

DECIPHERING NORTH AMERICAN PLEISTOCENE EXTINCTIONS

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The debate over the cause of North American Pleistocene extinctions may be further from resolution than it has ever been in its 200 year history and is certainly more heated than it has ever been before. Here, I suggest that the reason for this may lie in the fact that paleontologists have not heeded one of the key biogeographic concepts that they themselves helped to establish: that histories of assemblages of species can be understood only by deciphering the history of each individual species within that assemblage. This failure seems to result from assumptions first made about the nature of the North American extinctions during the 1960s.

There is probably no archaeologist, paleontologist, or ecologist who is not aware of the debate that rages over the causes of the massive extinctions that occurred in North America toward the end of the Pleistocene. Were they, as some claim, caused entirely by human predation? Or were they, as others argue, caused entirely by climate change or, as still others suspect, by some combination of these and/or other factors? This is a debate that has its roots in the late 18th century but that appears further from resolution than it did over a century ago (Grayson 1984).

I have long participated in this debate, but my goal here is not to take sides (see Grayson 2001, 2006b and Grayson and Meltzer 2002, 2003 for recent side-taking). Instead, I will argue that the debate is not likely to be solved unless we take to heart, and act on, one of the prime lessons taught us by historic biogeography during the past 50 years: that understanding the histories of assemblages of species requires that the history of each of those species be analyzed on its own. The benefits of this approach are clearly shown by contrasts between our understanding of the North American losses and the roughly comparable extinctions that took place in Eurasia. The former remain unexplained, but there is only muted debate over the causes of the latter. Recent advances in understanding Eurasian extinctions provides a research guide for extracting ourselves from the explanatory morass that now characterizes the North American situation.

THE PROBLEM

Although all archaeologists and life scientists are familiar with the general nature of the debate over the North American extinctions, they are generally not familiar with the empirical details of the situation here or in Eurasia. Since an acquaintance with those details is essential for understanding why our comprehension of the North American losses lags so far behind that of the Eurasian ones, I provide a synthesis of them.

North America

Toward the end of the Pleistocene, North America lost some 35 genera of mostly large mammals, either in the sense that they became globally extinct at that time (29 genera), or in the sense that they became extinct in North America while living on elsewhere (6 genera; see Table 1). While some of these animals were quite small—for instance, the short-faced skunk, the Aztlan rabbit, and the 15 kg diminutive pronghorn (Kurtén and Anderson 1980; Scott 1983)—most were large and some were immense. The ground sloth *Eremotherium*, for example, combined the height of a giraffe with the bulk of an elephant, and the largest short-faced bears may have weighed 1000 kg (Christiansen 1999). Most of the now-extinct forms were herbivores, but there are also seven genera of carnivores on the list, as well as two extinct carnivore species that belong to genera that still occur in North America: the American lion *Panthera leo* (or *P. atrox*: see Burger et al. 2004; Sotnikova and Nikolskiy 2006) and the dire wolf *Canis dirus*.

The mammals were not alone in suffering such extinctions. Some 19 genera of birds were also lost during the North American late Pleistocene. While nine of these were predators or scavengers whose extinction may have been driven by the loss of large mammals, the others ranged from storks and flamingoes to shelducks and jays (Emslie 1998; Grayson 1977; Van Valkenburgh and Hertel 1998). There was even a species of tree—the spruce *Picea critchfieldii*—that disappeared as the North American Pleistocene ended (Jackson and Overpeck 2000; Jackson and Weng 1999).

At the same time as these extinctions were occurring, other animals were undergoing often-massive distributional changes. Caribou (*Rangifer tarandus*), for instance, are known from as far south as northern Mississippi during the late Pleistocene and muskoxen (*Ovibos moschatus*) from as far south as Tennessee (FAUNMAP 1994; McDonald et al. 1996, 2000). Very small mammals, which underwent no extinctions, also moved dramatically across space as the Pleistocene ended. For instance, during the late Pleistocene, Tennessee was home to both the taiga vole *Microtus xanthognathus* and the heather vole *Phenacomys intermedius*. Today, the taiga

vole is found no further south than central Alberta and the heather vole no further south than the Canadian border in eastern North America (FAUNMAP 1994; Stafford et al. 1999).

