transmission evolves to nearly maximum strength ($\Delta \approx 1$) over a much wider range of parameter combinations than does a strong reliance on social learning, provided there is at least a small amount of migration. In fact, although extreme variations in these parameters will prevent the evolution of conformist transmission, the set of parameter values under which conformist transmission fails to evolve is surprisingly small. Second, the presence of conformist transmission effectively increases the accuracy of social learning in most situations and consequently facilitates a greater reliance on social learning.

The following summarizes the results of 152 separate simulations used to test the influence of varying four different parameters, m, n, ϵ, and ρ. The migration rate, m, was varied between 0.0 and 0.48, with increments as small as 0.01 and as large as 0.04 between consecutive simulations. The degree of environmental stability, ϵ, was varied from 0.99 to 0.55, with decrements between 0.01 and 0.04. The number of subpopulations, n, was varied between 2 and 5, with increments of 1. And finally, ρ, the accuracy of environmental information, ranges between 0.05 and 1.0, with increments between 0.1 and 0.2. Each parameter was varied through a sequence of simulations while the other parameters were held constant.

We set the initial conditions such that 99.99% of the individuals in each subpopulation possessed the allele for *all* individual learning (vs. social learning) and no conformist effect. The remaining 0.01% of the population was distributed equally over the other 399 genotypes representing all possible combinations of both social learning reliance (L) and conformist transmission (Δ). Similarly for the cultural traits, 80.0005% of the individuals in each subpopulation started with behavior 1 (and the environments for each subpopulation always began in environmental state 1), whereas 19.995% of the population started with behavior 2. All the results presented here are based on these initial conditions, but we also ran 23 test simulations using various combinations of different initial conditions. These tests demonstrated, to our satisfaction, that variations in the initial distribution of genotypes have no perceptible effect of the long-run equilibrium state of the population.

The parameters Δ and L were assumed to have reached steady state or equilibrium when their values changed by less than 0.00001 (changes in the sixth decimal place) per 1000 generations. Of course, these values are not true equilibria because selection varies randomly; however, the induced changes in gene frequency were very small. In every case tested, this occurred well within 300,000 generations, so we routinely ran al simulations to 300,000 generations to assure that equilibrium was reached.

Selection Favors Conformist Transmission as Long as Environments do not Change too Rapidly

We investigated the effect of environmental variation on the evolution of conformist transmission by varying the rate of environmental change in successive runs of the simulation. Figure 1 plots evolutionary equilibrium values of L (the amount of social learning) and Δ (the strength of conformist transmission) for differing values of the parameter ϵ, the probability that the environment remains unchanged from

FIGURE 1. Equilibrium values of L and Δ for different rates of environmental variation. At evolutionary equilibrium, the strength of conformist transmission (Δ, which ranges from 0 for unbiased transmission to 1.0 where the more frequent of two behaviors is imitated) is high at moderate rates of environment change (the probability that the environment is unchanged each generation, ϵ, between 0.6 and 0.8). However, the reliance on social learning (L as proportion ranging from 0 to 1.0) decreases rapidly over the same range of environmental stability. The equilibrium values of L and Δ were computed assuming that there are two populations ($n = 2$), the migration rate, m, is 0.02, and that the accuracy of environmental information, ρ, is 0.841.
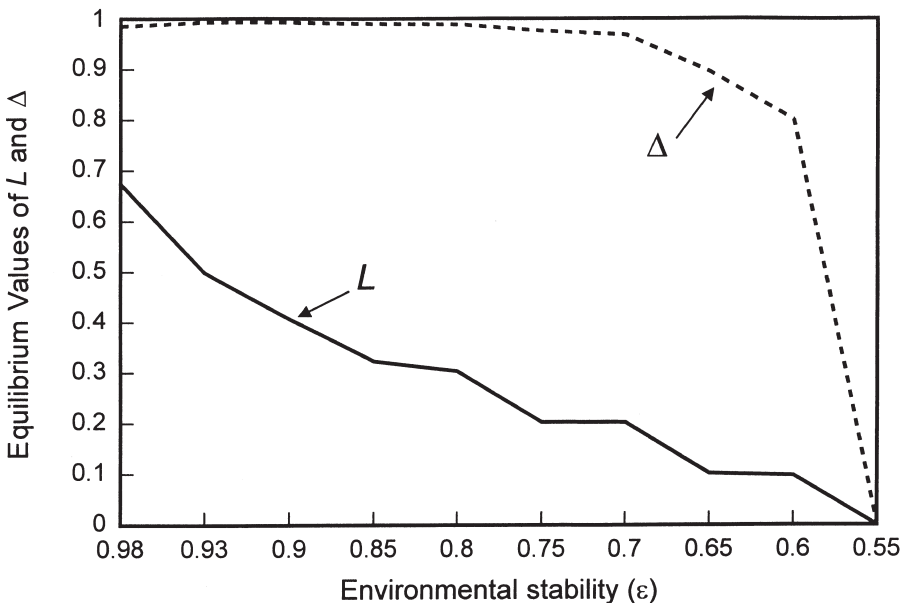
one generation to the next. For ϵ values between 0.98 and 0.80, Δ fluctuates around an equilibrium value just below one. Equilibrium values of Δ begin to decline after about $\epsilon = 0.80$, but remain above 0.80 until approximately $\epsilon = 0.60$. For values of $\epsilon < .060$, Δ drops precipitously to near zero, but never goes completely to zero. Evolutionary equilibrium produces a substantial degree of conformist transmission ($\Delta > 0.80$) over an extremely wide range of ϵ values.

Greater Rates of Environmental Change Favor Less Reliance on Social Learning

Increasing the rate of environmental change gradually reduces the evolutionary equilibrium value of L, the importance of social learning relative to individual learning. Figure 1 also shows that the proportion of social learning (L) rises to an equilibrium value of 0.67 when $\epsilon = 0.98$ and gradually drops to a value of 0.20 (at $\epsilon = .70$). Eventually L approaches zero.

