Chapter 4: Culture Is an Adaptation

In this chapter we are going to spill a lot of ink talking about why culture is an adaptation. Experience discussing this with students, friends, and colleagues leads us to expect that many readers will think that this is a ridiculous waste of time and effort. The advantages of social learning seem obvious. Individual learning is costly, and without social learning everybody would have to learn everything for themselves. Teaching, imitation, and other forms of social learning allow us to inherit a vast store of useful knowledge while avoiding the costs of learning. In fact, we have made exactly this argument ourselves, and so have many other authors whose work we admire.[1]

Unfortunately, this reasoning, though intuitive, is wrong. As we will see, if the only benefit of social learning is that allows most individuals to costs of individual learning, social learning can evolve alright, but, and this is a big but, at evolutionary equilibrium social learning does not increase the fitness of the imitators, or the population. The reason is that imitators are parasites who free ride on the learning of others. They contribute nothing to the capacity of the population to adapt to the local environment. To see this, imagine a population in which people acquire some behavior only by imitation, so that everyone copies someone who copied someone else, who in turn copied someone else, and so on ad infinitum. Since no one learns, there is no connection to the state of the environment, and no reason that behavior should be adaptive.

Thus we are left with a puzzle: It seems clear that culture is highly adaptive. It allows human populations to accumulate complex, highly adaptive tools and institution, that in turn have allowed people to expand their range to every corner of the globe. The puzzle is, how?

The exceptional nature of the human species deepens the puzzle—if culture is so great, why don't lots of other species have it? One of Charles Darwin's rare blunders was his conviction that the ability to imitate was a common animal adaptation. Many other complex adaptations like camera style eyes evolved long ago, evolved independently distantly related lineages, and are retained in most of their descendants. While many vertebrates do have simple forms of culture, only a few other species are even tolerably sophisticated social learners compared to humans. Why can't natural selection scale these proto-cultural systems up to the human level the way it scaled up simple eyes to complex ones? Why not long ago and in lots of species? If the presence of advanced culture in humans is not puzzling, then surely its rarity in others species is. Imagine that only humans had advanced eyes and the rest of the vertebrates were blind or nearly so. We call this complex of vexing issues the adaptationist's dilemma. The harder you think about humans the stranger we seem, not least in culture's adaptive properties.

In this chapter we try to ferret out how imitating others can increase individual fitness, and when this advantage will be great. We begin by presenting data that strongly suggest that even monkeys and our fellow apes acquire relatively little of their behavior by social learning. This fact suggests that human social learning is not a byproduct of sociality and individual learning capabilities, but requires special-purpose mental mechanisms. We then assume that these mechanisms might have been shaped by natural selection, and ask how and when culture is adaptive? Then we address the problem of why culture on the human scale is so rare. Finally, we test the hypotheses that emerge from our models of social learning with macroevolutionary data on human origins and parallel events in other lineages. We contrive an explanation for how to solve the adaptationist's dilemma; you can see what you think. We are under no illusions that it is the last word!

Why study adaptations?

We know a woman who plays an inventive game with her daughter. In every high-end cooking store is a gizmo department—a wall covered with inexpensive little gadgets, each of which is supposed to help with a specific kitchen task, like pitting cherries, making radish rosettes, or stripping asparagus. Occasionally, when one of the women happens to be in one of these stores, she goes to the gizmo department, buys the strangest and most obscure gizmo that she can find, removes the instructions and any other indication of what the gizmo is for, and sends it to the other. The object of the game is for the recipient to figure out what the gizmo is supposed to do.[2] Sometimes this turns out to be really hard. Figure 4.1 shows one of these gadgets. It is complicated and clearly designed for something, but what? Study it for a while, and if you have to give up (we both did), turn to page xxx, where its function is revealed. Amazing, isn't it? Until you know what the gadget does, you are hard put to figure out what its various parts are for and how they work; but once you know what it's supposed to do, how it works is obvious.

Figure 4.1. A mystery gadget.

Biologists study adaptation for exactly this reason. Plants and animals are very complicated contraptions with many parts that interact in complicated ways. One of the most important goals in biology is to figure out how organisms work, and one of the most useful tools for solving this task is the working hypothesis that the parts are adaptive. For example, scientists studying the complicated feeding organs of bivalve mollusks assume that these organs are well-designed machines for the purpose of extracting small bits of food from the water, and the assumption provides a powerful tool for understanding how the various parts of these organs work. Behavior is studied in same way. People studying great tits assume that the foraging strategies of these birds maximize their rate of energy intake. This facilitates understanding the details of foraging behavior: Which items should the birds take? How long should they stay in a patch? How are these decisions affected by handling time, travel time, and risk of being eaten by a predator?[3]

Surprisingly, the study of adaptations is controversial these days. The late paleontologist Steven Jay Gould and evolutionary biologist Richard Lewontin have convinced many people, including many social scientists, that adaptive explanations are usually unjustified.[4] Their position is that many features of organisms are historical accidents or side effects of adaptive changes in other characters, and that one must be extremely cautious in invoking adaptive explanations.

We couldn't agree less. Of course, there *are* many reasons that organisms may not be well adapted to their present circumstances. Unknown trade-offs may cause the evolution of the characters of interest to be affected by changes in other characters. Genetic or developmental constraints may prevent natural selection from achieving the optimal morphology or behavior. Environments may be changing so rapidly that selection cannot keep up. However, the mere existence of such mechanisms does not justify Gould and Lewontin's extreme conservatism about adaptive explanations. Such skepticism would be justified only if, in addition, nonadaptive outcomes were much more common than adaptive ones, or if the cost of mistakenly invoking an adaptive explanation was very much higher than the cost of mistakenly invoking a nonadaptive explanation. We do not think that either of these two conditions is true.

Much of the variation we see in nature likely *is* adaptive. Functional studies demonstrate that organisms are well designed, and a vast body of evidence from every part of biology illustrates that all kinds of traits can be understood by asking how these parts function to promote reproductive success. In his book, *The Blind Watchmaker*, evolutionary biologist Richard Dawkins cites the human eye as an example of complex organic design. The eye has a myriad of complex parts, carefully arranged to permit sight. No mechanism other than natural selection can account for the existence of such adaptive complexity. Comparative studies show that the differences in the structure of eyes among species are adaptations to different environments. Consider, for example, fish eyes. Unlike the eyes of humans and other terrestrial mammals, fish eyes have a spherical lens. The index of refraction of the lens varies smoothly from the same value as water at the surface of the lens to much higher values at the center of the lens. This lens design allows the fish to keep one entire 180-degree hemisphere in focus without needing muscles to distort the shape of the lens. Terrestrial creatures cannot use this design. Both fish eyes and human eyes must have a cornea, a transparent cover that allows light to enter the eye but protects and contains the interior of the eye. Because air has a lower index of refraction than any tissue, human corneas can act as a lens, and this fact frees the design of the remaining lens elements. In contrast, fish corneas have an index of refraction very close to that of water and thus have no effect on the entering light.[5]

Nor is attempting an adaptive analysis of a neutral or maladaptive character particularly costly. Typically, adaptive analyses make many detailed predictions about the character in question—explanations that can often be tested by studying the structure and behavior of the organism in the field. In contrast, explanations based on random historical events or developmental constraints are usually difficult to test, because they involve events in the distant past or poorly understood physiological tradeoffs. Gould and Lewontin are surely right that we should be cautious about casually accepting adaptive "just-so" stories about the function of traits that we observe. But we should be equally cautious, perhaps more cautious, about casually accepting nonadaptive just-so stories that invoke mysterious unspecified events in the distant past.

Culture is a derived trait in humans

Some animals have socially transmitted traditions that produce behavioral differences between populations of genetically similar individuals living in similar environments. Some observers are inclined to quarrel about whether such traditions qualify as culture in the sense that we apply that term to humans. People who are inclined to keep some distance between ourselves and the common run of beasts argue that traditions observed in other animals lack essential features of human culture: traditions that are symbolically encoded and are widely shared.[6] Others, who believe in the continuity between humans and other animals, argue that those who deny culture to nonhuman animals are applying a double standard—if the kind of behavioral variation observed among some other primate populations were observed among human populations, anthropologists would surely regard it as cultural.[7]

Despite having a lot of respect for the protagonists of these debates, we think this argument is a waste of time. Just as limbs evolved from fins, the machinery that allows people to learn by observing others must have evolved from "homologous" machinery in the brains of our ancestors. Moreover, the function of cultural transmission in humans could well be related to its function in other species, whether or not the psychological structures involved have evolved from a common ancestral structure. The study of the evolution of human culture must be based on categories that allow human cultural behavior to be compared to potentially homologous and functionally similar behavior in other organisms. At the same time, such categories should be able to recognize distinctions between human behavior and the behavior of other organisms, because the evidence strongly suggests that human culture differs in important ways from similar behavior in other species.

Social transmission of behavior is common

Many species of animals have socially transmitted behavioral differences that are analogous to human culture. In a review of social transmission of foraging behavior, comparative psychologists Louis Levebre and Boris Palameta give 97 examples of socially learned variation in this behavior in animals as diverse as baboons, sparrows, lizards, and fish.[8] Some of the most detailed work on culture in other animals comes from studies of songbirds and the social transmission of their song dialects.

Three decades of fieldwork across Africa suggest that chimpanzees exhibit cultural variation in subsistence techniques, tool use, and social behavior.[9] For example, chimpanzees in the Mahale Mountains of Tanzania often adopt a grooming posture in which both partners extend one arm over their heads, clasp hands, and then groom each other's exposed armpits. These grooming handclasps occur often and are performed by all members of the group. Chimpanzees at Gombe Stream Reserve, who live less than one hundred kilometers away in a similar type of habitat, groom often but never perform this behavior. At Mt. Assirik in Senegal, chimpanzees strip the bark from twigs before using them to fish for termites, while Gombe chimps use the same plant for termite-extracting tools but discard the twig and use the bark. Chimpanzees from some populations living in the Taï Forest of the Ivory Coast crack open hard-shelled nuts with stone hammers that they pound against other stones and exposed tree roots, while chimpanzees from nearby populations don't, though they have access to both the same nuts and suitable stones. Primatologist William McGrew has reviewed all of the field observations of chimpanzee tool use in wild populations,[10] and argues that the complexity of chimpanzee tool traditions rivals those of the simplest modern human tool kit known, that of the Aboriginal Tasmanians.[11]

Orangutans use tools, but not bonobos ("pygmy" chimpanzees) or gorillas, so far as is known. Orangutans in some areas of Sumatra use sticks to extract oily, energy-rich seeds from amid the irritant hairs that cover *Neesia* fruit.[12] Orangutans elsewhere in Sumatra and in Borneo often do not use tools even where *Neesia* are common. These geographical patterns do not seem to be the result of ecological differences, because *Neesia* seeds are the top-ranked food in terms of energy gained per unit time, and it is not likely that there is any environment in which orangutans would not eat them if they could.

In a few cases, scientists have observed the spread of a novel behavior. The most famous example occurred on Koshima Island in Japan in a group of Japanese macaques whose home range included a sandy beach. The monkeys were fed sweet potatoes, and one young female accidentally dropped her sweet potato into the sea as she was trying to rub sand off it. She must have liked the result, because she began to carry all of her potatoes to the sea to wash them. Other monkeys followed suit. However, other members of the group took quite some time to acquire the behavior, and many monkeys never washed their potatoes. Another example comes from the work of psychologist Marc Hauser, who saw an old female vervet monkey dip an *Acacia* pod into a pool of liquid that had collected in a cavity in a tree trunk. She soaked the pod for several minutes and then ate it. This behavior had never been seen before, though this group of monkeys had been observed regularly for many years. Within nine days, four other members of the old female's family had dipped their pods, and eventually seven of the ten group members learned the behavior.

Some of the most impressive field evidence for social learning in nonhumans comes from species other than primates, such as whales. Zoologists Luke Rendell and Hal Whitehead have recently surveyed the whale data.[13] As with chimpanzees, studies of humpbacked whales, sperm whales, killer whales, and bottle-nosed dolphins show an impressive amount of geographical variation in behaviors ranging from vocalizations to feeding strategies that are plausibly culturally transmitted. The toothed whales (sperm whales, killer whales, and dolphins) live in stable matrilineal groups and animals living in different matrilines often behave quite differently when the groups occupy the same environment. These behaviors can be quite complex. Some killer whale matrilines deliberately beach themselves to capture seals. Observations suggest that imitation and even teaching by mothers is a part of learning this risky behavior. Humpbacked whales cooperate to blow bubble curtains that form a sort of net to concentrate prey for subsequent capture. In the Gulf of Maine, observers noted the addition of an innovative fluke-slapping behavior at the end of the curtain-formation sequence, probably designed to stun or confuse their prey. This behavior spread to other whales in the vicinity in an exponential fashion consistent with cultural transmission. And, field observations suggest that other animals for such as parrots[14] and elephants[15] have complex cultural repertoires.