Of the 35 genera involved, we know that populations belonging to 16 genera survived in some parts of North America until between 12,000 and 10,000 radiocarbon years ago (see Table 2; all dates in this paper are in radiocarbon years). However, in almost no case can we show that *all* North American populations of a given animal were lost during this period, and we cannot estimate the time of extinction for the remaining 19 genera. It remains fully possible that the North American losses were time-transgressive, just as we now know they were in Eurasia (see below).

Nonetheless, and for reasons I will discuss, it is routinely assumed that all of the losses in all places occurred between 12,000 and 10,000 years ago. This interval includes substantial climate and vegetational change, including the Younger Dryas cold episode (Broecker 2006). It also includes the earliest secure evidence for the presence of people here, provided by the famous Clovis archaeological phenomenon, generally dated to 11,570 – 10,900 yr BP (Meltzer 2004; the suggestion that Clovis may instead date to 11,050 to 10,800 yr BP [Waters and Stafford 2007] requires, among other things, rejecting the 11,570 yr BP date from the Aubrey site [Ferring 2001; Humphrey and Ferring 1994]).

Because of this conjunction—the presumed time of extinction coincides with impressive climatic and vegetational change and with a possible human colonization event—there exists a chaos of conflicting attempts to account for whatever it was that happened in North America toward the end of the Pleistocene. All of the obvious candidates—climate change and its effects, human predation (“overkill”) and various combinations of these variables—are well-represented in the literature (see the excellent reviews in Barnosky et al. 2004 and Koch and Barnosky 2006). Less obvious candidates have had their supporters as well, including disease (MacPhee and Marx 1997) and an extraterrestrial impact event (Firestone and Topping 2001; J. Kennett, pers. comm. 2007).

Eurasia

In many, but not all, ways, the situation in Europe and northern Asia was similar. Although there were fewer genera lost here (Table 3), the end of the Eurasian Pleistocene was also a time of mammalian extinction and of massive changes in mammal distributions, as can be seen by looking at almost any area within this vast region. Table 4, for instance, lists the larger mammals known from the late Pleistocene of southwestern France, many of which were as large as those lost in North America. Of these 21 taxa, ten are either extinct or no longer exist in this part of the

world. The closest reindeer are in Scandinavia, the closest saiga in central Eurasia, and the closest muskoxen in North America.

As in North America, range adjustments and extinctions among large mammals were accompanied by huge range changes among small mammals toward the end of the Pleistocene. The Arctic fox *Alopex lagopus* is common in the late Pleistocene faunas of southwestern France but today the closest populations are in Scandinavia. The narrow-headed vole *Microtus gregalis* is known from a substantial number of late Pleistocene sites in this region, but is now found no closer than Siberia and China (Delpech 1983; Gromov and Palyakov 1992). Much the same is true for the British Isles (Coard and Chamberlain 1999; Stuart 1995), Spain (Altuna 1996; García and Arsuaga 2003), Italy (Bedetti, Palombo, and Sardella 2001) and elsewhere.

Although it was at one time assumed that most or all of the Eurasian extinctions occurred synchronously at the end of the Pleistocene (e.g., Kowalski 1967), it is now clear that this was not the case. Mammoths seem to have been lost from significant parts of Europe at or soon after 12,000 years ago (and perhaps much earlier from Iberia), but to have lasted until 10,000 years ago in Estonia, until shortly after 10,000 years ago on mainland northern Siberia and on the north Russian Plain, and until shortly after 4000 years ago on Wrangel Island in the Arctic Ocean (Arslanov et al. 1998; Boeskorov 2006; Lõugas, Ukkonen, and Jungner 2002; MacPhee et al. 2002; Orlova et al. 2004; Stuart 2005; Stuart et al. 2002; Stuart et al. 2004; Vartanyan et al. 1993). Similarly, the giant deer *Megaloceros giganteus* seems to have disappeared from southwestern France between 12,000 and 11,000 years ago but from the Urals and western Siberia after 7000 years ago (Delpech 1999; Stuart et al. 2004). The muskox seems to have disappeared from southwestern France at around 19,000 yr BP (Delpech 1999) but survived in northern Siberia until at least 2700 years ago and perhaps well beyond that.

That is, in Europe and northern Asia, different taxa were lost at different times at different places toward the end of the Pleistocene. Indeed, the same phenomenon can be seen at single places as long as sufficient work has been done to construct a reliable chronology. In southwestern France, for instance, muskoxen were gone by 19,000 years ago, woolly rhinos by about 15,000, mammoth shortly after 12,000, and reindeer by about 11,000 (Delpech 1999; see Figure 1). That the Eurasian losses occurred in piecemeal fashion is agreed by all (e.g., Martin 2005; Stuart 1999; Stuart et al. 2004).

