Chapter 6: Culture and Genes Coevolve

Milk was once marketed in the U.S. with the slogan, "Every Body Needs Milk." Catchy, but it's not true. Most people not only don't need milk, they can't tolerate it. The majority of world's adults lack the enzyme necessary to digest lactose, the sugar in milk, and if they drink milk, the lactose is fermented by bacteria rather than absorbed by the gut, leading to uncomfortable attacks of flatulence and diarrhea. That we didn't know this until the 1960s is testimony to how scientists are blinkered by their cultural background—most nutritionists came from countries where adult lactose malabsorption is rare. It is also testimony to how small a role evolution plays in biomedical science, because even a little adaptationist thinking would have suggested that it is the ability to digest milk that is abnormal, not the reverse. Milk has always been baby food for mammals and lactose only occurs in mother's milk. Thus, adult mammals had no need for the enzyme that cleaves lactose. Unsurprisingly, ever frugal natural selection shut down the production of this enzyme after weaning in almost all mammal species. The majority of people exhibit the standard mammalian developmental pattern; they can digest milk as infants but not as adults. The real evolutionary puzzle is why in some human populations most adults can digest lactose.

In the early 1970s, nutritionist Fredrick Simoons suggested that the ability to digest lactose evolved in response to a history of dairying.[1] The people of northwest Europe have long kept cows and consumed fresh milk. Dairying was carried to India by "Aryan" invaders, and has been practiced by pastoralists in western Asia and Africa for millennia. In each of these regions, most adults can drink fresh milk. Mediterranean dairying people traditionally consume milk in

the form of yogurt, cheese, and other products from which the lactose has been removed. Some adults in these populations can digest lactose while others cannot. Dairying is rare or absent in the rest of the world, and few Native Americans, Pacific Islanders, Far Easterners, and Africans are lactose absorbers. Simoons' hypothesis was controversial at the time, but subsequent genetic data confirm that adult lactose digestion is controlled by a single dominant gene, and careful statistical work indicates that a history of dairying is the best predictor of a high frequency of this gene. Moreover, calculations indicate that there been plenty of time for this gene to spread since the origin of dairying.[2]

The evolution of adult lactose digestion is an example of "gene-culture coevolution." Biologists developed the term "coevolution" to refer to systems in which two species are important parts of each other's environments so that evolutionary changes in one species induce evolutionary modifications in the other.[3] This can lead to an intricately choreographed coevolutionary dance, often with surprising results. For example, normally predatory ants often tend aphids, protecting them from predators. The aphids reward their ants by exuding sugar-rich honeydew, which the ants collect.

The evolving pools of cultural and genetic information carried by human populations are partners in a similar swirling waltz. Genetic evolution created a psychology that allows the cumulative cultural evolution of complex cultural adaptations. In some environments, this process led to the evolution of the dairying traditions. This new culturally evolved environment then increased the relative fitness of the gene that allows whole-milk consumption by adults. As that gene spread, it in turn may have changed the environment-shaping cultural practices, perhaps favoring more whole-milk consumption, or more serendipitously, giving rise to the evolution of ice cream.

We think that gene-culture coevolution has also played an important role in the *genetic* evolution of human psychology If genetically maladaptive cultural variants are an inevitable consequence of cumulative cultural adaptation, then the pools of cultural and genetic information carried by human populations each respond to their own evolutionary dynamic. Natural selection, mutation, and drift shape gene frequencies, while natural selection, guided variation, and a variety of transmission biases mold the distribution of cultural variants. However, these two processes are not independent. Each partner in the coevolutionary dance influences the evolutionary dynamics of the other. Genetically evolved psychological biases steer cultural evolution in genetic fitness-enhancing directions.[4] Culturally evolved traits affect the relative fitness of different genotypes in many ways. Consider just a few examples:

- <bl>Culturally evolved technology can affect the evolution of morphology. For example, modern humans are much less robust than earlier hominid species. Paleoanthropologists have argued that this change was due to the cultural evolution of effective projectile hunting weapons.[5] Before projectile weapons, robust genotypes were favored because people killed large animals at close range, but once they could be killed at distance, selection favored a less robust (and less expensive) physique.
- The availability of valuable culturally evolved information may lead to selection for enhanced capacities for acquiring and using that information. Language provides the canonical example. There is no doubt that the human vocal tract and auditory systems have been modified to enhance our ability to produce and decode spoken language, and we seem to have special-purpose psychological machinery for learning the meaning of words and grammatical rules. Selection could not have produced these derived features in an environment without spoken language. The most plausible explanation is that simple

culturally transmitted language arose first, and then selection favored a special-purpose throat morphology to generate speech sounds and a special purpose psychology for learning, decoding, and producing speech, which in turn gave rise to a richer, more complex language, and led to yet more modifications of the traits that allow language acquisition and production.

- Culturally evolved moral norms can affect fitness if norm violators are punished by others. Men who cannot control their antisocial impulses are exiled to the wilderness in small-scale societies and sentenced to prison in contemporary ones. Women who behave inappropriately in social circumstances are unlikely to find or keep husbands.[6] In this chapter, we will argue that coevolutionary forces have radically reshaped innate features of human social psychology.</bl>

Gene-cultural coevolution can generate such significant genetic changes because it has been going on for a long time. Dairying has been a force in populations with high frequencies of adult lactose digestion for some three hundred generations. In chapter 4, we presented evidence that the capacity for the cumulative evolution of complex cultural adaptations is roughly half a million years old. This means that complex cultural traditions have been exerting coevolutionary selective pressures on human gene pools for about twenty thousand generations. In this amount of time, culturally evolved environments could have had dramatic coevolutionary effects on the evolution of human genes.

We hope that the idea of gene-culture coevolution seems intuitive and plausible to most of our readers. Be warned, however, that you are being invited to start down what many evolutionary social scientists believe is a garden path. Researchers in this tradition emphasize that cultural evolution is molded by our evolved psychology, but not the reverse. As psychologist

Charles Lumsden and evolutionary biologist E. O. Wilson put it, genes have culture on a leash.[7] Culture can wander a bit, but if it threatens to get out of hand, its genetic master can bring it to heel. We think that this is only half the story. As we argued at length in the last chapter, heritable cultural variation responds to its own evolutionary dynamic, often leading to the evolution of cultural variants that would not be favored by selection acting on genes. The resulting cultural environments then can affect the evolutionary dynamics of alternative genes. Culture is on a leash, all right, but the dog on the end is big, smart, and independent. On any given walk, it is hard to tell who is leading who.

Better to think of genes and culture as obligate mutualists, like two species that synergistically combine their specialized capacities to do things that neither one can do alone.[8] Humans by themselves cannot convert grass into usable food. Cows by themselves cannot drive away lions and wolves. The cow-human mutualism works to the advantage of both. However, such mutualisms are never perfect. Humans will always be tempted to take more milk at the expense of calves, and cows will always be subject to natural selection favoring shorting the humans to feed their offspring. Each caters to the whimsical biology of the other so long as there is a net payoff to the cooperation. Humans chauvinistically see themselves as controlling domestication. A cow might as well flatter herself on how clever she is to elicit so much work on her behalf from her humans. The relationship between genes and culture is similar. Genes, by themselves, can't readily adapt to rapidly changing environments. Cultural variants, by themselves, can't do anything without brains and bodies. Genes and culture are tightly coupled but subject to evolutionary forces that tug behavior in different directions.

Biologists John Maynard Smith and Eörs Szathmáry point out that mutualisms have played an important role in the evolution of major transitions in levels of biological

organization.[9] The origin of eukaryotic cells provides a good example.[10] Until about two billion years ago, the world's biota was dominated by prokaryotes, organisms without nuclei or chromosomes, like modern-day bacteria. Then, eukaryotes arose as a result of a close symbiosis between prokaryote species; one of these species eventually evolved to become the nucleus and others became cellular organelles such as mitochondria and chloroplasts. The larger and functionally more complex eukaryotic cells that resulted from the coevolution of these mutualists were able to outcompete prokaryotes in some existing adaptive niches and enter many new ones.

In the remainder of this chapter, we will argue that the symbiosis between genes and culture in the human species has led to an analogous major transition in the history of life—the evolution of complex cooperative human societies that radically transformed almost all the world's habitats over the last ten thousand years.

Gene-culture coevolution and human ultrasociality

Human societies are a spectacular anomaly in the animal world. They are based on the cooperation of large, symbolically marked in-groups. Such groups have economies based on substantial division of labor and compete with similarly marked out-groups. This is obviously true of modern societies, in which enormous bureaucracies like the military, political parties, churches, and corporations manage complex tasks, and in which people depend on a vast array of resources produced in every corner of the globe. But it is also true of hunter-gatherers, who have extensive exchange networks and regularly share food and other important goods outside the family and the residential group.

In most animal species, cooperation is either absent or limited to very small groups, and

there is little division of labor. [11] Among the few animals that cooperate in large groups are social insects such as bees, ants, and termites, and the naked mole rat, a subterranean African rodent. Multicellular plants and many forms of multicellular invertebrates can also be thought of as complex societies made up of individual cells. In each of these cases, however, the cooperating individuals are genetically related. Typically, the cells in a multicellular organism are members of a genetically identical clone, and the individuals in insect and naked mole rat colonies are siblings.

Thus we have another evolutionary puzzle. Our ancestors six million years ago in the Miocene presumably cooperated in small groups mainly made up of relatives, as contemporary nonhuman primates do. There was no trade, little division of labor, and coalitions were limited to a small number of individuals. As we will argue below, these patterns are consistent with our understanding of how natural selection shapes behavior. Sometime between then and now, something happened that caused humans to cooperate in large, complex, symbolically marked groups. What caused this radical divergence from the behavior of other social mammals?

We think that gene-culture coevolution provides the most likely solution to this puzzle. There are two parts to this argument. First, cultural adaptation potentiates cultural evolution of cooperation and symbolic marking. Human culture allows rapid, cumulative evolution of complex adaptations and is particularly adaptive in variable environments. Such rapid adaptation has radically increased the amount of heritable cultural variation between human groups, which means that intergroup competition (always present) gives rise to the cumulative evolution of cultural traits that enhanced the success of groups. Since larger, more cooperative, and more coherent groups should outcompete smaller, less cooperative groups, group selection could give rise to culturally transmitted cooperative, group-oriented norms, and systems of rewards and

punishments to ensure that such norms are obeyed. Stable variation between groups can also lead to the evolution of symbolic markers that allow individuals to choose whom to imitate or whom to interact with.

Second, culturally evolved social environments favor an innate psychology that is suited to such environments. In culturally evolved social environments in which prosocial norms are enforced by systems of sanction and reward, individual selection will favor psychological predispositions that make individuals more likely to gain social rewards and avoid social sanctions. Similarly, in a world made up of coherent, culturally distinct, symbolically marked groups which demand loyalty from their members, individual selection will favor psychological adaptations that allow people to parse the groups that make up their social world, and identify with the appropriate ones.

As a result, people are endowed with two sets of innate predispositions, or "social instincts."[12] The first is a set of ancient instincts that we share with our primate ancestors. The ancient social instincts were shaped by the familiar evolutionary processes of kin selection and reciprocity, enabling humans to have a complex family life and frequently form strong bonds of friendship with others. The second is a set of "tribal"[13] instincts that that allow us to interact cooperatively with a larger, symbolically marked set of people, or tribe. The tribal social instincts result from the gene-culture coevolution of tribal-scale societies by the process described above. Consequently, humans are able to make common cause with a sizable, culturally defined set of distantly related individuals, a form of social organization that is absent in other primates.[14]

In the remainder of this chapter, we will describe and defend this hypothesis. First, we provide a brief primer on the theory of the evolution of cooperation. Our goal is to convince you that human sociality is indeed a puzzle, and provide necessary background for understanding our

coevolutionary account and a competing hypothesis from evolutionary psychology. We then describe in more detail how gene-culture coevolution has given rise to tribal social instincts. Next, we summarize data from psychological studies that suggest that such instincts actually exist. Then, we present ethnographic and historical evidence that suggests that the recent hunter-gatherer societies exhibit tribal-scale social organization. Finally, we use the evolution of complex societies as a natural experiment to test the hypothesis.

Cooperation is usually limited to kin and small groups of reciprocators

When we were graduate students during the late 1960s and early 1970s, it was quite common for biology texts to explain animal behaviors in terms of their benefit to the species. Alarm cries helped defend the social group against predators, and sexual reproduction maintained the genetic variation necessary for the species to adapt. A key advance in biology forty years ago was to show that such explanations are mostly wrong. Natural selection does not normally lead to the evolution of traits that are for the good of the species, or even the social group. Selection usually favors traits that increase the reproductive success of individuals, or sometimes individual genes; and when a *conflict* occurs between what is good for the individual and what is good for the group, selection usually leads to the evolution of the trait that benefits the individual.