The problem with field evidence is that it is very difficult to tell whether behavior really is acquired culturally. For example, it is hard to exclude the possibility that some obscure difference between the environments gives rise to the observed differences in tool use between neighboring groups of chimpanzees. But, social learning has also been studied in the laboratory where researchers can control opportunities for individual and social learning. Experimental evidence indicates that a number of behaviors, including song dialects, novel food preferences, and other foraging strategies, are socially transmitted. The most famous case is the transmission of song dialects in birds like the white-crowned sparrow.[16] These birds have a specialized social learning system for imitating the song patterns of local adults. The song of this species varies from place to place—different local variants are called dialects. Experiments show that young birds who do not hear the conspecific song develop only a simplified version of the typical song of their species. However, if young birds are exposed to the adults singing local song dialect, they acquire that dialect in all its complexity. Comparative psychologist Bennett Galef and his students have demonstrated that Norway rats learn about novel foods from the smell nest mates' fur when they return from foraging trips.[17] Louis Lefebvre and his colleagues, working with pigeons and their relatives, have demonstrated the social transmission of food acquisition strategies.[18] Even humbler sorts of organisms, such as guppies,[19] show evidence of social learning under controlled conditions. These experiments provide convincing evidence that animals can learn new behaviors from one another.[20]

Cumulative cultural evolution is rare in nature

While researchers debate culture in nonhuman animals, one thing is fairly clear: only humans show much evidence of *cumulative* cultural evolution. By cumulative cultural evolution, we mean behaviors or artifacts that are transmitted and modified, over many generations, leading to complex artifacts and behaviors. Humans can add one innovation after another to a tradition until the results resemble organs of extreme perfection like the eye. Even an implement as simple as a hunter-gatherer's spear is composed of several elements: a carefully worked, aerodynamic wooden shaft, a knapped stone point, and a hafting system to fasten the point to the shaft. Several other tools have to be used to produce the parts of a spear—scrapers and wrenches to shape and straighten the shaft, knives to dissect sinew for the hafting system, hammers to knap the stone point. As we explained in chapter 2, complex artifacts like this are not invented by individuals; they evolve gradually over many generations. In nonhuman animals, the evidence for cumulative cultural evolution is scanty and controversial; social learning leads to the spread of behaviors that individuals could, and routinely do, learn on their own. In many cases, these traditions are short-lived. Norway rats, for example, constantly sample new foods on their own and eventually will come to eat most of the edible foods they find without social cues. They also forget foods that they have eaten only a few days before—their traditions don't last longer than a week or so unless they are reinforced by the continued presence of the food item.

A few nonhuman social traditions are durable and based on innovations that are difficult for individuals to learn on their own. In an Israeli pine plantation, black rats use a simple but difficult to invent technique to extract seeds from pinecones. The seeds are arranged in a spiral, and are protected by a tough scale. Sufficiently hungry naive rats will attempt to scale the cones, but their technique requires more energy than they gain from eating the seeds. Knowledgeable rats start by removing the unrewarding basal seedless scales, following the spiral around until they reach the second row and start uncovering seeds.[21] Zoologist Joseph Terkel and his coworkers demonstrated experimentally that young pups learn this "spiral" technique from their mother. The trick is simple but no rat tested learned the technique by individual trial and error. One unusually lucky, persistent, or smart rat must have invented this tradition. In black rats, unlike Norway rats, marked traditional differences between local populations might arise because such traits are hard to learn and are inherited by social learning.[22] The song dialects in birds such as the white-crowned sparrow have multiple elements. Each generation of birds learns the details of the local dialect by listening to others. However, errors and sampling variation introduce innovations that sometimes spread in local populations. As a consequence, song dialects can be traced over many generations and substantial geographic distances, much like human dialects.[23] Some of the field observations, such as the humpback whales' addition of fluke slapping to bubble curtains, and the hammer-plus-anvil nut-cracking technique of chimpanzees, may prove to be examples in which a few sequential innovations have created modestly complex culture. Hal Whitehead predicts that killer-whale hunting strategies will eventually be shown to resemble those of humans in their complexity and diversity.

Human culture requires derived psychological mechanisms

Considerable evidence suggests that the ability to acquire novel behaviors by observation is essential for cumulative cultural change. Students of animal social learning distinguish *observational learning* or *true imitation* (hereafter, plain *imitation*) from other kinds of social transmission. Imitation occurs when animals learn a novel behavior by observing the behavior of more experienced animals.[24] Simpler kinds of social transmission are much more common.[25] For example, *local enhancement*, occurs when the activity of older animals in a particular location increases the chance that younger animals will visit that spot and then learn the older animal's behavior on their own. Thus, young chimpanzees that frequently accompany their mothers to termite mounds are more likely to acquire termiting skills than individuals whose mothers never termite. A similar mechanism, *stimulus enhancement,* occurs when a social cue makes a given stimulus salient to the animal. For example, smelling food particles on nest mates makes Norway rats more likely to sample these foods when foraging. Young individuals do not acquire the information necessary to perform the behavior by observing older individuals in either of these cases. Instead, the activity of others causes them to be more likely to acquire this information through their own interaction with the environment.

Local and stimulus enhancement and imitation both can lead to persistent behavioral differences among populations, but only imitation gives rise to the *cumulative* cultural evolution of complex behaviors and artifacts.[26] To see why, consider the cultural transmission of stone tool use. Suppose that an early hominid learned, on its own, to strike rocks to make useful flake tools. Her companions, who spent time near her, would be exposed to the same kinds of conditions, and some of them might learn to make flakes, too, entirely on their own.. This behavior could be preserved by local enhancement, because groups in which tools were used would spend more time in proximity to the appropriate stones. However, that would be as far as toolmaking would go. Even if an especially talented individual found a way to improve the flakes, say by blunting the back to protect the hand, this innovation would not spread to other members of the group because each individual has to learn the behavior independently, and individual learning is time consuming and chancy. Local and stimulus enhancement are limited by the learning capabilities of individuals, and by the fact that each new learner must start from scratch with only the barest clues from other animals to go by. Imitation allows each new innovation to be added to an individual's behavioral repertoire, because the information about how to perform the behavior is acquired by observing the behavior of others. To the extent that observers can rapidly and accurately use the behavior of models as a starting point, imitation leads to the cumulative evolution of behaviors that no single individual could invent on its own.

Several lines of evidence suggest that imitation is usually not responsible for protocultural traditions in other animals. First, as we have already said, many socially learned behaviors, like potato washing in Japanese macaques, are relatively simple and could be learned independently by individuals in each generation. Second, new behaviors like potato washing often take a long time to spread through the group, a pace more consistent with the idea that each individual had to learn the behavior on its own, aided only by weak clues of stimulus or local enhancement. Finally, sophisticated laboratory experiments capable of distinguishing imitation from other forms of social transmission like local enhancement have usually failed to demonstrate observational learning, except for the specialized song-learning system of some birds.[27]

Adaptation by cumulative cultural evolution is not a byproduct of intelligence and social life. We say "monkey see, monkey do," and use "ape" as a verb, but in fact monkeys and even apes do not seem to be especially clever imitators compared to humans. The best evidence comes from experiments in which the imitative capacities of children and apes have been compared.[28] Primatologists Andrew Whiten and Deborah Custance designed an artificial "fruit," a rugged, transparent plastic box that held treats inside. Experimental participants could open the box by manipulating a latch consisting of either bolts or a pin-and-handle arrangement. The participants were eight chimpanzees three to eight years of age and three groups of children with mean ages of 2.5, 3.5, and 4.5 years. They watched a familiar human demonstrate a specific technique for opening the fruit, and then were allowed to attempt open it themselves. The experimenters recorded whether the participants used the same technique that they had been shown. By most measures, chimpanzee imitative performances exceeded chance. However, 2.5-year-old children did even better, and older children were dramatically more proficient imitators than the chimpanzees.

Psychologist Michael Tomasello and his coworkers conducted similar experiments in which chimpanzees and children were shown how to use rakelike tools to obtain food that was out of reach. The chimps who watched expert demonstrators were more successful than untrained chimps in using the tool to obtain the food reward, but they did not imitate the precise method that their demonstrators had used. Children, on the other hand, followed the method they had been shown. Tomasello describes the ape technique as *emulation* rather than *imitation;* apes learn that a tool can be used to cause some desired effect by watching a demonstrator, but they don't pay close attention to the details of how the tool is used. Children imitate so faithfully that they persist in using an inefficient technique, one that the chimpanzees usually abandon in favor of the more efficient alternative. Children aren't *smarter* than chimpanzees in general, just much more imitative.[29] Taken together, these experiments suggest that social learning in apes and humans is not the same. Children imitate very faithfully, while apes emulate or at least imitate less faithfully.

Although the evidence on hand suggests that most cultural traditions in other animals are not the product of imitation, some caution is in order. Negative results are always difficult to interpret; experiments can fail for many reasons. Recent clear demonstration of imitation by marmosets suggests that better experiments might detect imitation in a wider range of species.[30] Experimental data from bottle-nosed dolphins suggests that they are excellent vocal and motor imitators, consistent with the field evidence.[31] Thus, we don't claim that imitation is unique to humans. However, the current evidence suggests that (1) cumulative cultural evolution is rare, and perhaps absent, in other species; and (2) even our closest relatives, the chimpanzees, rely on different modes of social learning than humans.

So far, we know of no convincing evidence that any other species has a cultural item as complex as a stone-tipped spear. Rudimentary forms of observational learning are certainly present in chimpanzees, orangutans, whales, crows, various songbirds, and parrots, [32] but as Darwin put it, a "great gap" exists between humans and other animals. No other species seems to depend on culture to anywhere near the degree that humans do, and none seem adept at piling innovation atop innovation to create culturally evolved "adaptations of extreme perfection." In fact, there is no evidence that *humans* made tools as complex as a stone-tipped spear until about four hundred thousand years ago.

As an aside, we are disappointed by the seeming lack of imitation and cumulative cultural evolution in other species, and we'd love it if future work showed more sophisticated social learning in nonhuman animals. The more the great gap is closed up, the more we can put the comparative techniques familiar to both evolutionists and social scientists to work. The sober chore is to estimate the width of the gap as accurately as we can, and the trend of the best current evidence seems to us to favor a gap even larger than Darwin imagined.[33]This fact leaves the adaptationist on the horns of the puzzling dilemma with which we opened this chapter. In the remainder of this chapter, we will explore the conundrum of culture as an adaptive system.

Why is culture adaptive?

In 1988, anthropologist Alan Rogers published a theoretical model demonstrating that avoiding the costs of learning is an important benefit of imitation, but this alone is not sufficient to explain the evolutionary origin of human culture. To see why, let's consider Rogers's argument.

Reducing learning costs may allow culture to evolve, but that alone does not increase adaptability

Rogers's conclusions are based on a model of the evolution of imitation in a very simple hypothetical organism. These hypothetical creatures live in an environment that can be in either of two states; let us call them wet and dry. The environment has a constant random probability of switching from wet to dry each generation and the same probability of switching from dry to wet. Over the long run, the environment is equally likely to be in either state. The probability of switching is a measure of the predictability of the environment. When the environment switches often, knowing the state of the environment in one generation tells you little about the state of the environment in the next generation. In contrast, when the environment switches states less often, the environment of the past generation was likely to have been the same as the environment now. The organisms have one of two possible behaviors: one best in wet conditions and one best in dry conditions. They can be one of two genotypes: learners and copiers. Learners figure out whether the environment is wet or dry on their own and always adopt the appropriate behavior. However, the learning process is costly, because trial-and-error learning takes time and energy. Copiers simply pick a random individual and copy it. Copiers don't pay the cost of learning. Copying thus does not have any direct effect on survival or reproduction, but copiers may acquire the wrong behavior for their environment. Rogers then used some simple but clever mathematics to determine which genotype wins in the long run.[34]

The answer is surprising (at least it was to us). The long-run outcome of evolution is always a mixture of learners and copiers in which both types have the same fitness as purely individual learners in a population without copiers. In other words, natural selection favors culture, but culture provides no benefit at equilibrium. The organisms are no better off than they were without any imitation. To understand the logic of this counterintuitive result, think of the imitators in Rogers's model as *information scroungers* and the learners as *information producers*.[35] Information producers bear a cost to learn. When scroungers are rare and producers common, almost all scroungers will imitate a producer. Most scroungers will obtain the same benefits of good information as producers but will not bear the cost of production. However, when scroungers are common, they will often imitate one another. If the environment changes, any scroungers that imitate scroungers will get caught out with bad information, whereas producers will adapt. The system equilibrates when the cost of production by producers just equals the cost of being wrong to scroungers when environments change. At evolutionary equilibrium, scroungers gain no advantage over producers. Both types are exactly where all the producers were when the evolution of scrounging began. Moreover, the theoretical result is robust; you can change the model in lots of ways, but as long as the only benefit of imitation is avoiding the costs of learning, you get the same answer. Information scrounging is known to exist from experiments on humans and on pigeons.[36] Perhaps many cases of simple culture and even aspects of culture in humans approximate Rogers's model.

This result is disturbing to most people, because it conflicts with their intuitions about the role of culture in the human species. Since the first appearance of tools and other evidence of culture in the archaeological record, the human species has increased its range from part of Africa to the entire world, increased in numbers by many orders of magnitude, exterminated many competitors and prey species, and radically altered the earth's biota. Rogers's model must be incomplete. Culture *is* adaptive. However, figuring out *what* is wrong with the simple producer-scrounger model is an interesting exercise, because what is missing will help us isolate which features of culture are the ones crucial to our extraordinary success.

Culture is adaptive when it makes individual learning more effective

Thinking about imitation in terms of costs and benefits reveals the crucial missing element in Rogers's model. Social learning improves the average fitness of a population only if it increases the fitness of individual learners who produce information, not just those who imitate. In other words, increasing the frequency of imitators must make information production cheaper or more accurate. We have been able to think of two ways that this can happen.

Imitation allows selective learning

Imitation may increase the average fitness of learners by allowing organisms to learn more selectively. Learning opportunities often vary—sometimes the best behavior is easy to determine, other times not. Organisms that can't imitate must rely on learning, take the information that nature offers, for better or worse. For example, consider individuals trying to decide which of two foraging techniques is better. They try them both out, and choose the one that yields the highest return. Because yields will vary for many reasons, individuals' trials may often yield misleading results—the technique with the higher return during the trial may have a lower return over the long run. Without imitation, every individual must decide based on the information each has available. Even if trials suggest that both techniques have the same return, one must decide which to adopt.