As in North America, the end of the Eurasian Pleistocene was also a time of significant vegetational and climatic change. Unlike North America, Eurasia has an archaeological record extending deep into the Pleistocene,

with the earliest well-dated archaeological site (Dmanisi, Georgia) some 1.75 million years old (Vekua et al. 2002). In addition, no extinctions are evident as modern humans enter Eurasia after 50,000 years ago (Trinkaus 2005). That is, even though they share many similarities with the North American extinctions, the Eurasian losses do not coincide with a distinctive human colonization event. As a result, climate-based (e.g., Delpech 1999) and multivariate explanations that include some role for human impacts (e.g., Stuart 1999) are common for these extinctions.

This, then, is the problem. Eurasia and North America saw substantial extinctions and extirpations toward the end of the Pleistocene. These are known to have been asynchronous in the former region and are routinely assumed to have been simultaneous in the latter. Eurasia has a lengthy archaeological record; North America, a record that extends securely no further back than the time of at least some of the extinctions. No one attributes the Eurasian extinctions to human impacts alone, but many continue to argue that the North American extinctions were due entirely to such impacts. Others strongly disagree.

THE CHRONOLOGY OF NORTHERN HEMISPHERE EXTINCTIONS

As I have mentioned, only 16 of the 35 North American genera can be shown to have survived beyond 12,000 years ago. Even for these 16, extinctions may well have occurred much earlier in some parts of North America than in others, just as happened in Europe. Nonetheless, it is widely believed that all the extinctions everywhere occurred between 12,000 and 10,000 years ago. This belief strongly dictates our approach to the extinctions. Perhaps most importantly, it provides a rationale for treating the extinctions as a discrete event, rather than approaching each loss on its own. The history of attempts to establish a North American extinctions chronology during the radiocarbon dating era provides insights into why this critical belief is so strongly held.

In the first thorough review of radiocarbon dates associated with the extinct North American mammals, Martin (1958) concluded that the losses began in Mexico and Alaska during the Pleistocene and ended in Florida perhaps as recently as 2000 years ago (1958:405). Soon after, however, Hester (1960:58) concluded that the great majority of herd animals seemed to have been lost swiftly and together around 8,000 years ago even if some, like the mastodon, may have lingered on beyond then. Hester was thus the first to suggest, based on radiocarbon evidence, that a significant number, if not all, of the North American extinctions were synchronous.

Although Martin (1963) continued to suggest that at least some of the extinctions had been time-transgressive, he was soon to change his mind. That change was due to the work of his colleague C. V. Haynes. Haynes (1964)

established that the earliest securely-known North American archaeological sites—Clovis—dated to between 11,500 and 11,000 years ago. This conclusion has, with minor modification, endured (Meltzer 2004; Waters and Stafford 2007). Haynes (1964: 1412) also observed that there appeared to have been “a marked decline” in mammoth abundance after 11,000 years ago, and that archaeological sites that followed Clovis lacked the remains of this animal.

Although Haynes (1964:1412) considered the cause of the extinctions to be “moot,” his message about Clovis chronology and mammoth extinction was not lost on Martin (1967). Armed with Haynes’ demonstration that mammoths had lasted until about 11,000 years ago but not much, if any, beyond that, Martin’s new reading of the radiocarbon data led him to conclude that “the main wave of extinction . . . appears to have occurred around 11,000 year B.P.” (1967:89). Martin had long believed that people lay behind the extinctions, even when, as in 1958, he believed that the losses had been spread across 10,000 years or more. Now, he used the coincidence of Haynes’ 11,500 – 11,000 yr BP date for Clovis (see also Haynes 1967) with his new 11,000 year date for the extinctions to argue that the former explained the latter.

An important aspect of the current view of the North American extinctions had now fallen into place. The extinctions had occurred as a “swift and sudden decline of all types” (Hester 1960:58).

Had the radiocarbon chronology become so strong in such a short period that this conclusion followed from it? It had not. Of the 34 genera on Martin’s list, he was able to provide dates of between 12,000 and 10,000 years ago for only 13. Based on these 13, he concluded that the remaining 21 had been lost at this time as well.