Selection favors cooperation among kin

The big exception to this rule occurs when groups are made up of genetic kin—then selection can favor behavior that reduces fitness of the individual performing the behavior as long as it causes a sufficient increase in the fitness of the group. Consider a very Prussian species in which

individuals all live in groups of exactly 9 drawn from the global population. Further suppose that there are two types: helpers and egoists. The helpers perform a prosocial behavior that increases the fitness of each of the other 8 individuals in their group by ¼ unit, but decreases the fitness of helpers by ½ unit. This behavior is clearly group beneficial—it increases the average fitness of each of the 8 other group members by ¼, so the net increase in group fitness due to the behavior is $8 \times ¼ - ½ = 1½$ fitness units.

People untrained in evolutionary biology often think that behaviors that produce group benefits will be favored by natural selection. But group benefits are not enough. Suppose groups are formed at random. Then each prosocial act has the same average effect on the fitness of helpers and egoists. This means that prosocial behavior has no effect on the *relative* fitness of helpers and selfish types, because helpers behave as saints, helping good guys and bad guys indiscriminately. In which case, no change in the frequency of these two types in the population will occur due the *receipt* of altruism. At the same time, the *costs* of performing prosocial behavior fall solely on helpers, and thus decrease their fitness relative to egoists.

Now suppose that groups are made up of full siblings. Full siblings share 50% of their genes, so helpers will find themselves in groups in which, on average, 4 of the other 8 members carry the helping gene. The other 4 carry a random sample of genes from the population. Now, the prosocial act increases the relative fitness of 4 individuals with the prosocial gene $4 \times ¼ = 1$ fitness unit, at a cost of only ½ fitness units. Selection can favor this behavior, because the benefits of prosocial acts are nonrandomly directed toward others who carry the same gene.

This simple example illustrates a fundamental evolutionary principle: costly group-beneficial behavior cannot evolve unless the benefits of group-beneficial behavior flow nonrandomly to individuals who carry the genes that give rise to the behavior. Altruism toward

kin can be favored by selection because kin are similar genetically. The late great evolutionary biologist W. D. Hamilton worked out the basic calculus of kin selection in 1964[15] and deduced many of its most important effects on social evolution. As you have seen, full siblings can count on sharing half their genes through common descent, and can therefore afford to help a sibling reproduce so long as the fitness payoffs are twice the costs. More-distant relatives require a higher benefit-cost ratio.[16] This principle, often called Hamilton's rule, successfully explains a vast range of behavior (and morphology) in a very wide range of organisms.[17]

Selection can favor cooperation among small groups of reciprocators

When animals interact repeatedly, past behavior also provides a cue that allows nonrandom social interaction. Suppose that animals live in social groups and the same pair of individuals interacts over an extended period of time. Often, one member of the pair has the opportunity to help the other, at some cost to itself. Suppose that there are two types: defectors who do not help, and reciprocators who use the strategy "Help on the first opportunity. After that, help your partner as long as she keeps helping you, but if she doesn't help, don't help her anymore." Initially, partners are chosen at random, so that at the first opportunity, reciprocators are no more likely to be helped than defectors. However, after the first interaction, only reciprocators receive any help, and if interactions continue long enough, the high fitness of reciprocators in such pairings will be enough to cause the average fitness of reciprocators to exceed that of defectors.

Beyond this basic story, there is little agreement among scientists about how reciprocity works. The contrast with kin selection theory is instructive. The simple principle embodied by Hamilton's rule allows biologists to explain a wide range of phenomena. Despite much work, evolutionary theorists (including yours truly) have not managed to derive any widely applicable

general principles describing the evolution of reciprocity. Worse, evidence that reciprocity is important in nature is scanty;[18] only a handful of studies provide evidence for reciprocity, and none of them are definitive.[19]

Despite its many problems, theoretical work does make one fairly clear prediction that is relevant here: reciprocity can support cooperation in small groups, but not in larger ones.[20] Instead of assuming that individuals interact in pairs, suppose that individuals live in groups, and each helping act benefits all group members. For example, the helping behavior could be an alarm cry that warns group members of an approaching predator, but makes the callers conspicuous and thereby increases their risk of being eaten. Suppose there is a defector in the group who never calls. If reciprocators use the rule, only cooperate if all others cooperate, this defector induces other reciprocators to stop cooperating. These defections induce still more defections. Innocent cooperators suffer as much as guilty defectors when the only recourse to defection is to stop cooperating. On the other hand, if reciprocators tolerate defectors, then defectors can benefit in the long run.

Theoretical work suggests that this phenomenon will limit reciprocity to quite small groups, and while no good empirical data exist, it does fit with everyday experience. We know that reciprocity plays an important role in friendship, marriage, and other dyadic relationships. We eventually stop inviting friends over to dinner if they never return our invitations; we become annoyed at our spouse if she does not take her turn watching the children; and we change auto mechanics if they repeatedly overcharge us for repairs. But cooperation in larger groups cannot be based on the same principle. Each one of a thousand union members does not keep walking the picket line because she is afraid that her one defection will break the strike. Nor does each Enga warrior maintain his position in the line of battle because he fears that his

desertion will precipitate wholesale retreat. Nor do we recycle our bottles and newspapers because we fear our littering will doom the planet.

Some authors have emphasized that punishment takes other forms such as reduced status, fewer friends, and fewer mating opportunities[21]— what evolutionary biologist Robert Trivers calls "moralistic punishment."[22] While moralistic punishment and reciprocity are often lumped together, they have very different evolutionary properties. Moralistic punishment is more effective in supporting large-scale cooperation than reciprocity for two reasons. First, punishment can be targeted, meaning that defectors can be penalized without generating the cascade of defection that follows when reciprocators refuse to cooperate with defectors. Second, with reciprocity, the severity of the sanction is limited by the effect of a single individual's cooperation on each other group member, an effect that decreases as group size increases. Moralistic sanctions can be much more costly to defectors, so that cooperators can induce others to cooperate in large groups even when they are rare. Cowards, deserters, and cheaters may be attacked by their erstwhile compatriots, shunned by their society, made the targets of gossip, or denied access to territories or mates. Thus, moralistic punishment provides a much more plausible mechanism for the maintenance of large-scale cooperation than reciprocity.

However, two problems remain:[23] First, why should individuals punish? If punishing is costly and the benefits of cooperation flow to the group as a whole, administering punishment is a costly group-beneficial act, and therefore, selfish individuals will cooperate but not punish. The Enga man who punishes a coward suffers a cost to himself and provides a benefit to other members of his clan. The Enga woman who shuns a deserter may forgo an otherwise desirable marriage partner while helping to ensure that cowards do not become common among the Enga. Thus, as long as the effect of the punishment administered by a single individual will have little

effect on the outcome of the battle, selfish individuals will not punish. Second, moralistic punishment can stabilize *any* arbitrary behavior—wearing a tie, being kind to animals, or eating the brains of dead relatives. Whether the behavior produces group benefits is of no significance. All that matters is that when moralistic punishers are common, being punished is more costly than performing the correct behavior, whatever it might be. When any behavior can persist at a stable equilibrium, then the fact that cooperation is a stable equilibrium does not tell us whether it is a likely outcome.

While much of the debate about moralistic punishment has focused on the first problem, we think the second presents a bigger obstacle to the evolution of cooperation in large groups. If moralistic punishment is common, and punishments sufficiently severe, then cooperation will pay. Most people may go through life without having to punish very much which in turn means that a predisposition to punish may be cheap compared with a disposition to cooperate (in the absence of punishment). Thus, relatively weak evolutionary forces can maintain a moralistic predisposition, and then punishment can maintain group-beneficial behavior. However, if evolutionary change is driven only by individual costs and benefits, then moralistic punishment can stabilize cooperation, but it can also stabilize anything else. Societies do often seem to use moralistic punishment or its threat to enforce social conventions of no apparent utility of any kind, such as wearing ties to work. Since cooperative behaviors are a tiny subset of all possible behaviors, punishment does not explain why large-scale cooperation is so widely observed. In other words, moralistic punishment may be necessary to sustain large-scale cooperation, but it is not sufficient to explain why large-scale cooperation occurs.

Selection among large, partially isolated groups is not effective

Group selection may be the number one hot-button topic among evolutionary biologists. The controversy began in the early 1960s, when ornithologist V. C. Wynne-Edwards published a book that explained a number of puzzling avian behaviors in terms of the benefit to the group.[24] For example, he thought that the great, whirling evening displays of thousands of roosting starlings allowed the birds to census population size and control their birthrates to avoid overexploiting their food supply. While this kind of explanation was not unusual in those days, Wynne-Edwards was much clearer than his contemporaries about the process that gave rise to such group-level adaptations: groups that had the display survived and prospered, while those that didn't overexploited their food supply and perished. The book generated a storm of controversy, with biological luminaries such as David Lack, George Williams, and John Maynard Smith penning critiques explaining why this mechanism, then called group selection, could not work.[25] At the same time, Hamilton's newly minted theory of kin selection provided an alternative explanation for cooperation. The result was the beginning of an ongoing and highly successful revolution in our understanding of the evolution of animal behavior, a revolution that is rooted in carefully thinking about the individual and nepotistic function of behaviors.

In the early 1970s, an eccentric retired engineer named George Price published two papers that presented a genuinely new way to think about evolution.[26] Up until that time, most evolutionary theory was based on an accounting system that kept track of the fitness of different genes. To understand the evolution of a particular trait, one needed to know how the behavior of others affects each individual carrying a particular gene and average this over all situations in which individuals find themselves (just as we did above in explaining kin selection and reciprocity). Price argued that it was *also* fruitful to think about selection occurring in a series of

nested levels: among genes within an individual, among individuals within groups, and among groups; and he invented a very powerful mathematical formalism, now called the Price covariance equation, for describing these processes. Using Price's method, kin selection is conceptualized as occurring at two levels: selection *within* family groups favors defectors, because defectors always do better than other individuals within their own group, but selection *among* family groups favors groups with more helpers, because each helper increases the average fitness of the group. The outcome depends on the relative amount of variation within and between groups. If group members are closely related, most of the variation will occur between groups. This is easiest to see if groups are composed of clones (as in colonial invertebrates such as corals). Then there is almost no genetic variation within groups; all the variation is between groups, and selection acts to maximize group benefit.

Price's multilevel selection approach and the older gene-centered approaches are mathematically equivalent. One approach may be more heuristic or mathematically tractable for particular evolutionary problems than the other, but if you do your sums properly, you will come up with the same answer either way.[27] Adopting the multilevel formalism does not imply that animals are more or less likely to do things for the good of the group, because these two approaches are equivalent.

The multilevel selection approach has led to a renaissance in group selection in recent years which has generated new wrangling between those who thought that they had killed group selection and those who, thinking in multilevel terms, see nothing wrong with it.[28] This argument is mainly about what kinds of evolutionary processes should be *called* group selection. Some people use *group selection* to mean the process that Wynne-Edwards envisioned—selection between large groups made up of mostly genetically unrelated individuals—while others use

group selection to refer to selection involving any kind of group in a multilevel selection analysis, including groups made up of close kin.

The real scientific question is, what kinds of population structure can produce enough variation between groups so that selection at that level can have an important effect? The answer is fairly straightforward: selection between large groups of unrelated individuals is not an important force in organic evolution. Even very small amounts of migration are sufficient to reduce the genetic variation between groups to such a low level that group selection is not important.[29] However, as we will explain below, the same conclusion does not hold for cultural variation.

Among primates, cooperation is limited to small groups

The punch line is that evolutionary theory predicts that cooperation in nonhuman primates and other species that have small families will be limited to small groups. Kin selection results in large-scale social systems only when there are large numbers of closely related individuals; social insects in which a few females produce a mass of sterile workers, and colonial invertebrates are examples of such exceptions. Primate societies are nepotistic, but cooperation is mainly restricted to relatively small kin groups. Theory suggests that reciprocity can be effective in such small groups but not in larger ones. Reciprocity may play some role in nature (though many experts are unconvinced), but there is no evidence that reciprocity has played a role in the evolution of large-scale sociality. All would be well if humans did not exist, because human societies, even those of hunter-gatherers, are based on groups of people linked together into much larger, highly cooperative social systems.

Rapid cultural adaptation potentiates group selection

So why aren't human societies very small in scale, like those of other primates? We believe that the most likely explanation is that rapid cultural adaptation led to a huge increase in the amount of behavioral variation among groups. In other primate species, there is little heritable variation among groups, because natural selection is weak compared with migration. This is why group selection at the level of whole primate groups is not an important evolutionary force. In contrast, there is a great deal of behavioral variation among human groups. Such variation is the *reason* why we have culture—to allow different groups to accumulate different adaptations to a wide range of environments. By itself, such variation is not enough to give rise to group selection. For group selection to be an important force, some process that can maintain variation among groups must also operate. We think that there are at least two such mechanisms: moralistic punishment and conformist bias. Let's see how they work.