In contrast, an organism capable of imitation can afford to be choosy, learning when learning is cheap and accurate, and imitating when learning is likely to be costly or inaccurate. For example, individuals could use a contingent rule such as "Try out the two techniques and if one yields twice as much as the other, adopt that technique; otherwise, use the technique that Mom used." The use of such a rule would cause those individuals who do rely on imitation to make fewer errors than those who always rely on individual learning. It would also cause them to imitate often, but not always. A more stringent rule, say, adopt the technique only if it yields four times as much the other, would further reduce the errors made by learners (and increase their fitness on that account), but would further increase the number of individuals who imitate (leading those who rely on imitation to be more susceptible to environmental change). In this model, everyone both produces and scrounges, depending upon circumstances. Now, increasing the frequency of imitating increases the average fitness of learning, because relying only on more definitive information cuts the cost of learning. At the same time, a higher frequency of imitating steadily reduces the fitness benefits of imitating, because the population doesn't keep up with environmental changes as well as when learning is more common. Eventually, an equilibrium is reached in which individuals mix learning and imitation optimally, trading off the higher cost of learning when cues are less obvious against the risk of imitating outdated information. But now average fitness is higher than in an ancestral population too dependent on one or the other. By becoming a selective learner, an individual gains most of the advantages of both learning and imitation.

Imitation allows cumulative improvement

Imitation also raises the average fitness of cultural creatures by allowing learned improvements to accumulate from one generation to the next. So far we have only considered two alternative behaviors. Many kinds of behavior admit successive improvements toward some optimum, as in adding a sharp, hard stone tip to a spear instead of merely trying to sharpen the wood itself. Individuals acquire an initial "guess" about the best behavior by imitation, and then invest time and effort in improving their performance. For example, a spear maker might tinker with the taper on the shaft of his spears in order to get them to fly straighter. For a given amount of time and effort, the better an individual's initial traditional spear, the better on average his final performance. Now, imagine that the environment varies, so that different behaviors are optimal in different environments. Game populations fluctuate. Sometimes a spear stout enough to stab large, slow animals is best; other times a slim aerodynamic one to toss at fleeter, smaller animals is better. Still other times, some compromise design may be best. Organisms that cannot imitate must start with whatever initial guess is provided by their genotype. They can then learn and improve their behavior. However, when they die, these improvements die with them, and their offspring must begin again at the genetically inherited initial guess. In contrast, imitators can acquire their parents' behavior after their behavior has been improved by learning. Therefore, imitators will start their search closer to the best prevailing design than purely individual learners, and can invest the information production efforts efficiently in further improvements. Then they can transmit *those* improvements to the grandkids, and so on down the generations until quite sophisticated artifacts evolve (and re-evolve to meet the needs of changing environments). Historians of technology have demonstrated quite nicely how this step-by-step improvement gradually diversifies and improves tools and other artifacts.[37] Even such seemingly simple items as spears, hammers, dinner forks, paper clips, and our mystery gadget are the product of many stepwise, cumulative improvements over a number of generations.

When is culture adaptive?

What kinds of environments favor a system of sophisticated imitation and teaching that in turn produces cumulative cultural evolution? When is such a cultural system liable to be worth any costs it may impose, such as the cost of having a big, expensive brain in order to imitate accurately? These are crucial questions because the human species' extreme reliance on culture fundamentally transforms many aspects of the evolutionary process. The evolutionary potential of culture makes possible unprecedented adaptations like our modern complex societies based on cooperation with unrelated people, *and* some almost equally spectacular maladaptations, such as the collapse of fertility in these same modern societies. The conditions under which selection might favor a strong reliance on imitation are all-important for understanding what sort of animal we are.

The force of guided variation

In our elementary models of adaptive cultural transmission, individuals acquire beliefs and values by unbiased imitation or some other form of social transmission. They can modify their beliefs and values based on any effort they invest in learning for themselves as opposed to blindly sticking with tradition. People may modify existing beliefs, or even invent completely new ones, as a result of their experiences. When such people are subsequently imitated, they transmit the modified beliefs, and the next generation can engage in more individual learning and further hone the trait. When the beliefs of one generation are linked to the next by cultural transmission, learning can lead to cumulative, often adaptive, change. We say that such change results from the force of *guided variation*. The system is a little like an imaginary genetic system in which mutations tend to be in a fitness-enhancing rather than random.

Like biased-transmission, guided variation depends on learning rules and it's likely that many of the same psychological mechanisms underpin both processes. Because they both depend on decision-making rules, we will refer to them collectively as *decision-making forces.* However, there are also important differences between the two. Biased transmission results from the comparison of different cultural variants already present in the population. As a result, biased transmission is a culling process like natural selection. Some variants in the population are more likely to be transmitted than others, and those variants spread. Thus, like natural selection, the strength of biased transmission depends on the amount of variation in the population. When a favorable trait is very rare, only a few people will have the opportunity to benefit from a comparison with a less-favored trait. As the favored trait becomes more common, more people will have the advantage of the comparison, and the rate of increase of the favored trait will increase. As the favored trait becomes even more common, fewer and fewer people will have the disfavored trait and the rate of change will drop again.

Guided variation works quite differently, because it is *not* a culling process. Individuals modify their own behavior by some form of learning, and other people acquire their modified behavior by imitation. As a result, the strength of guided variation does not depend on the amount of variability in the population. A population in which every individual believed exactly the same thing can change by guided variation just as readily as a population in which people vary. This difference means that the time paths of cultural change that results from biased transmission and guided variation are quite different, when a favored trait is rare. If the bias force must wait until a favorable variant is introduced by chance, then progress is slow until an appreciable number of individuals so acquire it. Individual learners, by contrast, have the most influence when the trait is rare, potentially getting the evolution of a newly favored trait off to a very fast start compared to a case with only random variation and bias (or bias and natural selection). While biased transmission has important analogies to natural selection, guided variation definitively is not. It is a source of cultural evolutionary change that has no good analog in genetic evolution.[38]

Culture is adaptive when learning is difficult and environments are unpredictable

The strength of guided variation and biased transmission affects the heritability of cultural variants. When these decision-making forces are weak, most people end up with the same beliefs as their parents and their friends—cultural differences are heritable. For example, weak decision-making forces are one way to explain the slow change in beliefs and values that affect farming practices in the Illinois farming towns of Freiburg or Prairie Gem. German kids who grow up surrounded by people who believe that farming is a valuable way of life end up with the same yeoman values themselves, as do Yankee kids who grow up among people holding entrepreneurial values. Now compare this situation to beliefs subject to a strong decision-making force—say, about whether one should suppress weeds by mechanical cultivation or by using chemical herbicides. Suppose that almost everyone tries herbicides and decides that they are superior to mechanical cultivation. Now what people believe has little to do with the culture in which they were raised and everything to do with the decisions they have made based on their own experience—cultural differences are not very heritable in the latter case.

When decision-making forces are weak, cultural variants are highly heritable, and this means that other evolutionary processes depend on the existence of heritable variation, can operate. When decision-making forces are strong, there will be little heritable variation, and other processes can have little effect. Remember that natural selection favored yeoman values because people who hold such values had larger families and were more likely to remain in farming, but selection can have an interesting effect only if decision-making forces are weak. Suppose that biased transmission is very strong—so that almost everyone who starts out with yeoman values switches to entrepreneurial ones and almost everyone who starts with entrepreneurial values stays that way. After a very short time, everyone will have entrepreneurial values and there will be no cultural variation for natural selection or further bias to act upon. The same goes for herbicide use. Suppose that organic agriculture advocates are right in believing that using herbicides actually reduces profitability. Perhaps the sight of hated weeds dying a lingering death is so much more satisfying than their merciful end by mechanical cultivation that farmers systematically overestimate the value of herbicides. Now natural selection among farms will favor mechanical cultivation. Farmers who use herbicides will earn lower profit and therefore be more likely to go out of business. However, if biased transmission acts sufficiently strongly in a maladaptive direction, almost all farmers will erroneously use herbicides, and natural selection will have little effect.[39]

In the next chapter, you will see how cultural evolution can lead to outcomes not easily predicted by simple adaptive considerations, and this is important because it enables a theory rooted in basic Darwinism to generate a rich enough variety of outcomes to explain the complexity and diversity of human behavior. However, these processes can only be important if there is sufficient heritable cultural variation. Are there circumstances in which natural selection will favor a sufficient reliance on accurate, unbiased cultural transmission to support heritable cultural variation? Or put very simply, when does natural selection favor doing something "just because" other people are doing it? You can think of this exercise as a basic scenario for the evolution of any system of social transmission. All organisms have means of adjusting their behavior and anatomy to local conditions. When can selection favor a costly system for transmitting these adjustments to offspring or other social learners?

We have analyzed this problem using several mathematical models of the evolution of imitation, and all of them tell the same story.[40] Selection favors a heavy reliance on imitation whenever individual learning is error prone or costly, and environments are neither too variable nor too stable. When these conditions are satisfied, our models suggest that natural selection can favor individuals who pay *almost* no attention to their own experience, and are *almost* totally bound to what Francis Bacon called the "dead hand of custom."

This result is quite intuitive. If people can accurately determine the best behavior, then there is no need to imitate; just do it. You don't need to observe your neighbors to duck into shelter when it rains or find shade when it is hot. If the environment changes rapidly, there is no sense in copying what has worked in the past, because what worked for Mom and Dad will be of little help today. No matter how error prone your best guess is about what to do, you are bound to do better than imitating someone whose behavior is surely out-of-date. For imitation to be beneficial, the environment must change slowly enough that the accumulation of imperfect, socially learned information over many generations is better than individual learning, but not so slowly that an innate instinct under the influence of natural selection alone is sufficient.

These models paint a consistent, intuitively pleasing picture of why capacities for culture evolve, but, given that environments almost always vary, they seem to predict that culture ought to be much more common than it is. True, the culture we assume in the models is rather simple, and simple systems of social learning are common. Students of nonhuman social learning have reason to be happy with the theory. However, we remain stuck with the stubborn fact of humans' overwhelming success using an exceedingly rare form complex culture.

Are the models a true depiction of the adaptive properties of culture? Unfortunately, we don't know. Usually evolutionary biologists test models of this kind by applying the comparative method. But in this case, one would have to collect data on a range of species that vary in the extent to which they rely on social learning, and then look to see whether more social learning occurs in the circumstances predicted by the model. However, there is so little data on the costs and benefits of social learning in other animals that this kind of test is currently rather weak. Interestingly, the best-known animal social learning systems occur in Norway rats and feral pigeons. These are the animal equivalent of weeds, species that do well in a wide range of environments, especially in disturbed habitats associated with humans. If a broader comparative study of animal social learning showed a significant correlation between environmental variability and capacities for social learning, the models would be supported.

Two more adaptive cultural mechanisms

Before we try to dig our way out of the adaptive puzzle of human culture, let's heap some more material on the pile by introducing two variants of the bias force that further enhance the adaptive power of cultural evolution. So far we have considered why and when accurate imitation can be favored by natural selection. We have imagined that people have the ability, albeit limited, to judge the relative merit of alternative beliefs and values, and to choose between these and those they can copy from the previous generation.

Such imitation strategies can be thought of as *heuristics* for guessing the right thing to do in a complex and variable environment. Psychologists have studied how human decision makers cope given our limited cognitive abilities. For example, a group led by Gerd Gigerenzer has investigated "fast and frugal" heuristics that generate correct answers to a class of problems quickly with minimal demands for data or for computational effort.[41] In one experiment, Gigerenzer's group gave a list of pairs of German cities to American college students and asked them to judge which was larger. In this case, the information that Americans have is poor, but a simple heuristic turns out to be quite accurate. A city you have heard of, such as Frankfurt, is almost always larger than the one you haven't—Bielefeld, for instance. Many fast, frugal heuristics are very nearly as accurate as the best statistical procedures, and for some classes of problems they often do a little better. Social learning can also be thought of as a decision-making heuristic. When in doubt about what to do, stop fretting and copy Mom, Dad, or your best friend. Our models of guided variation suggest that this is a useful heuristic whenever your own experience is not very telling.

But why stop there? Very often, decision makers who detect that Dad's way of doing things is quite outdated will be ill advised to start a brute force trial-and-error search for a solution to their problem. A biased search for a better model is a relatively cheap alternative. But even what we call content bias—careful comparison shopping among existing ideas—is likely to involve a costly search for good data and a be demanding, calculating chore if conducted by the methods we learned in our statistics and research methods courses. Given the size and complexity of our cultural repertoire, it defies imagination that we can use costly heuristics to bias many of our behavior-adoption decisions. Life is short, and rewards come from getting on with it. If fast and frugal heuristics exist that are less costly than guided variation and direct bias, but are still better than merely blindly copying Dad, then natural selection will have favored incorporating them into our bag of tricks for managing our cultural repertoire. No doubt the fast and frugal heuristics that Gigerenzer and his colleagues study are often applied in the form of strategies to learn for oneself and to directly bias the acquisition of cultural variants. In addition, culture affords the opportunity to use other types of cute tricks. We have been able to think of two:

Imitate the common type

Recall the old saw "When in Rome, do as the Romans do." This strategy makes good evolutionary sense under a broad range of conditions. A number of processes, including guided variation, direct bias, and natural selection, all tend to cause the adaptive behavior to become more common than maladaptive behavior. Thus, all other things being equal, imitating the most common behavior in the population is better than imitating at random. We label this general process *frequency-dependent bias,* because the bias depends on the commonness of the behavior, not its characteristics as in a content bias. In the case of weighting the common type more heavily, we have a *conformist* bias. Conformity is not just simple cultural influence, but a differential weighting of one's models by the commonness of the trait. If you regard your oddball friend Jane as a lovable eccentric and are as prone to imitate her as any of your more conventional friends, you are not exercising conformist bias. If you treat her as a barely tolerable deviant and actively avoid imitating her, you are a conformist. If you admire her spunky independence and are especially *prone* to imitate her, then you are applying a *nonconformist* bias, another type of frequency-dependent bias we shan't discuss further, though it has some obvious domains of applicability, such as selecting an occupation in a world where faddish choices tend to drive down wages in overfavored lines of work.