Interestingly, even when most individuals learn on their own and only a few imitate (e.g., $L = 0.2$), conformist transmission remains adaptive and evolves to 80% of its maximum value. When one imitates, even in an environment that shifts 40% of the time, preferentially copying the most frequent behavior remains advantageous. Consequently, it is the evolution of social learning, and not the evolution of the conformist effect, that demands more stable environments. More stable environments favor both the alleles for a heavy reliance on social learning and the alleles for strong conformist transmission.

Conformist Transmission Increases the Reliance on Social Learning

Figure 2 plots the evolutionary equilibrium values of L and Δ under conformist transmission and those for L when Δ is constrained to be zero (no genetic variability for Δ exists in population) for varying degrees of environmental stability (ϵ). Conformist transmission increases the equilibrium value of L by enhancing the effectiveness of social learning, even when the environment frequently switches. This result may seem counterintuitive until one realizes that conformist transmission acts to increase the accuracy of social learning by giving individuals a guide in accessing the more adaptive behavior.

Selection Favors Strong Conformist Transmission Unless Individual Learning is Very Error Prone or Highly Accurate

The conformist parameter, Δ, evolves to near its maximum value over a substantial span of ρ values. The parameter ρ represents the probability of learning the correct behavior using only (nonsocial) environmental cues. Remember, there are only two behaviors, so the minimum value of ρ is 0.50, meaning individuals have of 50/50 chance of acquiring the correct behavior. Figure 3 gives the equilibrium values of L and Δ for different values of ρ. Over the entire middle range of ρ values, be-
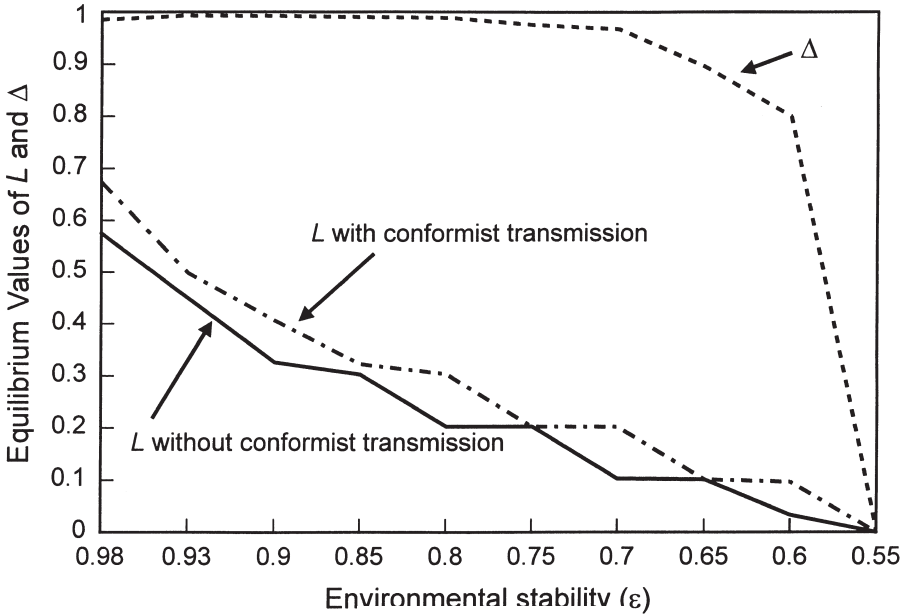
FIGURE 2. Equilibrium values of L for different rates of environmental variation when conformist transmission cannot evolve. When there is no genetic variation affecting the strength of conformist transmission, Δ, the evolutionary equilibrium value of L is lower than when Δ is free to evolve to its optimal value. Because conformist transmission causes the population to track the environment more effectively, it makes social learning more useful. The equilibrium values of L and Δ were computed assuming that there are two populations ($n = 2$), the migration rate, m, is 0.02, and that the accuracy of environmental information, ρ, is 0.841.

tween 0.618 and 0.945, Δ rises to an equilibrium above 0.9, and only after $\rho = 0.977$ does Δ begin to drop significantly. Even at large values of ρ, when environmental learning is very accurate, the conformist effect still achieves values above 0.60. At small values of ρ (below 0.618), the equilibrium value of Δ declines because the most frequent behavior in the population is no longer a much better predictor of the currently adaptive behavior than the behavior of a randomly selected individual. Despite this problem, Δ still achieves values above 0.60 when $\rho = 0.540$. Interestingly, it does not matter whether it is easy (ρ is big) or hard (ρ is small) to determine the best behavior using environmental cues; conformist transmission evolves in both cases.

