A Catalyst for Ideas

Anthropological Archaeology and the Legacy of Douglas Schwartz

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Hunter-Gatherers, Archaeology, and the Role of Selection in the Evolution of the Human Mind

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INTRODUCTION

The study of hunter-gatherers lies at the heart of anthropology, but anthropologists are conflicted as to why. One frequently given reason is that the human species has spent 99 percent of its more than 5-million-year history as hunter-gatherers (or foragers, as they are commonly called today). As recently as 15,000 years ago, everyone in the world lived by foraging. Even 500 years ago, foragers inhabited perhaps a third of the world’s landmass. In the landmark volume Man the Hunter, Richard Lee and Irven DeVore (1968) claimed that this made foraging the most successful adaptation that humans have ever achieved.

Nineteenth-century Europeans saw things differently. The Victorians viewed primitive peoples as lower forms of humanity, as examples of what becomes of those who fail to progress. The evolutionary struggle for the “survival of the fittest” was seen as a victory of morality over the “baser” instincts of man. The Victorians saw humanity as forming a portion of the great Chain of Being, in which different cultures—or, to the Victorians, “races”—were ranked in terms of evolutionary progress, each race occupying a rung on the evolutionary ladder. In
anthropology, this paradigm came to be known as unilineal evolutionism. The degree of progress was measured in terms of a number of characteristics, including technology, property, material possessions, a belief in magic, descent, religion, and marriage. But biology was primary. No matter how many British linguistic, social, economic, and cultural trappings a native of India adopted, he could never have stood on the same rung of the evolutionary ladder as his British lords. Although in theory one could climb the ladder, the racism of Europeans argued that this was, at the end of the day, impossible. (Such a view was necessary, in fact, to justify control of colonies.)

A notion of selection was at work in this process, but it was quite different from today's use of that term. The great Chain of Being, a concept that can be traced back to Greek philosophers, extended beyond humanity, for above the humans were angels, and above the angels, God. "Survival of the fittest" had moral overtones, for the Victorians thought that moral fiber, rather than reproductive success, controlled evolutionary change (although there were dissenters at the time who saw that the "profligate" Irish, with their large families, would soon overrun the spendthrift Scots, who married late and had small families).

Archaeology and human paleontology were fledgling sciences in the late nineteenth century, so Victorian scholars constructed evolutionary sequences largely through the comparative method (see R. L. Kelly 1995). In the comparative method, living peoples were taken, quite literally, to be living prehistory, and Victorian scholars confidently placed hunter-gatherers on the lower rungs of the evolutionary ladder. Descriptions of forager lifeways were frequently gleaned from ships' captains, military officers, explorers, and missionaries, observers who often knew little about the indigenous peoples they encountered. But better data would probably have been inconsequential, for the Victorians' image of foragers was of more use to them than ethnographic reality.

We can be proud of the fact that American anthropology was founded on Franz Boas's vehement denial of unilineal evolutionism and on his standards of fieldwork, which demonstrated that foraging peoples were equal to others in intelligence, creativity, and moral fiber. But anthropology still grants hunter-gatherers a special place in the pantheon of progress. The truth is, many of us were never more than unwittingly complicit in the idea that the modern way is not only better but different from the past. Indeed, lifeways represent a good deal of adaptation of human societies. But one must strip away the superstructure that is to study the past.

Anthropologists might now claim today, in a sense, that foragers are Still the people to whom the past? Two prominent anthropologists of evolutionary psychology both fields see human evolutionary psychology, and they key to understanding the modern, for studying foragers. They think because of a feeling for the past. Ethnography is the study of human prehistory.

My argument is that this process has played in the past and continues to play a role in the Victorians more than we recognize. Studies of male-female relations in food sharing in the last century have been bedded in culture.
Hunter-Gatherers, Archaeology, and the Role of Selection

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appeared (and among today’s public, it is often reversed, with foragers
seen as the ones full of wisdom and industrialized societies as the
wails who have lost their way), but we still seem to think that hunter-
gatherers are substantially different from the rest of humanity. Why?

In Man the Hunter, Lee and DeVore (1968:ix) gave their reasons for
studying the foraging lifeway: “We cannot avoid the suspicion that
many of us were led to live and work among the hunters because of a
feeling that the human condition was likely to be more clearly drawn
here than among other kinds of societies.” So hunter-gatherers were
different from horticulturalists or industrialists because those latter
lifeways represent layer after layer of complications built upon a
foundation of human nature (see Lee 1979). To get to human nature, then,
one must strip away those complications. And the most direct way to do
that was to study hunter-gatherers.

Anthropologists, including, I suspect, Lee and DeVore, would deny
this claim today, just as they deny the Victorian claim that living hunter-
gatherers are Pleistocene relics. If this is true, then why should hunter-
gatherers still occupy, as they do, such a prominent role in the study of
the past?

Two prominent research paradigms have foragers at their core:
evolutionary psychology (EP) and human behavioral ecology (HBE).
Both fields see human behavior as shaped by an evolutionary process
of selection, and each sees hunter-gatherers as holding an important
key to understanding that process. Lee and DeVore’s 1968 justification
for studying foragers might today be written thus: “We cannot avoid the
suspicion that many of us were led to live and work among the hunters
because of a feeling that living foragers allow us, in a sense, to look back
in time.” Ethnography in these cases substitutes for the direct study
of human prehistory through archaeology and paleoanthropology.

My argument is that we cannot determine the role that selection
has played in shaping humans without considering archaeology
and paleoanthropology. To do otherwise commits the same error that
the Victorians made. We will examine EP and HBE here, focusing on
studies of male-female differences in wayfinding in the former and
sharing in the latter. We will then look at how human sharing is em-
bedded in cultural precepts and how it could not arise except among
hominids with the biological capacity to be cultural. Finally, we will consider which research paradigm is better suited to investigate the linkages between a critical behavior such as sharing, and culture and selection.

EVOLUTIONARY PSYCHOLOGY

EP assumes that "the evolved structure of the human mind is adapted to the way of life of Pleistocene hunter-gatherers" (Cosmides, Tooby, and Barkow 1992:5; Tooby and Cosmides 1992). Thus, EP is concerned with how natural selection produced the psychological mechanisms that underlie behavior. EP argues that there are multiple, perhaps hundreds (if not more) of psychological "modules" that govern behavior. It supposes that these modules were created through selection during the "environment of evolutionary adaptedness," or EEA. EP researchers never specify when or where the EEA existed; it may, in fact, have existed at different times and places for different psychological modules. But in many instances, it is simply thought of as "back then" when all our ancestors lived as hunter-gatherers. So, perhaps the EEA was back when australopithecines lived on the forested edges of the African savanna; or perhaps it was back when well-organized, technologically sophisticated Upper Paleolithic hunters lived in the European periglacial environment.

But for those who study prehistory, the difference between these two eras and places is great, in terms of the challenges of the physical environment, human cognitive and social abilities, and the social landscape (see Foley 1995:206). This is important because evolution is a historical process and selection is a local process. Therefore, to argue that a particular psychological module is a product of selection means that one should be able to specify the time and the place when selection occurred in order to test the idea against the most direct records we have of human prehistory—archaeology and human paleontology.

For example, EP claims that men and women reckon space differently. In controlled experiments, men do better on mental rotation tasks and wayfinding, whereas women perform better on memorization tasks (for example, Linn and Petersen 1985; Hampson 1990; L. Silverman and Eals 1992; Eals and Silverman 1994; James and Kimura 1997; McBurney et al. 1997; Dabbs et al. 1998; Moffat, Hampson, and Hatzipanayia 1998). Although the experiments were generally limited to college students, the results transfer subjects into a social setting that is cross-culturally universal (male-female) and hypotheses in brain function (e.g., possible links between the left and right sides of the brain, 1990), it is not certain the combination of the experiments in our evolutionary history. In an initial paper on the "tracking and killing" and sex-specific spatial abilities, EP favored diverse set of hypotheses about evolutionary history and mental attributes involved in unfamiliar terrain exploration or "dead reckoning." The idea is that permit men to "track and rotate" rotations, map relationships, and "fire" landmarks, whereas women are "prediction," requiring a more fundamental reorganization of their spatial relations to the environment.

In essence, EP suggests that "dead reckoning" abilities are inborn, as are the geometrical configurations of familiar space by memorizing landmarks, not by using large-scale landmarks that would spend less time in the environment..."
Hunter-Gatherers, Archaeology, and the Role of Selection

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ment attributes that "would enable the pursuit of prey animals across unfamiliar territory and, also, accurate placement of projectiles to kill or stun the quarry" (1992:535). These attributes would include those that permit men to score significantly higher than women on mental rotations, map reading, and maze learning. Food plants, on the other hand, "are embedded within complex arrays of vegetation. Successful foraging, then, would require locating food sources within such arrays and finding them in ensuing growing seasons" (1992:535). This, EP argues, requires that women be good at memorizing object arrays and their spatial relationships.

In essence, EP argues that evolution selected for men who can "dead reckon" space, finding their way across unknown terrain by using the geometry of their day's trip to place themselves mentally at a known distance and bearing from camp. On the other hand, EP claims, evolution selected for women who could figure their way across space by memorizing it, following a known trail back from a day of foraging by using landmarks. Men and women who had these attributes would spend less time traveling and more time foraging (or maximize
time spent in fitness-linked non-foraging activities, or reduce the potential for accidents or predation while foraging by reducing the time spent traveling), raise more offspring to reproductive age, and hence increase the frequency of their wayfinding genes.

(Some anthropologists might question the assumption that men hunted and women gathered prehistorically. Personally, I am not troubled by it, since women's devotion to foraging is almost certainly linked to breast-feeding and the incompatibility between children and large game hunting [see R. L. Kelly 1995]. Given this, women can better provision children through foraging than through hunting [but this does not account for why men tend to focus on hunting; see below; Hawkes and Bliege Bird 2002]. Nonetheless, it is still an assumption that should be continually tested against the data of prehistory.)

Oddly, there is not a single ethnographic reference in any of the EP publications devoted to the hunter-gatherer theory of spatial sex differences. Actual ethnographic evidence, however, shows that men also memorize their landscapes, often being able to draw detailed maps of thousands of square kilometers (R. L. Kelly 2002). Indeed, hunters have to memorize landscapes in order to return to good places to look for game (such as springs, salt licks, or ridgetops that offer views). It may even be that they had to memorize larger landscapes than women (and they used various mental tools such as myths and religiously linked legends to do so). So shouldn't men today have memory skills at least as good as those of women, if selection were at work? And conversely, why wouldn't women need the apparent wayfinding skills of men? In my experience with the Mikea of Madagascar, if women returned to camp on a known path, it was only because the path out was the shortest path back and avoided brambles and thickets. Furthermore, I observed Mikea women navigate back to camp through dead reckoning.

EP does not ignore ethnography—references appear, for example, throughout Buss's (1999) textbook—but it does make selective use of it, tending to look for simple universals among a limited number of cases rather than for explanations of variation. Cosmides and Tooby's (1992) brief recitation of ethnographic data on sharing among foragers, for example, is completely in line with viewing the mind as a generalized decision-making device rather than as evidence of a

content-specific social or escape hatch; as E. Buss noted, "modern students are clearly less likely to have the skills of their ancestors to novel conditions [in their] everyday lives." Hence, behaviors can be adaptive today (in EP's view) if they had been adaptive in the past.

But EP tends to argue that we have of the historical past what Buss's (1999) textbook blithely says Oldowan tools dated to 2.5 million years ago were. He wrote, "Their main value is in separating the value of human thought, he cites work on foragers or scavengers--"prehistoric human intellect is a mystery, we don't know what OOHM"

The EP explanation of the fact that of modern foragers we don't know when we started being humans. We do know that by 2.5 million years ago (by what we finds), our hominin ancestors (although not the genus Homo), although the age of hominins is in the upper 7 to 6 million years, certainly falls within the 2.5 million-year range because hominids hunted larger animals. We are no longer out on the hunt for the first time: almost certainly males, gathering meat and foraging for plant foods. More importantly, we are not just an early hominin demographic and archaeological record. It is impossible to say that selection is not acting on an existing human trait

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Hunter-Gatherers, Archaeology, and the Role of Selection

content-specific social exchange module. And EP has left itself an escape hatch: as E. A. Smith (2000) points out, although tests with modern students are claimed to reflect the result of ancient selective forces, EP also argues that contemporary human behavior involves responses to novel conditions, conditions that were not typical of the EEA. Hence, behaviors created through selection in the distant past may not be adaptive today (Cosmides, Tooby, and Barkow 1992:5–6). This means that archaeological evidence should be crucial to EP.