A hypothetical example illustrates how a conformist bias might be favored by selection. Consider a population of early humans in the process of expanding their range from tropical savanna into temperate woodland, a habitat that favors quite different behaviors. This is easy to see for things related to subsistence—the foods that have the highest payoff, the habits of prey, shelter construction methods, and so on. However, different habitats may also favor different beliefs and values affecting social organization: What is the best group size? When should a woman accept being a man's second wife? What foods should be shared? Individuals will have difficulty making these descisions , and as a result, pioneering groups on the margin of the range will evolve slowly toward the most adaptive behavior. This improvement will be counteracted by the influx of beliefs and values brought by immigrants from the savanna that will often cause some people in woodland populations to hold beliefs more appropriate to life in the savanna than to life in the woodland. However, once a peripheral woodland population is isolated enough that adaptive processes cause the best variants to be most common, those who imitate the most common variant are less likely to acquire inappropriate beliefs than those who imitate at random. If this conformist tendency is genetically or culturally heritable, it will be favored by natural selection.

We have modeled the evolution of a conformist bias to see whether these intuitions are correct.[42] We assume that a population is subdivided into a number of partially isolated local populations that are linked by migration. The model has two environmental states, and each local population lives in a habitat that switches back and forth between these two states with a constant probability. The model has two cultural variants—one is better in one environment and the other better in the other environment. As before, individuals have imperfect information about which variants are best in the local environment. However, we now also assume that individuals observe the behavior of more than two models. Individuals vary in two dimensions: the extent to which they imitate the behavior of others (as opposed to rely on their own information about the state of the environments) and, given that they do imitate, the extent to which they are influenced by the more common type among their models. Finally, we assume that variation in both dimensions has a heritable genetic basis. We then combine the effects of biased social learning, individual learning, and natural selection to estimate the net effect of these processes on the joint distribution of cultural and genetic variants in the population. To project the long-run consequences, we iterate this process over many generations. We then ask, what amount of conformist transmission will be favored by natural selection? If there were an office pool, what value of conformity would you guess is optimal?

And (the envelope please) the winner is . . . a strong conformist tendency. As before, a reliance on social learning is favored when environments change slowly and the information available to individuals is poor. Any combination of these two factors that leads to the evolution of a strong reliance on social learning also favors a strong conformist tendency. In fact, selection favors a strong conformist tendency even when there is only a modest reliance on social learning. Thus, the psychology of social learning should plausibly be arranged so that people have a strong tendency to adopt the views of the majority of those around them. Anyone who has raised (or been) a teenager knows that people have a strong urge to conform, and a great deal of evidence from social psychology confirms this impression. Classic studies by social psychologists Muzafer Sherif, Solomon Asch, and Stanley Milgram established that individuals adjust their behavior to that of others.[43] Sherif used an "autokinetic" procedure to demonstrate the effect of conformity. Subjects sit a dark room in which a point of light is shown on a screen for a few seconds. Although the point of light is stationary, it appears to move, a trick of visual perception. When subjects are asked how far the light moves, estimates vary considerably, but on average people estimate that it moves about four inches. Nevertheless, small *groups* of individuals that have different perceptions will cause deviant individuals to change their perceptions quite dramatically. For example, a person who initially estimates that the light moves eight inches can be induced to conform to an estimate of two inches, if the other two people in the group have initial estimates of half an inch and two inches.[44]

Most conformity studies do not distinguish between simple cultural transmission and the curvilinear effects of conformity. For example, many experiments have several confederates who behave in a certain, usually highly odd, way, and just one real subject. Subjects markedly conform in such a case, but they would do so whether the cultural effect was conformist or not. Also, only a few studies have checked to see how durable conformity effects are. They are of little interest if conformity is mere polite agreement with the group that vanishes when individuals leave it.

A few studies do demonstrate durable influences.[45] Psychologist Robert Jacobs conducted one of the most informative experiments. He used the same autokinetic procedure as Sherif,[46] and set up microsocieties of two to four people. Each "generation," the subjects viewed the fixed dot and reported their estimates of its movement. Then the "oldest" experienced subject was removed from the society and a new naïve subject introduced. The experiments continued for ten generations. To create interesting initial conditions, some of the members of the initial generation were the experimenter's confederates. In one pair of experiments, Jacobs set up two three-person microsocieties. In both cases, confederates reported that the light moved sixteen inches, a highly deviant value. In one experiment, two of the three initial members of the society were confederates, and in the other experiment, only one of the three initial members was a confederate. When real subjects' faced two confederates, estimates were more than twice as far from the "true" movement of four inches compared with real subjects who were in groups with just one confederate. In both societies, the effect of the initial deviant models was temporary. Both microsocieties evolved toward the average estimate of uninfluenced naïve subjects, although the society with the initially largest deviation took considerably longer to reach equilibrium. In this experiment, guided variation was a powerful enough force to overbalance the conformist-bias effect in the long run.

Conformity does not stir much interest among contemporary social psychologists; the work conducted between 1950 and 1980 is still the main stuff of modern textbooks.[47] Conformist *transmission* remains a very poorly studied phenomenon, and we believe it illustrates a common phenomenon. Without Darwinian concepts and tools, the population-level consequences of individual behavior are not intuitive. Social psychologists following their noses did not discover the role of conformity in cultural evolution, whereas Jacobs, who worked on his project with the pioneering evolutionary psychologist Donald Campbell, asked an evolutionary question and devised the proper experiment to answer it. Darwinian analysis reveals a mass of largely unexplored questions surrounding the psychology of cultural transmission and the biases that affect what we learn from others. Small, dull effects at the individual level are the stuff of powerful forces of evolution at the level of populations.[48] Understanding rather precisely how *individuals* deploy their kit of imitation heuristics is necessary to understand the rates and direction of cultural evolution and work on the problem has hardly begun.

Imitate the successful

People often imitate the successful—aspiring pop stars imitate Madonna's vocal style and sartorial panache, and aspiring NBA stars imitate Michael Jordan's slash to the hoop, his solution to male-pattern baldness, and, if the Sara Lee Corporation[49] has spent its money wisely, his taste in underwear. On the face of it, this strategy seems odd, but advertising executives earn handsome rewards for getting inside our heads. Mass-media celebrities notwithstanding, our attraction to the successful makes much adaptive sense. Determining *who* is a success is much easier than to determining *how* to be a success. By imitating the successful, you have a chance of acquiring the behaviors that cause success, even if you do not know anything about which characteristics of the successful are responsible for their success. If you can accurately imitate everything they do, you ought to be a success, too, at least insofar as success is based on culturally transmissible characters. Even when the exact behaviors that contribute most to fitness are very hard to evaluate, there may be easily observable traits that are correlated with fitness, such as wealth, fame, and good health. If so, you can try to imitate everything that wealthy people do in an effort to acquire the traits that make them wealthy, but without actually trying to determine exactly how wealth is produced. We call this process *model-based bias,* because the bias depends not on the characteristics of the cultural variant itself, but instead depends on some other characteristic of individuals modeling the variant, such as indicators of prestige. Anthropologist Joe Henrich and psychologist Francisco Gil-White argue that we grant prestige, and the favors that go with it, to people we perceive as having superior cultural variants to imitate as a means of compensating them for the privilege of their company and the opportunity to imitate them. They contrast human prestige with the more widespread phenomenon of dominance, where strong or guileful individuals usurp resources from the weaker.[50] We can think of other forms of model-based bias besides the prestige bias, but we'll stick with the more evocative term in what follows.

To see how prestige bias might evolve, consider, once again, the hypothetical population of early humans expanding their range from tropical savanna into temperate woodland. Assume that individuals living in the woodland have a hard time determining the best way to behave, and as a result peripheral populations contain a mix of behaviors, some good and some not so good. People who happen to acquire the best behavior will be, on average, more successful. They will be healthier and have larger families or more political power. Thus, people who imitate the successful will, all other things being equal, be more likely to acquire the locally adaptive behavior. If the tendency to imitate the successful is genetically (or culturally) variable, it will increase by natural selection.

Simple mathematical models show that the strength of prestige bias depends on the correlation between the traits that *indicate* success and the traits that *cause* success. [51] They also show that prestige bias can lead to an unstable, runaway process much like the one that may give rise to exaggerated characters such as peacock tails.

Many social psychological experiments suggest that we are predisposed to imitate successful, prestigious people, even in domains not obviously related to their success. In one study, for example, subjects were asked their opinions on "student activism" in one of three scenarios: after hearing the opinion of somebody identified as an expert on the topic, after hearing the opinion of an expert on the Ming dynasty, and after a control condition in which they didn't hear anybody's opinion. Subjects tended to voice opinions similar to either of the two experts, and they were equally likely to adopt the opinions of experts on activism and the Ming dynasty.[52] Other experiments are consistent with the prediction that the tendency to imitate the prestigious should be greater when individuals have difficulty figuring out the best alternative on their own. Field studies are also consistent with the idea that prestige plays an important role in social learning. For example, people often use prestige bias to acquire new traits, tending to adopt the practices of high-status "opinion leaders."[53] This is particularly true for the poor and less educated, whose ability to bear the costs of direct evaluation of innovations is limited. Interestingly, the poor and less educated typically imitate people of high *local* status, not socially distant elites whose life situation far from potential adopters. A poor Turkoman herder is probably well advised to imitate the herd management practices of his wealthier neighbors and to ignore the advice of technical experts from Colorado, Switzerland, or New Zealand. Studies of dialect evolution also support this hypothesis; locally prestigious women tend to be the most advanced speakers of evolving dialects.[54] Indeed, the data suggest that popular preteen girls of the working or lower middle class are usually the most important leaders of language evolution in American cities. (We get perverse pleasure out of teasing our sometimes language-elitist academic colleagues with this fact.) The patterns of prestige in human societies are also consistent with the idea that information, not power, gets you prestige. For example, older people are prestigious in many societies, even when they do not have the power either in their person or their political alliances to dominate others.

The existence of these fast and frugal heuristics for acquiring culture now has us deeply entangled in the adaptationist's dilemma. Easy tricks are available to improve the power of culture to evolve adaptations, seemingly simpler and less costly tricks than the individual learning and direct bias that are based on ubiquitous animal capacities for learning on one's own.

Darwin's intuition that imitation should be widespread seems well supported by our modeling exercises, yet we are stuck with the stubborn empirical findings that very few if any other species make anything like the use of culture that we do. Many species have simple forms of social learning that ought to be excellent preadaptative foundations on the basis of which more-sophisticated forms could evolve. And, culture seems to be the very bag of tricks we've used to become the earth's dominant organism. Something quite unusual and quite remarkable must have led to our weird species. Understandably, few people think their own species is weird. Somehow being a very recently evolved species that has exploded like none other seems as right and natural to most as when we still believed that God created us in his image. A little scientific theorizing is necessary to convince us that existence of human culture is a deep evolutionary mystery on a par with the origins of life itself. We make no pretense of having a completely satisfactory explanation for the adaptationist's dilemma of complex culture, but let's peck away at the strands of the problem and see if we can see a ray or two of light.

How the capacities for culture possibly evolved

We are all surprised, amused, and sometimes exhausted by the intense curiosity of young children. As Ph.D.'s who flatter ourselves as having a wide and deep fund of general knowledge, especially when we can combine our different ranges of expertise, we received some humbling lessons from Pete's firstborn child. He often was able to put his current questions to the two of us either simultaneously or sequentially (not to mention his mother, "Aunt" Joan, and other handy adults), and he frequently exhausted our collective knowledge embarrassingly quickly. Contemptuous of answers of the form "We just don't know why it happens that way," he would demand, "Then why *maybe*?"

Philosopher Robert Brandon argues that why-maybe answers play an important role in evolutionary biology (he calls them “how possibly” explanations).[55] He points out that evolutionary trajectories are so complicated that they rarely allow an exact elucidation of how and why things happen. Evolutionary processes are too complex and the paleo-environmental and fossil records are too fragmentary for us to be certain of any account of how some adaptation evolved. More than one hypothesis is usually consistent with all the data we have at hand, and several might still stand after we have all the data we are ever likely to get. Although the kinds of adaptive accounts that evolutionary biologists give to historical questions are sometimes stigmatized as “adaptive just-so stories,” Brandon argues that nonadaptive accounts are equally “just so.” No Darwinian account of the evolution of any lineage of organisms entirely escapes being a how-possibly explanation. Nevertheless, some how-possibly answers are better than others. They are better because they fit more of the available information, they are better grounded in theory, and they are productive of further work. While we can never be satisfied with how-possibly accounts, they can still yield appreciable progress.

The typical trajectory of the evolutionary sciences is that we begin with a simple hypothesis or two that prove to be quite wrong but in being wrong simulate a spate of further work. For a while, the number of plausible ideas grows rapidly, and the data accumulate more slowly. In this middle period of a problem, uncertainty actually appears to grow, as if the more we investigate a problem the less we are certain about any part of it. Of course, this state of affairs results from our former innocent ignorance of the magnitude of the problem. Then a pruning process begins as hard work finds fatal flaws in old, good ideas faster than new ones appear. We may never know *the* answer, but we end up *immensely* more sophisticated than when the enterprise began. Given the manifest importance of culture in human behavior, the theory of cultural evolution ought to be central to the how-possibly project. In that spirit, we offer the following how-possibly account of the origin of *Homo sapiens* in terms of the evolution of increasingly sophisticated capacities for culture.