The reliance on social learning, however, is a different story. Figure 3 shows that for values of $\rho < 0.788$, approximately 85% of learning will be social learning and 15% will be individual learning. Although conformist transmission remains nearly constant above 0.9 between $\rho = 0.788$ and 0.945, the proportion of social learning steadily declines from $L = 0.85$ to $L = 0.15$. So, although as ρ increases, individuals are relying less on social learning, but when they do use social learning a strong conformist effect persists. Social learning eventually drops below 10% at $\rho = 0.977$, but never goes exactly to 0.
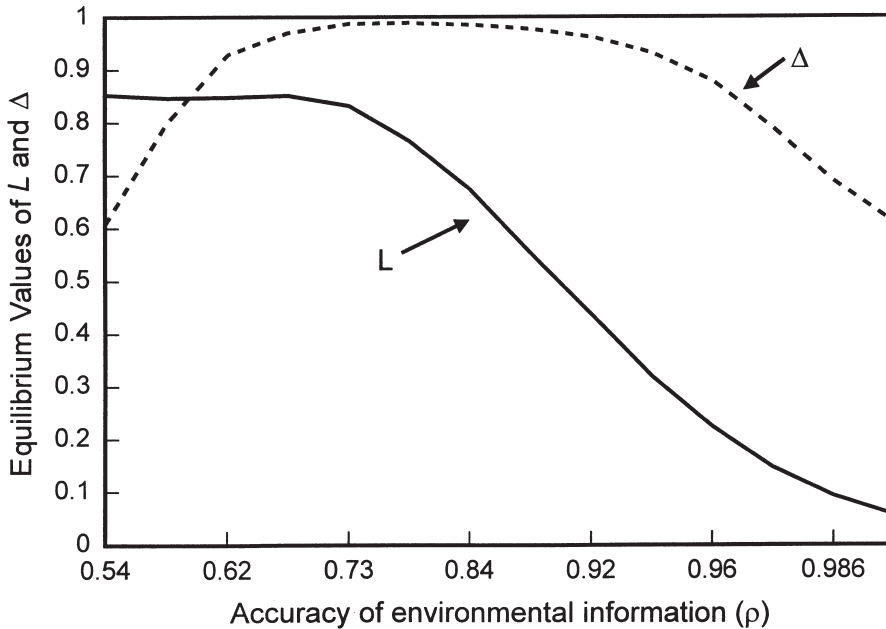
FIGURE 3. Equilibrium values of L and Δ for different levels of the accuracy of environmental information. As the accuracy of the cues that allow individuals to predict the current state of the environment, ρ is increased from 0.5 (cues are completely uninformative) to 1.0 (cues allow perfect prediction of environmental state), the equilibrium importance of socially learning declines steadily from a high of about 0.85 to approximately zero. In contrast, the equilibrium strength of conformist transmission is almost at its maximum value, 1, at intermediate values of ρ, and declines to lower still substantial values when ρ is near zero or one. The equilibrium values of L and Δ were computed assuming that there are two populations ($n = 2$), the migration rate, m, is 0.02, and that the stability of the environment, ϵ, is 0.98.

Conformist Transmission is Favored for a Wide Range of Migration Rates

Figure 4 illustrates that increasing the rate of migration among subpopulations gradually reduces the approximate equilibrium value of L for two different values of ρ. Over the entire range of migration rates, from $m = 0.01$ to 0.45, L drops from 0.68 to 0.50 and from $L = 0.85$ to 0.70 for $\rho = 0.841$ and 0.977, respectively. However, Δ, the conformist parameter, stabilized near its maximum value, just below one, over the entire range of migration rates (m). Increasing rates of migration has little effect on the evolution of conformist transmission and the degree of reliance on social learning. Note that, because of the mathematical method used in calculating the effect of migration and the use of only two subpopulations for most simulations, when a certain fraction emigrates out from a subpopulation, half of that fraction returns to the subpopulation through immigration. And with only two subpopulations, if $m = 0.5$, each subpopulations sees an *effective migration rate* of only 0.25 (only 1 of 4 individuals comes from a different subpopulation during the preceding generation), because half of the 0.5 who left end up returning to their original subpopulation (see the Appendix for details).
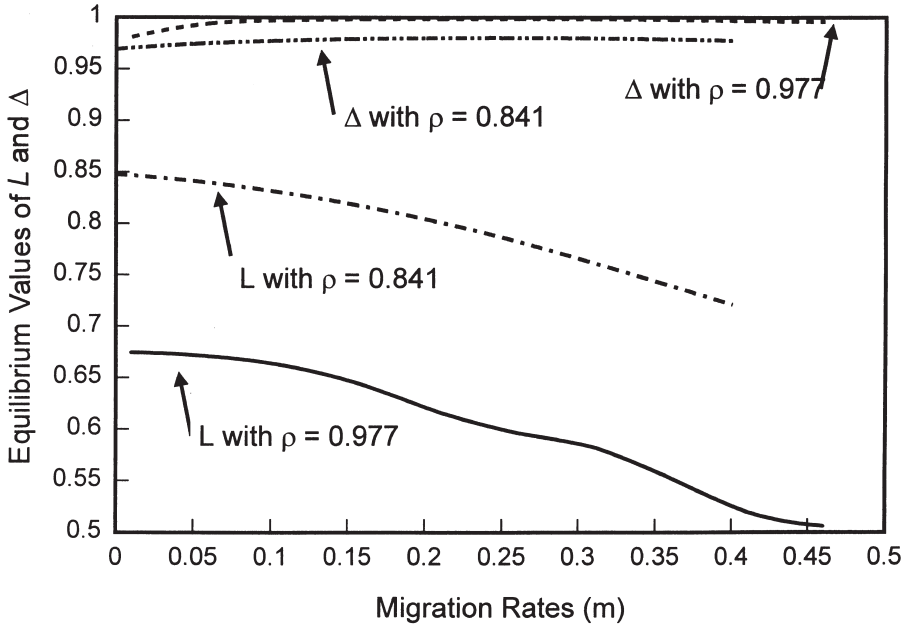
FIGURE 4. Equilibrium values of L and Δ for different rates of migration between populations. As the amount of migration between populations increases, the equilibrium importance of socially learning declines steadily, whereas the equilibrium amount of conformist transmission is almost constant. Increasing the quality of environmental information from $\rho = 0.841$ to $\rho = 0.977$ sharply decreases the equilibrium value of L and but has little effect on Δ. The equilibrium values of L and Δ were computed assuming that there are two populations ($n = 2$), the migration rate, m, is 0.02, and that the stability of the environment, ϵ, is 0.98.