But EP tends to ignore archaeology, the most direct record we have of the historical process of selection. References to archaeology in Buss’s (1999) textbook are brief and often wrong. For example, of Oldowan tools dating back some two million years Buss (1999:77) wrote, “Their main function seems to have been for killing and then separating the valuable meat from the bones and cartilage.” Later, however, he cites work arguing that the tools could have been for digging plants or scavenging carcasses. Obviously, testable hypotheses about prehistoric human behavior are not a priority in EP. (And truthfully, we don’t know what Oldowan tools were used for.)

The EP explanation requires a division of labor that is similar to that of modern foragers—women gathering and men hunting. Frankly, we don’t know when this division of labor appeared in the human past. We do know that by 1.8 million years ago (judging from the Dmanisi finds), our hominin ancestors inhabited a range of environments (although not the full range that they would later occupy). And although the age of the first biologically modern humans is debated, it certainly falls within the past 200,000 years. We know that some hominids hunted large game by at least 400,000 years ago, but the jury is still out on the hunting behavior of earlier hominids. Females, and probably males, gathered plant foods, but if the record is muted on the role of game in the diet, it is completely silent on the early role of plant foods. More importantly, it is not until the past 90,000 years (and perhaps not until 40,000 years ago) that anything like modern human behavior, complete with its use of symbols, appears on the scene.

The bottom line here is that EP either makes poor use of ethnography and archaeology or is oblivious to both fields. I am not saying that selection is not responsible for the apparent differences in male-female spatial abilities. I am saying that the hypothesis has not been tested.
Selectionist explanations are very hard to test. By ignoring archaeology as a possible source of tests, EP merely creates ad hoc selectionist "stories." If the opposite pattern had emerged from their wayfinding tests, I am confident that the data could be interpreted with exactly the same story. I fear that evolutionary psychologists, like the Victorians, have become more interested in and comfortable with their image of hunter-gatherers, and, in particular, their image of ancient hunter-gatherers, than they are in dealing with the reality of ethnography or archaeology.

**HUMAN BEHAVIORAL ECOLOGY**

Human behavioral ecology is similar to EP in that it seeks to understand the role of selection in creating human behavior (for overviews, see Cronk 1991; E. A. Smith and Winterhalder, eds. 1992; R. L. Kelly 1995; Cronk, Chagnon, and Irons, eds. 2000). However, HBE argues that selection produced not a mind of a myriad modules, but a generalized decision-making apparatus that is capable of considering multiple factors in making behavioral choices that maximize fitness. These include straightforward material factors (will I get more food utility for my time if I seek plants or large game?), as well as social ones (how will individual X feel toward me if I seek large game instead of plants, and will it depend on whether I am successful?), and more complex abstract ones (will my deceased ancestors punish me tomorrow if I shortchange my cousin today?). In HBE, it is not so much the mind that is the subject of interest, but how ecological and social variables condition the human decision-making process.

Both EP and HBE point out that the human brain is some six times larger than that of other primates, controlling for body size, and consumes nearly 20 percent of our energy budget; humans also require a longer period of enculturation. For both paradigms, these facts suggest that there is an adaptive significance to the mind, that it is a product of selection, and that its decision-making processes must have some fitness-enhancing direction. Thus, HBE looks at the diversity of human behavior and asks how it is that a particular decision is an "adaptive" response to particular conditions.

While some have brought the paradigm of HBE to studies of pastoral, agricultural, and industrial societies, the central pieces of research—and the most ambitious—are ambitious. But, for a moment, let us imagine, say, the role of hunters, gatherers, and agriculturists in Africa, and then ask ourselves what we are interested in how ecological and social variables shape human behavior. Among hunter-gatherers, the concept of the "game" relaxes, from a deterministic range of conditions to what we might best approximate as a set of probabilities of twenty-first century coming close as possible to the immediate past. So, leaving aside the framework of the historic world, can we say anything about the distant past?

We approach this question with the hypothesis testing we do in science.

Sharing use of technology is surprising, many human and nonhuman hunting and nonhunting groups, and Feistner 1995 argue that animals engage in reciprocal exchange as "the line of assistance must be returned." The animals, relationships, and it is the humans who themselves, matter most.

But the reality is prettier. Most animals are not exhausted by the strains of living through "demand," and they will neither demand nor badger a person for more "bacco," but I was able to replace my cameras, GPS, and
Hunter-Gatherers, Archaeology, and the Role of Selection

Research—and they are excellent examples of anthropological science—are ambitious, long-term, quantitative studies conducted with foragers, such as the Aché of South America, the Hadza and Bushmen of Africa, and the Meriam of Australia. The reason is that HBE is interested in how evolution shaped human behavior. Human behavioral ecologists argue neither that human nature is more clearly defined among hunter-gatherers nor that living hunter-gatherers are Pleistocene relics, frozen in time. They do argue, however, that part of the range of conditions under which our ancient human ancestors lived is best approximated today by living hunter-gatherers. After taking the realities of twenty-first-century foraging life into account, the goal is to measure the fitness consequences of behavior under conditions as close as possible to those under which selection might have operated. So, leaving aside the criticism that modern foragers do not live in a prehistoric world, can we still study them to grasp the role that selection in the distant past played in creating humans as we know them today? We approach this issue by examining one of the best examples of hypothesis testing in HBE, the study of sharing behavior.

Sharing used to be the sine qua non of hunter-gatherers. Not surprisingly, many have considered sharing to be the factor that separates human and nonhuman primates (Isaac 1978; see references in McGrew and Feistner 1992). Nearly all introductory anthropology textbooks use a foraging case to exemplify the most widespread form of sharing: generalized reciprocity. Sahlins (1972:193–94) defined generalized reciprocity as “transactions that are putatively altruistic, transactions on the line of assistance given, and if possible and necessary, assistance returned.” The gifting of material goods or food creates social relationships, and it is often said that these, rather than the goods themselves, matter most in generalized reciprocity (Mauss [1924] 1990).

But the reality of foraging society is more complex—and not as pretty. Most anthropologists who work with foragers quickly become exhausted by the dunning for gifts. Foragers share, yes, but it is often through “demand sharing” (Peterson 1993). They may publicly berate and badger a person until he or she gives in. When I was with the Mikea, I brought things to give away (mostly clothing, cloth, and tobacco), but I was constantly asked for everything else—including my cameras, GPS, and compass. Upon our arrival in one camp, a
ROBERT L. KELLY

cranky old woman called to her husband, “Tell them to give us all their
tobacco and leave!” I quickly learned to take no extra clothing into the
bush, for then I could honestly answer the requests for my tee-shirt and
pants with the excuse that I had no others.

In the 1970s and 1980s, research into sharing focused on the com-
mon ethnographic observation that meat from game is extensively shared
but plant food is not. (Although plant food is sometimes shared, it does not seem to be the focus of interest
among the foragers themselves, and usually is shared when another adult is ill or otherwise incapable of foraging.) In some cases, a hunter may eat very little, if at all, from his own kills but instead eats meat hunted by another
man (Kaplan and Hill 1985a). The variance (or risk) reduction hypothesis
sought to model the relationships encompassed by this pattern of
sharing.

In this model, one shares under those circumstances (or with
those resources) in which the resource is risky and foragers’ individual
efforts are not linked to one another (that is, when one hunter’s success
or failure is not correlated with another’s). One shares if the debt
created by the act of sharing can be repaid. Hunting success rates
are almost always low for any individual man (R. L. Kelly 1995: 103). One
way to ensure that a man and his family receive some meat is to share
a kill and then expect a return on those days when the man is unsuccess-
ful in his own hunt.

Plant food, on the other hand, can be gathered by different
people at far similar rates of return (all the more so if women forage in the
same patch). Luck plays a smaller role here than in hunting. Women
tend to bring in the necessary plant food for their households.
In this case, foraging efforts are linked; everyone does just as well or just as poorly, depending on the abundance of the particular
plant food being collected. According to this model, there is no sense
in sharing. When a forager is doing poorly and needs another to share,
that other person cannot, because he or she is also doing poorly. When
a forager is doing well and can afford to share, others do not need the
favor. If one were to share his or her efforts in this scenario, it is
because the receiver is simply too lazy to forage, and why share with
someone who will be of no help in the future (Winterhalder 1986)? So,
the apparent goodwill reflected in early descriptions of sharing seems
to have some cold calculation behind it.

HUNTER-GATHERER

An alternative explanation for the observed practice was to build up a systematic strategy to build up a systematic share,
because it is not possible for everyone to share directly, thus the surplus is shared indirectly through the Hunter-Gatherer
unit of a resource. For instance, imagine a man who hunts and
slaughters a hundred pounds of meat in his lifetime. The rest of the
tribe does not hunt and thus, the hunter has an obligation to share
no. The potential recipient notes that the value of the meat is
the value of the meat is not worth sharing. Again, from the standpoint
of generosity, but because the meat is not worth sharing.

Still another possibility is that, like the hunter-gatherers, the
daily return rate in the fishing community is less predictable than the
collection of plant food. Fishing success can be shared among the
community and thus, can be shared. In contrast, for women who,
literally, for sex with a man who has a success rate of 100%,
then, has a value to the hunter-gatherer, only a similar
type of generosity, only a similar type of generosity effort.
(Kaplan and Hill 1985a: 103). This is more in line with observed
sharing.

However, these rules are not absolute. The variance reduction
strategy for sharing food is one that has to be reinforced by
evidence of “free-rider” behavior. There is evidence that hunters who share have an equal amount of meat
(Gurven, Hill, et al. 2000) found that the meat is not shared
before they are even caught. There is actually no explicit call
for sharing or generosity.
Hunter-Gatherers, Archaeology, and the Role of Selection

An alternative hypothesis is tolerated theft. Here food is shared not to build up a system of debts to hedge against future hunting failures, but because it is not possible to consume a large package of food quickly and thus the surplus has to be defended. This raises the question of whether the resource is worth the cost of defense, for the value of an additional unit of a resource declines with increasing amounts of that resource. For example, imagine the hunter who brings an entire elk into camp—a few hundred pounds of food. He and his family can eat only so much in one sitting. The rest either rots or is dried and stored. In either case, the hunter has an obvious surfeit of food while others in the camp may have none. The potential for conflict is high. From the hunter's perspective, the value of the extra meat is not worth fighting for, so the meat is shared. Again, from this perspective, sharing occurs not out of inherent generosity, but because of a calculation that the value of the additional meat is not worth the cost of trying to keep it.

Still another possible explanation is exchange. Hawkes (1992, 1993, 1996) noted that Aché hunters actually could achieve a higher mean daily return rate if they ignored large game and focused on more easily collected plant foods. But doing so means that men would reduce the frequency with which they brought in large quantities of meat that could be shared. Hawkes notes that Aché men exchange meat, quite literally, for sex with women (including other men's wives). The meat, then, has a value to men beyond nutrition. And again, there is no generosity, only a simple investment in reproductive fitness (but see Kaplan and Hill 1985b; and Hawkes has rethought her position, so it is more in line with costly signaling theory; see below).

However, these three hypotheses receive little empirical support. The variance reduction hypothesis makes sense, but it does not fit with demand sharing: if sharing makes economic sense, then why does it have to be reinforced? Some quantitative tests of this hypothesis find evidence of "free-riders," who benefit but do not contribute, and no evidence that hunters who contribute meat to the community receive an equal amount back (Bliege Bird and Bird 1997; E. A. Smith and Bliege Bird 2000; Hawkes, O'Connell, and Blurton Jones 2001a, 2001b; Bliege Bird et al. 2002; Hawkes and Bliege Bird 2002; although Gurven, Hill, et al. [2000] found that free-riders can go only so far before they are eventually excluded from sharing). There are also virtually no explicit contests over food, as tolerated theft might predict.
(although there might be subtle, unstated contests, such as a sideways glance at a hunter or a carefully chosen word or two). But hunters often share the entire kill, keeping nothing for themselves, contra the tolerated theft hypothesis. And regular, straightforward exchange of meat for sex or anything else has not been documented in foraging societies outside the Aché.6

Partly as a response to these deficiencies, researchers have investigated costly signaling theory as a way to account for the sharing of meat (see E. A. Smith and Bliege Bird 2000; Bliege Bird et al. 2002; Hawkes and Bliege Bird 2002). Many years ago, Darwin used sexual selection as a way to explain the appearance of otherwise “wasteful” biological elements such as peacocks’ extravagant tails. By virtue of his extravagant tail, the male peacock says to potential mates, “I can invest a lot of energy in my tail and yet it does me no harm. Obviously, I am physiologically stronger than other males. Pick me.” Costly signaling moves this idea to the realm of behavior. In this hypothesis, selection has produced the proclivity for men to “signal” their attributes through “costly” displays. For costly signaling to work, a behavior must be costly to an individual—that is, it cannot be done by just anyone (this is known as the handicap principle). It has to be honest, and it is kept honest through inherent links between the display and the attribute it is meant to advertise. Hunting accomplishes this by bringing in large amounts of nutrient-dense food. As Hawkes and Bliege-Bird point out (2002:58), a display means more if it not only signals attributes to an audience but also provides some direct benefits.