Variation is maintained by moralistic punishment

As we explained earlier, moralistic punishment can stabilize a very wide range of behaviors. Imagine a population subdivided into a number of groups. Cultural practices spread between groups because either because people migrate, or because they sometimes adopt ideas from neighboring groups. Two alternative, culturally transmitted moral norms exist in the population, norms that are to be enforced by moralistic punishment. Let's call them norm X and norm Y. These could be "must wear a business suit at work" and "must wear a dashiki to work," or "A person owes primary loyalty to kin" and "A person owes primary loyalty to the group." In groups where one of the two norms is common, people who violate the norm are punished.

Suppose that people's innate psychology causes them to be biased in favor of norm Y, and therefore Y will tend to spread. Nonetheless, if norm X somehow becomes sufficiently common, the effects of punishment overcome this bias, and people tend to adopt norm X. In such groups, new immigrants whose beliefs differ from the majority (or people who have adopted "foreign" ideas) rapidly learn that their beliefs get them into trouble and adopt the prevailing norm. When more believers in norm Y arrive, they find themselves to be in the minority, rapidly learn the local norms, and maintain norm X despite the fact that it does not fit best with their evolved psychology.

This kind of mechanism only works when the adaptation occurs rapidly, and is not likely to be an important force in genetic evolution. Evolutionary biologists normally think of selection as weak, and although there are many exceptions to this rule, it is a useful generalization. So, for example, if one genotype had a 5% selection advantage over the alternative genotype, this would be thought to be strong selection. Suppose that a novel, group-beneficial genotype has arisen, and that it has, through a chance event, become common in one local group where it has a 5% advantage over the genotype that predominates in the population as a whole. For group selection to be important, the novel type must remain common long enough to spread by group selection, and this is only possible if the migration rate per generation is substantially less than 5%.[30] Otherwise, the effects of migration will swamp the effects of natural selection. But this is not very much migration. The migration rate between neighboring primate groups is on the order of 25% per generation. While migration rates are notoriously difficult to measure, most likely they are typically high among small local groups that suffer frequent extinction. Migration rates between larger groups are much lower, but so, too, will be the extinction rate.

Variation is maintained by conformist social learning

A conformist bias can also maintain variation among groups. We argued in chapter 4 that natural selection can favor a psychological propensity to imitate the common type. This propensity is an evolutionary force that causes common cultural variants to become more common and rare variants to become rarer. If this effect is strong compared with migration, then variation among groups can be maintained.

As before, think of a number of groups linked by migration. Now, however, assume that the two variants affect religious beliefs: "believers" are convinced that moral people are rewarded after death and the wicked suffer horrible punishment for eternity, while "nonbelievers" do not believe in any afterlife. Because they fear the consequences, believers behave better than nonbelievers—more honestly, charitably, and selflessly. As a result, groups in which believers are common are more successful than groups in which nonbelievers are common. People's decision to adopt one cultural variant or the other is only weakly affected by content bias. People do seek comfort, pleasure, and leisure, and this tends to cause them to behave wickedly. However, a desire for comfort also causes thoughtful people to worry about spending an eternity buried in a burning tomb. Since people are uncertain about the existence of an afterlife, they are not strongly biased in favor of one cultural variant or the other. As a result, they are strongly influenced by the cultural variant that is common in their society. People who grow up surrounded by believers choose to believe, while those who grow up among worldly atheists do not.

The difference between moralistic punishment and conformist learning is illustrated by the different answers to the question, given that people have grown up in a devout Christian society, why do they believe in the tenets of the Christian faith? If cultural variation is

maintained mainly by moralistic punishment, those who do not adopt Christian beliefs in a devout Christian society are punished by believers, and people who do not punish such heretics (say, by continuing to associate with them) are themselves punished. People adopt the prevalent belief because it yields the highest payoff in readily measurable currencies, inclusive of the cost of being punished. If cultural variation is maintained mainly by conformist transmission and similar cultural mechanisms, young people adopt the tenets of Christianity because such beliefs are widely held, fit with certain content-based biases, and are difficult for individuals to prove or disprove. (Of course, any mixture of conformity and punishment is also possible; the answer is quantitative, not qualitative.)

Conformist transmission can potentiate group selection only if it is strong compared with opposing content biases, and this can occur only if individuals have difficulty evaluating the costs and benefits of alternative cultural variants. In some cases this is not very difficult—should you cheat on your taxes or fake illness to avoid military service? The threat of punitive action may be sufficient to keep taxpayers and conscripts honest. However, many beliefs have effects that are hard to judge. Will children turn out better if they are sternly disciplined or lovingly indulged? Is smoking marijuana harmful to one's health? Is academia a promising career option? These are difficult questions to answer, even with all of the information available to us today. For most people at most times and most places, even more-basic questions may be very difficult to answer. Does drinking dirty water cause disease? Can people affect the weather by appeals to the supernatural? The consequences of such difficult choices often have profound effect on people's behavior and their welfare.[31]

<B>Heritable variation between groups + intergroup conflict = group selection</B>

In *On the Origin of Species,* Darwin famously argued that three conditions are necessary for adaptation by natural selection. There must be a "struggle for existence" so that not all individuals survive and reproduce. There must be variation so that some types are more likely to survive and reproduce than others, and the variation must be heritable so that the offspring of survivors resemble their parents.

Darwin usually focused on individuals, but the multilevel selection approach tells us that same three postulates apply to *any* reproducing entity—molecules, genes, and cultural groups. Only the first two conditions are satisfied by most other kinds of animal groups. For example, vervet monkey groups compete with one another, and groups vary in their ability to survive and grow, but—and this is the big but—the causes of group-level variation in competitive ability aren't heritable, so there is no cumulative adaptation.

Once rapid cultural adaptation in human societies gave rise to stable, between-group differences, the stage was set for a variety of selective processes to generate adaptations at the group level. As Darwin said,

> It must not be forgotten that although a high standard of morality gives but a slight or no advantage to each individual man and his children over other men of the same tribe, yet that an increase in the number of well-endowed men and an advancement in the standard of morality will certainly give an immense advantage to one tribe over another. A tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to aid one another, and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection.[32]

Darwin's is the simplest mechanism: intergroup competition. The spread of the Nuer at the expense of the Dinka discussed in chapter 2 provides a good example. Recall that the Nuer and Dinka are two large ethnic groups living in the southern Sudan. During the nineteenth century, each consisted of a number of politically independent groups. Cultural differences in

norms between the two groups meant that the Nuer were able to cooperate in larger groups than the Dinka. The Nuer, who were driven by the desire for more grazing land, attacked and defeated their Dinka neighbors, occupied their territories, and assimilated tens of thousands of Dinka into their communities.

This example illustrates the requirements for cultural group selection by intergroup competition. Contrary to some recent critics,[33] there is no need for groups to be sharply bounded, individual-like entities. The only requirement is that there are persistent cultural differences between groups, and these differences must affect the groups' competitive ability. Winning groups must replace losing groups, but losers need not be killed. The members of losing groups just have to disperse or be assimilated into the victorious group. If losers are resocialized by conformity or punishment, even very high rates of physical migration need not result in the erosion of cultural differences.

This kind of group selection can be a potent force even if groups are usually large. For a group-beneficial cultural variant to spread, it must become common in an initial subpopulation. The rate at which this occurs through random driftlike processes will be slow in sizable groups.[34] However, it only needs to occur once. Several processes might supply the initial variants. Even if groups are usually large, occasional bottlenecks that reduce group size could allow a group-favoring variant to arise by chance. Environmental variation in even a few subpopulations could provide the initial impetus for group selection. Small, deviant groups, if successful, can grow into large ones, as often happens with religious sects. Whatever their source, differences between societies in contact, like those of the Nuer and Dinka, are often quite substantial; we have noted many other examples.

Group competition is common in small-scale societies. Contrary to some romanticized

accounts, ethnographic and archaeological data indicate that raiding and warfare are frequent in foraging societies.[35] For example, data collected by pioneering anthropologist A. L. Kroeber and his students during the first half of this century indicate that warfare was very common among hunter-gatherers in western North America during the nineteenth century, often exceeding four armed conflicts per year. However, the data from hunter-gatherers are far too poor and too influenced by contact with colonial powers to estimate how often such conflicts resulted in group extinction. Better data come from highland New Guinea, which provides the only large sample of simple societies studied by professional anthropologists before these societies experienced major changes due to contact with Europeans. Although they were horticulturalists rather than hunter-gatherers, New Guinea peoples lived in simple tribal societies much as many hunter-gatherers did, and intergroup competition was still ongoing, or at least quite fresh in informants' minds when ethnographers arrived.

Anthropologist Joseph Soltis assembled data from the reports of early ethnographers from highland New Guinea. Many studies report appreciable intergroup conflict and about half mention cases of social extinction of local groups. Five studies contained enough information to estimate the rates of extinction of neighboring groups (table 6.1). The typical pattern is for groups to be weakened over a period of time by conflict with neighbors and finally to suffer a sharp defeat. When enough members become convinced of the group's vulnerability to further attack, members take shelter with friends and relatives in other groups. The group thus becomes socially extinct, even if mortality rates are well below 100%. At the same time, successful groups grow and eventually fission. The social extinction of groups was common (table 6.1). At the these rates of group extinction, it would take between 20 and 40 generations, or 500 to1,000 years, for an innovation to spread from one group to most of the other local groups.

Region	Number of groups	Number of social extinctions	Number of years	% groups extinct every 25 years	Source
Mae Enga	14	5	50	17.9%	Meggitt, 1977
Maring	13	1	25	7.7%	Vayda, 1971
Mendi	9	3	50	16.6%	Ryan, 1959
Fore/Usurufa	8--24	1	10	31.2%–10.4%	Berndt, 1962
Tor	26	4	40	9.6%	Oosterwal, 1961

Table 6.1. Extinction rates for cultural groups from five regions in New Guinea. From Soltis et al 1995.

These results imply that cultural group selection is a relatively slow process. But then, so are the actual rates of increase in political and social sophistication we observe in the historical and archaeological records. New Guinea societies were no doubt actively evolving systems,[36] yet the net increase in their social complexity over those of their Pleistocene ancestors was modest. Change in the cultural traditions that eventually led to large-scale social systems like the ones that we live in proceeded at a modest rate. These estimates can explain the five-thousand-year lag between the beginnings of agriculture and the first primitive city-states, and the five millennia that transpired between the origins of simple states and modern complex societies.

Group-beneficial cultural variants can spread because people imitate successful neighbors

Intergroup competition is not the only mechanism that can lead to the spread of group-beneficial cultural variants—a propensity to imitate successful neighbors can play a role. Up to this point, we have mainly focused on what people know about the behavior of members of their own local group. But people also often know something about the norms that regulate behavior in neighboring groups. They know that we can marry our cousins here, but over there they cannot; or anyone is free to pick fruit here, while individuals own fruit trees there. Now suppose that one set of norms cause people to be more successful than alternative norms. Both theory and empirical evidence suggest that people have a strong tendency to imitate the successful. Consequently, the better norm will spread because people imitate their more-successful neighbors.

You might wonder if this mechanism can really work. It requires enough diffusion between groups so that group-beneficial ideas can spread; and at the same time, there can't be too much diffusion, or the necessary variation between groups won't be maintained. Is this combination possible? We wondered the same thing, so we built a mathematical model of this process. Our results suggest that group-beneficial beliefs spread in a wide range of conditions.[37] The model also suggests that such spread can be rapid. Roughly speaking, it takes about twice as long for a group-beneficial trait to spread from one group to another as it does for an individually beneficial trait to spread within a group. This process is much faster than simple intergroup competition because it depends on the rate at which individuals imitate new strategies, rather than the rate at which groups become extinct.

The rapid spread of Christianity in the Roman Empire may provide an example of this

process. Between the death of Christ and the rule of the emperor Constantine, a period of about 260 years, the number of Christians increased from only a handful to somewhere between six million and thirty million people (depending on whose estimate you accept). This sounds like a huge increase, but it turns out that it is equivalent to a 3%–4% annual rise, about the growth rate of the Mormon Church over the last century. According to sociologist Rodney Stark,[38] many Romans converted to Christianity because they were attracted to what they saw as a better quality of life. In pagan society the poor and sick often went without any help at all. In contrast, in the Christian community charity and mutual aid created "a miniature welfare state in an empire which for the most part lacked social services."[39]

Such mutual aid was particularly important during the epidemics that struck the Roman Empire during the late imperial period. Unafflicted pagan Romans refused to help the sick or bury the dead, sometimes leading to anarchy. In Christian communities, strong norms of mutual aid produced solicitous care of the sick, thereby reducing mortality. Both Christian and pagan commentators attribute many conversions to the appeal of such aid. For example, the emperor Julian (who detested Christians) wrote in a letter to one of his priests that pagans need to emulate the virtuous example of the Christians if they wanted to compete for their souls, citing "their moral character even if pretended" and "their benevolence toward strangers."[40] Middle-class women were particularly likely to convert to Christianity, probably because they had higher status and greater marital security within the Christian community. Roman norms allowed polygyny, and married men freely engaged in extramarital affairs. In contrast, Christian norms required faithful monogamy. Pagan widows were required to remarry, and when they did they lost control of all their property. Christian widows could retain property, or, if poor, would be sustained by the church community. Demographic factors were also important in the growth of

Christianity. Mutual aid led to substantially lower mortality rates during epidemics, and a norm against infanticide led to substantially higher fertility among Christians.