Culture is adaptive because it provides information about variable environments

Humans, even as hunter-gatherers, adapt to a vast range of environments. The archaeological record indicates that foragers from the Pleistocene epoch occupied virtually all of Africa, Eurasia, and Australia. The data on historically known hunter-gatherers suggest that to exploit this range of habitats, humans used a dizzying diversity of subsistence practices and social systems. Consider just a few examples. The Copper Eskimos lived in the high Arctic, spending summers hunting near the mouth of the MacKenzie River and the long, dark months of the winter living on the sea ice, hunting seals. Groups were small and intensely dependent on men's hunting. The !Xo lived in the central Kalahari collecting seeds, tubers, and melons; hunting impala and gemsbok; surviving fierce heat; and living without surface water for months at time. Both the !Xo and the Copper Eskimo lived in small, nomadic bands linked together in larger patrilineal band clusters. The Chumash lived on the productive California coast around present-day Santa Barbara, gathering shellfish and seeds and fishing the Pacific from great plank boats. They lived in large permanent villages with division of labor and extensive social stratification.

This range of habitats, ecological specializations, and social systems is much greater than any other animal species. Big predators such as lions and wolves have the largest range among other animals, but lions never extended their range beyond Africa and the temperate regions of western Eurasia; wolves were limited to North America and Eurasia. The diet and social systems of such large predators are similar throughout their range. They typically capture a small range of prey species using one of two methods: they wait in ambush, or combine stealthy approach and fast pursuit. Once the prey is captured, they process it with tooth and claw. The basic simplicity of the lives of large carnivores is captured in the Gary Larson cartoon in which a *T. rex* contemplates its monthly calendar—every day has the same notation "Kill something and eat it." In contrast, human hunters use a vast number of methods to capture and process a huge range of prey species, plant resources, and minerals. For example, anthropologist Kim Hill and his coworkers have observed the Aché, a group of foragers who live in Paraguay, who take 78 different species of mammals, 21 species of reptiles, 14 species of fish, and over 150 species of birds using an impressive variety of techniques that depend on the prey, the season, the weather, and many other factors. Some animals are tracked, a difficult skill that requires a great deal of ecological and environmental knowledge. Others are called by imitating the prey's mating or distress calls. Still others are trapped with snares or traps or smoked out of burrows. Animals are captured and killed by hand, shot with arrows, clubbed, or speared.[56]

And this is just the Aché—if we included the full range of human hunting strategies, the list would be endless. The list of techniques applied to plants and minerals is similarly long and diverse. Making a living in the Arctic requires specialized knowledge: how to make weatherproof clothing, how to provide light and heat for cooking, how to build kayaks and umiaks, how to hunt seals through holes in the sea ice. Life in the central Kalahari requires equally specialized, but quite different knowledge: how to find water in the dry season, which of the many kinds of plants can be eaten, which beetles can be used to make arrow poison, and the subtle art of tracking game. Survival might have been easier on the balmy California coast, yet specialized social knowledge was needed to succeed in hierarchical Chumash villages compared to the small, egalitarian bands of the Copper Eskimo and the !Xo.

So, maybe humans are more variable than lions, but what about other primates? Don't chimpanzees have culture? Don't different populations use different tools and foraging techniques? There is no doubt that great apes do exhibit a wider range of foraging techniques, more-complex processing of food, and more tool use than other mammals.[57] However, these techniques play a much smaller role in great ape economy than they do in the economies of human foragers. Anthropologist Hillard Kaplan and his coworkers compare the foraging economies of a number of chimpanzee populations and human foraging groups. They categorize resources according to the difficulty of acquisition: *Collected foods* like ripe fruit and leaves can be simply collected from the environment and eaten. *Extracted foods* must be processed and include fruits in hard shells, tubers or termites that are buried deep underground, honey hidden in hives high in trees, or plants that contain toxins that must be extracted before they can be eaten. *Hunted foods* come from animals, usually vertebrates, that must be caught or trapped. The data show that chimpanzees are overwhelmingly dependent on collected resources, while human foragers get almost all of their calories from extracted or hunted resources.[58]

Humans can live in a wider range of environments than other primates because culture allows the relatively rapid accumulation of better strategies for exploiting local environment compared with genetic inheritance. Consider "learning" in the most general sense; every adaptive system "learns" about its environment by one mechanism or another. Learning involves a tradeoff between accuracy and generality. Learning mechanisms generate contingent behavior based on "observations" of the environment. The machinery that maps observations onto behavior is the "learning mechanism." One learning mechanism is more accurate than another in a particular environment if it generates more adaptive behavior in that environment, and it is more general than another if it generates adaptive behavior in a wider range of environments.

Typically, a tradeoff exists between accuracy and generality, because every learning mechanism requires prior knowledge about which environmental cues predict the state of the environment and what behaviors are best in each environment The more detailed and specific such knowledge is for a particular environment, the more accurate is the learning rule. Thus for a given amount of inherited knowledge, a learning mechanism can either have detailed information about a few environments, or less-detailed information about many environments.

In most animals, this knowledge is stored in the genes, including of course the genes that control individual learning. Consider a variation on the thought experiment described in chapter 2. Pick a wide-ranging primate species, let's say baboons. Then capture a group of baboons, and move them to another part of the natural range of baboons in which the environment is as different as possible. You might, for example, transplant a group from the lush wetlands of the Okavango Delta to the harsh desert of western Namibia. Next, compare their behavior to the behavior of other baboons living in the same environment. We believe that after a little while, the experimental group of baboons would be quite similar to their neighbors. This experiment has actually been done, although not in such an extreme case. Primatologist Shirley Strum moved a group of baboons that was being threatened by humans from one site to a somewhat different one several hundred kilometers away. The baboons quickly adapted to their new home. The reason that the local and transplanted baboons would be similar, we think, is the same reason that baboons are less variable than humans: they acquire a great deal of information about how to be a baboon genetically. To be sure, they have to learn where things are, where to sleep, which foods are desirable, and which are not, but they can do this without contact with already knowledgeable baboons because they have the basic knowledge built in. But they can't learn to live in temperate forests or arctic tundra because their learning systems don't include enough innate information to cope with those environments.

Human culture allows learning mechanisms to be both more accurate and more general, because *cumulative* cultural adaptation provides accurate and more-detailed information about the local environment. People are smart, but individual humans can't learn how to live in the Arctic, the Kalahari, or anywhere else.[59] Think about being plunked down on an Arctic beach with a pile of driftwood and seal skins and trying to make a kayak. You already know a lot—what a kayak looks like, roughly how big it is, and something about its construction. Nonetheless, you would almost certainly fail (We're not trying to dis you; we've read a lot about kayak construction, and we'd at best make a poor specimen, without doubt). Even if you could did make a passable kayak, you'd still have a dozen or so similar tools to master before you could make a contribution to the Inuit economy. And then there are the social mores of the Inuit to master. The Inuit could make kayaks, and do all the other things that they needed to do to stay alive, because they could make use of a vast pool of useful information available in the behavior and teachings of other people in their population. The reason the information contained in this pool is adaptive is that a combination of learning and cultural transmission leads to relatively rapid, cumulative adaptation. Even if most individuals blindly imitate with only the occasional application of some simple heuristic, many individuals will be giving traditions a nudge in an adaptive direction, on average. Cultural transmission preserves the many small nudges, and exposes the modified traditions to another round of nudging. Very rapidly by the standards of ordinary evolutionary time, and more rapidly than evolution by natural selection alone, weak decision-making forces generate new adaptations. The complexity of cultural traditions can explode to the limits of our capacity to learn them, far past our ability to make careful, detailed decisions about them. We let the population-level process of cultural evolution do the heavy lifting of our "learning" for us.

Social learning may be an adaptation to Pleistocene climate fluctuations

The picture sketched above indicates that cumulative cultural adaptation is most advantageous when there are big differences between environments in time and space *and* when that variation arises slowly enough to make transmission and accumulation by social learning useful. If environments change too rapidly in time or space, selection will favor individual learning, but no transmission. If environments change too slowly, then ordinary organic evolution can track the fluctuations more faithfully and at less cost than a system of social learning. Humans seem to be the first species on our planet to have evolved an advanced capacity for cumulative culture, although in so doing we have proved a spectacular, though not necessarily permanent, success. Given that complex culture is adaptive, why did it evolve in the human lineage at this particular juncture of the earth's rather long biotic history?

sOne good how-possibly answer is that social learning is an adaptation to increased climate variation during the last half of the Pleistocene. This hypothesis provides a possible way to ease off the horns of the adaptationist's dilemma. We suspect that a sophisticated capacity for culture has only been adaptive for a short, recent bit of the earth's history and we are merely the first lineage to discover its advantages. Deteriorating climate over the last two million years favored increased behavioral flexibility, including an increased reliance on social learning, probably in many species. Already a relatively large-brained group, the primates were preadapted to evolve the cognitively taxing mechanisms of observational learning and sophisticated biasing needed to manage culture. Just storing the large cultural repertoires involved with complex, accumulated cultural adaptations may require considerable brain volume. Primates are also rather sociable as mammals go, and "learning" by cultural evolution is an intensely social phenomenon. Finally, the visual adaptation of most primates and the manipulative hands of our ancestors were likely preadaptations for imitation and the production of sophisticated tools that are the cornerstone of human economies. The history of the human lineage specifically suggests that the evidence from the fossil and archaeological records is consistent with the hypothesis that the psychological machinery that underpins cumulative cultural change evolved over the last half million years, a period during which climates were more unstable than ever before.

Using a variety of proxy measures of past temperature, rainfall, ice volume, and the like, derived mostly from cores of ocean sediments, lake sediments, and ice caps, paleoclimatologists have recently constructed a stunning picture of climatic deterioration over the last two million to three million years.[60] The earth's mean temperature has dropped several degrees, and the amplitudes of fluctuations in rainfall and temperature have increased (fig. 4.2).[61] For reasons that are still poorly understood, glaciers wax and wane in concert with changes in ocean circulation; carbon dioxide, methane, and dust content of the atmosphere; and changes in the average amount and distribution of precipitation. Different cyclical patterns of glacial advance and retreat involving all these variables have prevailed. A 21,700-year cycle dominated the early part of the period, a 41,000-year cycle between about 2.6 million and 1 million years ago, and a 95,800-year cycle the last million years.

Fluctuations that occur over tens of thousand of years are not likely to have driven the evolution of adaptations for social learning. Populations will adjust to such slow changes by changing their ranges and by organic evolution. However, the increased variation over such long timescales seems to be strongly associated with variation at much shorter timescales. High-resolution data for the last 80,000 years are available from ice cores taken from the deep ice sheets of Greenland and Antarctica. Resolution of events lasting little more than a decade is possible in ice 80,000 years old, improving to monthly resolution for events after 3,000 years ago. During the last glacial, the ice core data show that the climate was highly variable on timescales of centuries to millennia.[62] Figure 4.3 illustrates how dramatic this variability was. Even when the climate was in the grip of the ice, it briefly spiked to near interglacial warmth every thousand years or so. The intense variability of the last glacial carries right down to the limits of the decade-level resolution of the ice core data. Sharp spikes lasting a century or less are common in the Greenland record. Even more recent high-resolution data from temperate and tropical latitudes verify that the high-amplitude fluctuation seen in the ice core is a global phenomenon, and some of the best records suggest that most or even all of the world's climates fluctuated to the same beat, as i recorded so beautifully in Greenland ice.[63]

Undoubtedly, oscillations such as those detected in ice cores had important impacts on evolving animal populations. The Holocene (the last relatively warm, ice-free 10,000 years) has been a period of very stable climate compared with the last glacial. Nonetheless, Holocene weather extremes have had significant effects on organisms.[64] The impact of the much greater variation that was probably characteristic of most of the Pleistocene is hard to imagine. Tropical organisms did not escape the impact of climate variation; temperature and especially rainfall were highly variable at low latitudes.[65] During most of the Pleistocene, plants and animals lived under conditions of rapid, chaotic, and ongoing reorganizations of ecological communities as species' ranges adjusted to the noisy variation in climate. Thus, for the last two and a half million years or so, organisms have seemingly had to cope with increasing variability in many environmental parameters at timescales on which strategies for phenotypic flexibility would be highly adaptive.