More specifically, costly signaling theory argues that a hunter sacrifices the nutritional benefit of meat in exchange for a reputation (as a hunter, or leader, certainly as a potential provider) that makes him desirable to potential wives or male collaborators. The sharing of meat can also produce less tangible but still significant benefits, such as goodwill toward his offspring or toward his family in his old age.

Many studies of sharing among foragers have been short-term. But Wiesner (2002) points out that we cannot fully understand the sharing of meat without a long-term perspective. She produces data from thirty-four years of study of Africa’s Ju/'hoansi (more widely known as the !Kung) showing that men use meat sharing to build social and political relationships. The Ju/'hoansi data indicate that men who are good hunters live in large, socially cohesive groups composed of their biological kin, and that many close kin who share can be of more assistance than unchallengable goods (through meat, for a result of these benefits). Wiesner shows that Ju/'hoan males, in Allen-Arave, et al. (1997) benefit when they share meat with more people, something than others; see also Wiesner.

As is true for sons, levels at the same time and levels are more subtle to kinship circle, back to general theory, Sahlin's [1980] arguments and not cause the general. [1977] argues that generalized reciprocities cannot as no sustaining. Generalized proper behavior are generally reciprocal.

Foragers provide much of their hunting-gathering throughout the year, generalized reciprocal, and the least of hunter-gatherers are nutritionally significant. The short- focus of sharing.

SO, WHAT ABOUT BAMFORTH? Bamforth (1966) aging models prevails but these models assume a modifications to the previous model...
biological kin, unlike poor hunters, who live in smaller groups without many close kin. Good hunters, then, live in groups that provide them with more assistance in raising their offspring and that can exert an unchallengeable claim to land. Good hunters also have more material goods (through greater numbers of hxaro exchange partnerships). As a result of these resources, good hunters raise more offspring to adulthood (that is, have greater reproductive success) than poor hunters. Wiessner shows that these outcomes are mostly achieved through the judicious and "generous" distribution of meat. (Similarly, Gurven, Allen-Areve, et al. [2000] show that Aché men who are good hunters benefit when they are injured or sick by receiving more food from more people, compared with those who produce and/or share less than others; see also Hames [2000]).

As is true for most cultural behaviors, sharing operates on multiple levels at the same time—for straightforward economic reasons but also as more subtle social communication. In my opinion, this brings us full circle, back to generalized reciprocity. (In line with costly signaling theory, Sahlins [1972:194] even noted that the "failure to reciprocate does not cause the giver of stuff to stop giving.") For these reasons, Cashdan (1997) argues that there is a sound evolutionary explanation for generalized reciprocity and truly unconditional giving. But this should come as no surprise: people who live up to their culture's standards of proper behavior—and generosity is valued among nomadic foragers—are generally rewarded for doing so.

Foragers participate in generalized reciprocity in part because much of their behavior is public and because, like many other peoples, hunter-gatherers rely on social connections for their well-being throughout their lives, especially in old age. Thus, it makes sense that generalized reciprocity with a vague and diffuse utility should be prevalent among foragers and that surplus-producing, hard-to-procure, nutritionally significant resources (such as large game) should be the focus of sharing.

SO, WHAT ABOUT SELECTION?

Bamforth (2002) argues that HBE fails to show that optimal foraging models predict reproductive success. He is correct that most models assume the linkage; that is, HBE assumes that foragers will conform to the prediction of optimal foraging models because HBE
assumes that efficient foraging translates into maximum reproductive advantage. In fact, there are data—admittedly limited—that show that good hunters (men with high return rates) have greater reproductive fitness (Wiessner 2002; E. A. Smith 2004). But the causal linkage in these cases is unclear, for men who are good hunters may be providing more food to their offspring or may have acquired spouses who are high-return-rate foragers (Hawkes, O'Connell, and Blurton Jones 2001b) and provide more food for their offspring. Or the good hunters and their offspring may receive attention when ill or injured, owing to the good hunter's previous generosity (Gurven, Allen-Arave, et al. 2000)—because those who benefit from good hunters' generosity will desire to see it continue. So being a good hunter, for whatever reason, does appear to have a reproductive advantage, and thus the attributes that make a man a good hunter are likely to be under selection.

It is clear that some of those attributes are purely biological: keen eyesight, good hand–eye coordination, stamina, and strength. But what really makes a man successful in these cases is his generosity. True, acts of sharing communicate his abilities, but others are not drawn to him solely for those abilities; they are drawn to him for his generosity. Without it, his abilities would be meaningless to anyone outside his family.

The sharing behavior of humans is substantially different from that of other primates (reviewed in Kuhn and Sarther 1999; see also McGrew and Feistner 1992). Acts of sharing are relatively rare among group-living primates, occur in restricted social settings, and have much more the characteristics of tolerated theft (and it is often offspring "stealing" from parents). Human sharing, however, is not an instantaneous decision but involves a record of past debts or gracious acts and a view to the future: for spouses, liaisons, debts, alliances, treatment in the afterlife, and so on. This entails, I think, not simply a quantitative difference between ourselves and other primates, but a qualitative difference, and a significant one at that. The question that faces us is, Was selection responsible for the mental capacities that produce or permit the sharing behavior that we see among humans? How would we know?

It may appear that sharing is a coldly calculated behavior: What can I get from this person if I share? What do I lose if I don't? While I suspect that this is true on one level, at the level of the individual, cul-
Hunter-Gatherers, Archaeology, and the Role of Selection

Tural mandates often take precedence. An instructive example comes from Eleanor Leacock's research with the Cree in the 1950s. Traveling some distance from camp, Leacock and her informant, Thomas, encountered two hungry acquaintances. Leacock's informant gave away the last of his flour and lard to them:

This meant returning to the post sooner than he had planned, thereby reducing his possible catch of furs. I probed to see whether there was some slight annoyance or reluctance involved, or at least some expectation of a return at some later date. This was one of the very rare times Thomas lost patience with me, and he said with deep, if suppressed anger "suppose now, not give them flour, lard—just dead inside." More revealing than the incident itself were the finality of his tone and the inference of my utter inhumanity in raising questions about his action. (Leacock 1969:13–14)

Thomas might have calculated that giving away the last of his provisions was the worst thing he could do for himself at that moment. But he did it anyway.

Thomas is telling us about more than just his character. It should go without saying that it is highly unlikely that sharing behavior is simply biological. That is, whether one shares a lot or a little is not simply a product of genetic heritage. One can see how a male peacock with a glorious tail could attract more mates and thus pass on more genes to the next generation. In that case, sexual selection produced (and continues to produce) the peacocks we know today. But humans are, to say the least, different. A male peacock has no choice but to strut with his tail; Thomas had a choice, and he knew it. Did Thomas calculate that giving away the lard and flour was better than being stingy and risking the social consequences of such an act? Or was Thomas motivated by a deeper sense of shame in not living up to the ideals of his society—sharing even when it hurts? I would guess the latter. The value placed on sharing and generosity—and subsequent acts of sharing and generosity—is not passed on through a psychological "module" or genetic proclivity, but through culture. (Note that billionaire entrepreneurs, athletes, and actors in Western society, even the philanthropic ones, are not generous to the point "where it hurts." They are not
condemned in Western culture, but they would be in Cree culture.)

Like evolutionary psychology, HBE argues that selection played a role in forming a mind that reaches decisions by taking economic values, social relations, and abstract cultural values into account. But HBE argues for the mind as a generalized decision-making device rather than as a set of modules. I suspect that HBE is closer to the truth than EP. Nonetheless, selection is assumed to have been responsible for this general decision-making device. Since HBE often calls on a literature that employs foraging models to explain the behavior of birds and fish, HBE assumes that this generalized decision-making device is so ancient, evolutionarily speaking, that its origin is not especially interesting. But we have seen that human sharing operates in terms different from those of other primates; it implies a different cognitive capacity. If that difference is a product of selection, then it is selection that occurred after the hominid line split from the rest of the primate lineage.

HBE and EP have different ideas about how the human mind operates, but neither HBE nor EP has demonstrated that selection was responsible for it. Neither has come to grips with demonstrating the selective process and the effects of the process whereby humans developed the biological capacity to be cultural beings.

A PLACE FOR ARCHAEOLOGY

Despite pleas to the contrary, I am plagued by the growing sense that researchers in HBE and EP feel that studies of living hunter-gatherers can substitute for the study of prehistory. On the one hand, HBE sees living foragers as providing our best access to the evolutionary process because they live under conditions close to humanity's Pleistocene ancestors; I agree that living foragers can be a source of hypotheses. EP is closer to the Victorian idea, in which living hunter-gatherers are treated as though they were prehistory, but, of course, they are not.

There is a problem in attempting to test the extent to which selection is responsible for shaping the human mind—that is, for creating humans' ability to be cultural beings—with ethnographic data collected over short time spans. We have already seen that the place of sharing might not be completely visible except over long spans of time—a
Hunter-Gatherers, Archaeology, and the Role of Selection

generation, really. But can we actually test whether selection, a historical and local process, is responsible for the mind with even a generation’s worth of ethnographic data? Isn’t it necessary to test hypotheses of selection against data on an evolutionary time scale that records gross biological and behavioral changes in the hominid line? Here is where I think EP and even HBE have fallen down.

For example, Kuhn and Sarther (1999) argue, as Isaac (1978) did, that the beginnings of human sharing might lie in the hominid entry into a carnivorous niche in the late Pliocene, some two to three million years ago. Whether these hominids were hunting or scavenging might not matter; in either case, they might have acquired quantities of food—fatty meat, specifically—that they could not have consumed in one sitting. Here, sharing might have operated according to a tolerated theft model (McGrew and Feistner 1992).

Kuhn and Sarther argue that as hominids became true hunters (rather than scavengers), meat became a regular and significant part of the diet. This selective milieu may have produced the pattern of sharing we see among humans today. The latter requires several attributes. It requires that one be able to recall the past, to know what others have done for you, and it requires the ability to predict others' behavior in the future (to see their potential for retribution or cooperation down the road and not just in the moment). And it requires acting in terms of something beyond a straightforward and instantaneous evaluation of costs and benefits: it requires culture.

I say this because ethnographic data are clear that hunters go hunting with the knowledge that others will consume the meat acquired. Kuhn and Sarther argue that this would have resulted in increased efficiency in hunting and that, in fact, this is one of the things that characterizes Upper Paleolithic industries. Although Lower and Middle Pleistocene hominids adapted to a variety of environments, they did so with technologies that were remarkable for their redundancy. Acheulean hand axes and, later, Mousterian tools appear across vastly different geographic regions that offered different sorts of resources. And these technologies persist over long spans of time, tens of thousands of years, during which food resources changed without concomitant changes in technology.

But by 40,000 years ago, Upper Paleolithic tool assemblages varied
across space, reflecting geographic differences in food resources, and they changed relatively quickly over time (see Kuhn and Stiner 2001). The spatial and temporal diversity in tool kits from 40,000 to 10,000 years ago is orders of magnitude greater than that of the preceding two million years.

Pointing out that artifact design has much to do with hunting efficiency, Kuhn and Sarther (1999:93) argue that the “rapid generation and adoption of novel forms of weaponry over long periods of time would suggest that there was a fairly constant selective advantage to improving the effectiveness or efficiency of foraging.” They suggest that the open-ended demand created by a social network that values sharing—by benefiting both the giver and the taker—would continually select for foraging efficiency even where food was not limited. “If the products of foraging were regularly distributed only within small groups—for example, a female and her children, a mated pair and offspring, or a group of close allies—then there would have been less general benefit to increasing the effectiveness of techniques for harvesting food resources in bulk so long as those resources remained at least moderately abundant in the environment” (1999:93).