In order to spread by this mechanism, practices have to be relatively easy to observe and to try out.[41] Evangelizing religions such as Christianity and Islam are at pains to help potential converts learn the new system and to welcome awkward neophytes. Even so, most modern conversions, and presumably ancient ones, are of fellow family members, close friends, and other intimate associates.

Rapid cultural adaptation generates symbolically marked groups

One of the most striking features of human sociality is the symbolic marking of group boundaries.[42] Some symbolic markers are seemingly arbitrary traits, such as distinctive styles of dress or speech, while others are complex ritual systems accompanied by elaborately rationalized ideologies. It is a commonplace that social relations are regulated by norms embedded in a group's sanctified belief system.[43] Even in simple hunting and gathering societies, symbolically marked groups are large. For instance, the phenomenon of ethnicity is diverse and impossible to define except in terms of ideal types. Ethnicity grades into class, region, religion, gender, profession, and all the myriad systems of symbolic marking humans use to regulate (among other things) the scope of altruistic norms.

Considerable evidence indicates that symbolic marking is not simply a byproduct of a similar cultural heritage. Kids acquire lots of traits from the same adults, and if cultural boundaries were impermeable, akin to species boundaries, this would explain the association between symbolic markers and other traits. For example, if Mexican immigrant kids in

California never imitated anyone except ethnic Mexicans and if Anglo Californians were similarly conservative, the persistence of an ethnic boundary would be easy to explain. However, there is a great deal of evidence that ethnic identities are flexible and ethnic boundaries are porous.[44] Chicano kids in California learn good English and adopt many other Anglo customs. Anglo Californians in turn learn at least a few words of Spanish, prefer salsa to ketchup, bash piñatas at birthday parties, and acquire a smattering of other Mexican customs. The movement of people and ideas between groups exists everywhere and will tend to attenuate group differences. Thus, the persistence of existing boundaries and the birth of new ones suggest that other social processes resist the homogenizing effects of migration and the strategic adoption of ethnic identities.

The persistence of marked boundaries may be a consequence of rapid cultural adaptation. First, notice that symbolic marking allows people to identify in-group members. In-group serves two purposes. First, the ability to identify in-group members allows selective imitation. When cultural adaptation is rapid, the local population becomes a valuable source of information about what is adaptive in the local environment. It's important to imitate locals and avoid learning from immigrants who bring ideas from elsewhere. Second, the ability to identify in-group members allows selective social interaction. As we have discussed, rapid cultural adaptation can preserve differences in moral norms between groups. Best to interact with people who share the same beliefs about what is right and wrong, what is fair, and what is valuable so as to avoid punishment and reap the rewards of social life. Thus, once reliable symbolic markers exist, selection will favor the psychological propensity to imitate and interact selectively with individuals who share the same symbolic markers.

The second and less obvious step is to see that these same propensities will also create

and maintain variation in symbolic marker traits.[45] Suppose that there are two groups; call them red and blue. In each group a different social norm is common; the red norm and the blue norm. Interactions among people who share the same norm are more successful than interactions among people with different norms. For example, suppose that the norm concerns disputes involving property, and people with shared norms resolve property disputes more easily than people whose norms differ. These groups also have two neutral but easily observable marker traits. Perhaps they are dialect variants. Call them red-speak and blue-speak. Suppose red-speak is relatively more common in the red group, and blue-speak in the blue group. Further suppose that people tend to interact with others who share their dialect. Individuals who have the more common combination of traits, red-norm and red-speak in the red group and blue-norm–blue-speak in the blue group, are most likely to interact with individuals like themselves. Since they share the same norms, these interactions will be relatively successful. Conversely, individuals with the rare combinations will do worse. As long as cultural adaptation leads to the increase of successful strategies, the red-marked individuals will become more common in the red group and the blue-marked individuals will become more common in the blue group. The real world is obviously much more complicated but, nonetheless, the same logic should hold. As long as people are predisposed to interact with others who look or sound like themselves, and if that predisposition leads to more-successful social interaction, then markers will tend to become correlated with social groups.

The same basic logic works for markers that allow people to imitate selectively.[46] People who imitate others with the locally more common marker have a higher probability of acquiring locally advantageous variants. If people imitate both the marker and the behavior of the marked individuals, then individuals with the locally common marker will, on average, be more

successful than people with other markers. This will increase the frequency of locally common markers, which in turn means that they become even *better* predictors of whom to imitate. If a sharp environmental gradient or a sharp difference in local norms exists, differences in marker traits will continue to get more extreme until the degree of cultural isolation is sufficient to allow the population to optimize the mean behavior.[47]

Many people think that ethnic markers arise because they allow altruists to recognize other altruists.[48] The problem with this idea is that symbols are easy to fake. Talk is cheap and so is hair dye. Advertising that you are an altruist is a dangerous proposition, because it's so easy for bad guys to signal that they are good guys. If you wear a big *A* on your chest, you are liable to attract false friends who take the benefits of your good heart, returning nothing. Indeed, sociopaths seem to be quite good at simulating good-guy behavior in the pursuit of their predatory schemes.[49] What *can* evolve are markers signaling that you are a member of a group that shares cooperative norms that are enforced by moralistic punishment. Then, behaving altruistically is in your own self-interest, and advertising that you are a member of a moral community does not expose you to merciless exploitation by sociopaths, because the moralists in your community will punish those who victimize you. Wearing the badge of a community whose altruism is protected by moral rules and moralistic punishment supplements cheap talk with a big stick.[50]

Tribal social instincts evolved in social environments shaped by cultural processes

This new social world, a result of rapid cultural adaptation, drove the evolution of novel social

instincts in our lineage. Cultural evolution created cooperative, symbolically marked groups. Such environments favored the evolution of a suite of new social instincts suited to life in such groups, including, a psychology which "expects" life to be structured by moral norms, and is designed learn and internalize such norms, new emotions, such as shame and guilt, which increase the chance the norms are followed, and a psychology which "expects" the social world to be divided into symbolically marked groups.[51] Individuals lacking the new social instincts more often violated prevailing norms and experienced adverse selection. They might have suffered ostracism, been denied the benefits of public goods, or lost points in the mating game. Cooperation and group identification in intergroup conflict set up an arms race that drove social evolution to ever greater extremes of in-group cooperation. Eventually, human populations diverged from societies such as those of other living apes and came to resemble the hunting-gathering societies of the ethnographic record. We think that the evidence suggests that after about one hundred thousand years ago, most people lived in tribal-scale societies.[52] These societies were based upon in-group cooperation where in-groups of a few hundred to a few thousand people are symbolically marked by language, ritual practices, dress, and the like. Social relations were egalitarian, and political power is diffuse, and people were ready to punish transgressions of social norms, even when personal interests are not directly at stake.

But why should selection favor new prosocial motives? People are smart, so shouldn't they just calculate the best mix of cooperation and defection given the risk of punishment? We think the answer is that people aren't smart enough for evolution to trust them with the necessary calculations. For example, there is ample evidence that many creatures, including humans, overweight the present in decision making. For example, most people offered the choice between $1,000 right now and $1,050 tomorrow grab the $1,000. On the other hand, if offered the choice

of $1,000 in 30 days or $1,050 in 31 days, most people choose to wait. But this means that when 30 days have passed, people regret their decision. This bias can cause individuals to make decisions that they later regret, because they weigh future costs less in the present than they will weigh the same costs in the future.[53] Now suppose that, as we have hypothesized, cultural evolution leads to a social environment in which noncooperators are subject to punishment by others. In many circumstances the reward for noncooperation can be enjoyed right away, while the cost of punishment will be suffered later; and thus people who overvalue immediate payoffs may fail to cooperate, even though it is in their own interest to do so. If generally cooperative behavior is favored in most social environments, selection may favor genetically transmitted social instincts that predispose people to cooperate and identify within larger social groupings. For example, selection might favor feelings such as guilt that make defection intrinsically costly, because this would bring the costs of defection into the present, where they would be properly compared with the cost of cooperation.

These new tribal social instincts were superimposed onto human psychology without eliminating those that favor friends and kin. Thus, there is an inherent conflict built into human social life. The tribal instincts that support identification and cooperation in large groups are often at odds with selfishness, nepotism, and face-to-face reciprocity. Some people cheat on their taxes, and not everyone pays back the money he borrows. Not everyone who listens to public radio pays her dues. People feel deep loyalty to their kin and friends, but they are also moved by larger loyalties to clan, tribe, class, caste, and nation. Inevitably, conflicts arise. Families are torn apart by civil war. Parents send their children to war (or not) with painfully mixed emotions. Highly cooperative criminal cabals arise to prey upon the production of public goods of larger scale institutions. Elites take advantage of key locations in the fabric of society to extract

disproportionate private rewards for their work. The list is endless. The point is that humans suffer these pangs of conflict; most other animals are spared such distress, because they are motivated only by selfishness and nepotism.

Some of our evolutionist friends have complained to us that this story is too complicated. Wouldn't it be simpler to assume that culture is shaped by a psychology adapted to small groups of relatives? Well, maybe. But the same friends almost universally believe an equally complex coevolutionary story about the evolution of the language instinct. The Chomskian principles-and-parameters model of grammar[54] holds that children have special-purpose psychological mechanisms that allow them to rapidly and accurately learn the grammar of the language they hear spoken around them. These mechanisms contain grammatical principles that constrain the range of possible interpretations that children can make of the sentences they hear. However, sufficient free parameters exist to allow children to acquire the whole range of human languages.

These language instincts must have coevolved with culturally transmitted languages in much the same way that we hypothesize that the social instincts coevolved with culturally transmitted social norms. Most likely, the language instincts and the tribal social instincts evolved in concert. Initially, languages must have been acquired using mechanisms not specifically adapted for language learning. This combination created a new and useful form of communication. Those individuals innately prepared to learn a little more protolanguage, or learn it a little faster, would have a richer and more useful communication system. Then selection could favor still more specialized language instincts, allowing still richer and more useful communication, and so on. We think that human social instincts very similarly constrain and bias the kind of societies that we construct, with important details left to be filled in by the local cultural input.[55] When cultural parameters are set, the combination of instincts and culture

produces operational social institutions. Human societies everywhere have the same basic flavor, if the comparison is with other apes, say. At the same time, the diversity of human social systems is quite spectacular. Like the language instincts, the social instincts coevolved with such institutions over the last several hundred thousand years.

So much for theory. What is the evidence that such instincts actually exist?

Altruism and empathy

Lots of circumstantial evidence suggest that people are motivated by altruistic feelings which motivate them to help unrelated people even in the absence of rewards and punishments.[56] People give to charity, often anonymously. People risk their own lives to save others in peril. Suicide bombers give their lives to further their cause. People give blood.

The list of examples is long. Long, but not long enough to convince many who are skeptical about human motives. For these people all examples of altruism are really self-interest in disguise. Charity is never anonymous; the right people know who gave what. Heroes get on Letterman. Resources are lavished on the families of suicide bombers. You get a sticker to wear when you give blood. Or, in the words of the bioeconomist Michael Ghiselin, "Scratch an altruist and watch a hypocrite bleed."[57] The possibility of covert selfish motives can never be excluded in these kinds of real-world examples.

In recent years, however, experimental work by psychologists and economists has made it a lot tougher to hang on to dark suspicions about the motives behind good deeds. In these experiments, the possibility of selfish reward is carefully excluded. Nevertheless, people still behave altruistically. Psychologist Daniel. Batson thinks that empathy is the key to altruism.[58] Once it is engaged, helping behavior is motivated by a genuinely unselfish desire to relieve the

victim's suffering. He doesn't doubt (nor do we!) that egoistic motives are quite important. The question is whether empathy driven altruism is also important. Batson executed a series of experiments designed to explore the role of empathy in altruistic behavior. Participants were divided into experimental and control groups. Experimenters encouraged an empathetic response in the experimental group by asking them to write an account of the experiment from the point of view of its victim. Controls were asked to view the situation objectively. Then the experimental conditions were manipulated to test whether participants in the empathy condition were more likely to provide aid. In one experiment, for example, "Elaine," a sham participant/victim, was purportedly to suffer a series of ten moderately painful shocks—not a pleasant thing to experience or to witness someone else experience. Some real participants were told they would escape watching Elaine's suffering after two shocks; other participants would purportedly have to observe all ten. Then all real participants were told, just before the shocks were to Elaine were to start, that she is unusually sensitive to shocks due to a traumatic childhood experience, and finds them exceedingly uncomfortable. The experimenter expresses concern about this, and offers the real participants the chance to continue the "experiment" in place of Elaine. The shocks will be uncomfortable for them, but not nearly as painful as for Elaine..