As the migration rate approaches zero, the equilibrium value of Δ declines more rapidly. Figure 5 compares the effect of a zero migration rate ($m = 0$) with the effect of $m = 0.02$ on the evolution of conformist transmission and the reliance on social learning for increasing values of ρ. While the L curve is similar in both figures, the conformist curve for $m = 0$ reveals that, without some small amount of migration ($m = 0.02$), Δ does not maintain an equilibrium near its maximum value of 1. Conformist transmission allows immigrants to readily learn the most adaptive behavior for the current environment. When there is no migration, conformist transmission is not much better than unbiased imitation because most people are behaving correctly. However, even when m is as small as 0.02, the entire subpopulation is replaced every 50 generations, and, therefore, conformist transmission is useful.

Varying the Number of Subpopulations Has Little Effect on the Model's Behavior

The number of subpopulations has little effect on either L or Δ. As shown in Figure 6, L decreases from 0.62 to 0.59 between $n = 2$ and 5. Δ achieves a nearly identical
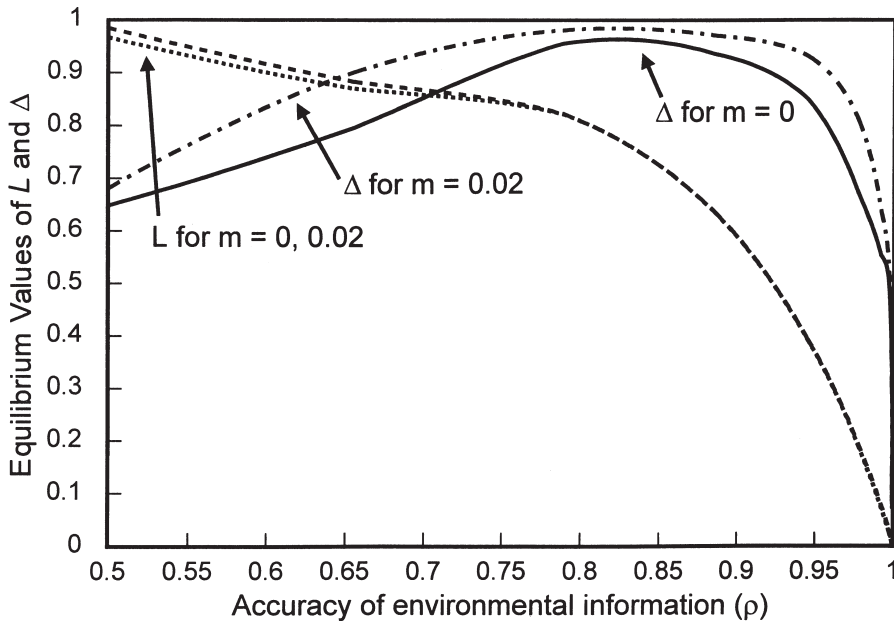
FIGURE 5.   Equilibrium values of L and Δ for different levels of accuracy of environmental information and very low levels of migration. Changing the amount of migration from a low value (0.02) to zero has a marked effect on the evolutionary equilibrium values of Δ, but little effect on the evolutionary equilibrium value of L. The equilibrium values of L and Δ were computed assuming that there are two populations ($n = 2$), the migration rate, m, is 0.02, and that the stability of the environment, ϵ, is 0.98.

equilibrium value just below 1 for all values between $n = 2$ and 5. The number of subpopulations does not strongly affect the equilibrium value of L and Δ in this model. Perhaps in models with more than two different environments n may be more significant.

Although it is difficult to determine the strength of conformist transmission in the current human cognitive apparatus, most people would agree that humans learn many important beliefs, ideas, values, and behaviors from other individuals and not from the nonsocial environment. After thorough testing of this simulation, we can find no circumstance under which social learning evolves to a significant degree and conformist transmission does not, so long as there is at least a little migration. However, several circumstances show the evolution of a strong conformist tendency ($\Delta > 0.50$), but produce only a very small degree of social learning (L < 0.1).

WHY IS CONFORMIST TRANSMISSION IMPORTANT?

Conformist transmission accounts for the fact that there is "heritable" cultural variation among human groups. Humans live in cultural groups in which group members tend to believe similar things about the world and behave in similar ways. Individu-
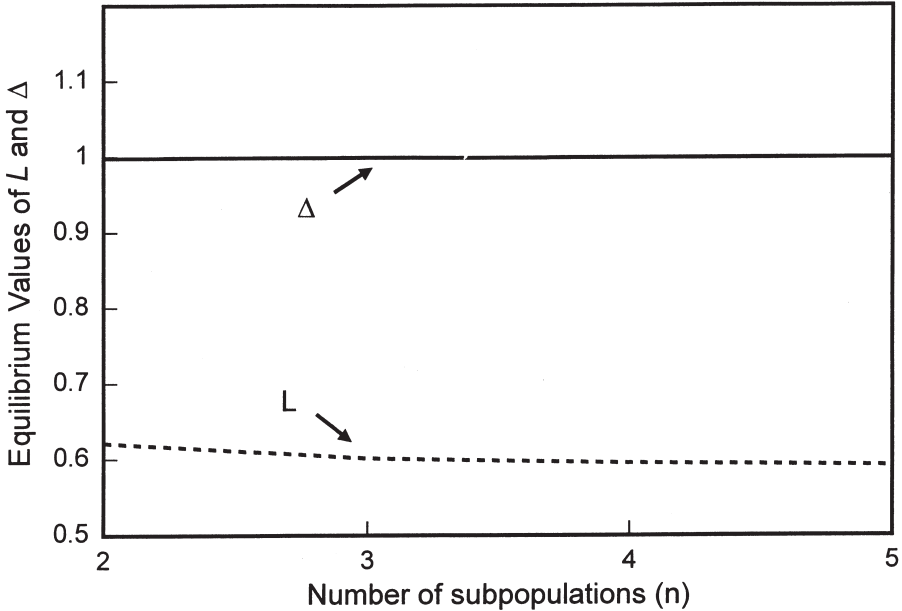
FIGURE 6. Equilibrium values of L and Δ for different numbers of subpopulations. Changing the number of subpopulations has little effect on the equilibrium levels of either social learning or conformist transmission. The equilibrium values of L and Δ were computed assuming that the migration rate, m, is 0.02, the accuracy of environmental information, ρ, is 0.841, and the stability of the environment, ϵ, is 0.98.

als in neighboring groups tend to believe different things and behave in different ways, even though people from different groups may interact and even intermarry. Conformist transmission generates a population-level process that creates and maintains group boundaries and cultural differences through time. Such boundaries may establish the initial conditions that lead to the development of group stereotypes, ethnic conflict, and racial strife. Delineating both the micro-level psychological mechanism of conformism, as well as the population-level processes to which they give rise, may further our understanding of these important social phenomena.