If the linkages between technology and sharing are correct, then it might be the Upper Palolithic’s new pattern of sharing that gave modern humans a selective advantage over Neandertals (even if modern humans interbred with Neandertals, it is modern human behavior that became common). This new pattern of sharing made possible by culture could have permitted human populations to grow and competitively exclude Neandertals from the late Pleistocene environment of Europe. Evidence suggests that this could have happened very quickly (Pettit 1999), and one mathematical model shows how sharing hominids could rapidly replace nonsharing ones (Horan, Bulte, and Shogren, n.d.).

**CONCLUDING THOUGHTS**

Sharing is a behavior whose direct evidence might be difficult to see archaeologically. Although some have suggested how this might be done (see Waguespack 2002; Enloe 2003), it will probably always remain difficult to demonstrate directly in the most ancient reaches of human time. But by linking sharing to its implications for technology,
Hunter-Gatherers, Archaeology, and the Role of Selection

Kuhn and Sarther might have demonstrated when the complex of behavior that we gloss as "sharing" first appeared among humans. And in evolutionary time, it is not ancient, perhaps only 40,000 years old. If Kuhn and Sarther are correct, the pattern of human sharing behavior appears at the same time as other distinctive hallmarks of humanity, especially elaborate burials that suggest ideas of the afterlife and religion, and art that demonstrates the human ability to think symbolically. All of this suggests a dramatic change in the human mind—a change that is more in line with HBE's working assumption of the mind as a generalized problem-solving device rather than with EP's assumption that the mind is composed of "modules" that were selected for over time during the EEA. Mithen (1996), in fact, while quite sympathetic to the research program of EP, finds that the record supports the more generalized decision-making apparatus of HBE.

But HBE still uses a model of the mind that, not being unique to humans, sees culture as merely the idiom in which the mandates of selection are written. Perhaps this is true (although I think not), but it is too important a point to concede without rigorous testing. Indeed, other studies have pointed out that the transmission of cultural behavior can operate contrary to the directives of a purely fitness-directed model (for instance, Boyd and Richerson 1985). Yet the account of sharing reviewed here suggests that it may be the very other-directedness of cultural behavior that gave hominids a selective advantage in evolution.

Ethnography offers rich testing grounds for understanding what sort of variation we might expect among hominids (although the past could always lie outside the range of modern variation), as well as for understanding the variables that produce that variation (Tooby and DeVore 1987; R. L. Kelly 1995). And carefully executed cross-cultural tests that control for enculturation might very well discover a mental architecture whose origins could fruitfully be sought from the perspective of natural selection. But we should not be fooled. As noted above, modern behavior may not necessarily be adaptive (in the strict sense of fitness maximization), and so we cannot use it as our sole guide to the behavior or mental architectures produced through a process of selection. The first cultural hominids appeared in a social context of noncultural hominids. Our ancient ancestors may have

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confronted environmental challenges similar to those faced by living foragers, but we should not expect to find an analogue for their social context. The ability to be cultural arose fairly late in human evolution and could have dramatically altered the selective context of human behavior. Evolutionary biology has developed some useful criteria for recognizing a behavior or an element of anatomy or physiology as an adaptation (reviewed in Cosmides and Tooby 1992:165). But these are definitions, not proof, and they are best treated as hypotheses to be tested against the record of evolution.

Ancient human behavior is not directly observable; archaeologists must rely on material remains to track evolutionary changes. The paradigm of HBE provides a greater number of more obvious linkages among material remains, behavior, and properties of the human mind than does EP. This does not necessarily mean that EP cannot do so, only that it has not.

Modern evolutionary paradigms assume that the mind must be a product of selection. This is logical, yet the role of selection in producing the human mind has been in question for a long time. Alfred Wallace, who once used natural selection to explain the mind (1864), later asserted that “the brain of pre-historic and of savage man seems to me to prove the existence of some power, distinct from that which has guided the development of the lower animals through their every varying forms of being” (1870:343). Although Darwin was scandalized, Wallace may be right. Although Wallace relied on living “primitives” for his argument, he had the excuse that the archaeological record was nearly unknown. We cannot use that excuse. A concern with how the human mind and, in particular, the ability to be cultural was produced through selection remains with us. But, unless we want to argue that living foragers are human nature in the raw or are relics of our Pleistocene ancestors—and I do not think we want to do either—then living foragers cannot substitute for a study of the past. While ethnographic work can generate hypotheses, if we wish to know how evolution created that which makes us human—the biological capacity to be cultural—then we must ultimately test those hypotheses on the most direct evidence we have of evolution: archaeology and paleoanthropology.
HUNTER-GATHERERS, ARCHAEOLOGY, AND THE ROLE OF SELECTION

Notes

1. One might start the clock with the appearance of biologically and behaviorally modern humans, some 100,000 to 200,000 years ago; but since agriculture arose about 10,000 years ago, biologically modern humans have still spent about 90 to 95 percent of their time as hunter-gatherers.

2. A phrase first coined by Herbert Spencer, not Darwin, to whom it is often mistakenly attributed, although he later borrowed it.

3. It is not that men are better than women at reckoning space, but only that the sexes reckon space differently.

4. Tavassoli (2002) shows a difference between Chinese and English speakers in spatial memory that she attributes to differences in the nature of written Chinese and English. Dasey (1975) also shows a difference among three cultures in their spatial abilities.

5. I. Silverman and Eals (1992) argue that the differences appear too early for enculturation to be completely responsible, although another study found that older people reckoned space differently than younger individuals in their sample; this difference is attributed to varying amounts of experience (Dabbs et al. 1998).

6. Many foragers trade meat for agricultural produce, but exchange here refers to exchange within the foraging group, not between that group and another.

7. Though, to be sure, we do not yet know this for certain. One can manipulate the symbols of generosity and/or dominate public rhetoric so that one appears to be generous when skimming off the top for oneself. This is the case, for example, in chiefly societies, where a chief extols his own generosity while accepting tribute to maintain his entourage. Such manipulation is perhaps less possible in foraging societies where much behavior is public.

8. And perhaps at most not more than 75,000 to 90,000 years, if new evidence from central and southern Africa on the appearance of modern human behavior is accurate (Yellen et al. 1995; Henshwood et al. 2001).
Native Americans and the Environment
Perspectives on the Ecological Indian

Edited and with an introduction by
Michael E. Harkin and David Rich Lewis

Foreword by Judith Antell
Preface by Brian Hosmer
Afterword by Shepard Krech III
4. Did the Ancestors of Native Americans Cause Animal Extinctions in Late-Pleistocene North America?

And Does It Matter If They Did?

Robert L. Kelly and Mary M. Praschunas

The relationship between the animal and human life of the New World has long been the subject of debate. As early as 1749 the French naturalist George-Louis Leclerc hypothesized that both humans—Native Americans—and the animals they fed upon had degenerated from their superior European forms because nature was less “active” and “energetic” on one side of the globe than on the other. In his Notes on the State of Virginia (1781), Thomas Jefferson responded to Leclerc in discussing the nature and origins of Native Americans, a subject that greatly intrigued him (and led him to undertake the first “scientific” excavation of an archaeological site in the United States). Jefferson admired the Native peoples of the New World and, unlike many of his contemporaries, believed them to be equal to Europeans in intellect. But he needed more substantive grounds on which to refute Leclerc.

One of the key elements of Leclerc’s proposition was the claim that animals of the New World were smaller than those of Europe. Jefferson was aware of finds of the skeletal remains of mammoths, mastodons, and giant ground sloths in various places, such as Big Bone Lick, Kentucky. (And his interest is recognized through the scientific name for the giant ground sloth, Megalonyx jeffersoni.) He once kept a mammoth skull in Monticello’s front foyer, and while president he laid out mammoth bones in the White
House's East Room (dubbed the "Bone Room" by White House staff). Such large animals were proof that Leclerc's image of New World fauna, and hence his degeneration hypothesis, were incorrect.

The skeletal remains that decorated Monticello and the White House were undeniable evidence of a large fauna. But it was equally undeniable that there were no pachyderms tromping through Virginia's forests. Thus, one could have argued that mammoths and other large Pleistocene fauna were extinct precisely for the reason that Leclerc claimed. Whether this counterevidence played a role in his thinking is unclear, but Jefferson believed that extinctions do not occur, that "such is the economy of nature, that in no instance can be produced her having permitted any race of her animals to become extinct." And so, when Jefferson sent Lewis and Clark west in 1803 he instructed them to keep an eye out for herds of mammoths on the Great Plains.

Unfortunately, they were ten thousand years too late.

**Late-Pleistocene Extinctions**

Scholars have debated the cause of late-Pleistocene extinctions since the early nineteenth century (Grayson 1984b; Martin and Steadman 1999). And with the unambiguous establishment, in the 1920s, of the presence of humans in late-Pleistocene North America, the role of Native Americans in the extinctions became central. The importance of understanding the cause of these extinctions is not purely academic. Martin (1990, 2002), for instance, argues that the wave of extinctions that began in the late Pleistocene is still occurring today and that the earth is in the midst of human-induced extinctions that will rival those of the late Cretaceous, when a meteor destroyed the earth's "Jurassic Park" fauna and gave rise to the dominance of mammals, including humans (see also Ward 1994). Many other ecologists unflinchingly use the late-Pleistocene extinctions as examples of what humans did in the past and what they are capable of doing in the future (e.g., Wilson 2002; Diamond 1992; Ward 2000). Martin and Burney (1999) even propose that we should reintroduce free-ranging elephant herds on North America's Great Plains so that the proboscidea can help reestablish stable ecological relationships there (see also Steadman 1989; Steadman and Olson 1985).

Of more immediate concern is the role of Native Americans in the American environment. On the issue of hunting rights, even Jefferson's eighteenth-century and the Native American" should be repeatedly examined.

Leaving aside the role of humans, some determinants of human extinction are often polarizing: anthropogenic predation (Graham and MacPhee 1985) and human introduced prey (MacPhee and MacPhee 1992). There are many cases where each hypothesis can explain extinction on North America, but the best known. We can be sure that even if Native Americans are responsible for the late-Pleistocene extinction of many species, the role of modern Native Americans remains essential.

**Late-Pleistocene Extinctions**

Because of a late-Pleistocene extinction event, the world's great mammals were extirpated, and the extinctions of the inhabitants of the ice age occurred within the limits of radiocarbon dating. The last great extinctions occurred within the last 10,500 BP (Grayson 1984a; Martin 1990; Martin and Steadman 1999; Stuart 1985; Stuart 1985; Stuart 1985; Stuart 1985; Stuart 1985; Stuart 1985).
Of more immediate importance is the argument that if the ancestors of Native Americans caused the late-Pleistocene extinctions, then living Native Americans are not qualified to act as unchecked stewards of the environment. On this basis, some argue that treaty-guaranteed fishing and hunting rights, such as those granted to the Chippewas in the nineteenth century, and that were contested in Minnesota and Wisconsin in the 1990s, should be repealed.

Leaving aside the politics, this chapter examines current thinking on the role of humans in late-Pleistocene extinctions. Explanations for extinctions are often polarized between two competing hypotheses: climatic change (Graham and Lundelius 1984; Guthrie 1984; Lundelius 1989) and human predation (Martin 1967, 1973, 1984; Martin and Steadman 1999). Recently, MacPhee and Marx (1997) have added an alternative that implicates the role of human-introduced hypervirulent diseases.

There are many variations on these general themes. Here we examine each hypothesis and the supporting arguments and criticisms. We focus on North America, where the archaeological and paleontological record is best known. We conclude that we simply do not know for certain, yet, what caused the late-Pleistocene extinctions, although the climate-change argument currently seems to have the most support. In addition, we conclude that even if Native Americans were the primary cause of the late-Pleistocene extinctions, that fact would have little bearing on the land-use rights of modern Native Americans.