Why did Martin (1967) make this inferential leap? And why did he conclude that the latest date for a particular animal implied that that animal had become extinct everywhere at that time? Given that Martin now focused on Clovis as the cause, and that Clovis had now been dated to ca. 11,000 years ago, it followed to him that all of the extinctions must have occurred at this time. For Martin, dates for the extinctions followed from their explanation, at the same time as that explanation was meant to account for the dates. Martin (2005:136) is admirably explicit about this purposeful circularity.

He was not alone in doing this. Although the 11,000 year date pegged by Martin coincided with Clovis, it also coincided with evidence for significant climate change (e.g., Adam 1967; Davis 1967; Ogden 1967). Since people and/or climate seemed to provide the only options for explaining the losses and that both explanations saw 11,000 yr

BP as the critical time, there was now little reason to question that all of these losses had occurred rapidly and together at the very end of the Pleistocene. This belief soon permeated the literature.

In other words, the widely-accepted chronology for the North American extinctions has in large part been inferred from the explanations that are available for those extinctions. As a result, we assume that the extinctions had a breadth (35 genera) and rapidity (perhaps a few hundred radiocarbon years) that they may or may not have had (Grayson 1991). Tightly related to this is the assumption that all of the losses can legitimately be treated as a linked set and that explanations that apply to one or a few of the animals will likely apply to all of them. That, as Robert Frost might have said, has made all the difference.

INDIVIDUALISTIC SPECIES RESPONSES

As these developments in our perception of North American Pleistocene extinctions were occurring, important changes were taking place in the way American ecologists were conceptualizing biotic communities and their history. By the mid-1950s, detailed studies of eastern North American forests had shown that “species distributions are individualistic in the sense that each species is distributed according to its own way of relating to the range of total environmental circumstances” (Whittaker 1957:199).

This conclusion represented a forceful rejection of the influential views of Frederick E. Clements, who had seen a climax plant community as “a complex organism inseparably connected with its climate,” the inherent unity of which “rests upon the fact that it is not merely the response to a particular climate, but is at the same time the expression and indicator of it” (Clements 1936:254). As the emerging consensus led to the rejection of the Clementsian holistic view of the nature of plant communities, it also accepted the radically different view espoused by Henry A. Gleason. This approach argued that “every species of plant is a law unto itself, the distribution of which in space depends on its individual peculiarities of migration and environmental requirements” (Gleason 1926:26). Gleason (1926:16) famously referred to this view as “the individualistic concept of the plant association” (see Nicolson 1990 for a general history of this concept).

Although the rejection of Clements’ views during the 1950s was based on observations of modern plant communities, it did not take long for paleobotanists to observe that the detailed vegetational histories they were constructing for eastern North America fully supported this rejection. Cushing (1965), for instance, noted that the further back in time one looked in pollen records, the weaker became any analogy with modern vegetation, just as one would infer from Gleason’s notions (see also Davis 1965; Whitehead 1965; Grimm and Jacobsen 2004). By

1976, Margaret Davis was able to observe, without controversy, that eastern deciduous forest communities “are a recent, chance conglomeration of species of trees that have immigrated into the area from different directions” (1976:23). The days of “accordion phytogeography”, in which entire plant communities were seen as moving, compressing, and expanding in response to climate change, were over.

It took longer for this view to penetrate the communities of scientists working on North American mammal faunas. Beginning in the 1970s, vertebrate paleontologists began to notice exactly what paleobotanists had noted before them: that individual species of mammals seemed to be responding to climate change in very individualistic ways. The same phenomenon had been noted for the European Pleistocene a century earlier (Grayson 1984), but this time the observation was accompanied by far greater stratigraphic and chronological precision (e.g., FAUNMAP 1996; Graham 1976, 1985, 1988, 1992). Today, thanks largely to arguments made on the basis of the paleontological record, all ecologists and paleoecologists seem to agree that understanding the past and future of any given set of mammals requires that the history of each species of mammal in that set be analyzed on its own, independent of the history of every other species in that set (e.g., Brown 2004; Hewitt 2000).