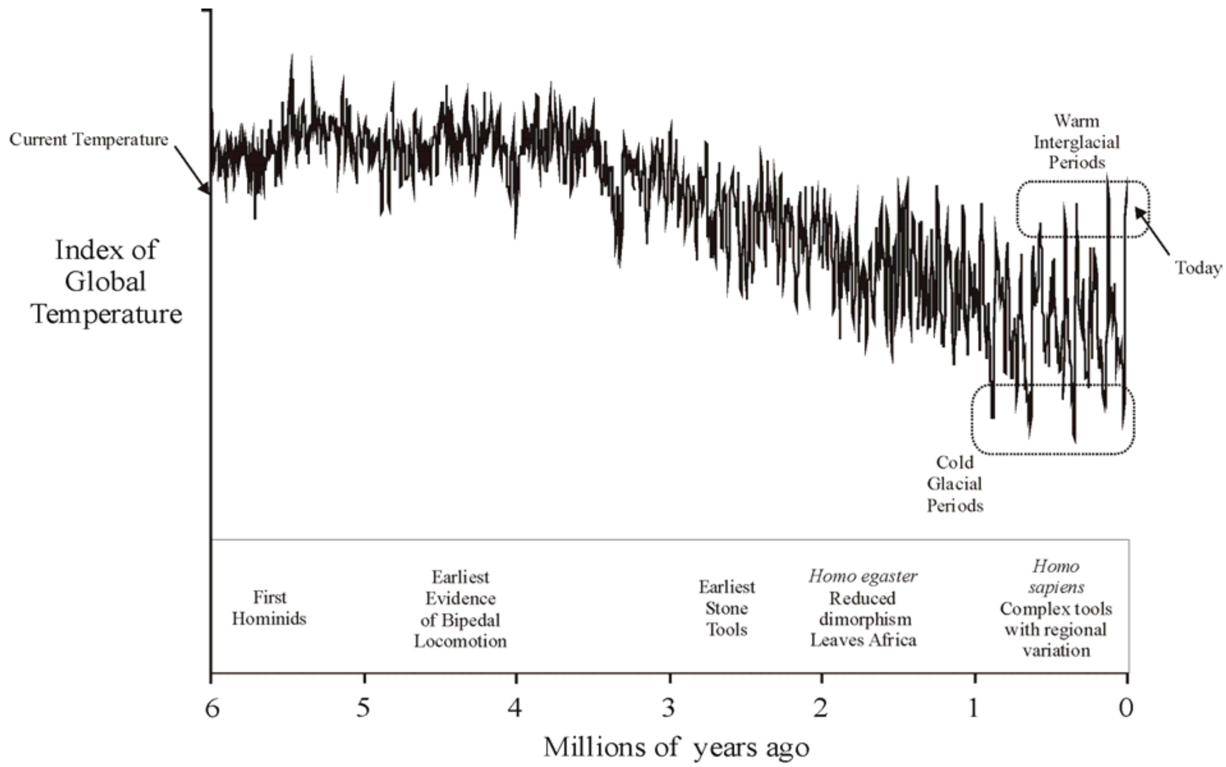

Figure 4.6. The world's climate has become colder and more variable over the last six million years. The vertical axis plots δO^{18}, the excess of O^{18} relative to O^{16} in samples taken from deep-sea sediments that date to different times over the last six million years. The concentration of O^{18} in seawater increases during cold periods, because water containing the lighter isotope of oxygen, O^{16}, evaporates more readily and is thus trapped in glacial ice. Other data from deep-sea cores indicate that during cold periods, the world was drier and the CO_2 concentration of the atmosphere was lower. (Redrawn from Opdyke et al. 1995)

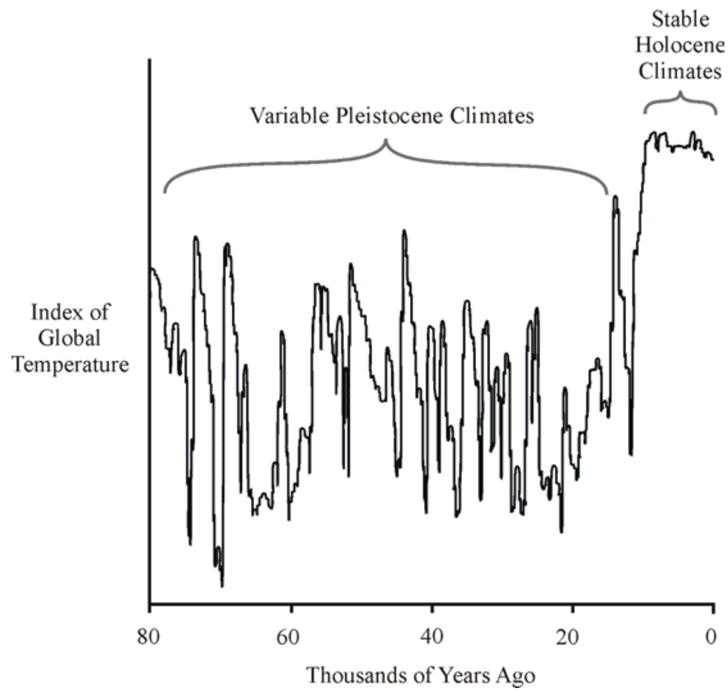

Figure 4.3. During the last glacial period, there were large fluctuations in the world's climate, often occurring in less than 1,000 years. The last glacial period extended from about 70,000 years ago to 12,000 years ago. The vertical axis plots the deficiency in O^{18}, an index of temperature, in a core taken in the Greenland ice cap. Notice that during the last glacial period, that high-latitude temperature swung from glacial to nearly interglacial levels in very short time periods. Other data indicate that similar fluctuations occurred at lower latitudes. Because this figure was smoothed using a 150-year high pass filter, the actual amount of short time period fluctuations was greater than shown.

The Pleistocene climate deterioration is correlated with increases in brain size in many mammalian lineages besides our own. The average encephalization (brain size properly corrected for body size) of mammals has increased ever since the demise of the dinosaurs 65 million years ago.[66] However, many relatively small-brained mammals persist to the present even in orders where some species have evolved large brains. The largest increases in encephalization per unit time by far occurred over the last 2.5 million years—the increase in average encephalization during this period was larger than the increase during the previous 20 million years. Brain enlargement in the human lineage began to diverge from the trend of the other apes at the beginning of the Pleistocene, about 2 million years ago, about the same time as an abrupt increase in the amplitude of glacial fluctuations,[67] and then increased rapidly again between 800 thousand and 500 thousand years ago after another increase in the amplitude of glacial fluctuations.

All other things being equal, selection should ruthlessly favor small brains, because large brains are costly.[68] Nonetheless, brain size in mammals is quite variable. Human brains account for 16% of our basal metabolism. Average mammals have to allocate about only 3% of basal metabolism to their brains, and many marsupials get by with less than 1%.[69] These differences are easily large enough to generate strong evolutionary tradeoffs. In addition to metabolic requirements, there are other significant costs of big brains, such as increased difficulty at birth, greater vulnerability to head trauma, increased potential for developmental snafus, and the time and trouble necessary to fill them with usable information. In effect, all animals are under stringent selection pressure to be as stupid as they can get away with. The oft-mentioned "fact" that we actually use only a small part of our brain is a myth. Brains are a use-it-or-lose-it organ. If they have gotten bigger, they must be good for something, really good.

A recent study by comparative psychologists Simon Reader and Kevin Laland suggests that one thing they are good for is learning—both individual *and* social learning.[70] Reader and Laland surveyed the primate literature, recording the number of times that different primate species had been observed doing three different things: using tools, performing novel or innovative behavior, and engaging in social learning. They showed that all three traits are correlated with a measure of brain size. In other words, primates with bigger brains are more likely to use social learning, more likely to engage in novel behavior, and more likely to use tools. Interestingly, observations of novel behavior and social learning are correlated even after the effect of brain size is taken into account, suggesting that social learning allows more-flexible responses to novel environments.

A related study by Hillard Kaplan and economist Arthur Robson[71] supports the idea that larger brains lead to more behavioral flexibility. They showed that among primate species, larger brains (corrected for body size) are associated with a longer juvenile period and longer life span, even when other correlates of brain size, like group size, are controlled. Kaplan and Robson argue that brain size and longevity are linked in an adaptive complex. As we all know, learning takes time. You can't learn how to play chess or ski in a day—mastering mental and physical skills takes years of learning and practice. The same goes for foraging skills. This means that environments, like the variable ones of the Pleistocene, that favor increased behavioral flexibility also favor longer juvenile periods to allow enough time for learning and larger brains to do the learning. Learning and teaching culture are costly investments , and thus increased brain size and longer juvenile periods will favor a longer life span. Selection favors a longer life, because it allows individuals to get more benefit from what they learned during the necessary but costly extended juvenile period.[72]

According to the argument we have developed so far, humans are just the tail of the distribution. We are the largest brained, slowest developing member of the largest brained, slowest developing mammalian order. However, this can't be the whole story. That increases in brain size and decreases in developmental rate are correlated with climate variation supports the idea that fluctuating environments really do favor increased behavioral flexibility and social learning. However, as we argued earlier, we are unique in our ability to build up complex subsistence systems over many generations by the incremental modifications of many innovators. This capacity, on our account, is responsible for our ability to evolve a huge range of complex cultural adaptations that in turn account for our success as a species. But if many animal species have rudimentary to moderately sophisticated systems for social learning and if complex culture is a highly advantageous means of adapting to Pleistocene climatic deterioration, why is complex culture so rare?

One interesting hypothesis to consider is that the evolution of the cumulative cultural evolution faces a “bootstrap problem.” Models show that under some sensible cognitive-economic assumptions, a capacity for complex cumulative culture cannot be favored by selection when rare.[73] The idea is quite intuitive. Suppose that to acquire a complex tradition efficiently by imitation, some derived cognitive machinery is required. For example, a number of psychologists have argued that a “theory of mind” is required for observational learning.[74] The idea is that unless you can guess other people’s intentions and motives, the decision to imitate is very difficult. Suppose you see our mystery device (figs. 4.1, 4.8) hanging in someone’s kitchen, and later see an identical one in a store. Are you tempted to buy? If you still don’t know its purpose, almost certainly not. If you have discovered what other people do with it, then perhaps so. We humans rather automatically put ourselves inside others’ heads. If Aunt Ethel uses the mystery device in the course of making a salad in your presence, you fit its use into a scenario of Aunt Ethel wanting to make a salad, wanting a certain ingredient in the salad, and using the mystery device to that end. Having modeled Aunt Ethel’s motivations and actions, you know the function of the device and can fit it into a scenario where you personally might find the device useful, even if you never touched the mystery device or sampled the salad. The decision to buy or not is for us trivial once we've *seen* what the thing is for. As easy and automatic as this seemingly trivial mental theorizing is to us, experiments show that small children and most other animals tested either lack the capacity to see others' functional acts in this way or have only limited abilities to do so.

Figure 4.8. It is an avocado slicer (from Progressive International Corp.). Halve the avocado, remove the pit, and then use the slicer to make long wedges in the fruit. The flat hoop makes it easy to stay near the skin, and the thin wires slice even very ripe avocado without tearing.

Suppose that the theory of mind module is necessary for rapid, accurate imitation of complex skills and that it also takes up a not-trivial amount of the resources of the brain. Suppose further that if complex, difficult-to-accumulate, culturally evolved traditions are available to imitate using the module, then the capacity to acquire them is a big fitness advantage, more than repaying the nontrivial cost. Obviously, complex traditions cannot evolve without the cognitive machinery that gives rise to cumulative cultural evolution. The rub is that complex traditions don't come out of thin air. A whole population of individuals capable of imitating has to exist and exist for some time to evolve complex traditions. This means that a rare mutant with the ability to imitate, say, because he has a better theory of mind, will observe only the behavior that can be acquired without his ability. Such a mutant will bear the costs of the module but will get no benefits.

Worse yet, as anthropologist Joe Henrich has argued, to get complex traditions, just a few individuals with the necessary cognitive complexity aren't enough; the cultural evolution of complex adaptations may require a fairly large population of imitative minds. Henrich points out that imitation is an error-prone process and that learners have a hard time getting the skills to manufacture complex artifacts down pat. In a small population, this effect will lead to the degradation of more-complex skills. However, in a large population, especially skilled or lucky toolmakers will be relatively numerous. These geniuses will improve the technology they are good at, and have the effect of preventing the degradation of the technology as their imitators spread the recovered complexity to others. Henrich's work suggests that only fairly sizable populations can sustain complex, culturally evolved artifacts and behaviors.

This result is consistent with the loss of tool complexity on Tasmania documented by the late Australian archaeologist Rhys Jones. When European explorers reached Tasmania in the nineteenth century, they collected the simplest tool kit known for any living people. When Jones got to digging on Tasmania in the 1970s, he discovered that the Tasmanians once had the full Australian tool kit, hundreds of items richer than that collected from the living Tasmanians.[75] The complexity of the tool kit began to decline when the flooding of the Bass Strait about eight thousand years ago cut the land bridge that connected Tasmania to the mainland. Yet the Tasmanian population was not tiny—at European arrival it numbered about four thousand people. Nor had the technology simplified quickly. Rather, the more-complex items, such as boats, seem to have disappeared slowly but steadily over the millennia. These data and Henrich's model suggest that surprisingly large populations are necessary to sustain a tool kit consisting of many hundreds of rather complex items against slow but inexorable decay due to small but cumulative transmission error.

If such an impediment to the evolution of complex traditions existed, evolution must have traveled a roundabout path to get the theory of mind module (or whatever) past the threshold necessary for bringing it under positive selection for the cumulative cultural adaptation. Some have suggested that primate intelligence was originally an adaptation to manage a complex social life.[76] Perhaps in our lineage the complexities of managing food sharing, the sexual division of labor, or some similar social problem favored the evolution of a sophisticated ability to take the perspective of others. Such a capacity might incidentally make imitation possible, launching the evolution of the most elementary form of complex cultural traditions. Once elementary complex cultural traditions exist, the threshold is crossed. As the evolving traditions become too complex to imitate easily they will begin to drive the evolution of still more-sophisticated imitation. This advantageous-but-can't-increase-when-rare sort of stickiness in the evolutionary processes is presumably what gives evolution its commonly contingent, historical character.[77] If such barriers exist to the evolution of a new capacity, then many species with the apparently necessary preadaptations may collect at the barrier until finally one breaks through. Other such barriers are easy to imagine. Much of the traction we get from culture comes from tools. Most apes are quadrupeds that need all four limbs for locomotion. Once our lineage became bipedal, hands could fall under selection for new functions such as making stone tools and carrying spears. Like winning the lottery, probably several such preadaptations had to come our way before natural selection could get real purchase on the capacity for complex culture.

How humans possibly evolved

With these ideas in hand, let us now turn to the evolution of the human lineage. We have two goals here. First, we want to convince you that population thinking about human culture adds quite a bit to the explanations conventionally used in paleoanthropology. Second, in chapter 6 we will argue that cultural evolutionary processes have shaped human social environments in ways that had important consequences for the genetic evolution of human psychology. Here we discuss the evidence that humans have had the capacity for cumulative cultural evolution long enough for such coevolutionary processes to be important.