Late-Pleistocene Extinctions: What Happened?
Because of a late-Pleistocene extinction event that was rapid, pervasive, and global, Lewis and Clark had to disappoint Jefferson. A period of alternating glacial and interglacial periods, the Pleistocene lasted from about 2 million to 10,000 years ago (Anderson 1984, 41). Most of the extinctions, however, occurred within its final few thousand years and were complete by 11,000–10,500 BP (Grayson 2001, 35; G. Haynes 2002a, 2002b; Hollliday 2000b; Martin 1990; Martin and Burney 1999; Mead and Meltzer 1984; Meltzer and Mead 1985; Stuart 1991; all dates used here are in uncalibrated radiocarbon years before present [BP]; for a rough conversion to calendar years, add 2,000 to the radiocarbon years).
Table 4.1. Extinct late-Pleistocene North American mammals with date of latest appearance (adapted from Grayson 1991). Genera in boldface are the only genera unequivocally associated with kill sites (adapted from Grayson 1991 and Grayson and Meltzer 2002, 2003).

<table>
<thead>
<tr>
<th>Order</th>
<th>Family</th>
<th>Genus</th>
<th>Common name</th>
<th>Youngest good date</th>
</tr>
</thead>
<tbody>
<tr>
<td>Artiodactyla</td>
<td>Antilocapridae</td>
<td>Capromeryx</td>
<td>Diminutive pronghorn</td>
<td>None</td>
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<td></td>
<td></td>
<td>Tetrameryx</td>
<td>Shuler's pronghorn</td>
<td>None</td>
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<td></td>
<td></td>
<td>Stegocerus</td>
<td>Pronghorn</td>
<td>None</td>
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<tr>
<td>Bovidae</td>
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<td>Saiga</td>
<td>Saiga</td>
<td>None</td>
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<td></td>
<td></td>
<td>Euceratherium</td>
<td>Shrub ox</td>
<td>None</td>
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<td></td>
<td></td>
<td>Bootherium</td>
<td>Harlan's musk ox</td>
<td>None</td>
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<tr>
<td>Camelidae</td>
<td></td>
<td>Camelops</td>
<td>Yesterday's camel</td>
<td>10,900 ± 750</td>
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<tr>
<td></td>
<td></td>
<td>Hemisusuchus</td>
<td>Large-headed llama</td>
<td>None</td>
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<td></td>
<td></td>
<td>Falcrolopus</td>
<td>Stout-legged llama</td>
<td>10,890 ± 130</td>
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<tr>
<td>Cervidae</td>
<td></td>
<td>Ceruolus</td>
<td>Elk-nimble</td>
<td>None</td>
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<td></td>
<td></td>
<td>Naloochroes</td>
<td>Mountain deer</td>
<td>None</td>
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<td></td>
<td></td>
<td>Platyopus</td>
<td>Long-nosed peccary</td>
<td>None</td>
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<td></td>
<td></td>
<td>Flat-headed peccary</td>
<td>None</td>
<td>None</td>
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<tr>
<td>Carnivora</td>
<td>Canidae</td>
<td>Canis</td>
<td>Dhole</td>
<td>None</td>
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<td></td>
<td>Felidae</td>
<td>Homotherium</td>
<td>Scimitar cat</td>
<td>None</td>
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<td></td>
<td></td>
<td>Mirarionyx</td>
<td>American cheetah</td>
<td>None</td>
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<tr>
<td></td>
<td></td>
<td>Smilodon</td>
<td>Sabertooth</td>
<td>13,130 ± 275</td>
</tr>
<tr>
<td>Mustelidae</td>
<td>Mustelaursita</td>
<td>Bouscrotoptera</td>
<td>Short-faced skunk</td>
<td>None</td>
</tr>
<tr>
<td>Ursidae</td>
<td></td>
<td>Actosys</td>
<td>Giant short-faced bear</td>
<td>None</td>
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<tr>
<td></td>
<td></td>
<td>Tremusquor</td>
<td>Florida cave bear</td>
<td>None</td>
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<tr>
<td>Lagomorpha</td>
<td>Leporidae</td>
<td>Azlanolagus</td>
<td>Azlan rabbit</td>
<td>None</td>
</tr>
<tr>
<td>Perrissodactyla</td>
<td>Equidae</td>
<td>Equus</td>
<td>Horse</td>
<td>10,370 ± 350</td>
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<td></td>
<td></td>
<td>Tapirus</td>
<td>Tapir</td>
<td>10,900 ± 450</td>
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<tr>
<td>Proboscidea</td>
<td>Elephelidae</td>
<td>Mamnorthis</td>
<td>Mammoth</td>
<td>10,550 ± 350</td>
</tr>
<tr>
<td></td>
<td>Mammutidae</td>
<td>Mammut</td>
<td>American mastodon</td>
<td>10,395 ± 130</td>
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<tr>
<td>Rodentia</td>
<td>Castoridae</td>
<td>Castoroides</td>
<td>Giant beaver</td>
<td>None</td>
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<tr>
<td></td>
<td>Hydrochoeridae</td>
<td>Hydrochoerus</td>
<td>Holmes's capybara</td>
<td>None</td>
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<tr>
<td></td>
<td></td>
<td>Nechchraus</td>
<td>Pinckney's capybara</td>
<td>None</td>
</tr>
<tr>
<td>Xenarthra</td>
<td>Pampatheriidae</td>
<td>Holmestina</td>
<td>Northern pampatheria</td>
<td>None</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pampatherium</td>
<td>Southern pampatheria</td>
<td>None</td>
</tr>
<tr>
<td></td>
<td>Glyptodontidae</td>
<td>Glyptotherium</td>
<td>Simpson's glyptodont</td>
<td>None</td>
</tr>
<tr>
<td></td>
<td>Megalonychidae</td>
<td>Megalonyx</td>
<td>Jefferson's ground sloth</td>
<td>12,390 ± 215</td>
</tr>
<tr>
<td></td>
<td>Megatheriidae</td>
<td>Ermossemum</td>
<td>Ruscon's ground sloth</td>
<td>None</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Northnorthyops</td>
<td>Shasta ground sloth</td>
<td>10,035 ± 250</td>
</tr>
<tr>
<td></td>
<td>Mylodontaide</td>
<td>Glossotherium</td>
<td>Harlan's ground sloth</td>
<td>20,450 ± 460</td>
</tr>
</tbody>
</table>

Prior to 1970, megafauna weighed over 400 kg (880 lb) were considered (see Chapter 5). Extinct megafauna included the bison, mammoth, giant moose, megadipoid (a giant ground sloth), and Anancus (another giant ground sloth). The extinction of the last species of megafauna in the Pleistocene ended the era of the megafauna. However, there is no direct evidence for the extinction of megafauna in the Pleistocene, and many scientists believe that the extinction of megafauna was gradual and not instantaneous (Barnosky et al. 2002).

In addition, a proposed link between megafauna and human predation has been questioned. Some studies suggest that humans did not play a significant role in the extinction of megafauna, while others propose that human predation was a significant factor in the extinction of megafauna, particularly in the case of the bison and the mammoth.

The overkill hypothesis, which proposes that human predation caused the extinction of megafauna, has been widely debated. Some researchers argue that the evidence for overkill is weak or nonexistent, while others argue that the evidence supports the overkill hypothesis. The debate continues, and the role of human predation in the extinction of megafauna remains a topic of ongoing research.

The overkill hypothesis is based on the observation that megafauna populations decreased rapidly following the arrival of humans in the New World. However, the timing of the arrival of humans in the New World is not well-dated, and some researchers argue that the apparent decline in megafauna populations may be due to other factors, such as climate change or natural population fluctuations.
Prior to the extinction event, more than one hundred genera of large mammals (>44 kg) existed in North and South America (Martin 1984, 355; 1990, 188). Extinctions reduced this assemblage by more than two thirds (Martin and Steter 1999, 37). In North America, thirty-five genera of mainly large mammals distributed across twenty-one families and seven orders became extinct near the terminal Pleistocene (Grayson 1991, 194; 2001, 35; Kurten and Anderson 1980; see table 4.1). This is more than the total number of mammals that became extinct throughout the past 4.8 million years, making the late Pleistocene witness to an extinction event unparalleled in the entire Cenozoic era (Martin 2002, 10; Martin and Steadman 1999). The event was not limited to North America: South and Central America lost forty-seven genera (Martin 2002, 18), and twenty-eight genera disappeared from Australia (Flannery and Roberts 1999). Large mammals were especially hard hit, but many species of birds, reptiles, and small mammals also disappeared. In addition, many species that managed to survive into the Holocene did so in far more restricted ranges than they enjoyed in the late Pleistocene (e.g., musk ox, which once lived as far south as Tennessee).

Late-Pleistocene extinctions are notable in that they were concentrated on megafauna and attendant parasites, predators, and commensals, to the exclusion of invertebrates, smaller fauna, and marine taxa. Martin suggests that this argues against a climatic (global) cause (Martin 1990, 189–92; 2002, 11; Martin and Steadman 1999, 17–18). Similarly, there were virtually no accompanying floral extinctions. Only one plant species in North America (a spruce, Picea rigida) is known to have become extinct (Jackson and Weng 1999; Martin 2002, 9) suggests the possibility of human involvement, but paleoecologists attribute the loss of this spruce to climate change (Jackson and Weng 1999).

Something very drastic happened at the end of the Pleistocene. But what?

**The Overkill Hypothesis**

The overkill hypothesis argues that Clovis hunters were responsible for late-Pleistocene North American megafaunal extinctions. It also suggests a more
general pattern of faunal extinction caused by human colonists throughout time and in many different parts of the world. An advocate of the overkill hypothesis for several decades, Paul Martin (1967, 1973, 1984, 1990, 2002; Martin and Steadman 1999; Mosimann and Martin 1975) proposed that big-game Clovis hunters from Siberia crossed into North America through an ice-free corridor between the Cordilleran and Laurentian ice sheets and moved quickly across the North American landscape, killing all large game before them in a "blitzkrieg" occupation. The Clovis Complex is the earliest accepted and well-dated North American cultural complex, dating to approximately 11,500–10,000 BP (Dixon 1999, 215; Fiedel 1999; Grayson 2001, 35; C. V. Haynes 1993; Taylor, Haynes, and Stuiver 1996). Clovis artifacts are the only stylistic artifact forms that appear in all forty-eight contiguous states, and they are associated with mammoth and mastodon remains in a few archaeological sites (Grayson 2001, 36; Grayson and Meltzer 2002; see Fiedel and Haynes 2004; Grayson and Meltzer 2004).

Although controversy exists as to the magnitude of Clovis dependence on meat and specialized big-game hunting, the association of distinctive Clovis fluted projectile points with mammoths and other large mammals does indicate that Clovis people did hunt mammoth at times (G. Haynes 2002a). Kelly and Todd (1988) argued that an Arctic adaptation to large-game hunting (but not exclusively of megafauna) in an unpopulated environment undergoing rapid environmental change explains the high mobility of Clovis populations. In this scenario, rapid late-Pleistocene environmental change (resulting in local extinctions) coupled with depletion due to hunting forced Clovis foragers to move to new territory frequently to maintain high return rates on hunting (Kelly 1996, 1999). But with no previous occupants to call upon for local landscape knowledge, Clovis hunters needed an adaptation that permitted the occupation of unknown terrain and that allowed them to eschew plant foods, the uses of which would have been unknown to Arctic foragers. Kelly and Todd argued that the same hunting adaptation would have been necessary to cross ecological boundaries without having to acquire new subsistence-related knowledge. Thus, a hunting adaptation both permitted and encouraged rapid movement. However, Kelly and Todd explored this out a blitzkrieg occupation.

A recent consideration of animal population change and substantial population changes have been driven by rapid environmental change (G. Haynes and Martin 1973) and may not become sufficiently large to support human populations that can support foraging because they were small and thus were easily exterminated (G. Haynes and Martin 1973). In summary, migrations that can support foraging may be specific to areas where they are not fully exploited by other foragers.
and Todd explicitly argued that such rapid movement could happen without a blitzkrieg of the faunal population.

A recent computer simulation suggests that, as is often true for colonizing animal populations, a highly mobile Clovis population could have had a substantial population growth rate (Surovell 2000). If so, then demographic pressure coupled with an adaptation that not only permitted but also required territorial mobility could have pushed colonists rapidly southward.

Martin (1973) argues that such population densities would have quickly become sufficiently large to cause extinctions throughout the Americas by soon after 11,000 BP. This blitzkrieg could have been especially devastating because the megafauna had no experience with human hunters and thus were easily dispatched (Martin 1973, 1984, 2002; Mosimann and Martin 1975). In support of the blitzkrieg model are several computer simulations that can produce extinction purely as a product of human hunting (Alroy 2001; Holdaway and Jacomb 2000; Mithen 1997).