Batson reasoned that if helping is motivated by the selfish desire to avoid viewing someone else suffering, the ability to leave after only two shocks should reduce the tendency to offer to take Elaine's place. On the other hand, if participants had a genuine desire to help the victim, even subjects allowed to leave after two shocks should offer to help. In the control, low-empathy condition, difficulty of escape had a dramatic effect on helping, raising the proportion helping from about one in five to about three in five participants offering to take Elaine's place. This suggests that people expected to feel quite unpleasant while watching Elaine's suffering,

and they offered to help when this was the most effective way to avoid their own discomfort. In the empathy condition, the difficulty of escape made no significant difference in helping; nearly everyone offered to help. In this case, people's empathy for the victim seemed to be the overriding factor in their response.

Batson also produced evidence that people are motivated by a sincere desire to help, not just a desire to earn self-administered psychological brownie points. In experiments in which the desire to help was aroused and then frustrated because someone else provided the help, participants who saw help provided but didn't have to provide it themselves had the greatest mood increase, and those prevented from helping when no one else provided the help had the lowest mood. Once empathy is engaged, people apparently have a genuinely unselfish desire to help. The attitude seems to be "it's a dirty job, but someone's got to do it." Attitudes like this crop up in the reminiscences of combat soldiers, to take an extreme case. Few veterans are eager for the next fight; they expect the whole experience to be hateful. But they do their duty.

These kinds of experiments did not convince most economists, game theorists, and others in the rational-choice camp. First, psychologists routinely lie to their subjects---Elaine was not really going to be shocked. Since subjects are often drawn from psychology classes and have presumably done the assigned reading, they may not believe what experimenters tell them. Maybe most of Batson's subjects suspected that "Elaine" was the experimenter's confederate. Second, the costs and rewards are vague and hard to measure. Subjects said their mood was elevated, but how do we really know they were telling the truth? Finally, the effects of reciprocity and reputation are not usually carefully controlled. Subjects may expect to meet Elaine again on campus and get some reward for their help. A psychology of altruism may just be a proximal mechanism for forming reciprocal bonds.

Such skepticism led economists to design their own experiments in which these kinds of effects were controlled for. The Dictator Game provides a good example. Participants are recruited to the laboratory, and all are paid a "show-up" fee. Then some participants are given a sum of money, the endowment. Usually this is a modest sum, say, ten dollars, but in some experiments the endowment is much larger. Each participant who receives an endowment is offered the opportunity to give some (or all) of it to a second participant. Participants make their choice and then walk out of the lab with whatever money they have decided to keep. The interaction is totally anonymous. Neither participant ever sees the other or is told anything about the other, and in some experiments even the experimenter does not know what the individual participants do. As to the game's outcome, economic theory makes an unambiguous prediction: selfish, money-maximizing players should keep all the money.

The Dictator Game has been played hundreds of times in many different settings. University students in the United States, Europe, and Japan typically keep about 80% of their endowment and give away 20%. Older nonstudents (aka grown-ups) give much more, sometimes averaging an even split. The Dictator game has also been played in a number of small-scale, non-Western societies; offers in these societies vary more than offers in Western societies, but even then most participants give some money away.[59] The news couldn't be much worse for the view that people have purely selfish motives.

Moralistic punishment and reward

A great deal of circumstantial evidence also suggests that we are inclined to punish fellow group members who violate social norms, even when such punishment is costly. Road rage is a classic example. Think about how you feel if somebody cuts you off, or makes an illegal left turn in

front of you. If you are like most people you get annoyed, perhaps very annoyed , and want to punish the rule breaker, even though you know you'll never see the person again. Or, think about how do you feel if someone cuts in line while you wait for a movie. Most people get quite angry, even if they are near the front of the line and are sure to get a good seat. Such emotions can give rise to voluntary, informal punishment of people who break social rules. But in complex societies, it's hard to know whether such punishment plays a significant role in maintaining social norms because police and courts also act to punish rule breakers. Many simple societies lack formal legal institutions, so the only kind of punishment *is* informal and voluntary. In small-scale societies, considerable ethnographic evidence suggests that moral norms are enforced by punishment.[60]

A series of experiments by economist Ernst Fehr and his coworkers at the University of Zurich provide strong evidence that many people are willing to punish rule breakers, even when it doesn't profit them in any way.[61] One certain-to-be-classic experiment is based on the public-goods game often used by experimental economists. As usual in experimental economics, participants are anonymous and are paid real money. For each round of the game, participants are randomly divided into groups of four, and each participant is given a sum of money that he can keep or contribute to a common pool. The experimenters increase all contributions to the common pool by 40% and divide it equally among all players in the group. If one player contributes $10, for example, the experimenter increases it to $14, and gives $3.50 to each player. Then, new groups of four are formed at random, and they repeat the same procedure. This procedure continues over a series of trials.

In this game players do best, on average, if everyone contributes all his resources to the common pool; but an individual is best off if she contributes nothing while everyone else

contributes everything. This selfish individual gets to keep his stake and reaps a share of the rewards from the suckers who do contribute. The participants in Fehr's experiment behaved much like the participants in many previous public-goods games: initially, many participants contributed to the common pool, but over time contributions declined until by the tenth round participants contributed almost nothing.

But Fehr did not stop there. In another treatment, each round consisted of two stages. The first stage was a public-goods game like the one just described. In the second stage, the contributions of each player in the group were posted (without revealing the player's identity). Then participants could reduce any player's payoff at some cost to themselves. Since groups were randomly re-formed each time period, there was no possibility that punishment could induce a player to behave differently toward the person who behaved punitively. Nonetheless, many participants punished low contributors to the common pool, and as a result contributions rose over time so that by the tenth round most participants contributed their entire endowment. Postgame interviews indicate that participants were motivated by moral emotions described above, and Fehr reports that some participants were quite angry about the bad behavior of others.

One of the frequent criticisms of these kinds of experiments is that people don't really believe they are playing a one-shot game with strangers; our psychology is simply not set up to deal with this possibility, so we always behave as if our neighbors were watching. Perhaps so, but Fehr's experiment suggests that some of the neighbors watching us take sadistic pleasure in punishing our transgressions, or at least feel obligated to exert considerable effort to punish. Worrying about what unselfishly moralistic neighbors will do is an entirely reasonable precaution for humans! Even if these impulses are really designed for the repeated game in small groups, they nevertheless seem to misfire readily in the anonymous, nonrepeated case. We

submit that cultural rules capitalize on this tendency and routinize the misfiring, if misfiring it is.

Unless these experiments are highly misleading, even strangers with whom your will never interact again are liable to be nice to you unless you are not nice to them. Many ordinary things we do depend upon this being so. Take travel. Solitary individuals can travel through strange cities and usually come to no harm as long as they behave themselves. We've traveled through Third World cities where our pocket money and personal valuables were worth a small fortune in local terms, and where the police were inefficient and corrupt. We usually had a good time. We remember whispered advice from storekeepers, hotel clerks, and officious matrons when we were inadvertently doing something risky, such as choosing the wrong bar to go into. To take a more extreme case, recall the video from the August 1998 embassy bombing in Kenya or the 9/11 attack in New York City in which streams of wounded were helped away from the bomb site, often by others nearly as bloody as themselves. Disasters of all kinds yield similar footage: people other than highly trained, paid emergency services personnel will come to your rescue if need be.

Evidence for social instincts relevant to symbolically marked groups

Finally, there is much evidence that symbolic markers of group boundaries motivate important behavior. Tribal instincts cause people to use symbolic markers to define the boundaries of in-groups and establish, for example, who is eligible for empathy, who should excite suspicion, and, in some horrible cases, who should be killed.[62]

Evidence suggests that ethnolinguistic boundaries among foragers are symbolically marked, and that stylistic marks of group membership are highly salient. Anthropologist Polly Wiessner collected arrow points from a number of Kalahari San Bushmen groups, including

groups unknown to the !Kung San, the people she studied. Wiessner asked !Kung San men for comments on the distinctive styles.[63] Confronted by unfamiliar arrow points, !Kung men guessed that their makers were very different people from themselves. They reported that they would be alarmed to find these points in their territory, because they certainly would have been lost by people unknown to the !Kung and therefore potentially dangerous. On the other hand, exchange of stylistically familiar beadwork and other valuables within groups is used to build up a notion of the !Kung social universe and to build a web of relationships that link people within the ethnolinguistic unit. In simple band-scale societies like the !Kung, the institutions that link members of a tribe are informal but very important. In a harsh and unpredictable world, succor in times of disaster may often mean the difference between life and death. Using gift exchanges, ceremonial activities, and rules of exogamy to create a large group of trusted friends and affines is an effective form of insurance. These data, together with the appearance of stylistic artifacts at least one hundred thousand years ago, indicate that expressive symbolic displays have been part of human strategies for managing social life for a respectable period.[64]

At the proximal psychological level, the "minimal group" experimental system developed by social psychologist Henri Tajfel provides interesting insights into the cognitive mechanisms involved in the use of symbols to demarcate groups, and the actions people take based on group membership.[65] In social psychological experiments, as in real life, members of groups favor one another and discriminate against out-groups. The social psychologists in Tajfel's tradition were interested in separating the effects of group membership per se from the personal attachments that form in-groups. Social psychologist John Turner, for instance, contrasts two sorts of hypotheses to explain group-oriented behavior.[66] Functional social groups might be composed entirely of networks of individuals that are linked by personal relationships, objective shared

fate, or other individual-centered ties. Groups could be a collection of individuals bound together by mutual interpersonal attraction reflecting some degree of functional interdependence and mutual aid. The alternative hypothesis is that identity symbols alone are sufficient to induce humans to accept membership in a group, acting positively toward in-group members and negatively toward out-groups.

In his prototypical experiments, Tajfel told participants that they were participating in a test of aesthetic judgment. They were shown pictures of paintings by Paul Klee and Wassily Kandinsky, and asked to indicate which they preferred. Then the participants were divided into two groups, supposedly on the basis of their art preference, but in fact at random. The participant's task was then to divide a sum of money among members of her own group or the other group. Participants discriminated in favor of the in-group members: people gave more money to people who (supposedly) shared their own preference for Klee or Kandinsky. The most plausible evolutionary interpretation of these results is that people react to symbolic badges of group membership because in the evolutionary past they marked important social units. When experimenters take away any information about the nature of groups, they may expose the "default settings" of in-group psychology. Looked at this way, minimal group experiments suggest that people are well primed to make quick and intuitive judgments about behavior appropriate to life in symbolically marked groups. In the politically complex world outside the lab, where many groupings are potentially salient, people attempt to make sensible decisions about what cues to take seriously in any given circumstance, and socially learned determinants play a role alongside whatever genetic dispositions exist.

Recent field experiments by psychological anthropologist Francisco Gil-White in Mongolia suggest that humans use the same cognitive strategy for classifying ethnic groups as

they use for classifying species of plants and animals. Much evidence suggests that people believe that individual members of a given species have important hidden properties in common—essences—and that these essences are transmitted from parents to offspring. These essences are immutable, so for example, if a zebra is transformed so that it looks and behaves exactly like a horse, even small children will insist that it is still a zebra. Because people intuitively believe the essences are important, they readily generalize what they observe about one individual of a species to all members.

