

Native Americans and the Environment

Perspectives on the Ecological Indian

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4. Did the Ancestors of Native Americans Cause Animal Extinctions in Late-Pleistocene North America?

And Does It Matter If They Did?

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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 counterargument 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).

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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.¹ 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; Holliday 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).

Order	Family	Genus	Common name	Youngest good date
Artiodactyla	Antilocapridae	<i>Capromeryx</i>	Diminutive pronghorn	None
		<i>Tetrameryx</i>	Shuler's pronghorn	None
		<i>Stockoceros</i>	Pronghorns	None
	Bovidae	<i>Saiga</i>	Saiga	None
		<i>Euceratherium</i>	Shrub ox	None
		<i>Bootherium</i>	Harlan's musk ox	None
	Camelidae	<i>Camelops</i>	Yesterday's camel	10,900 ± 750
		<i>Hemiauchenia</i>	Large-headed llama	None
		<i>Palaeolama</i>	Stout-legged llama	10,890 ± 130
	Cervidae	<i>Cervalces</i>	Elk-moose	None
		<i>Navahoceros</i>	Mountain deer	None
		Tayassuidae	<i>Mylohyus</i>	Long-nosed peccary
	<i>Platygonus</i>		Flat-headed peccary	None
Carnivora	Canidae	<i>Cuon</i>	Dhole	None
	Felidae	<i>Homotherium</i>	Scimitar cat	None
		<i>Miracinonyx</i>	American cheetah	None
		<i>Smilodon</i>	Sabertooth	11,130 ± 275
	Mustelidae	<i>Brachyprotoma</i>	Short-faced skunk	None
	Ursidae	<i>Arctodus</i>	Giant short-faced bear	None
<i>Tremarctos</i>		Florida cave bear	None	
Lagomorpha	Leporidae	<i>Aztlanolagus</i>	Aztlan rabbit	None
Perrisodactyla	Equidae	<i>Equus</i>	Horse	10,370 ± 350
	Tapiridae	<i>Tapirus</i>	Tapir	10,900 ± 450
Proboscidea	Elephantidae	<i>Mammuthus</i>	Mammoth	10,550 ± 350
	Mammutidae	<i>Mammut</i>	American mastodon	10,395 ± 110
Rodentia	Castoridae	<i>Castoroides</i>	Giant beaver	None
	Hydrochoeridae	<i>Hydrochoerus</i>	Holmes's capybara	None
		<i>Neochocerus</i>	Pinckney's capybara	None
Xenartha	Pampatheriidae	<i>Holmesina</i>	Northern pampathere	None
		<i>Pampatherium</i>	Southern pampathere	None
	Glyptodontidae	<i>Glyptotherium</i>	Simpson's glyptodont	None
	Megalonychidae	<i>Megalonyx</i>	Jefferson's ground sloth	12,190 ± 215
	Megatheriidae	<i>Eremotherium</i>	Rusconi's ground sloth	None
		<i>Nothrotheriops</i>	Shasta ground sloth	10,035 ± 250
Mylodontidae	<i>Glossotherium</i>	Harlan's ground sloth	20,450 ± 460	

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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 Szuter 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 critchfieldii*) 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

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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 11,500–10,900 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

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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 megafaunal 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).² The paleontological 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, Waguespack, 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, Waguespack, 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).

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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; Hudecek-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

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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. 2001; 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. 2001), 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, Pregill, 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

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et al. 1991). 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 proboscidean 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.

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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

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or tissues of extinct fauna. To date, researchers have not found any direct empirical evidence of HVD in extinct late-Pleistocene mammals. In sum, there is no good evidence to support the HVD hypothesis.

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 11,000 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.³ 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 reshuffling 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, 215). 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-cheeked 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 and a latitudinal “bottleneck” that geographic community diversity may have influenced in choice localities for sufficient food for survival (Guthrie 1984). The distinction between late Pleistocene predators, and how they affected available nutrients, and the reduction in range of smaller mammals across geographic thresholds.

Guthrie (1984) argued that many plants that were doomed to extinction were not allochemically defended, and was then supplemented by plants that could obtain adequate nutrients. As plant diversity declined, allochemically defended plants had more competitive abilities, but their competitive abilities were poorly understood (Guthrie 1984, 291; see review in Grayson 1991, 215). (Guthrie 1984, 291; see review in Grayson 1991, 215). (Guthrie 1984, 291; see review in Grayson 1991, 215).

Gary Haynes argued that there is no evidence of climate change (Haynes 1991, 392; Fiedel and Haynes 1991, 392; Fiedel and Haynes 1991, 392). (Haynes 1991, 392; Fiedel and Haynes 1991, 392; Fiedel and Haynes 1991, 392). (Haynes 1991, 392; Fiedel and Haynes 1991, 392; Fiedel and Haynes 1991, 392).

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 edantines, 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 past bringing about that focus on completions can result in hunting (e.g., Native Americans did cause extinctions of foraging species from foraging (1993, 1994). We need to maintain a focus about extirpation.

At the same time, societies that are not as rich as the Inuit and the Eskimo, but everyone is trying to understand the consequences of a more desirable, and a society that is more

Second, if the extinctions of the Pleistocene are major factors in what we know of climate change appears to be a result of human activities. Climate change must be an objective

Third, this case is a warning to the environment; there has been no "natural" extinctions in the last thousand years, if by a relatively low popula-

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., Alvard 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 climatic-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, tromping 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 2002 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 Fetterman 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.

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