Why didn't all animals go extinct? Martin argues that the surviving species had characteristics that made them undesirable to human hunters. They were "cryptic or secretive in habits (moose, puma); erratic and unpredictable in movements (bison, caribou); sequestered in sparsely inhabited regions (polar bear, musk oxen); truculent or dangerous when approached (brown and polar bears); fleet of foot (pronghorn, gray wolf); denizens of rugged terrain (mountain goat, mountain sheep, jaguar); and in no case as promising a target for human hunters as the slow-moving ground sloths or as vulnerable to low levels of predation as the proboscidea" (Martin 2002, 17).

Evidence for Overkill

Foremost among the arguments in support of the overkill hypothesis are (1) the apparent chronological coincidence of megafaunal extinctions and the appearance of human hunters, (2) the observation that island fauna are frequently decimated by human colonization, and (3) arguments derived from ecological theory.

Chronology. The close chronological coincidence of late-Pleistocene mega-
faunal extinctions and the colonization of the New World was what initially
generated the overkill hypothesis (Grayson 1991, 204–5). The latest occurrences of mammoths, for example, in North America are about 11,000 BP (Martin 1990, 195; Taylor, Haynes, and Stuiver 1996). The palaeontological record therefore points to a suspicious coincidence between the first arrival of humans and the disappearance of some megafauna (Martin 1967, 1990; Lyons, Smith, and Brown 2004; Surovell, Wagus, and Brantingham 2005). For some, this coincidence strongly suggests a causal relationship.

The time-transgressive nature of late-Pleistocene extinctions has also been used to argue for human involvement and against a global cause of extinctions such as climatic change (Martin 1990, 188; Martin and Burney 1999, 60; Surovell, Wagus, and Brantingham 2005). Although catastrophic extinctions did occur regionally, some researchers argue that extinctions were not synchronous but instead occurred only, and soon, after human colonization in the Americas, Australia, Madagascar, New Zealand, and the South Pacific (Martin 1990; Martin and Burney 1999, 61). While North American megafauna were extinct by 10,500 BP, large-mammal extinctions occurred in Australia as early as 50,000 BP (Miller et al. 1999), when that continent may have been first colonized by people. Indeed, the timing of the extinctions is quite suspicious (Lyons, Smith, and Brown 2004).

In contrast, overkill proponents point out that few large ungulate species have become extinct over the past forty thousand years in areas with longer histories of human occupation, such as Africa, Europe, and tropical Asia (Martin 1990, 188; Martin and Burney 1999, 61). Martin (2002, 24) argues that the success of large animals in these places is explained by a much longer history of human occupation on these continents, which allowed the fauna to develop a coevolutionary response to hominid predation. These animals evolved alongside ancient hominids; they never had to naively encounter sophisticated, fully armed hunters as did the fauna of the Americas, Australia, Madagascar, and the Pacific Islands. Megafaunal extinctions in Greater Australia (Australia, Tasmania, New Guinea, and New Zealand) appear to have occurred without associated environmental change, suggesting to overkill proponents that these regions provide independent tests of the model (Diamond 1992; Martin 1967, 1984; Fiedel and Haynes 2004; Lyons, Smith, and Brown 2004).

Unfortunately, the evidence for human-driven extinctions is not as strong. In order to establish causation, it is expected that extinctions should be synchronous, and that the extinctions should be found only within the Clovis settlement area. None of this is currently true. Of the three taxa that are primary targets of the overkill hypothesis, radiocarbon dates from Australia, Madagascar, and the South Pacific (Grayson 1991, 204–5). Admittedly, these dates are not as thorough as those from the Americas.

It is possible, however, as it was done before, Clovis sites occur in the interior of the United States as well as on the coast. However, it is important to note that not all Clovis sites are located in the vicinity of the overkill hypothesis. However, the majority of Clovis sites are located in the vicinity of the overkill hypothesis.

However, the presence of Clovis sites in the interior of North America is not a reason to think that these are not part of a larger archaeological assemblage (though perhaps one with different characteristics). The presence of large animals in the west coast of North America is not surprising, given the history of extinctions resulting in the extinction of many megafaunal species. However, even if Clovis sites are found in the interior of North America, it is not clear that they are responsible for the extinctions. In fact, the New World was not populated by humans until after 12,000 years ago.

Additionally, it is possible that the presence of Clovis sites in the interior of North America does not necessarily mean that Clovis hunters had a major role in the extinctions. However, it is important to recognize that Dixon 1999, 250–1) that these sites are based upon a broad dataset.
Unfortunately, the empirical foundations of these arguments are not strong. In order for the chronological coincidence of Clovis and the extinctions to be significant, most if not all the extinctions would have to occur within the Clovis era, 11,500 to 10,900 BP. But this does not appear to be true. Of the thirty-five genera that became extinct at the end of the Pleistocene, radiocarbon dating can only show that fifteen survived past 12,000 BP (Grayson 1987, 1991, 2001; Grayson and Meltzer 2002; Meltzer and Mead 1985). Admittedly, though, the dating programs on all the involved species are not as thorough as one would like.

It is possible that humans were in the New World before, and perhaps long before, Clovis hunters. Recent data from South America, notably from the site of Monte Verde in southern Chile, suggest that humans were in South America by 12,500 BP. This might imply that people were in North America considerably before that date (if we accept the Bering land bridge as the entry point, and all evidence points to that as the case). If this is true, then pre-Clovis hunters might be responsible for the pre-12,000 BP extinctions.

However, there is no unequivocal evidence for a pre-Clovis human presence in interior North America, and Kelly (2003) argues that there is good reason to think that such evidence will never be found (though many competent archaeologists would disagree, e.g., Adovasio 2002). It is possible (though perhaps unlikely) that a pre-Clovis human migration moved along the west coast of North America and bypassed the North American interior, resulting in the populating of interior South America prior to North America. But even if this is true, Clovis hunters would still be the first occupants of interior North America—and the only humans potentially responsible for the extinctions there. Evidence of a pre-Clovis population elsewhere in the New World does not account for extinctions in interior North America prior to 12,000 BP.

Additionally, we would expect evidence that Clovis diet was biased toward large game. In recent years it has become popular to argue that Clovis hunters had a more generalized foraging adaptation (Dincauze 1993, 285; Dixon 1999, 250; Hadecek-Cuffe 1998; Meltzer 1993; Willig 1991, 93), relying upon a broad diet of fish, plants, and small animals such as turtles, How-
ever, this argument depends more on ethnographic analogy with modern foragers who know their environments intimately and whose movements are constrained by agricultural neighbors. Unfortunately, it is difficult to reconstruct Clovis diet from the currently known archaeological record, because our sample of sites is small and potentially biased toward large kill sites, and because small plant and animal remains do not always survive the ravages of time. Additionally, many Clovis sites were excavated decades ago when archaeologists did not have methods to recover what small faunal and botanical remains may have been present. One quantitative analysis of existing Clovis faunal assemblages shows a distinct bias toward large game animals, suggesting that Clovis hunters were big-game specialists (Waguespack and Surovell 2003). Yet another argues that when the various biases are taken into account, the evidence for big-game specialization disappears (Cannon and Meltzer 2004).

So, is there any direct evidence for big-game hunting? Distinctive fluted Clovis points turn up at only a few proboscidean sites in the New World (G. Haynes 1991, 197). Although thirteen of the thirty-five extinct genera occur in archaeological contexts, Grayson and Meltzer (Grayson 1991, 212; 2001, 37; Grayson and Meltzer 2002, 2003) note that only fourteen North American kill sites provide evidence that Clovis hunters targeted mammoths and mastodons. Because other fauna such as horses and camels are well represented in the paleontological record of the late Pleistocene, their lack of association with kill sites cannot be attributed to sample bias. In brief, we have no direct evidence that Clovis hunters took any megafauna other than mammoths and mastodons. For some, the handful of proboscidean kill sites is too few to indicate a heavy human reliance on mammoth hunting (e.g., Meltzer 1993; Dixon 1999, 216).

But Martin (1973, 1984; Martin and Steadman 1999) argues that extinctions occurred so rapidly that they would have left little evidence of hunting (rendering this version of the overkill hypothesis untestable). Short-term events often leave little to no trace archaeologically (e.g., despite knowledge of their route and intensive searches, archaeologists have a hard time finding evidence of the Lewis and Clark expedition). This explanation for the lack of evidence has been unequaled.

Grayson and Meltzer (2004, 13; 2002a, 2002b) pointed out that the Clovis record is extraordinarily large compared to other sites, including a large number of kill sites.

What about extinctions and those in North America? Fiedel and Haynes (1994) concluded that not only are there no macrovertebrate sites, but certainly no pigs or horses.

Although the evidence suggests that the timing of extinctions (Brooks et al. 1997; Robert et al. 2000; and Brothwell and Field 2001), the timing of human arrival from 43,000 to 30,000 years ago (Johnson 2001) and a lengthy period (Brook and Bowman 1994).
with modern movements is difficult to cal record, be-ard large kill always survive vated decades that small fau-titative analy-s toward large specialists in the various alization dis-ictive fluted ew World (G. genera occur 91, 212; 2001, North Amer-mammoths nels are well ne, their lack sias. In brief, ifauna other roboscidian amoth hun-t that extinc- of hunting. Short-term e knowledge d time find-ation for the lack of evidence does not explain why only mammoth/mastodon kill sites have been unequivocally identified (Grayson 2001, 38).

Grayson and Meltzer’s argument and Martin’s counterargument are based on the assumption that fourteen is a “small” number. But Gary Haynes (1999, 13; 2002a, 2002b) argues that there are fewer elephant kill sites in all of Africa than in North America, despite Africa’s having a larger landmass and tens of thousands of years of human hunting of elephants. In comparison, the Clovis record is rich in proboscidean kill sites. Surovell and Waguespack (2004) likewise show that the density of Clovis proboscidean kill sites is extraordinarily high, whether landmass, time, or a combination of the two is considered, compared to the Old World. Fourteen might actually be a large number.

What about the evidence from Europe and Australia? Contra Martin, extinctions and extirpations did occur in Europe at about the same time as those in North America. These included large game such as Irish elk, reindeer, mammoth, saiga, and the giant deer (Grayson and Meltzer 2003; see Fiedel and Haynes 2004; Grayson and Meltzer 2004). Since humans had hunted these animals for millennia, hunting probably played no direct and certainly no primary role in their extinctions.

Although the record of megafaunal extinctions in Greater Australia suggests that the timing of human colonization of the region coincides with extinctions (Brook and Bowman 2002, 14626; Flannery and Roberts 1999; Roberts et al. 2007; Thorne et al. 1999; Turney et al. 2001; Webb 1998; Wroe and Field 2001), the record is still not thoroughly dated. This is complicated by the fact that, as is true for the New World, there is no consensus on the timing of human colonization of Greater Australia, with estimates ranging from 43,000 BP (O’Connell and Allen 1998) to 71,500 BP (Brook and Bowman 2002). As in North America, there are few unambiguous associations between megafauna skeletal remains and evidence of human activity (Johnson 2002, 2221; Miller et al. 1999). Some conclude that there was a lengthy period of overlap between humans and Australian megafauna (Brook and Bowman 2002; Roberts et al. 2007), which would argue against the blitzkrieg model of overkill. To an extent, what happened in Australia
does not matter, for the North American case must be resolved independent of the Australian one.

**Island Extinctions.** Mass extinctions on many Pacific islands occurred only a thousand to fifteen hundred years ago, coinciding with human colonization (Martin 1990, 199). The paleontological records of many islands throughout the Pacific indicate that catastrophic extinctions did indeed accompany human colonization (Martin 1990, 2002).

Olson and James (1982, 1984), for example, argue that Polynesians may have quickly brought about the extinction of more than half the native species of the Hawaiian Islands through human predation, competition, predation by introduced non-native fauna, and landscape changes caused by anthropogenic fires. Massive extinctions of land birds coincident with initial human colonization occurred on many oceanic islands (Grayson 2001, 29–30; Steadman 1995). A similar pattern of extinction and human colonization occurred on other islands, such as the West Indies (Steadman, Precill, and Olson 1984), Madagascar (Burney 1997, 1999; Dewar 1997a, 1997b), Corsica (Blondel and Vigne 1993; Vigne 1992; Vigne and Valladas 1996), and other Mediterranean Islands (Alcover, Seguí, and Bover 1999). Some researchers use this evidence as analogs of Clovis hunting in North America. Martin (1990, 196–98), in fact, argues against climatic change as a driving force behind extinctions because no severe changes in island fauna occurred during the late Pleistocene.