Gil-White's experiments suggest that our folk theory of ethnicity is also essentialist. He interviewed Mongols and Kazakhs, the most numerous ethnic groups in the area where he worked, asking them questions designed to see if they thought that Kazakhs possessed inalterable features in common that distinguished them from Mongols. When asked if a Kazakh child adopted at birth and raised by a Mongol mother and father was of Mongol or Kazakh ethnicity, most respondents replied "Kazakh." Neither biologists nor anthropologists regard essentialism as the proper basis for a taxonomy of either species or cultures, but for everyday purposes, it may be sufficient. Gil-White thinks that Kazakhs and Mongols are distinguished mainly by differences in customs that would make everyday intimate interactions unpleasant. Customs of family life, food, hygiene, hospitality, and formality of everyday intercourse differ between the two groups in ways that would make social interactions awkward. For example, polite reserve is the centerpiece of Mongol hospitality, while the Kazakhs take delight in rough teasing, which they fully expect to be reciprocated by their guests. Gil-White, whose first hosts were Mongol, reports that he took several days to adapt to Kazakh teasing even though his own personal style is more in accord with theirs than that of the Mongols. These are the sorts of differences that are likely to arise by rapid cultural evolution and motivate the evolution of a regard for ethnic

markers.[67]

Complexities aside, we think there can be little doubt that humans give great emotional salience to large, impersonal groups (Protestant Irish, Serb, Jew, German, Hutu, Tutsi, etc.), and under the right circumstances, they undertake desperate deeds on the behalf of such groups. When such group identities become highly salient, individuals in one group will turn their hearts against former friends and neighbors in the other group with appalling frequency. So few Germans went out of their way to protect Jewish friends in Nazi Germany that they are counted as heroes.[68] So few Euro-Americans turned out to aid Japanese-American internees during World War II that the few who did are well remembered by those who benefited. If groups are always built on the foundation of dyadic ties, we would find it hard to explain how loyalties to large and necessarily abstract groups could override the ties of personal friendship to create the atrocities that too commonly result from ethnocentrism. Even after long periods of relative dormancy, group identity can make strong claims on our emotions. And there is always the awful possibility that an aggressive out-group may suddenly, for reasons of its own, target one as belonging to a previously weakly relevant group, as has happened recently to Bosnian Muslims and, in the mid-twentieth century, to German Jews. Not unlikely, a long history of conflicts between symbolically marked groups may have led to the evolution of in-group sentiments that are all too easily turned to the service of conflict with out-groups. Nonetheless, relatively relaxed relations between different ethnic groups are more common than genocidal hostility.[69]

The scale of Pleistocene societies is consistent with the social instincts hypothesis

Many in the evolutionary social science community are skeptical that culture has much to do with social emotions such as empathy and ethnocentrism. Instead, they think that the human social instincts evolved in small foraging groups in which kinship and reciprocity favored the evolution of cooperative behavior.[70] While variants of this argument are many, we think the most convincing one goes something like this: Until the spread of agriculture over the last ten thousand years ago, humans probably lived in relatively small groups. In such a world, ordinary natural selection could favor psychological mechanisms such as empathy and moralistic anger because groups were small, and many of the potential recipients of altruism were kin or members of small, reciprocal social networks. Motives that generated unconditional altruism in toward strangers in large, anonymous modern societies (or in the experimental economics laboratory) were favored during the period when our social psychology evolved because no interaction in a small hunter-gatherer group would actually be anonymous. Ties of kinship and reciprocity within groups are stronger than kinship ties among groups, and as a result, neighboring groups competed for territory or other resources. If neighboring groups of interrelated families had differences in dialects, customs, or artifacts on a quite fine scale, selection might favor a rule: "Be nice to people who talk like you, dress like you, and act like you. Be suspicious of everyone else." When agriculture made much larger, culturally homogeneous social groups possible, these social emotions gave rise to tribal-scale social organization. The cultural similarity once characteristic of the small bands came to apply to a much larger group and the emotions appropriate to the kin group scaled up accordingly. This is another variant of the "big-mistake hypothesis" we discussed in the last chapter. If it is correct, almost everything in modern life—

trade, religion, government, and science—is a mistake from the viewpoint of the selfish gene.[71]

The relative plausibility of the tribal social instincts hypothesis and this big-mistake hypothesis depends on the scale of Pleistocene foraging societies. The tribal social instincts hypothesis requires that these societies already had fairly complex social organization in which sizable groups of people shared moral norms and symbolic group makers. The tribal social instincts are an adaptation to tribal social life. In contrast, the big-mistake hypothesis is more plausible if forager societies were considerablysmaller. Theory strongly suggests that reciprocity, especially in the production of public goods such as cooperation in warfare and enforcement of moral rules, can only evolve in very small groups,[72] and kin groups are necessarily small given human reproductive biology.

So the question is, what were Pleistocene foraging societies like? Unfortunately, this is a hard question to answer. Ethnographic work gives us a detailed, sometimes quantitative picture of the economy and social organization of contemporary foragers. However, the ethnographic sample of foraging societies is biased toward groups living in unproductive environments like the Kalahari and central Australian deserts and the Amazonian rain forest. We know from historical accounts, particularly from western North America, that foragers in more-provident environments had more complex social organization than those studied ethnographically.[73] That the spectacular cave art of late Pleistocene Europe is reminiscent of elaborate rituals associated with complex societies[74] provides circumstantial evidence that at least some Pleistocene societies were similarly complex. However, any claims about the nature of social life bygone hunter-gatherers should be taken with a grain of salt. Historical accounts are of uncertain quality, and the elderly men and women interviewed by ethnographers in the early twentieth century lived their entire lives in communities that had already been influenced by modern societies. Another

problem is that we don't know how to project the ethnographic and historical samples back into the Pleistocene. The climate of the last ten thousand years is warmer, wetter, and much less variable than the climates that prevailed during most of the Middle and Upper Pleistocene.

With these problems in mind, let's try to estimate the range of social organization of late Pleistocene foragers as best we can using descriptions of the foraging societies that persisted into the modern period. The band-level societies of the Great Basin in North America, the Kalahari Desert in South Africa, and the desert of central Australia are among the simplest in the ethnographic and historical record.[75] The Great Basin societies, were composed of autonomous family bands with minimal and informal tribal institutions, yet there was generalized propensity to be more cooperative with speakers of one's own and closely related languages. Bands often came together for socializing or for communal enterprises such as rabbit and antelope drives. Thus, even in the simplest foraging societies known, there is significant tribal-scale cooperation. Kinship and friendship may have been sufficient to account for social organization at the band level, but at the tribal level, principles of social organization unique to humans were widespread, consistent with the presence of tribal instincts.

Other band-level societies have marked tribal institutions. For example, the !Kung San of southern Africa have a system of gift exchange (involving artistic productions like those known from the late Pleistocene) that weld the small residential bands into a tribe composed of a much larger number of people.[76] Like a modern nation in miniature, the whole tribe never gathers in one place, but there is normally a clear sense of who belongs to the tribe and who does not. People maintain contacts with members of other bands, because in times of subsistence emergencies, they can call on other members of their tribe living in other bands for permission to forage on their territories or receive emergency aid. Anthropologist Aram Yengoyan suggests

that peoples of the desert in central Australia, living in the poorest environments on the continent, have more-elaborate institutions to maintain solidarity with other bands than those living in more-provident environment. Precarious subsistence in the desert means that one often has to appeal to poorly-known acquaintances and distant relations for aid.[77]

Tribal institutions in such simple band-level societies are modest. There is no discernable superstructure of government, not even an informal council of influential people. Surrounded by powerful neighbors, the !Kung are not warlike, but within-group rates of violence are quite high, because self-help coercion is the only mechanism for punishing transgressors.[78] The most egalitarian and least politically sophisticated foragers have problems maintaining internal peace and rallying responses to external threats, despite vigorous efforts to maintain friendly ties with as many people as possible.[79] More broadly, however, the great majority of ethnographically known foraging societies make war, and military cooperation was likely an important function of tribal institutions in Pleistocene societies.[80]

At the other end of the spectrum, some ethnographically known foragers lived in complex, hierarchical societies. For example, societies on the Northwest Coast of North America, such as the famous Kwaikiutl, had large, permanent settlements, substantial division of labor, hierarchal social systems, hereditary political ranks, and extensive large-scale warfare—all characteristics usually associated with agricultural subsistence. Their elaborate art rivals that of the Pleistocene caves suggesting that Upper Pleistocene hunter-gathers may have had similar sociopolitical sophistication. While some of this complexity may have arisen in response to trade stimulated by the arrival of Europeans, there is much historical and archaeological evidence for the existence of complex foraging societies in many other areas.[81] It is quite plausible that the societies of Upper Paleolithic Europe might have achieved similar complexity. Much as the rich

marine resources of the Northwest Coast supported locally dense populations that created the population base for complexity, the harvest of migratory big game at favorable sites might also have supported large populations.[82]

In between these extremes, a variety of ethnographically or historically known foraging societies might be proposed as approximating the central tendency of the late Pleistocene. Good candidates might be the North American Plains groups that specialized in big-game hunting. Their environments resemble the cold, semi-arid environments that were more common in the last glacial period, and the focus of the economy on large mammals was probably more like Pleistocene foraging economies than the plant-focused subsistence strategies of groups like the !Kung. Some historical information is available for Plains societies before the introduction of the horse in the eighteenth century. Much more is available from the succeeding two or three generations as fur traders established regular contact with the groups.[83] The Blackfeet came from a purely foraging ancestry, unlike many other Plains tribes of the horse era who were formerly farmer-hunters. The core of their subsistence was hunting bison Several families cooperated to construct traps for the herds and to drive the animals into them. Successful drives yielded lots of meat, but failures were common. Likely, unsuccessful groups often had to depend upon the generosity of successful ones, motivating bands to maintain tribal-scale affinities for insurance purposes, as do the !Kung and central Australians. Dried meat may have supported regular rendezvous with other bands on some scale.

Blackfoot warfare was a tribal-scale institution. The Blackfeet fought a chronic guerrilla war against the Shoshoni who emerged from the northern Great Basin to hunt bison. Owing to the limited mobility of pedestrian hunters, most fights were band-scale raids. Nevertheless, informants who lived as young adults in the prehorse days told an early visitor that fights with

two hundred warriors on a side sometimes occurred, a fair fraction of the tribe's total force of warriors. Three subtribes of Blackfeet (Piegans, Bloods, and Blackfeet proper), each composed of several bands, were at peace. During the horse era and perhaps earlier, the Blackfeet were allied with two other tribes, the Gros Ventres and the Sarsis, thus maintaining internal peace on a considerable scale.

Commentators on primitive warfare do not always describe the realm over which peace is maintained,[84] yet the scope and quality of internal peace is, perhaps, a more important index of the strength of tribal institutions than the size and frequency of wars themselves. Logistics limit the size of war parties among foragers, but the realm of peace can, and commonly does, include more people than could ever be assembled in one place. In societies like the Blackfeet, disputes are solved through self-help violence by aggrieved parties. It is testimony to the strength of tribal instincts and their associated cultural institutions that societies lacking formal leadership do not suffer a Hobbesian collapse of social peace.[85]

Even in the horse days, Blackfeet tribal governance was very informal. Anthropologist Christopher Boehm argues that such egalitarian societies have a reverse dominance hierarchy in which followers control the behavior of leaders. [86] Even in the horse days, Blackfeet. Band "leaders," so-called peace chiefs, were typically older men with many horses.. Generous rich men who lent horses and food to the poor could earn great respect, and only men whose decisions were sound could maintain this regard. Even at that, chiefs could only guide the emergence of a consensus; they could not coerce followers. Errant chiefs were "replaced" whenever popular sentiment came to favor the opinions of another man. Individual families were free to move to other bands if they were dissatisfied with life in their current band. Moreover, groups of families could split off to form a new band. War chiefs, usually younger men than

peace chiefs, were entrepreneurs who organized raids on an ad-hoc basis in quest of horses, captives, and glory. War chiefs were not subordinate to peace chiefs or vice versa.

The horse lent the Blackfeet mobility and brought them a wealth of food, but there was little time for the horse era to affect basic institutions. Thus, horse-era Blackfeet must have been little more than modestly scaled-up, richer versions of pedestrian big-game hunters, with a little more dominance successfully exercised by richer horse owners. It is quite plausible that the range of latest Pleistocene foraging societies encompassed societies of the complexity of the Blackfeet. Of course, how close to the late Pleistocene central tendency they might have been is more difficult to say.

We read the ethnographic evidence as suggesting that many, if not most, Pleistocene societies were multi-level tribal formations in which small residential bands were nested within a larger society. At the simple end of the spectrum were societies something like the Shoshoni and !Kung, in which bands were linked into a weakly organized tribal unit. At the other end of the continuum, tribal societies with sufficient resources—rich fishing or hunting grounds—could grow to several thousand people with the aid of sufficiently sophisticated cultural institutions. For example, Nuer tribes ranged from less than ten thousand to more than forty thousand, and they maintained a modicum of unity on this scale with a highly extended kinship ideology and other modest institutions.[87] Most likely, no Pleistocene societies reached this size. More likely, the modal Pleistocene society living in relatively provident temperate environments was something like the Blackfeet, in which relatively limited tribal institutions organized many hundreds or perhaps a few thousand people to cooperate in subsistence and in warfare. If this argument is correct, the dependence of the big-mistake hypothesis on kin and reciprocity scale seems insufficient to account for the scale of social organization typical of the late Pleistocene.

Modern institutions are based on tribal social instincts

Adaptationist reasoning usually runs "forward in time"—we predict contemporary behavior from a knowledge of past environments. The recent radical changes in human environments and the inadequacy of the archaeological record make this strategy difficult in the case of human social behavior. However, adaptationist reasoning can also be run "backward"—we can predict past environments from present behavior. In this enterprise, the radical changes in the environment work for us. You can think of the evolution of complex societies in the Holocene as a giant field experiment in which the social instincts adapted to smaller-scale societies are subjected to a wide range of new environmental conditions. How does cultural evolution engineer ancient Rome or modern Los Angeles starting with human raw material originally designed for societies, at most, on the scale of the cattle camps of the southern Sudan? The size, degree of division of labor, and degree of hierarchy and subordination of Rome and Los Angeles are orders of magnitude beyond the range of the most complex foraging societies. If either the big-mistake or tribal instincts hypothesis is correct, the structure of our evolved psychology should have left tracks all over the resulting constructions.