Competing Explanations For Within-Group Similarity And Between-Group Differences

There are at least three other, competing—though not mutually exclusive—explanations for the existence of cultural variation at the group level, which we categorize as: (1) variation in the physical and biological environment, (2) different local optima, and (3) punishment. First, some scholars (Harris 1979; Hill and Hurtado 1996) deny that many of the important aspects of culture are socially transmitted and hence "heritable." Instead they believe that most so-called "cultural" variation

results from phenotypic plasticity. For humans, this kind of behavioral plasticity is usually portrayed as variations in behavior in response to different environmental information.

Second, the same environmental problems may have multiple solutions, and, consequently, the specific histories of different cultures may have led to divergent evolutionary trajectories—different solutions for the same problem. This process can maintain similarities among individuals within groups and differences between groups because individuals who deviate from the common behaviors in some dimension are worse off, because their rare behavior does not complement those of the rest of the culture. In this way, cultural variation is maintained in much the same way that natural selection maintains many different kinds of eyes in the animal kingdom. Third, norms enforced by social sanctions or punishment can stabilize a very wide range of social behaviors, and if such norms affect a wide enough range of behavior, they may be responsible for heritable cultural variation.

In this section we briefly examine each of these three hypotheses. We argue that the first hypothesis can be rejected on empirical grounds. The other two hypotheses are cogent, but have different empirical entailments than the hypothesis that conformist transmission maintains cultural variation. One should keep in the mind that these explanations are not mutually exclusive. All of them (and perhaps combinations of other transmission biases; see Boyd and Richerson 1987) may interact to establish and maintain cultural similarities and cultural differences.

Hypothesis 1: Environmental variation. Authors from otherwise disparate points of view (behavioral ecology, Hill and Hurtado 1996: 14; and cultural materialism, Harris 1979: 55–56) have argued that differences in physical, ecological, or economic environments are the main cause of variation among groups. These researchers suggest that members of human groups are similar because they live in the same environment, and people living in different human groups are different because they inhabit different environments. Of course, in the short run, people may differ because of differences in the social environment, but, according to this view, in the longer run the social environment is shaped by ecological circumstances. We do not believe that this hypothesis can explain the widespread existence of culturally distinct groups whose behavior differs in many important ways despite the fact that they inhabit very similar physical and ecological environments.

Reviewers of an earlier version of this article suggested that such cultural variation among groups is due to the historical patterns created when individuals responded opportunistically to the current distribution of behaviors expressed by other members of the group, and that by ignoring this historical dimension we have created a straw man. Although some authors (Alexander 1979: p. 77) have invoked this kind of argument as an explanation for human cultural variation, we do not think that such explanations are coherent or plausible. History is not a causal factor in explaining human behavior, but rather something to be explained, and we believe that any explicit, coherent explanation will necessarily incorporate a role for culturally transmitted information. If history is just the temporal working out of individual choices, then why is the "historical dimension" of human environments so impor-

tant to understanding the differences between human groups, but not so important in understanding the differences between chimpanzee groups? Although chimpanzees do have history and it does shape the behavior of social groups (De Waal 1982; Wrangham et al. 1994) it does not lead to the large-scale variation in space and time seen in humans.

The view that historical and cultural factors are unimportant also is implicit in the work of human behavioral ecologists (and others such as economists) who rely almost entirely on optimization models to predict human behavior. Although such models often provide a heuristic way to derive the steady-state outcomes of adaptive processes such as learning and natural selection, they are devoid of any historical dimension. The fact that some authors within these research traditions rely exclusively on optimization models suggests that they place little credence in historical or cultural explanations. For example, in their extensive efforts to explain the deviations of Aché foraging from the predictions of optimal foraging theory, Hill, Kaplan, and their co-authors (Hill and Hawkes 1983; Hill et al. 1984, 1987; Kaplan and Hill 1985; Kaplan et al. 1984; 1990) never invoke history or transmitted culture (although Kaplan [1987] does allude to the potential importance of cultural transmission in a general theoretical discussion). Instead they have sought only solutions consistent with the optimization behavioral ecological paradigm.

As for the cultural materialists, Marvin Harris (1979) is very clear about what primarily drives the development of social-cultural systems: technologies applied to ecosystems. Harris claims that, "similar technologies applied to similar environments tend to produce similar arrangements of labor in production and distribution, and that these in turn call forth similar kinds of social groupings, which justify and coordinate their activities by means of similar systems of values and beliefs" (Harris 1968: 4). In later work this becomes the "principle of infrastructural determinism" (Harris 1979: 55–56). Harris maintains that the interface between the economies and ecologies is the primary force in the evolution of human societies and, thus, the differences among human societies. We address these explanations with two ethnographic examples, taken from numerous possibilities, which show that substantial cultural differences exist between societies that possess similar technologies and inhabit similar (or some times identical) environments.