While Oceania provides evidence for the role of human colonization in faunal extinctions, island faunas are particularly vulnerable to anthropogenic ecological changes, which often result in extinction (Grayson 2001; Paulay 1994, 134; Simmons 1999; Steadman 1989, 178; Steadman et al. 1991, 126). Most islands were colonized not by hunter-gatherers but by horticulturalists whose lifeways (especially that of swidden horticulturalists) caused rapid and pervasive changes to the indigenous vegetation, especially by the burning and clearing of vegetation and by the introduction of non-native species that competed with native fauna. With small populations, a lack of defensive mechanisms, and, especially, no ready source of conspecifics to replenish diminished populations, island faunas are more sensitive to ecological disruption than continental faunas (Steadman 1989, 178; Steadman et al. 1991). With a larger faunal mass than on continents, extinctions brought about by the introduction of the bison, to the brink of extinction. As a result of the Pleistocene extinctions, it is difficult to envision species that did not undergo significant ecological changes. Thus, it is inapplicable to ecologists to consider extinctions on islands as if they were caused by human hunting.

**Ecology.** Other relationships that exist are those of a two-way relationship between human populations and the megafauna. Large herbivores and megafauna had a substantial impact on their ecosystems (G. Hay, 2000). The extinction of megafauna was a result of severe population pressure at the population changes. The ecological pressure caused by human hunting resulted in their extinction. This process is related to extinction (Owens, 1990).

For the key species, extinction of the megafauna may have been caused by hunting. But radiocarbon dating has shown that some species of mammoths survived well into the Pleistocene (Grayson 2001, 38; see 77).

To discover the causes of extinction of the megafauna, John T. Scott (1990) compared the Pleistocene faunas of the Americas, including those on Caribbean islands, with low reproductive
solved independently. Without guns, human predation has a different effect on island fauna than on continental fauna (with guns, obviously, Euro-Americans brought about the extinctions of some animals and drove others, such as bison, to the brink of extinction).

Because human colonization of North America occurred at the end of the last Ice Age, a time of enormous environmental change and human migration, it is difficult to isolate human involvement from environmental causes of extinction. But there is no evidence for significant human-induced vegetational change during Clovis times in North America (Grayson 2001, 42). Thus, it is inappropriate to use the documented fact of human-induced extinctions on islands as evidence that extinctions on continents were likewise caused by humans.

Ecology. Other arguments in favor of overkill explore the ecological relationships that existed among humans, megafauna, and the environment. Large herbivore feeding can actually increase an ecosystem’s primary productivity (G. Haynes 2002a, 392). Therefore, mammoth and mastodon extinction could have had significant ripple effects on North American ecosystems (G. Haynes 2002a, 408–9). Owen-Smith (1987, 1999) argues that megafauna were “keystone” species that increased diversity and carrying capacity at the patch level through their feeding, trampling, and wallowing. The ecological dependence of smaller fauna on the proboscideans resulted in their extinction when humans hunted mammoths and mastodons to extinction (Owen-Smith 1999, 67).

For the keystone hypothesis to explain the extinction event, however, mammoths and mastodons must have been the first fauna to go extinct. But radiocarbon data do not support this chronology; in fact, they suggest that mammoths and mastodons were some of the last species to go (Grayson 2001, 38; see Table 1).

To discover the characteristics that made certain species more susceptible to extinction, Johnson (2002) compares the characteristics of late-Pleistocene species that disappeared in Australia, Eurasia, the Americas, and Madagascar to those species that survived. He concludes that mammal species with low reproductive rates were more likely to become extinct, although
nocturnal and arboreal species that would have less contact with human hunters were more likely to survive. While his analysis does not support selective hunting of large-bodied species as the cause of extinction, and casts doubt on the blitzkrieg model, it does suggest that humans could have contributed to extinctions because even low-level hunting could severely affect species with low reproductive rates.

However, this explanation suggests that humans hunted animals to the point where the animals' numbers fell below a level of reproductive viability. This is difficult to square with what we know of foraging behavior. Ethnographic data show that foragers generally try to maintain as high a return rate as possible on their foraging efforts (Kelly 1995). For this reason, foragers abandon a habitat or drop an item from their diet when the benefits obtained from that habitat or item fall below the average return from harvesting other foods or searching other habitats. As resource density declines due to predation, foragers migrate or switch prey when the cost of foraging reaches a level that surpasses the cost of moving to a new territory, not when the animals became locally extinct (Kelly 1995, 80). Thus, Clovis (or any) hunters move before hunting a species to extinction, thus allowing a megafauna population to rebound (Webster and Webster 1984). Note that this is not because Clovis hunters wished to conserve their resource, but only to increase the return on their hunting efforts. (On islands, however, with limited places for hunters to go, this pattern could still result in extinction.)

Mithen (1997), however, argues that prey switching probably did not occur in the case of mammoth hunting if mammoth hunting was more of a prestige-oriented than a subsistence-oriented activity. The acquisition of ivory or vast amounts of meat could have conferred prestige on successful hunters (of course, we never will know if Clovis peoples considered proboscidian hunting prestigious or just “all in a day's work”). As mammoth populations diminished, there may have been an even greater demand for them. Mithen's computer simulation uses the sensitivity of mammoth populations to predation (due to long regeneration periods) to show that if mammoth hunting was intensive for even a short period, it may have been impossible for a population to recover.

Others argue that the overkill hypothesis is not optimal foraging or adaptive (Eiselt 1999). At the time, the environment was changing, and humans were abandoning a patch of Clovis hunters, who were so good at hunting at an age in the renegade period and thus would be concentrated in restricted areas for exploiting these resources. Eiselt (1999, 8) notes that responsible for low reproductive failure is dramatic change.

Thus, arguing that the overkill hypothesis is not responsible for the extinction of the mammoths and the extirpation of any of these species, Eiselt (1999) took other resources. At the moment, there is a hypothesis that the extirpation of any of the megafauna was due to a dramatic change, and that the overkill hypothesis is false.

The Hypervirulence Hypothesis
An interesting hypothesis is that the hypervirulence disease affecting the horse and other megafauna led to the megafauna extinction. The hypothesis is that the hypervirulence disease was transmitted by the same vector that transmitted the disease.
ith human support serves, and casts I have conceivably affect
als to the viable viability. Eth high a reason, n the ben- turn from density de- the cost of v territory, uis, Clovis hus allow- g84). Note resource, nds, how- ll result in lid not oc- more of a nition of successful id probosaur pop- for them. pulations mammoth impossible

Others argue that Clovis hunting of megafauna is compatible with optimal foraging theory (G. Haynes 1999; 2002a, 401–4; G. Haynes and Eiselt 1999). At the end of the Pleistocene, mammoths clustered into refugia due to environmental changes (G. Haynes 1999, 21; 2002a, 407). Instead of abandoning a patch when prey abundance fell, G. Haynes (2002a, 407) argues, Clovis hunters focused more heavily on megafauna hunting, choosing to forage in the remnant megafauna refugia where they knew megafauna would be concentrated and thus easier to locate. Concentrations of mammoths in restricted areas would yield greater return rates for human hunters exploiting these patches (G. Haynes 1999, 33; 2002a, 2002b; G. Haynes and Eiselt 1999, 83). Human hunting pressure could therefore have been responsible for late-Pleistocene extinctions of certain species—those with low reproductive rates who clustered in refugia during late-Pleistocene climatic change.

Thus, arguments derived from foraging theory can support or refute the overkill hypothesis. Although they help to guide thinking and models, they are not a substitute for the empirical record. But as noted above, that record’s interpretation is equally controversial and can be used to support an interpretation of Clovis hunters as large-game specialists or generalists. At the moment, all we can say is that Clovis hunters definitely took some mammoths and mastodons, but we have no direct evidence for the hunting of any of the other large fauna that became extinct. Clovis hunters also took other resources—plants and small game—but we don’t know if proboscideans were central or peripheral to diet. In sum, the jury is still out as to whether the archaeological record supports or refutes big-game specialization, and consequently on whether the record supports or refutes the overkill hypothesis.

The Hypervirulent Disease Hypothesis

An interesting alternative to the overkill model looks to humanly introduced disease as the culprit. MacPhee and Marx (1997) argue that the driving force behind late-Pleistocene extinctions was not hunting or ecological degradation but rather hypervirulent diseases (HVDs) introduced to the
native fauna by humans and/or their dogs. Hypervirulent diseases would have resulted in massive extinctions that closely coincided with initial human colonization—but without evidence of predation.

MacPhee and Marx (1997) argue that the HVD hypothesis explains the differential survival of r versus K-selected species. Young and old animals of large fauna with low reproductive rates (K-selected) would be especially susceptible to disease, resulting in smaller population sizes of large animals. In contrast, the life history characteristics of small-bodied fauna, such as higher reproductive rates that permit high degrees of mortality, would have protected these populations from disease-induced extinction (MacPhee and Marx 1997, 186). The HVD hypothesis also potentially explains the lack of abundant kill sites in the late-Pleistocene archaeological record of North America because the effects of human hunting would not have been severe; it is the mere presence of humans that matters in this explanation. Disease might also explain the fact that after initial human contact and significant faunal loss, the rate of extinction dropped abruptly and stayed low until recent times (MacPhee and Marx 1997).

The HVD model is an unlikely and, at present, inadequately tested explanation of extinctions (Alroy 1999; Burney 1999, 161; Owen-Smith 1999). Alroy (1999), for instance, argues that it fails to explain the intensity and body-size selectivity of late-Pleistocene extinctions. He also points out that mammals potentially carrying diseases immigrated into North America throughout the entire Cenozoic era without causing mass extinctions. By the time humans arrived in North America, fauna should have been exposed to many pathogens. Additionally, most mammalian diseases are restricted to a single order. There is no evidence of a deadly pandemic disease that is capable of spreading through populations of different orders such as would be required to explain the trans-taxonomic pattern of late-Pleistocene extinctions (Alroy 1999, 139). Lyons et al. (2004) point out that hypervirulent diseases are expected to attack animals of particular body size; thus, multiple diseases would be required to account for Pleistocene extinctions, and this seems unlikely.

The HVD hypothesis should be testable in that the pathogens responsible for mass extinction should be detectable in ancient DNA found in bones or tissues of descending animals. Empirical evidence suggests that there is no good evidence for the HVD hypothesis.

The Climatic-Aridity Hypothesis (VD) briefly in the literature-driven transition from proceeding warming at approximately 14,500 BP, climate

A cold pulse appeared (VD) briefly in the literature-driven transition from proceeding warming at approximately 14,500 BP, climate

Combining the two hypotheses, a period of megafauna extinctions throughout North America suggests that during the Pleistocene, faunal populations were more vulnerable to the effects of this drought. It is possible that Clovis times were characterized by a prolonged drought.

A common trait of this period is that the fauna th...
seases would explain the extinction of large ani-mal species was not exclusive to the Pleistocene. The extinction of large animals at the end of the Pleistocene is well documented. The extinctions of large mammals is thought to have been caused by a combination of factors, including climate change, overkill by humans, and disease. The overkill hypothesis suggests that humans hunted large mammals to extinction. However, it is not clear to what extent overkill contributed to the extinctions. Disease is another factor that may have contributed to the extinctions. The remnants of large mammals in the Pleistocene record suggest that some species may have been affected by diseases with high initial host specificity before the initial host died. The disease would then have spread to other species, resulting in the extinction of those species. The hypothesis that disease was a major factor in the extinction of large mammals in the Pleistocene is supported by the fact that disease has been identified in the bones of many large mammals from the Pleistocene period.

The Climatic-Change Hypothesis
The late Quaternary was a time of frequent climatic fluctuations during the transition from glacial to interglacial conditions, with an overall trend toward warming (Bond and Lotti 1995; Dansgaard et al. 1993; Grayson 1984a, 2001; Mayewski et al. 1993). During the full glacial, mean annual temperatures were as much as 5–7°C colder than modern temperatures. Around 14,500 BP, climatic warming began and glacial ice ablated (Wright 1993).