The past ten thousand years have seen a race toward ever larger and more complex societies. In favorable circumstances, foraging can support fairly large, sedentary, hierarchical societies, but in most environments the social complexity of foragers is limited. Foraging was probably the only option during the Pleistocene, because climates during that epoch were hostile to agriculture—dry, low in atmospheric CO_2, and extremely variable on quite short timescales. The warm, moist, stable climates of the last ten thousand years have made agriculture, and

therefore larger, more complex societies, possible over much of the earth. Once they were possible, the race was on. Larger societies can usually marshal larger military units and defeat smaller societies in military competition. Size allows economies of scale, and division of labor generates greater economic productivity. These also contribute to political and military success, and attract imitators and immigrants. The Nuer-Dinka style conquest-absorptions are evident from the beginning of the written historical record. The result was a steady increase in social scale and complexity that continues today.[88]

The increase in the size and complexity of human societies has probably not been accompanied by significant changes in our social instincts. While natural selection can sometimes lead to substantial genetic change in a few thousand years, most biologists think that important changes in complex characters take much longer to assemble. Our social psychology is probably that bequeathed to us by our Pleistocene ancestors.

If we are correct, the institutions that foster hierarchy, strong leadership, inegalitarian social relations, and an extensive division of labor in modern societies are built on top of a social "grammar" originally adapted to life in tribal societies. To function, humans construct a social world that resembles the one in which our social instincts evolved. At the same time, a large-scale society cannot function unless people are able to behave in ways that are quite different from what they would be in small-scale tribal societies. Labor must be finely divided. Discipline is important, and leaders must have formal power to command obedience. Large societies require routine, peaceful interactions between unrelated strangers. These requirements necessarily conflict with ancient and tribal social instincts, and thus generate emotional conflict, social disruption, and inefficiency.

Consequently, social innovations that make larger-scale society possible, but at the same

time effectively simulate life in a tribal-scale society, will tend to spread. If we assume that the social instincts have changed little if any since the beginning of the Holocene, then the evolutionary job of creating complex will have to have been done entirely by institutional "work-arounds" that have alternately taken advantage of and finessed our social instincts. People will prefer such arrangements and will adopt them given a choice. Societies with such institutions will suffer less internal conflict and will, all else being equal, be more effective in competition with other groups. To put the idea a little differently, to the extent possible, institutions buttressed by the ancient and tribal social instincts will be used as building blocks in the evolution of complex societies.

However, these building blocks are not especially well suited to the task. For example, the command and control institutions necessary for cooperation inevitably generate inequality as those in high positions acquire a disproportionate share of society's rewards. Our social instincts do not prepare us to submit to command or tolerate inequality. As a result, our social institutions should resemble a well-broken-in pair of badly fitting boots. We can walk quite a ways in the institutions of complex societies, but at least some segments of society hurt for the effort.

In the section that follows, we describe what seem to us to be the main work-around mechanisms, and the conflicts, compromises, and modes of failure that each entails.

Command backed up by force is necessary but not sufficient

To make a complex society a going concern, the moralistic punishment of tribal societies has to be supplemented with institutionalized coercion. Otherwise, individuals, organized predatory bands, and classes or castes with special access to means of coercion would entirely expropriate the benefits of cooperation, coordination, and division of labor. However, institutionalized

coercion *creates* roles, classes, and subcultures with the power to turn coercion to their own narrow advantage. Social institutions of some sort must police the police so that they will act in the larger interest. Such policing is never perfect and, in the worst cases, can be very poor. That elites always advantage themselves shows that narrow interests, rooted in individual selfishness, kinship, and, often, the tribal solidarity of the elite, exert their predictable influence.

While coercive institutions are common enough, there are two reasons to suspect that they are not, by themselves, sufficient to sustain a complex society. First, the elite class itself must be a complex, cooperative venture. Additionally, the tribal instincts and the institutions built on them often give classes quite a high degree of social solidarity. The importance of the military in the politics of so many countries is an example of how highly organized even a highly coercive institution must be to maintain control of a complex society. Weakly organized coercive elites lead to warlordism, and as we now see in Somalia, Afghanistan, Colombia, Zaire/Congo, and some successor republics to the U.S.S.R., this can lead to near anarchy.

The second problem with pure coercion is that defeated and exploited peoples seldom accept subjugation as a permanent state of affairs without costly protest. The instability of dictatorships is evidence that even highly organized coercion is not sufficient in the long term. Deep feelings of injustice generated by manifestly inequitable social arrangements move people to desperate acts, driving the cost of dominance to levels that cripple societies in the short run and cannot be sustained in the long run.[89] Durable conquests, such as those leading to the modern European national states, Han China, or the Roman Empire, leaven raw coercion with more prosocial institutions. The Confucian system in China and the Roman legal system in the West were far more sophisticated and group-functional institutions than the highly coercive systems that they replaced.

Hierarchies are segmented

Top-down control is generally exerted through a segmentary hierarchy that is adapted to preserve nearly egalitarian relationships at the face-to-face level. As we have argued, late Pleistocene societies probably linked residential bands into larger ethnolinguistic units that served social functions without much formal political organization. The same principle is used in complex societies to deepen and strengthen the hierarchy of command and control. The trick is to construct a formal nested hierarchy of offices, using various mixtures of ascription and achievement principles to staff the offices. Each level of the hierarchy replicates the structure of a hunting and gathering band. A leader at any level interacts mainly with a few near-equals at the next level down in the system and collaborates with peers across the hierarchy. New leaders are usually recruited from the ranks of subleaders, often tapping informal leaders at that level. Bonds of individual reciprocity and small-group esprit leaven tendencies to arbitrary authority deriving from status in the larger hierarchy. Even high-ranking leaders in modern hierarchies typically adopt much of the humble headman's deferential approach to leadership.[90] Charismatic individuals such as Bill Clinton have a gift for reducing their subjective distance from people far beneath them in the official chain of command. As Max Weber so famously argued, bureaucratic institutions attempt by training, symbolic means, and legalistic regulations to routinize charisma in order to legitimize the command-and-control system.[91]

The imperfect fit of institutions and social instincts often makes segmentary hierarchicies painfully inefficient. Selfishness and nepotism—corrupt sergeants, incompetent aristocrats, vainglorious generals, power-hungry bureaucrats—degrade the effectiveness of social organizations. Leaders in complex societies must convey orders downward, not just seek

consensus among their comrades. Only very careful attention to detail can make subordinates responsive to leaders without destroying the illusion that the same arrangements would have arisen by egalitarian consensus. The chain of command is necessarily long in large complex societies, and remote leaders are not normally able to exercise personal charisma over a mass of subordinates. Devolving substantial leadership responsibility to subleaders far down the chain of command is necessary to create small-scale leaders with face-to-face legitimacy. However, delegation potentially generates friction if lower-level leaders have different objectives than the upper leadership or are seen by followers as helpless pawns of remote superiors. Stratification often creates rigid boundaries so that natural leaders are denied promotion above a certain level, resulting in inefficient use of human resources and a fertile source of resentment to fuel social discontent.

In-group symbols create a sense of solidarity in complex social systems

In complex societies, high population density, division of labor, and improved communication give rise to symbolic systems adapted to simulate the badges and rituals of tribal membership, sometimes on a huge scale, as in modern nationalism.[92] The development of monumental architecture in which to stage mass ritual performances is one of the oldest archaeological markers of complex societies. Usually an established religious organization supports a complex society's institutions. At the same time, complex societies make use of the symbolic in-group instinct to delimit a diverse array of culturally defined subgroups, within which a good deal of cooperation is routinely achieved. Military organizations generally mark a set of middle-level, tribal-scale units with conspicuous badges of membership. A squad or platoon's solidarity can rest on bonds of reciprocity reinforced by prosocial leadership, but ship's companies, regiments,

and divisions are made real by symbolic marking. These kind of ethnic group–like sentiments are most strongly reinforced in units that number between one thousand and ten thousand men (British and German regiments, U.S. divisions), groups on the same scale as the tribal societies from which we believe our tribal instincts evolved.[93] In civilian life, symbolically marked units include regions, tribal institutions, ethnic diasporas, castes, large economic enterprises, religions, civic organizations, and, of course, universities.[94]

The evolutionary properties of symbolically marked subgroups gives rise to many problems and conflicts in complex societies. Marked subgroups often have enough tribal cohesion to organize at the expense of the larger social system, as when lower-level military units arrange informal truces with the enemy or ideologies of elite superiority support highly exploitative institutions. "Special interests" organize to warp policy in directions favoring their ideology or material well-being. Charismatic innovators regularly launch new belief and prestige systems, which sometimes make radical claims on the allegiance of new members, make large claims at the expense of existing institutions, and grow explosively. The worldwide growth of fundamentalist faiths that challenge the institutions of modern states is a contemporary example.[95] On the other hand, larger loyalties can arise for better or worse, as in the case of modern nationalism and Islam.

Societies often have legitimate institutions that command broad support

At their most functional, institutions create the sense that laws and customs are fair. Rationally administered bureaucracies, lively markets, protection of socially beneficial property rights, widespread participation in public affairs, and the like often combine to provide public and private goods efficiently, and preserve individual liberties and village-scale autonomy to a

certain degree. Individuals in modern societies often feel part of culturally labeled tribal-scale groups, such as local political parties, that have influence up through a hierarchy on the remotest leaders. In older complex societies, village councils, local notables, tribal chieftains, or religious leaders often hold courts open to humble petitioners, and these local leaders in turn represented their communities to higher authorities. As long as most individuals feel that existing institutions are reasonably legitimate and that reform can be achieved through ordinary political activities, considerable scope exists for collective social action, including deliberate evolution of new social institutions.

On the other hand, the many unavoidable flaws in the evolving institutions of complex societies make legitimacy a difficult thing to sustain. Individuals who do not accept the legitimacy of the current institutional order are liable to band together in resistance organizations, such as the contemporary fundamentalist and tribal groups that view secular modernism as illegitimate. Stubbornly tribal people such as the Pathans of Afghanistan and Pakistan have effectively resisted incorporation into larger social systems for millennia. Trust varies considerably in complex societies, and variation in trust is the main cause of differences in happiness across societies.[96] Even the most efficient legitimate institutions are prey to manipulation by small-scale organizations and cabals, the so-called special interests of modern democracies.[97]

Conclusion: Coevolution weaves cultural and genetic causes into a single cloth

in the main point of this chapter is that the cultural part of the gene-culture coevolutionary

processes has played an important role in the evolution of human social institutions. In the short run, cultural evolution, partly driven by ancient and tribal social instincts and partly by selection among culturally variable groups, gave rise to the institutions we observe. In the longer run, cultural evolutionary processes created an environment that led to the evolution of uniquely human social instincts.

This hypothesis provides a theoretically coherent account of the evolution of complex human societies, and is consistent with much empirical evidence. It explains the undeniable elements of functional design in human social institutions *and* the manifest crudity of complex societies in the same theoretical framework. Without the ancient social instincts, we can't explain the many features of our social systems that we share with other primates. Without the tribal social instincts, we can't explain why our societies are so different from those of other primates, the emotional salience of tribal-scale human groups, or their importance in social organization and social conflict. The social instincts of both sorts, acting as biases shaping evolution of social institutions, account for the peculiar form of human societies, for the timescales over which institutions evolve, and for the patterns of conflict that routinely plague human societies. The institutions of complex societies are manifestly built on ancient and tribal instincts and have predictable imperfections deriving from cultural evolutionary processes.

While we are quite proud of this hypothesis, we know that it skips lightly over many details. Surely, for example, future discoveries will eventually yield a better picture of how cultural and genetic processes are integrated in the brain. Social psychologists will be able to tell us how this integration plays out in the everyday social interactions that are the foundation of social institutions. Sociologists, anthropologists and historians will better map out how our evolved psychology, acting through ongoing cultural evolution, generates the actual social

institutions we observe. Nonetheless, we believe a better explanation will retain a number of the essential elements of the hypothesis given here. In particular, it will (1) synthesize organic and cultural causes, (2) be an evolutionary explanation, and (3) explain the intricate mix of function and dysfunctional conflict in human societies.