Many culturally distinct groups inhabit quite similar or identical environments. The Arawakan-speaking Machiguenga and the Panoan-speaking Yora, for example, represent two culturally distinct Amazonian Indian groups that possess identical technology and inhabit nearly identical and overlapping regions in and around Manu National Park in the southeastern Peruvian Amazon. Among a long list of cultural differences, the Machiguenga and Yora speak entirely different languages, with unrelated grammatical structures, different vowels, and different rules for verb conjugation: Further, the Machiguenga live in egalitarian single-family groups or small, nucleated family clusters organized through bilateral descent (Snell 1974), whereas the Yora live in larger hierarchically organized groups based on a dual moiety system and patrilineal descent (MacQuarry 1988).

Socially, the Yora have an elaborate system of marriage preferences, including cross-cousin preference, community endogamy, moiety exogamy, and marriage

class homogeneity. The Yoras' belief in these rules strongly affects the frequencies of different mating combinations. Adherence to these rules affects how a particular marriage is viewed by the community (Kensinger 1984; MacQuarry 1988). Machiguengas also have a preference for cross-cousin marriages (Johnson 1978), but possess none of these other marriage prescriptions or classifications.

Demographically, the Machiguenga live in individual family-based houses, whereas Yora live all together in larger *malocas*. The Yora have a well-defined tradition of raiding, and they frequently raid Machiguenga communities. The Machiguenga have no parallel tradition and never raid Yora communities. Moreover, both male and female Machiguengas wear *cushmas* (long cotton ponchos), where Yora females wear short skirts (called *samas*) and Yora males wear monkey tooth belts to which they tie their penises. The Yora have personal names, whereas traditionally the Machiguenga do not (Snell 19674). Further Glenn Shepard (1996, personal communication), who has worked extensively with both of these groups, has found that the Yora and Machiguenga possess fundamentally different traditional medical systems, including their concepts of illness classification and causation. The list goes on and on. The local ecology cannot account for the substantial differences maintained between groups inhabiting adjacent and often overlapping regions.

The Dinka and the Nuer provide another excellent example of two groups who lived in the same environment, but maintained different cultures. Before 1820, the Nuer and Dinka (Kelly 1985) occupied adjacent regions in the southern Sudan. Despite inhabiting similar environments and possessing identical technology, the two groups differed in significant ways. Economically, both the Dinka and the Nuer raised cattle, but the Dinka maintained smaller herds of approximately nine cows per bull, whereas the Nuer maintained larger herds with two cows per bull. The Nuer ate mostly milk, corn, and millet, and they rarely slaughtered cows. The Dinka, however, frequently ate beef. Politically, the Dinka lived in small tribes that corresponded to their groups' wet season encampment. In contrast, the Nuer organized according to a patrilineal kin system that structured tribal membership across much larger geographic areas. Consequently, the size of a Dinka tribe was limited by geography, whereas the Nuer system could organize much larger numbers of people over greater expanses of territory. Despite the similarity of their environments, these two group showed substantial economic and political differences.

The cultural differences between the Nuer and the Dinka cannot be accounted for by subtle ecological differences between their territories. After 1820, the Nuer began successfully conquering and settling on Dinka lands. After more than 100 years of occupying the "Dinka environment," no Nuer had become Dinka; however, many conquered Dinka had adopted Nuer practices. We cannot see how this, and similar examples, can be reconciled with the idea that environmental differences cause cultural variation. Either they fail to explain why the Dinka and the Nuer exhibit such large cultural differences while inhabiting the same environment, or, given some microecological difference, they fail to explain why the Nuer do not become Dinka after about 100 years of living on Dinka lands. Environmental variation (or even environment plus technological variation) cannot account for much of the observed behavioral variation within and between human groups.

Hypothesis 2: Multiple solutions to adaptive problems.   Real-world environments probably result in complex fitness topographies containing a variety of peaks, valleys, chasms, and plateaus. Consequently, slight variations in initial conditions (the starting position on the fitness landscape) can drive two quite similar populations toward increasingly divergent adaptive "peaks" or solutions (see Boyd and Richerson 1992a for discussion and further references). And, because many adaptive behavioral practices involve the accumulation and integration of many different traits, and the addition of each new behavioral component alters the conditions for subsequent additions, most changes or novel traits are likely to produce maladaptive effects once a local optimum is reached. Jumping from one optimum to another becomes difficult, because it requires simultaneously altering a number of traits in just the right way so as to land on a superior peak and avoid dropping into fitness valleys. Normally, most adaptive cultural practices require a gradual accumulation of innovations, and consequently "peak-shifting" is rare even for simple, nonintegrative adaptive traits. This is most easily illustrated for progressive technological developments.

Needham (1988) has documented the parallel evolution of boats in Asia and Europe. Chinese junks and European sailing ships show a number of major differences, despite the similar goals of their builders, which can be traced backward through a gradual accumulation of innovations, with each new innovation built on top of previous innovations. For example, early European boats used a heavy keel as the main structural support, whereas the early Chinese solved this problem by using flat-bottomed rafts reinforced with cross-wise ribs or bulkheads. This early difference in how boat builders solved the problem of structural integrity led these groups to increasingly diverge, leading them up different adaptive peaks. Later, when European and Chinese sailors came into close and repeated contact, neither group adopted the hull design of the other. Although as many believe, the Chinese design was superior (at a higher adaptive peak), European ship builders could not readily adopt these designs because they already relied on an immense amount of specialized construction knowledge, specific carpentry skills, and reliable trade networks for particular raw materials (what economists called network externalities). Similarly, European sailors had benefited from centuries of learning sailing skills and maritime knowledge that had been honed and time-tested for this particular type of craft. Switching to a Chinese design surely would have brought increased risk, inefficiency and a slow leaning curve. Each group had stabilized along a particular evolutionary trajectory, and, consequently, any individuals deviating from their groups' trajectory would incur costs.