The earliest hominids were bipedal, but otherwise much like contemporary apes. Genetic data indicate that the last common ancestor of humans, chimpanzees, and bonobos lived five to seven million years ago. Three different hominoid fossils date from this period, *Orrorin tugenensis, Sahelanthropus tchadensis,* and *Ardipithecus ramidus*. However, currently described specimens do not tell us whether any of these species were bipedal, or whether they are more closely related to humans or chimpanzees. Beginning roughly four million years ago, the first bipedal hominids appear in the fossil record, and when it rains it pours. For the next two million years, Africa was lousy with hominid species. The details of the taxonomy are controversial, but most paleoanthropologists agree that there were between five and ten species belonging to three separate genera, *Australoptihecus, Paranthropus,* and *Kenyanthropus*. We will refer to these folks collectively as “bipedal apes,” because while they were bipedal, they were still very apelike in most other ways. Males were much larger than females, indicating that males probably invested more energy in competing for mates than caring for offspring. Their brains were the same size as the brains of contemporary apes (correcting for body size), and they had a relatively short juvenile period and life span, even shorter than living chimpanzees. They were smaller than modern humans (roughly the same size as chimpanzees), with long arms and short legs, suggesting that they still spent quite a bit of time in the trees. Many anthropologists include the specimens formerly included in *Homo habilis* in one of these genera because although some of these specimens had larger brains than other early hominids, they were otherwise apelike.[78] Paleoanthropologists have reached no consensus about which bipedal ape species is ancestral to later hominids. Upright posture and hands did not by themselves set off a rush to complex culture as paleoanthropologists once supposed. For a million and a half years or so of bipedality, no evidence for artifacts exists at all.

Perhaps the bipedal apes eventually began to use chipped stone tools. The earliest flaked stone tools have been found at Gona, a site in Ethiopia that dates to about 2.6 million years ago. Similar crudely shaped cores and flakes belonging to the Oldowan industry are found in many sites in Africa that date to this period, but it is unclear which hominid species made these tools. The bipedal apes furnish the only bones so far discovered to match to the stones. However, *Homo ergaster* fossils have been discovered dating to about 1.8 million years ago. Stone tools are tough objects, and a user probably made many of them in a lifetime. Bones are much more perishable, and no one leaves more than one set. Thus, the stones record is denser than the bones record. The earliest tools will typically appear in the fossil record before the first fossil of the creature that made the tools. In any case, since both chimpanzees and orangutans use simple tools, the bipedal apes probably did as well, even if they didn't flake stone.

Other evidence suggests that Pleistocene bipedal apes had no more sophisticated social learning abilities than living apes. Their brain sizes and developmental rates were similar to contemporary apes, suggesting that their cognitive abilities and investment in learning were similar, and their geographical ranges were limited in the same way as contemporary ape species.

Thus, the tool traditions of bipedal apes were likely not transmitted by imitation, but rather maintained by other learning mechanisms, as in contemporary apes. Primatologists Sue Savage Rumbaugh and Nicholas Toth were unable to teach Kanzi, a bonobo with a considerable talent for acquiring human behaviors, to make simple stone tools. He was able to make small sharp stone flakes by flinging raw cobbles against hard concrete surfaces, and then used the flakes to open food containers. But despite much tuition, he was never able to flake cores using his hands in a controlled way.[79] Why Kanzi couldn't accomplish this task isn't clear. Perhaps his ability to imitate is deficient. Perhaps the morphology of the chimpanzee hand makes this task difficult for him.[80] Or, perhaps he is handicapped by cognitive limitations; chimpanzees seem to have a limited ability to present causal physical relationships.[81]

Early specimens of *Homo ergaster* have been found at a number of East African sites and as far afield as Dmanisi in the foothills of the Caucasus Mountains. Anatomically similar fossils, usually called *Homo erectus,* have been found in China and Indonesia at sites that date from perhaps 1 million years ago up to less than 100,000 years ago. These creatures have larger brains than the bipedal apes, but also have larger, modern human–sized bodies, so they were only a bit brainier on average than the bipedal apes that preceded them. These hominids were fully committed terrestrial bipeds with long legs and short arms. The difference between the size of males and females was about the same as in modern people. *H. ergaster* probably developed more rapidly than modern humans. By counting growth lines in tooth enamel, biological anthropologists can accurately estimate the rate at which teeth develop, and in living primates the rate of tooth development is highly correlated with other developmental rates. Using this technique, Christopher Dean and colleagues showed that the rate of development of *H. ergaster* was similar to living apes, a little slower than the bipedal apes that preceded it, and much faster than modern humans.[82]

The earliest fossils of *H. ergaster* are associated with simple Oldowan tools, the same ones that some creature or creatures had been making for 800,000 years or so. However, beginning sometime between 1.6 million and 1.4 million years ago, a more sophisticated tool kit, called the Acheulean industry, appears in Africa. The Acheulean is dominated by large cobbles that have been carefully reduced to a symmetrical, tear-drop-shaped hand ax. The same tool kit is found throughout Africa and western Eurasia for the next million years—not just *similar* tool kits, but statistically the *same* tool kit. Once the effects of raw materials are accounted for, the differences between the tools found at sites that are separated by a million years are, on average, no more than the differences between tools at contemporaneous sites. In East Asia, simple tools similar to the Oldowan continued to be made. Controversial evidence also suggests that hominids were able to control fire during this period.

The evidence concerning the imitative abilities of *Homo ergaster* is quite bewildering. Most scholars assume that the skills necessary to manufacture Acheulean tools were transmitted culturally in the same way that stone tool traditions are transmitted among living foragers. However, this assumption is hard to reconcile with either theory or data. Models predict that traditions among small, semi-isolated groups will rapidly diverge, so that even if functional constraints are strong, variation between groups will increase through time.[83] Both archaeological evidence from later people and ethnographic data are consistent with this prediction. How could cultural transmission *alone*, particularly if based on a relatively primitive imitative capacity, preserve such a neat, formal-looking tool as a Acheulean hand ax over half the Old World for a million years?[84] Combine this fact with *H. ergaster*'s relatively small brain and rapid development, perhaps we need to entertain the hypothesis that Acheulean bifaces were innately constrained rather than wholly cultural and that their temporal stability stemmed from some component of genetically transmitted psychology. On the other hand, the sophisticated controlled forms of the Achuelean have no parallel among the tools made by any other species of primate and demand the same sorts of manual skills that we transmit culturally.

From the point of view of cultural evolution, this already strange pattern seems even stranger. Most evolutionary scenarios connect modern humans to chimpanzees with a straight line and assume that *H. ergaster/erectus* fell somewhere along that line. Cultural evolutionary considerations lend weight to the suspicion that the path from our quadrupedal ancestor to ourselves was more circuitous. We are getting confidently more uncertain about what was going on in the early Pleistocene, and knowing what you don't know is just as important as knowing what you do know!

Beginning roughly a half a million years ago, larger brained hominids appear in Africa and Europe. We say "roughly" because sites during this period were, until recently, extremely difficult to date accurately.[85] From the neck down these creatures were similar to *H. ergaster/erectus*—very heavily muscled and stout boned—but rather more modern from the neck up. Their brains were about the same size as ours, but their skulls were long and low, and they had large faces with prominent brow ridges. We will follow the recent practice of referring to these hominids as *Homo heidelbergensis.* The developmental rate of early *H. heidelbergensis* has not been measured directly. However, Neanderthals, which appeared in western Eurasia between 300,000 and 130,000 years ago, developed at a rate similar to modern humans. Since Neanderthals are similar to *heidelbergensis* morphologically, and used a similar stone tool kit, the slow life history that is characteristic of modern humans probably evolved during this period.

About the same time, the first uncontroversial examples of cumulative cultural adaptation begin to appear in the archaeological record, especially in Africa.[86] About 350,000 years ago in Africa, the Achuelean industry is replaced by a variety of Middle Stone Age (MSA) industries based on what archaeologists call "prepared core" technologies. To manufacture this kind of tool, the knapper first shapes a block of stone, the core, with a hammer stone, and then strikes the core so that a large flake with a predetermined shape is removed. By 250,000 years ago this technology had spread throughout western Eurasia. During this period, particularly in Africa, the amount of regional variation in tools increased dramatically. In some areas, highly refined tool industries based on long, thin stone blades appear, based upon a still more sophisticated preparation of cores. At Katanda in the eastern Congo, archaeologists recovered exquisite barbed bone spear points[87]. Untipped wooden throwing spears, weighted for accurate flight like modern javelins, have been recovered from a bog deposit in Germany.[88] Regional diversity and highly sophisticated cultural adaptations, more sophisticated than an individual could develop on their own, are the hallmarks of cumulative cultural adaptation. Signs of symbolic behavior also emerge in Africa during the latter part of this period. Red ochre, used by modern peoples for personal adornment, is found at numerous sites, even quite early ones, and ostrich-shell beads and other decorative items enter the archaeological record beginning about 100,000 years ago.[89]

A variety of genetic data suggest that modern humans evolved and spread throughout Africa during this period, and then perhaps only 50,000 years ago spread across the rest of the world.[90] The earliest modern human fossils, dating to about 160,000 years ago, have been found in Africa, and abundant evidence suggests that modern humans spread across the world about 50,000 years ago, carrying sophisticated technology with them. How much gene flow between African and Eurasian populations occurred during this period is uncertain. Mitochondrial DNA from six Neanderthals indicates that the last common ancestor of modern human and Neanderthal mtDNA lived perhaps 500,000 years ago, and good evidence shows that modern humans in Europe are not related to Neanderthals.[91] On the other hand, a sophisticated statistical analysis of all the available molecular data suggests that quite a bit of gene flow occurred between modern African and archaic Eurasian populations as the spread occurred.[92]

So far we have said nothing about language, and the reason is simple: paleoanthropologists have no idea when human language evolved. Some anatomists think that they can identify brain structures associated with language from the skull of bipedal ape species living more than two million years ago.[93] Others, based on reconstructions of the soft anatomy of the vocal tract, argue that even very recent hominids such as the Neanderthals may have had only limited speech.[94] We cannot easily infer anything about the evolution of language from the archaeological record because whether language is necessary for cumulative cultural evolution is unclear, at least those aspects of culture that turn up in the fossil record. Archaeologist Stephen Shennan argues that stone tool technology and similar manual skills are learned by observation and that language would not be required to make them.[95] So too even with artistic productions, though many tend to assume that graphic art and language are related. One of us has a friend who is an accomplished artist, and he cannot be made to say anything about his art. He says when pressed, “You’re supposed to look at it, not talk about it!”

Psychologist Merlin Donald argues that quite complex behavior can be acquired by mimicry in the absence of language.[96] Nineteenth-century accounts of the abilities of deaf-mutes to acquire many sorts of useful economic and social skills without language suggest that they could easily learn most nonlinguistic skills by observation, without any linguistic aids. Thus the increasingly sophisticated stone tools of the later Pleistocene are not beyond the abilities of mute persons with good imitative skills. Indeed, even normal speakers generally find demonstrations of such skills superior to pictures and pictures equal to a thousand words. Language is often given pride of place as the watershed between humans and other animals, and again we are much tempted to reason from modern human analogies about fossil hominids, especially big-brained ones. Some people's credulity is strained to think that rather ancient hominids didn't have at least some simple language. On this point, too, as with Acheulean hand axes, we are more impressed by the strangeness of what we do know about the lifeways of our more distant ancestors. Reasoning from modern patterns uniformly diluted to make them "primitive" has repeatedly failed to predict the finds of the paleoanthropologists. People might have been mute until comparatively recent times.

Many scholars believe that language evolved to manage social interaction.[97] Social actors can often benefit by communicating about who did what to whom, when, and why—that is, by gossiping—and this is difficult to do without grammatically structured language. (Imagine *People's Court* with a cast consisting only of mimes!) Language is also an extraordinarily powerful device for encoding and transmitting some kinds of cultural traditions, particularly myths and stories that often carry much information about social roles and moral norms. While nineteenth-century deaf-mutes could learn simple social customs such as table etiquette, we doubt that they could manage the rules for operating a unilineal kinship system, much less a law court. The productivity of language allows humans to express a huge number of ideas and link them in patterned arrays. Some authors think that without linguistic encoding, social learning is not accurate enough to give rise to stable traditions or gradual, cumulative adaptive evolution.[98] And even if language first evolved to gossip about band politics, it could have then been elaborated, because it made more-complex cultural traditions possible by making it easy to express, memorize, and teach cultural principles verbally. Perhaps sophisticated language antedates all other forms of complex culture.

We think that whatever any neural reorganization amounted to, one important factor is that by about 50,000 years ago, humans simply had larger populations than Mousterians. Recall our mention of Joe Henrich's model earlier in this chapter.[99] He assumes that imitation is an error-prone process and that learners have a hard time getting the skills to manufacture complex artifacts down pat. Perhaps the Mousterians were socially unsophisticated and had relatively limited contacts with neighbors, leading to a relatively unsophisticated tool kit.