A cold pulse at the end of the Pleistocene known as the Younger Dryas (YD) briefly interrupted this warming trend. The YD was a Northern Hemisphere-driven cold event that reversed warm and wet conditions beginning at approximately 11,100/11,300 BP and ending around 10,000 BP (G. Haynes 2002a, 393). The climatic warming at the end of the YD cannot be the cause of the extinctions, as most extinctions were already complete by about 12,000 BP. Nor can the YD account for those extinctions that occurred before 12,000 BP. If anything, the onset of the YD might be responsible for the extinction of those animals that survived beyond 12,000 BP, and that would be odd because it would mean that species that survived for millennia in glacial conditions were done in by cold conditions.

Combining the overkill and climatic arguments, C. V. Haynes (1984, 1991) sees a period of desiccation and drought during the terminal Pleistocene throughout North America. This drought period appears to coincide with megafauna extinctions as well as the appearance of Clovis hunters. Haynes suggests that drought may have concentrated physiologically stressed megafaunal populations at water holes, making them easier prey for hunters (C. V. Haynes 1991, 447). However, Holliday (2000a) is unable to find evidence of This drought on the southern High Plains; instead, the evidence suggests that Clovis times were quite wet and that the succeeding Folsom times were characterized by periodic drought.

A common argument against climate change as a cause of extinction is that the fauna that became extinct at the end of the Pleistocene had survived
some nine glacial-interglacial cycles over the past 700,000 years and must therefore have been able to adapt successfully to changing environmental conditions (Martin and Steadman 1999; Fiedel and Haynes 2004). However, terminal-Pleistocene climatic change may have been unlike past climatic changes in its form, rapidity, and intensity (Guthrie 1984, 291), especially during the YD. For example, unlike any previous climatic warming, the terminal Pleistocene was followed by the Holocene (ca. 10,000 BP−present), a relatively warm and climatically stable period (Bond and Lotti 1995).

In fact, paleontological data point to environmental change at the end of the Pleistocene that was unlike any other climatic warming. Proponents of the overkill hypothesis tend to focus solely on the fate of large mammals, but the extinction of these fauna coincided with significant geographic re-shuffling of many smaller species (FAUNMAP Working Group 1996; Grayson 1991, 214; 2001, 39; Stafford et al. 1999) and a fundamental reorganization of vegetation communities.

Many late-Pleistocene mammal communities have no modern analogs (FAUNMAP 1996, 1605; Graham and Lundelius 1984; Grayson 1991; Guthrie 1984; Lundelius 1989). Late-Pleistocene faunal assemblages show that many species lived cheek by jowl that are separated today by elevation or latitude (Grayson 1991, 213). The combinations of taxa present in the Pleistocene no longer exist, leading to the terms “disharmonious” (Graham and Lundelius 1984) or “intermingled” (Lundelius 1989) to describe them. For example, the yellow-checked vole today lives only in Alaska, and the western pack rat only in the western United States, but in the late Pleistocene both lived together in many localities including those outside their current ranges, such as Tennessee. Intermingled late-Pleistocene faunal assemblages are known from virtually all areas of the world that are represented by adequate data, including North America, Australia, southern Africa, and Eurasia (Graham and Lundelius 1984; see review in Guthrie 1984, 263−66; Lundelius 1989). These intermingled communities disappear at the same time that extinctions occur (Lundelius 1989, 415).

Frankly, we don’t know if this correlation is significant. The terminal Pleistocene saw a reduction in arid grasslands and homogeneous vegetation communities that geographically diversified in response to climatic change. The current latitudinal diversity in choice loci for food and shelter is the result of competition for efficient food sources (Guthrie 1988). The correlation between megafaunal extinctions and available nutrients is a result of population reduction in response to a reduction in smaller mammals and an increase in geographic threats.

Guthrie (1989) states that many plants and animals are doomed to extinction and not because they are less viable than their Pleistocene analogs, but because they could not obtain shelter and food. As plant diversity declines, allochemically defined insular communities develop. Competitive ability is a function of the poorly understood genetic relationships of these insular communities.

Gary Haynes (1989) points out that the mammals of the Pleistocene had no evidence of incipient extinction. This statement is underpinned by the fact that the late-Pleistocene fauna was large, with body size just products of declining competition.
communities and biomes, the latter marking a transition from a "plaid" to a latitudinal "band" plant distribution. Graham and Lundelius (1984) argue that geographic range restrictions coupled with decreasing plant community diversity may have contributed to extinction by increasing competition in choice locales, making it more difficult for megafauna to consume sufficient food for the winter (Grayson 1991, 216; Graham and Lundelius 1984; Guthrie 1984). Decreased diversity in local vegetation increased competition between large monogastrics (mastodons, mammoths, rhinos, large edantes, and horses) and ruminants (moose, deer, and bison) and reduced available nutrients for the former (Guthrie 1984, 284-85, 263). Thus, a reduction in range would have had a greater effect on megafauna than on smaller mammals, and once populations dropped below a critical demographic threshold, the species was doomed to local extinction.

Guthrie (1984) also suggests that the antiherbivory defense systems of many plants shifted to ones of increased toxins. Those mammals that were doomed to extinction were, for the most part, adapted to plants that were not allochemically well defended by having a tolerance for stems, which was then supplemented by other better-defended plant parts. Thus, animals could obtain adequate nutrition by mixing plant parts and diluting toxins. As plant diversity decreased, these mammals had to rely more heavily on allochemically defended plants. As a result, the mammals ingested more toxins than they could combat, resulting in reduced metabolic function, competitive abilities, and reproductive success. Thus, very complex and as yet poorly understood changes in vegetation communities (that have no modern analogs) could have brought about the late-Pleistocene extinctions.

Gary Haynes argues against the climate-change argument by pointing out that fossils of extinct large mammals from the late Pleistocene show no evidence of climate-induced stress in the form of poor health (2002a, 392; Fiedel and Haynes 2004). However, Guthrie (2003) has shown that late-Pleistocene horses in Alaska underwent a clear and rapid reduction in body size just prior to extinction. If this reduction in body size was a product of declining forage abundance and quality, then Guthrie’s is the first
demonstration of environmentally induced biological stress on a Pleistocene megafauna species.

We suspect that climate change is the most parsimonious and likely cause of late-Pleistocene extinctions in North America. Humans may have helped the process along in places, but it is likely that the result would have been the same even if human hunters were not present. The climatic-change hypothesis, however, is by no means proven and requires further testing.

Conclusion

Jefferson was wrong; extinctions do occur. In fact, 99 percent of all animal species that have ever existed on earth are extinct; death is an integral part of life. If the ancestors of Native Americans had never made it to the New World before Europeans arrived in the sixteenth century, would the French, British, and Spanish have brought back drawings of mammoths and mastodons instead of beavers and bison? Would Leclerc have changed his mind? Could Jefferson have stabled live pachyderms and ground sloths in the White House instead of just their skeletons? We suspect that the answer to these questions is no, because climate change is the most likely explanation for the extinction of North American megafauna. But we admit that we simply don't know the answer yet. It remains unknown whether human hunters, climatic change, or disease was the sole cause or whether they worked together.

Nonetheless, can we learn any lessons from what we do know of the events of ten thousand years ago? First, since the jury is still out on whether human hunting caused the extinctions, it is irresponsible for ecologists to point to the late-Pleistocene and Native American hunting practices as a warning of things to come if industrial society does not repent. For that lesson we need look no further than what almost happened to the American bison, and what did happen to the passenger pigeon.

And, therefore, it is also wrong to use Pleistocene extinctions as evidence that Native Americans are not capable of environmental stewardship. But what if we do discover incontrovertible evidence that the ancestors of Native Americans hunted mammoths and mastodons to extinction? In fact, it is already clear that such as the early Pleistocene ecosystems, some of the major processes leading to biological stress on the late-Pleistocene megafauna. For example, it is likely that Pleistocene megafauna populations were already in decline as a result of climate changes (e.g., DeMartin, 1993, 1994). We must now come to terms with the fact that we are facing extinctions.

At the same time, there are societies that are living in harmony with nature, such as the contemporary Pueblo and Hopi, but everyone is not so wise. We all need to understand the consequences of our actions and learn from history. We need to consider the possibilities that we are facing.

Second, if the Pleistocene megafauna extinctions are major factors in shaping the world we know, what we know of the impact of climate change appears to have been significant deception in the late-Pleistocene megafauna. Climate change must be an object of public concern.

Third, this case study in the environment; there has been no “natural” extinction. Over the course of ten thousand years, if by natural extinction, it may have been an abnormally low population.
is already clear from island archaeology and paleontology and from cases such as the passenger pigeon and dodo bird that all peoples are capable of bringing about extinctions. And North American archaeological studies that focus on later time periods show that local extinctions or extreme depletions can result from long-term (hundreds of years) sustained human hunting (e.g., Broughton 2002; Hildebrant and Jones 2002). Native Americans did cause extirpations in many cases. Likewise, ethnographic studies of foraging peoples show that hunters aim to maximize the return rate from foraging regardless of the conservation consequences (e.g., Alvand 1993, 1994). Where hunters are geographically constrained, their efforts to maintain a high return from their hunting efforts will inevitably bring about extirpation and possibly extinction.

At the same time, we see explicit and effective efforts in many indigenous societies that aim to increase biodiversity and conserve resources (e.g., Minnis and Elisens 2000; Murray 2003). No one is naturally a conservationist, but everyone is capable of becoming one. Rather than argue about whether one human group is or is not inherently conservationist, it is better to understand the conditions under which conservation behaviors are prestigious and desirable, and when short-term needs relegate them to long-term luxuries that a society cannot afford (see, e.g., Zavaleta 1999).

Second, if the climate-change argument is correct, then we see from the Pleistocene case that habitat degradation and geographic range restriction are major factors in the extinction process. This is commensurate with what we know of other instances of extinction, such as on islands. Climate change appears to have produced habitat degradation and range restriction in the late Pleistocene, but today such effects are often a result of human activities. Clearly, aiming for zero loss of habitat and range reduction must be an objective of development.

Third, this case study reminds us that humans are an integral part of the environment; they were in the late Pleistocene, and they are today. There has been no "natural" environment anywhere on earth for the last ten thousand years, if by "natural" we mean "no human presence." Even at relatively low population densities, humans can have large and long-standing
effects on the environment. Sometimes these effects have produced environments that we now take to be natural and desirable. Through their use of fire, for example, Native North Americans probably produced the extensive oak forests of the eastern United States that we fight to maintain today; the same is probably true of the extensive eucalyptus forests in northern Australia. Humans are part of the environment. We change it, just as mammoths changed it by fertilizing it with their dung, tramping around bogs, and eating grass. Like mammoths and ground sloths, we could become extinct by environmental changes that are beyond our control—a meteor, perhaps—or we could become extinct through more subtle environmental changes that derive from our presence and behavior.

Unlike mammoths and ground sloths, however, we have a choice. And it is wiser to spend our time deciding what that choice will be (free-ranging elephants in Kansas?) and how we will attain it than to argue about whether one group of people is inherently better suited to make that choice than another. We would like to think that Thomas Jefferson, had he known what archaeologists and paleontologists know today, would come to the same conclusion.

Notes
1. The September 2003 judicial decision (upheld by the appeals court in February 2004) that the ninety-four-hundred-year-old Kennewick skeleton is not Native American might suggest to some that the earliest inhabitants of North America were not ancestral to modern Native Americans, making this statement irrelevant. Space does not permit us to present the argument here, so it will have to suffice to say that this judicial opinion is not coeval with a scientific one, and that arguing that Kennewick cannot be proven to be ancestral to Native American under federal law (Native American Graves Protection and Repatriation Act) does not mean that he was not Native American (see Kelly 2004).
2. There are a few "late" mammoths, e.g., the Fettman mammoth in Wyoming, which dates to about 9000 BP (Byers 2002); these are outliers, and it is assumed that some unknown biochemical process has affected the radiocarbon dates.
3. However, the uniqueness of the late Pleistocene's climate change may be a function of the fact that we have a much more fine-grained and more intensively studied record than for the previous climatic changes.

References


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5. Rationality

Some Propositions

Ernest S. Gellner

It is axiomatic that societies that interact by apes is correct, it should mean approaches to the relationships with the new assert empirically and are associated with different empirical findings and rounding associations.

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