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1. Simoons 1970, 1969. Durham (1991, chap. 5) reviews and reanalyzes the data on adult lactose absorption.
2. Cavalli-Sforza, Menozzi, and Piazza 1994; Holden and Mace 1997.
3. Paul Ehrlich and Peter Raven (1964) coined the term *coevolution* to describe the evolutionary relationship between butterflies and plants. Caterpillars prey on plants, and the plants in turn evolve chemical defenses to mitigate the damage of insect attack, which leads to the evolution of caterpillar detoxification capacities. Since then its meaning has been extended to any case in which two distinct evolutionary systems interact in interesting ways.
4. Another way to think about gene-culture coevolution is in terms of "niche construction" (Odling-Smee et al. 2003). Whenever an organism modifies its environment, natural selection will result from the effects of the modified environment. For example, beavers construct dams and are much modified for aquatic life in the resulting ponds. In this way of thinking, the products of culture become part of the selective environment of genes, just as the products of genes become part of the selective environment of culture. One just has to be careful to understand what is acting as an inheritance system and what is not. Beaver dams cannot reproduce themselves; the information about how to construct dams is encoded in beaver genes, not in the dams themselves, although in principle beavers could learn dam building by observing the dams of other beavers.
5. Klein 1999, 474–76; Berger and Trinkhaus 1995.
6. For a model of this process see Richerson and Boyd 1989b **;** Laland 1994; and Laland, Kumm, and Feldman 1995.
7. Lumsden and Wilson 1981, 303. See also E. O. Wilson 1998.
8. Corning 2000, 1983 discusses the evolutionary consequences of synergy in some detail.
9. Maynard Smith and Szathmáry 1995.
10. Margulis 1970.
11. Kaplan et al. 2000.
12. There are two common objections to the term *instinct*. First, some critics say that the term is hollow. A pattern of behavior exists, and merely labeling it an instinct adds nothing to our understanding. To this we answer that we want to distinguish between influences on behavior that are genetic and those that are cultural. Second, some would restrict the term *instinct* to innate patterns of behavior that are little modified by environmental contingencies or culture. Wilson 1975, 26–27 notes that this sense of the term applies only to extreme cases and so endorses the usage we adopt here.
13. We are well aware that anthropologists have used the term *tribe* in such diverse ways that

many feel that the term has become hopelessly muddled. Common English usage is also quite polysemous. We use it here in a minimalist sense. Tribes are a unit of social organization that incorporates people of relatively low degrees of biological relatedness into a common social system without depending upon formal authority. Extended kinship, sentiment, and informal institutions animate tribes, rather than formal law and leadership with formal powers of coercion. Birdsell's 1953 classic study estimated that the average Australian hunter-gather tribe incorporated about five hundred people. The creation of social units composed of many distantly related families, usually not coresident in hunter-gatherers, is unique to humans. Usually, descent from a common ancestor, often fictitious, honorific, or metaphorical, forms the core of the ideology enjoining feelings of solidarity, which are in turn the main wellspring of common action. Some restrict the term *tribal* to a range of societies of intermediate size and complexity usually characterized by sizes of a few thousand, with fairly elaborate formal political institutions but still no specialized full-time leaders with coercive authority (Service 1962). We believe that even the societies like the Shoshone, Steward's (1955, chap. 6; see esp. p. 109) illustration of an approximation to his "family band" ideal type, are normally part of a multiband community that functions to maintain local peace, resist incursions by other tribes, and provide aid in subsistence crises, even if in extreme cases these functions are rather limited. Murphy and Murphy 1986 and Thomas et al. 1986 argue that Steward's characterization of the Shoshone as family band societies underestimates their social complexity, even taking his caveats into account. In any case, the Shoshone adaptation to the arid Great Basin is very late, highly derived, and rather sophisticated in its very minimalism (Robert Bettinger, personal communication). No ethnographically known societies lack some form of integration into units considerably larger than the family or coresident band. Simpler societies vary continuously along several dimensions regarding social organization (e.g., Jorgensen 1980), and clean classification is a vain hope. The emergence of social bonds among noncoresident, distantly related people requires a convenient label, and the choice is *tribal* or an awkward neologism.

14. Boehm 1992; Rodseth et al. 1991.

15. Hamilton 1964. The "derivation" we gave in the previous paragraph is in the spirit of that paper.

16. The great population geneticist J. B. S. Haldane gave what is perhaps the pithiest summary of this principle. When asked by a reporter whether the study of evolution had made it more likely that he would give up his life for a brother, Haldane is supposed to have answered, "No, but I would give up my life to save two brothers or eight cousins." We can't resist another Haldane anecdote here, even though it has nothing to do with the subject of this book. Haldane was also asked by a reporter, maybe even the same one, whether the study of evolution had taught him anything about the mind of the Creator, to which Haldane is said to have replied, "He has an inordinate fondness for beetles."

17. Silk 2002; Keller and Chapuisat 1999; Queller and Strassman 1998; Queller 1989.

18. As opposed to *Nature,* where it figures prominently.

19. Hammerstein manuscript

20. See Axelrod and Dion 1988 and Nowak and Sigmund 1993, 1998a and 1998b for reciprocity in small groups; Boyd and Richerson 1988a**,** 1989a and Joshi 1987 for larger groups. Hubermann and Glance (1993) present a model in which reciprocity evolves in large groups, but this result depends on constraints on their choice of a set of possible strategies. Simple unconditional

defection invades their cooperative Evolutionarily Stable Strategy
21. E.g., Binmore 1994.
22. Trivers 1971.
23. Boyd et al. 2003 and Boyd and Richerson 1992b.
24. Wynne-Edwards 1962.
25. Maynard Smith 1964; Williams 1966; Lack 1966.
26. Price 1972, 1970.
27. The Price approach has been very fruitful, generating a much clearer understanding of many evolutionary problems—for example, Alan Grafen's 1984 work on kin selection and Steven Frank's 2002 work on the evolution of the immune system, multicellularity, and related issues. This approach can also be used to study cultural evolution. See Henrich, in press, and Henrich and Boyd 2002.
28. Sober and Wilson 1998.
29. Eshel 1972; Aoki 1982; Rogers 1990b
30. See Boyd and Richerson 1990 for details.
31. There is also a very interesting interaction between conformism and moralistic punishment. If there is a widely held norm of moralistic punishment, it may be that most people cooperate. This in turn means that it is difficult to know whether punishing is individually advantageous (because nonpunishers are punished or not (because nonpunishers take a free ride on the police work of others). Thus, even weak conformist transmission can maintain a moral norm that holds that people should engage in moralistic punishment, and then the punishment so generated can maintain group-beneficial behavior. See Henrich and Boyd 2001 for more details. Rob, I find I don't understand this footnote either. Has it gotten corrupted somehow?
32. Darwin 1874, 178–79. Of course, Darwin did not understand organic inheritance, though he did use concepts closely related to the modern notion of culture. The subtleties of the differences between genes and culture were lost on him, but he did understand that selection would normally favor selfish behavior. See Richards 1987 and Richerson and Boyd 2001a.
33. Palmer, Fredrickson, and Tilley 1997.
34. See Cavalli-Sforza and Feldman 1981for models of cultural drift, and Coyne, Barton, and Turelli 2000 and Lande 1985 for rates at which populations shift from one equilibrium to another due to genetic drift.
35. Keeley 1996; Otterbein 1985; Jorgensen 1980.
36. Wiessner and Tumu 1998.
37. Boyd and Richerson 2002.
38. Stark 1997.
39. Johnson 1976, 75, quoted in Stark 1997.
40. Stark 1997, 83–84.
41. See Rogers 1995 on the reason these properties are necessary for easy diffusion of innovations.
42. Barth 1969, 1981; Cohen 1974.
43. Rappaport 1979.
44. Barth 1981.
45. McElreath, Boyd, and Richerson 2003.
46. See Boyd and Richerson 1987 for mathematical details.

47. Logan and Schmittou 1998 offer the art of the Great Plains Crow as an example of such a process.
48. E.g., van den Berghe 1981; Nettle and Dunbar 1997; Riolo, Cohen, and Axelrod 2001.
49. Harpending and Sobus 1987.
50. See Ostrom's 1990 discussion of punishment in the context of managing public goods . See also Gruter and Masters 1986 on ostracism and Paciotti 2002 for an African tribal system with very sophisticated punishment.
51. Cognitive psychologists like Boyer 1998 would say that we have a "naïve ontology" in which symbolically marked groups are a default category.
52. Kelly 1995; Richerson and Boyd 1998, 2001b, Richerson, Boyd, and Henrich 2003
53. The idea that much criminal behavior in modern societies is a product of impulsive and otherwise socially maladroit personalities is a classic criminological hypothesis. Scholars differ about the reasons some people attract more punishment than others, but the data suggesting that prison inmates and other delinquents tend to be more impulsive than the average person is rather strong (Caspi et al. 1994; Raine 1993).
54. Pinker 1994, 111–12.
55. Steward 1955, chaps. 6–8; Kelly 1995.
56. Mansbridge's 1990 edited volume gives an excellent sampler.
57. Ghiselin 1974, **.**
58. Batson 1991.
59. Camerer, in press **.** Henrich et al., submitted **.**
60. Boehm 1993; Eibl-Eibesfeldt 1989, 279–314; Insko et al. 1983; Salter 1995.
61. Fehr and Gächter 2002.
62. The syndrome of ethnocentrism has received much attention from sociologists, from the work of William Graham Sumner early in the twentieth century onward. Notable summaries include those of Robert LeVine and Donald Campbell 1972 and Nathan Glazer, Daniel Moynihan, and Corinne Schelling's edited volume 1975.
63. Wiessner 1984, 1983.
64 Bettinger 1991
65. Tajfel 1982, 1981, 1978; Robinson and Tajfel 1996.
66. Turner 1984; Turner, Sachdev, and Hogg 1983.
67. Gil-White 2001 and personal communications. The complexity of this case is fairly typical. Nonetheless, sensible people know the costs of ethnic conflict and the advantages of alliance and trade.
68. Paldiel 1993.
69. Brewer and Campbell 1976.
70. Alexander 1987, 1979; Cosmides and Tooby 1989; Dunbar 1992.
71. This hypothesis was first, and perhaps most clearly, articulated by Pierre van den Berghe (1981).
72. Some people have interpreted the work of Nowak and Sigmund 1998a, 1998b as showing that indirect reciprocity can lead to helping in larger groups. That conclusion is problematical. First, the Nowak and Sigmund model had significant technical flaws (Leimar and Hammerstein 2001). Second, the corrected model still allows the evolution of indirect reciprocity, but under much-restricted conditions. Also see Panchanathan and Boyd (n.d.). Third and most important,

this model is still limited to pairwise interactions. It does not explain the evolution of public-good provision.
73. Jorgensen 1980.
74. Price and Brown 1985.
75. R. L. Bettinger, University of California, Davis, personal communication.
76. Wiessner 1983, 1984.
77. Yengoyan 1968.
78. Knauft 1987.
79. Knauft 1985a**;** Otterbein 1968.
80. Keeley 1996, 28.
81. Arnold 1996; Price and Brown 1985.
82. It is also true that the institutions of small-scale societies vary for reasons that have no discernable correlation with ecological circumstances. Among the work cited here, Knauft 1985b, 1993 and Jorgensen 1980 describe the considerable degree of variation that exists in simple societies, apparently independent of environment.
83. For example, a trader first visited Blackfeet of the northwestern plains in 1787, during the second generation of the horse era, and at that time few elderly people experienced with pedestrian hunting were still alive to give him an impression of that (Ewers 1958).
84. Otterbein 1968; Boehm 1984.
85. Service 1966, 54–61.
86. Boehm 1993.
87. Evans-Pritchard 1940; Kelly 1985, chap. 4.
88. Richerson, Boyd, and Bettinger 2001; Richerson and Boyd 2001c.
89. Kennedy 1987. Insko et al.'s 1983 elegant experiments in social evolution showed dramatic resistance that coercive dominance generates compared to leadership that is perceived as more legitimate. They also show how domination and resistance to domination weaken the productivity of the group as a whole.
90. Eibl-Eibesfeldt 1989, 314.
91 Salter 1995 provides a detailed analysis of how the institutions of dominance in complex societies function to manipulate our evolved psychology.
92. Benedict Anderson 1991 argues that nations came to be the dominant actors on the political stage when mass literacy and newspapers allowed cultural-political writers to appeal to the whole of the community speaking a vernacular. We imagine that the ritual systems centered on dramatic public buildings we so admire as ruins were the analogs in ancient city-states. The Mayans and the Greeks that participated in the construction of such complexes and in the ceremonies that took place in them could easily imagine themselves to be part of a common community. Today, the Muslim hajj (pilgrimage to Mecca) is the largest extant ritual and probably plays a real role in giving Muslims a sense of a common community despite the huge size of that community (Peters 1994).
93. Kellett 1982, 112–17.
94. Garthwaite 1993; Curtin 1984; Gadgil and Malhotra 1983; Srinivas 1962; Fukuyama 1995; Putnam, Leonardi, and Nanetti 1993; Light and Gold 2000; Light 1972.
95. Marty and Appleby 1991; Roof and McKinney 1987; Juergensmeyer 2000.
96. Inglehart and Rabier 1986.

97. We have elsewhere reviewed two sets of comparative cases, World War II armies and village-scale commons management institutions, in the light of this taxonomy of work-arounds and their problems (Richerson, Boyd, and Paciotti 2002; Richerson and Boyd 1999).