The problem with this hypothesis is that there are many differences between groups that are not plausibly explained as alternative, locally optimal solutions to adaptive problems. The logic of multiple local optima is sound and may, at least partially, explain why members of a group maintain a certain cultural variation when deviations from that variant cause the deviant individual to perform worse than nondeviants. However, multiple local optima cannot explain the maintenance of a variant over more adaptive variants when there is a plausible evolutionary pathway linking the two traits. For example, why don't the aboriginal peoples of New Guinea

fletch their arrows? It seems likely that people in coastal New Guinea have had plenty of contact and have observed others using fletching for centuries. Arrow fletching is clearly a superior method of crafting arrows and should increase hunting and fighting efficiency, yet it has not spread to New Guinea. It is hard to see why this practice cannot be adopted in a number of small, adaptive steps, each an improvement over the previous step. Research seeking to show that multiple local optima alone can account for similarities within cultures and the differences between them must explain why groups reject more effective alternatives to widely used behaviors.

Hypothesis 3: Third-party punishment.   Scholars from economics, anthropology, and biology have suggested that third-party punishment (also called moralistic reciprocity) may account for the maintenance of group norms (Binmore 1994; Hirshleifer and Rasmussen 1988) and, consequently, the similarity within groups and the differences between groups. This hypothesis proposes that humans possess a reliably developing neural encoding that compels them both to punish individuals who violate group norms (common beliefs or practices) and punish individuals who do not punish norm violators—the punishment of nonpunishers. Boyd and Richerson (1992b; see Binmore [1994] and Hirshleifer and Rasmussen [1988] for analogous results in economics) have shown that punishment can stabilize group beneficial behaviors and any other cultural trait within a group. By punishing norm violators and nonpunishers of norm violators, punishment can maintain any belief or practice ranging from such odd behaviors as wearing uncomfortable neck ties and tipping at restaurants, to charging an entrenched enemy under fire or eating the brains of dead relatives.

Third-party punishment can only explain the maintenance of norms or high-frequency behaviors that involve punishment. Some scholars (Daniel Fessler, Francisco Gil-White, 1997, personal communication) have suggested that all deviations from high-frequency behavior evoke "moralistic indignation" or negative reactions that may result in some sort of social sanction (which may be subtle). Consequently, *all* norms are maintained through the fear of punishment. No one debates whether some norm violations are punished, but the empirical question remains as to whether deviations from any and all high-frequency behaviors found in cultural groups evoke negative, punishment-producing responses. If norms or high-frequency behaviors exist that do not evoke punishment-producing responses, then third-party punishment alone is insufficient to explain the patterns of intergroup variation.

Conformist transmission and third-party punishment may be complementary explanations for within-group similarity and between-group differences. Third-party punishment can explain the maintenance of punishment-enforced norms, such as wearing clothes, shaking hands, or saying "hello." However, further research should seek to differentiate punishment-enforced norms from those potentially maintained b conformist transmission. Conformist transmission may provide a foundation for the evolution of third-party punishment, and together they may provide a more complete explanation of the emergence and maintenance of norms as well as the maintenance of within-group similarities and between-group differences.

CONCLUSIONS

In the preceding discussion, we have reached several conclusions regarding the evolution of social learning, conformist transmission, and the emergence of within-group similarities and between group differences. We summarize them as follows:

1. Our model indicates that conformist transmission is favored by selection under a wide range of conditions. Conformist transmission evolves in fluctuating environments; it evolves when the accuracy of environmental information is poor and when it is fairly accurate.
2. Assuming that our model captures the conditions that shaped the evolution of social learning in humans, we have shown that natural selection favors increasing the reliance on social learning. And, there is no case in which a strong reliance on social learning evolves but conformist transmission does not. Thus, the fact that humans can imitate implies that conformism also is likely to be an important component of human social learning.
3. In our model, the presence of a conformist effect increases the evolutionary equilibrium amount of social learning. Social learning becomes more prevalent when conformist genotypes are possible.
4. Conformist transmission, third-party punishment, and multiple local optima all provide logically possible explanations that are not mutually exclusive. All three processes may, in fact, create and maintain intragroup similarities and intergroup differences. Further research should focus on detailing and differentiating these processes.

APPENDIX

The specifics of our computer model are detailed below. Copies of the C++ code are available upon request from the authors.

The simulation tracks the frequencies of 400 alleles at a haploid genetic locus that affect the degree of reliance on social learning and the propensity to use conformist transmission. There are two cultural traits labeled 1 and 2. Each generation consists of five life stages: genetic transmission, cultural transmission, individual learning, migration, and selection. The symbol u represents the frequency of each particular combination of behavior trait and genotype for each subpopulation. Each u carries four subscripts. The first indexes the behavioral trait, the second the subpopulation, and the latter two the genotype. Thus, u_{1ijk} is the frequency of behavioral trait one and genotype jk in subpopulation i. Both j and k range from 1 to 20 and together index the 400 different alleles in the model. The j subscript identifies the relative strength of social learning (L) associated with the allele, whereas k indexes the relative strength of conformist transmission (Δ).

Genetic and Cultural Transmission

Individuals acquire their genotype by genetic transmission. Then, during cultural transmission individuals experience both unbiased transmission and conformist transmission from three individuals drawn randomly from the subpopulation. In unbiased transmission, a subpopulation receives behavioral traits 1 and 2 in proportion to their representation in the previous generation. The conformist effect increases or decreases the frequency of a behavioral trait according to its prevalence in the previous generation. Here we use a three parent model (see Boyd and Richerson [1985] for details):

$$u'_{1ijk} = \underbrace{u_{1ijk}}_{\substack{\text{unbiased} \\ \text{transmission}}} + \underbrace{u_{1ijk}q_i(1-q_i)(2q_i-1)\Delta}_{\substack{\text{conformist} \\ \text{effect}}}$$

where q_i is the frequency of behavior 1 in subpopulation i, and Δ is the strength of the conformist effect for allele type k and varies linearly between zero and one. When $k = 0$, $\Delta = 0$; when $k = 19$, $\Delta = 1$. An equation similar to the above equation can be written for u_{2ijk}.