Conclusion: Why is human culture such an extraordinarily successful adaptation

If we are right, culture is adaptive because it can do things that genes cannot do for themselves. Simple forms of social learning cut the cost of individual learning by allowing individuals to use environmental cues selectively. If you can easily figure out what to do, do it! But if not, you can fall back on copying what others do. When environments are variable and the learning is difficult or costly, such a system can be a big advantage, and most likely explains the relatively crude systems of social learning commonly found in social animals. Humans have evolved the additional capacity to acquire variant traditions by imitation and teaching, and can accurately, quickly, and selectively acquire the variants used by the successful, or the most common variant. When these kinds of social learning biases are combined with occasional adaptive innovations and content biases, the result is the cumulative cultural evolution of complex, socially learned adaptations, adaptations that are far beyond the creative ability of any individual. Because cumulative cultural evolution gives rise to complex adaptations much more rapidly than natural selection can give rise to genetic adaptations, complex culture was particularly suited to the highly variable Pleistocene environments. As a consequence of taking fuller advantage of the inheritance-of-acquired-variation feature of cultural evolution than any other species, humans eventually became one of the most successful species of the Pleistocene large mammal fauna.[100]

Paradoxically, humans have been even more successful in the Holocene, despite a dramatic drop in climatic variation. This is a quite surprising turn of events if we are correct that culture was originally an adaptation to Pleistocene climatic chaos. Shouldn't the quiet climate of the last eleven thousand years have led to dramatic economies of expensive nervous-system tissue, degrading the cultural system? More generally, as the influential evolutionary psychologists Leda Cosmides and John Tooby argue,

> [T]here is no *a priori* reason to suppose that any modern cultural or behavioral practice is "adaptive" . . . or that modern cultural dynamics will necessarily return cultures to adaptive trajectories if perturbed away. Adaptive tracking must, of course, have characterized the psychological mechanisms governing culture during the Pleistocene, or such mechanisms would never have evolved; however, once human cultures were propelled beyond those Pleistocene conditions to which they were adapted at high enough rates, the formerly necessary connection between adaptive tracking and cultural dynamics was broken.[101]

Tooby and Cosmides' *logic* seems sound, but, *empirically,* human populations have exploded in the last ten thousand years; we are now vastly *more* successful than we were in the Pleistocene. Another variant of the adaptationist's dilemma! One reason is that humans themselves now create rapid, large-scale environmental change comparable to the climate changes of the last glacial. For example, agriculture changes the environment for wild plants and animals and the foragers who would depend upon them for subsistence. Even though weeds, pests, and diseases evolve to take advantage of the new anthropogenic environments, we readapt even faster, generating further deterioration. So long as we generally find human-modified environments more congenial than our competitors, predators, and parasites, we can thrive, if only by using cultural adaptations to stay one step ahead of onrushing pests. Humans succeed by winning arms races with species that attack our resources and us. They evolve too slowly; we outwit them by cultural counteradaptations, staying a step ahead in the race. We have done more than simply keep ahead of our own environmental deterioration; we have bounded ahead to dominate the earth to an extent perhaps not ever equaled by any single species since the origin of life. Similarly, dense human populations compete with each other, and technical and social innovations by one society tend to exert competitive pressure on their neighbors. The capacity for rapid cultural evolution is thus not just self-sustaining but has gotten progressively ever more rapid as we invent cultural devices, such as reading, writing and arithmetic, that have had the effect of speeding up cultural evolution and increasing sophistication of technology and society. At least to date! Human culture as an adaptive system evolved in response to Pleistocene environments but has subsequently upped anchor and sailed rather well on uncharted waters.

However wild cultural evolution has subsequently run, it arose by natural selection operating to build a complex adaptation in response to specific adaptive challenges. Culture is an unusual system of phenotypic flexibility only because it has population-level properties. But even in this it has numerous analogs in the history of evolution; for example, coevolving mutualisms.[102] Such coevolution sometimes precipitates spectacular evolutionary events.[103] The eukaryotic cell, derived from bacterial symbioses, is an example. We leave it for readers to decide for themselves the extent to which human gene-culture coevolution achieves a status in the history of the evolution of life akin to the rise of the eukaryotic cell. But reserve judgment until you've read chapter 6!

But this is only part of the story. Despite this extraordinary success, many of the products of cultural evolution *do* seem frankly maladaptive. Critics of Darwinian social science often lean heavily on the claim that much cultural evolution has nothing to do with adaptation. We do seem to have cut our way to our extraordinary adaptive success dragging a canoe-load of junk behind us. Some adaptationists may be discomforted by the existence of cultural maladapations, but we are not. In the next two chapters, we hope to convince you that both the baroque excesses of maladaptation and our spectacular success at organizing gigantic social systems flow directly from the processes we have outlined in this chapter and the previous one.

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1. Boyd and Richerson 1985; Tooby and DeVore1987; Rosenthal and Zimmerman 1978; Brandon and Hornstein 1986; Pinker and Bloom 1990.
2. A similar game, Guess the Gadget, is played with the audience on the program *Home Matters,* which airs on the Discovery Channel.
3. See Stephens and Krebs 1987 for many examples.
4. Gould and Lewontin 1979.
5. Nilsson 1989.
6. E.g., Tomasello, Kruger, and Ratner 1993.
7. E.g., McGrew 1992.
8. Levebre and Palameta 1988; see Moore 1996 for an analysis restricted to the evolution of imitation.
9. Wrangham 1994; Whiten et al. 1999; McGrew 1992.
10. McGrew 1992.
11. The Tasmanian tool kit is unusually reduced, a subject to which we return later in this chapter. It is also important to note that this kit may have included many artifacts that have not been preserved in the archaeological record.
12. Van Schaik and Knott 2001.
13. Rendell and Whitehead 2001.
14. Moore 1996.
15. McComb et al. 2001.
16. Marler and Peters 1977; Baker and Cunningham 1985; Baptista and Trail 1992.
17 Galef 1996.
18. Levebre and Palameta 1988.
19. Lachlan, Crooks, and Laland 1998.
20 Most laboratory investigators have strong doubts about attributions of culture based on field studies. See commentaries on Rendell and Whitehead's 2001 paper for an introduction to this controversy. In the absence of controlled experiments, experimentalists argue, it is impossible to know whether observed behaviors are transmitted culturally. Field-workers feel equally strongly

that laboratory environments don't provide much opportunity for animals to show off their best tricks, and that animals with seemingly complex behavior, such as chimpanzees and killer whales, are the hardest to deal with in the laboratory. They argue that the circumstantial evidence for rather sophisticated culture is strong.
21. Chou and Richerson 1992; Terkel 1995; Zohar and Terkel 1992
22. Galef 1988.
23. Slater, Ince, and Colgan 1980; Slater and Ince 1979.
24. Imitation sometimes connotes rote copying of motor patters, but we use it to label any form of learning in which individuals learn how to perform a behavior by observing others. So, for example, learning grammatical rules from hearing other speak is imitation in our usage.
25. Galef 1988; Visalberghi and Fragazy 1991; Whiten and Ham 1992.
26. Tomasello and Ratner 1993.
27. Galef 1988; Whiten and Ham 1992; Tomasello and Ratner 1993; Visalberghi 1993; Visalberghi and Fragazy 1991. But see Heyes 1996 for a quite different take on the evidence.
28. Custance, Whiten, and Fredman 1999 and Tomasello 1996.
29. Whiten 2000 thinks the difference between imitation and emulation is quantitative. Clearly, the exact differences between human and chimpanzee social learning skills are not yet precisely mapped.
30. Heyes and Dawson 1990; Voelkl and Huber 2000.
31. Herman 2001.
32. Pepperberg 1999; Moore 1996; Connor et al. 1998; Heyes 1993; Dawson and Foss 1965; Van Schaik ad Knott 2001; Russon and Galdikas 1995.
33. Darwin and some of his early followers thought that accurate imitation characterized even insects; the low level of sophistication of social learning in so many species would have surprised him (Richerson and Boyd 2001a; Galef 1988).
34. Rogers 1989; Boyd and Richerson 1995 show that Rogers's result generalizes considerably beyond his simple model.
35. Kameda and Nakanishi 2002.
36. Lefebvre and Geraldeau 1994
37. Basalla 1988; Petroski 1992.
38. Although there is some evidence that molecular-epigenetic systems may exhibit analogous dynamics. See Jablonka and Lamb 1995.
39. As we saw in chapter 3, when there are multiple attractors, bias and guided variation may tug in different directions; and when this is the case, strong bias can cause the population to evolve so that every individual has beliefs near one of the attractors. Weak selection can still be important if there is no strong bias among these attractors.
40. Boyd and Richerson 1988b
41. Todd and Gigerenzer 2000.
42. Henrich and Boyd 1998. See Boyd and Richerson 1985, 1987, and Kameda and Nakanishi 2002 for other treatments.
43. Myers 1993; Sherif and Murphy 1936.
44. Another classic is Asch 1956. The social psychology literature under the heading of conformity is extensive and rich. Conformist cultural transmission in our sense is that part of "informational conformity" that results in relatively durable changes in attitudes, beliefs, skills,

and the like. Aronson, Wilson, and Akert 2002 (chap. 8) provide an accessible and up-to-date summary. In chapter 7 we describe some models of punishment without, however, tying these to the sort of coercive socialization of deviants that social psychologists observe in their experiments.
45. Boyd and Richerson 1985, 223–27.
46. Jacobs and Campbell 1961.
47. Myers 1993, chap. 7.
48. Some people like call such effects emergent properties. We are not fond of this term, because the whole-part relations of different kinds of systems are so diverse. The weather is a notoriously difficult-to-understand result of the Newtonian mechanics of flow in compressible fluids. The physics of turbulence has only the most distant analogies to the ecology and biology that drive evolution. To gather the phenomena of hurricanes and adaptations under one term doesn't seem very useful to us.
49. Manufacturer of Hanes brand underwear.
50. Henrich 2001.
51. Boyd and Richerson 1985, 223–27.
52. Ryckman, Rodda, and Sherman 1972.
53. Rogers 1983.
54. Labov 2001.
55. Brandon 1990.
56. Kaplan et al. 2000.
57. Byrne 1999. But some birds do as well or better! See Hunt 1996 and Weir, Chappell, and Kacelnik 2002 on the amazing tool use abilities of the New Caledonian crow.
58. Kaplan et al. 2000.
59. In fact it is not at all clear that humans can learn individually a whole lot faster or better than baboons. The human individual learning mechanism is adapted to manipulated culture. It is likely for this reason to be more general purpose than that of animals that can't depend to anywhere near the same extent on highly specialized cultural adaptations. If Shirley Strumm had made a contest of it and transplanted some humans along with her baboons, then perhaps we'd know whether humans can learn any faster than baboons. What humans would do is rapidly transmit the successes of any one individual to the whole group, and in this way we might well best the monkey even if we're not any smarter individual by individual.
60. Lamb 1977; Alley 2000; Partridge et al. 1995; Bradley 1999; National Research Council, Committee on Abrupt Climate Change 2002.
61. Opdyke 1995.
62. Anklin et al. 1993; Lehman 1993; Ditlevsen, Svensmark, and Johnsen 1996.
63. Allen, Watts, and Huntley 2000; Dorale et al. 1998; Frogley, Tzedakis, and Heaton 1999; Hendy and Kennett 2000; Schulz, von Rad, and Erlenkeuser 1998.
64. Lamb 1977; Fagan 2002; Grove 1988.
65. Broecker 1996.
66. Jerison 1973.
67. Opdyke 1995; Klein 1999; deMenocal 1995.
68. Eisenberg 1981, 235–36.
69. Aiello and Wheeler 1995. Also see Martin 1981.

70. Reader and Laland 2002.
71. Kaplan and Robson 2002.
72. The argument works in reverse, too. An environment that favors longer life spans will make a prolonged juvenile period less costly, and therefore will also favor increased behavioral flexibility and larger brains. Kaplan and Robson argue that large brains were favored in Oligocene primates, because arboreal life reduced predation pressure and therefore selected for longer life spans.
73. Boyd and Richerson 1996.
74. Cheney and Seyfarth 1990, 277–30; Tomasello 2000.
75. Diamond 1978.
76. Humphrey 1976; Whiten and Byrne 1988, 1997; Kummer et al. 1997; Dunbar 1992, 1998.
77. Boyd and Richerson 1992a
78. Wood and Collard 1999.
79. Toth et al. 1993.
80. Susman 1994.
81. Povinelli 2000.
82. Dean et al. 2001.
83. Cavalli-Sforza and Feldman 1981; Shennan and Wilkinson 2001.
84. For a contrary view, see Mithen 1999.
85. Typically, potassium-argon dating methods cannot be used for sites less than about 500,000 years old, and carbon-14 methods cannot be used for sites older than about 40,000 years. In the last couple of decades new methods such as thermoluminescence (TL) and electron spin resonance (ESR) allow sites from this period to be dated. However, many Middle Pleistocene sites were excavated before such methods were available.
86. McBrearty and Brooks 2000.
87 Brooks et al. 1995
88. Thieme 1997.
89. Henshilwood et al. 2002; Henshilwood et al. 2001.
90. Ingman et al. 2000; Kaessmann and Paabo**.** 2002; Underhill et al, 2000.
91. Hofreiter et al. 2001.
92. Templeton 2002.
93. Falk 1983; Holloway 1983.
94. Laitman, Gannon, and Reidenberg 1989; Lieberman 1984.
95. Shennan and Steele 1999.
96. Donald 1991.
97. Dunbar 1996; Thompson 1995.
98. Sperber 1996; Atran 2001; Castro and Toro 1998.
99. Henrich, in press
100. Our picture of hominid evolution will be slowly improved by new paleoanthropological finds and methods. However, the most important advances in the short term are liable to be the paleoclimatologists'. As we write this, the high-frequency variation in climate that is key to our analysis in this chapter exists only for the last glacial and the Holocene. We have only the most speculative ideas on the rest of the relevant record. Is the highly variable climate ancient, implying long lags between climatic events and the evolution of culture? Or does the record of

brain size increase and tool sophistication reflect ongoing changes in high-frequency climate variation during the Pleistocene? Are some of the oddities of ancient hominids attributable to as-yet unappreciated oddities in environmental variation? Paleoclimatologists are hot on the trail of data that will bear on these questions, fuelled by the fear that ongoing anthropogenically induced climate change is a serious threat.
101. Tooby and Cosmides 1989.
102. Odling-Smee 1995.
103. Maynard Smith and Szathmáry 1995; Corning 1983.