Individual Learning

Next, individuals have an opportunity to learn from the environment. Here, depending on the strength of individual learning versus social learning, frequencies change as individuals learn both the adaptive behavior and sometimes the maladaptive behavior from the environment.

$$u''_{1ijk} = u'_{1ijk} - \underbrace{u'_{1ijk}p_{2j}}_{\substack{\text{those that learned} \\ \text{behavior 2 individually}}} + \underbrace{u'_{2ijk}p_{1j}}_{\substack{\text{those that learned} \\ \text{behavior 1 individually}}} .$$

The variables p_{1j} and p_{2j} represent the probability of acquiring behavior 1 (p_{1j}) or behavior 2 (p_{2j}) through individual learning. Figure 7 illustrates how the p values are calculated using the accuracy of environmental information (M, which remains set for a particular simulation) and the degree of reliance on social versus individual learning, which is governed by the parameter d. The relationship between d and p_1 and p_2 is shown in Figure 7. When $j = 0$, $d = 0$ and when $j = 19$, $d = 3.2$. The fact that the maximum value of d is 3.2 places an upper bound on the relative importance of social learning. However, this did not constrain any of the simulation results presented here.

   Those who do not learn individually, either the right or wrong behavior, are left with the culturally transmitted behavior they received during the previous cultural transmission event. The relative importance of social learning. $L = 1 - p_{1j} - p_{2j}$.

Migration

In the next event, migration, a certain fraction of each behavioral-type/genotype emigrates in proportions equal to their representation within that subpopulation, and
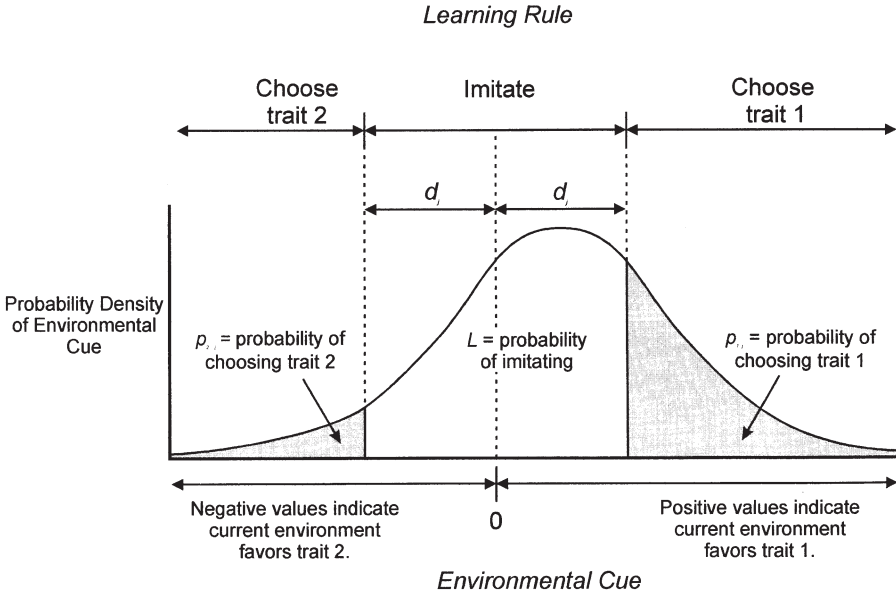
Learning Rule

FIGURE 7. Graphical representation of the model of individual and social learning. Each individual observes an independent, normally distributed environmental cue. The bell-shaped curve gives the probability density of different values of this cue. A positive value of the cue indicates that the environment is in state 1; a negative value indicates that the environment is in state 2. If the value of the environmental cue is larger than the threshold value, *dj*, and individual with genotype *jk* adopts trait 1. This occurs with probability, p_{1j}. If the value of the environmental cue is smaller than $-dj$, the individual adopts trait 2, which occurs with probability, p_{2j}. (The index *k* determines the individual's value of Δ.) Otherwise, the individual imitates. Thus, the larger the mean value of the cue compared to its standard deviation, the higher is the value of ρ. As the threshold value is increased, the ratio of correct to incorrect inferences increases. However, the likelihood that the cue is indecisive also increases and thus makes imitation more probable.

equal numbers of immigrants enter each subpopulation in proportions that reflect the behavioral and genetic traits of the *overall* population.

$$u'''_{1ijk} = u''_{1ijk} - \underbrace{mu''_{1ijk}}_{\substack{\text{migration} \\ \text{out}}} + \underbrace{m\bar{u}''_{1jk}}_{\substack{\text{migration} \\ \text{in}}}$$

where,

$$\bar{u}''_{1jk} = \frac{\sum_i u''_{1jk}}{n}$$

and *n* = the number of subpopulations.

Selection

During selection, individuals who possess the behavior adaptive in the current environment gain a slight survival advantage, that is, the frequency of those types pos-

sessing the currently adaptive behavior increases relative to those possessing the adaptive behavior. The equations below calculate the effect on u_1 and u_2 when the environment favors behavior 1 (similar equations can be written for u_1 and u_2 when the environment favors behavior 2).

$$u_{1ijk} = \frac{u'''_{1ijk}(W + D)}{\overline{W}}$$

$$u_{2ijk} = \frac{u'''_{2ijk}W}{\overline{W}}$$

where

$$\overline{W} = (W + D)\sum_i \sum_j \sum_k u'''_{1ijk} + W\sum_i \sum_j \sum_k u'''_{2ijk}$$

and $W = 1$, the baseline fitness, and $D = 0.01$, the strength of selection.

After selection the simulation checks, using a random number generator, to see if the state of the environment changes for the next generation. Then, the next generation begins again with cultural transmission. Usually simulations were run for 300,000 generations, until "equilibrium values" were changing less than 0.000001.

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