No one has ever thought that the late Pleistocene mammals of North America belonged to a single interacting biotic community. Nonetheless, in assuming that all of the North American extinctions occurred at the same time and that what caused the extinction of one of the large herbivores caused the extinction of all the others, many scientists have come close to doing just that. At the same time, they have set aside a position established in paleontology over 30 years ago: understanding the structure of assemblages of species requires that the history of each species in that assemblage be studied on its own. The fact that those interested in explaining the late Pleistocene North American losses have so routinely made these twin assumptions may well explain why there is so little agreement on the cause of the extinctions.

In short, North American paleontologists were in the forefront of establishing the reality of “Gleasonian individualism” in mammalian responses to environmental change yet they have not brought that approach to understanding the late Pleistocene extinctions of North American mammals. Since we seem to be no closer to resolving the cause or causes of these extinctions than we were during the 19th century (Grayson 1984), it is certainly time to take this lesson to heart.

Eurasian models

We do not have to look far for appropriate models for such analyses, although none of them come from North America south of Beringia. In fact, it is precisely because scientists working in Eurasia have adopted Gleasonian approaches that our understanding of Eurasian extinctions is so rich.

A superb example is provided by Delpéch (1999), who combined stratigraphic information and radiocarbon dates to construct a sequence of individual late Pleistocene mammal histories for southwestern France (Figure 1). Noting the staggered nature of mammalian extinctions here, she convincingly showed that each species history is tightly correlated with well-established episodes of climate change in this region.

Stuart et al. (2004) took a different approach. Rather than looking at the individual histories of multiple mammals in a single area, they examined the detailed histories of two mammals—woolly mammoth and giant deer—across much of western Eurasia. Until quite recently, it had been thought that giant deer became extinct in Eurasia at about 11,000 years ago (Barnosky 1986; Gonzalez et al. 2000; Guérin and Patou-Mathis 1996; Kowalski 1967; Kurtén 1968; Martin 1967; Martin 1984; Martin and Guilday 1967; Vereschagin and Barytshnikov 1984). Stuart and his colleagues obtained 43 new radiocarbon dates for western Eurasian *Megaloceros*, providing a giant deer chronology based on 92 dates that extends back some 40,000 years. The results showed that these animals seem to have disappeared from western Europe between about 20,000 and 12,500 years ago, very likely in response to the development of steppe-tundra vegetation during this time. They reappeared in northwestern Europe after about 12,500 years ago but not further south—perhaps, Stuart et al. (2004) suggest, because of denser human populations in more southerly areas. Then, shortly after 10,700 years ago, they disappeared from northwestern Europe, almost certainly because of climatic and vegetational changes associated with the Younger Dryas. Their disappearance in at least some areas cannot be associated with human activity, since extinction occurred at this time in Ireland, where people did not yet exist.

Even more remarkable than this nuanced biogeographic history for western Europe, however, is the fact that Stuart et al. (2004) showed that giant deer—at one time assumed to have become globally extinct at the end of the Pleistocene—had survived in the Urals and western Siberia until about 7000 years ago. Whether or not humans were involved in the loss of giant deer from this region is not clear, but the loss does coincide with the spread of steppe vegetation across western Siberia.

Finally, there is the important effort made by MacPhee et al. (2002) to increase our understanding of the late Pleistocene and Holocene history of a broad variety of large mammals in a portion of northern Siberia focusing on

the Taimyr Peninsula. Building on the extensive work of Russian scientists in this region (see the reviews in Kuznetsova et al. 2001; Sulerzhitsky and Romanenko 1999; Orlova et al. 2004) and adding 75 new dates to an already strong chronology, MacPhee and his colleagues showed that the youngest date for mammoth on the Taimyr Peninsula falls at 9670 ± 60 yr BP. Indeed, this is the youngest reliable date for mammoth anywhere on the Siberian mainland (the 9600 yr BP date for the Yuribei mammoth, Gydan Peninsula, has been rejected on the basis of inadequate pretreatment: see Stuart et al. 2002). The Siberian mammoth chronology is so strong that it shows the northwards retreat of mammoth distribution through time, with most—but not all (Stuart et al. 2002; Orlova et al. 2004)—mammoth populations restricted to the far north after ca. 11,000 years ago (Kuzmin et al. 2003; MacPhee et al. 2002; Orlova et al. 2004; Sher 1997). Sher (1997), Kuzmin et al. (2003) and others attribute this history to the progressive loss of mammoth habitat.

Although the latest known mainland Eurasian mammoth dates to 9700 years ago, the latest records for mammoth anywhere in the world come from north of here—from Wrangel Island, in the Arctic Ocean north of the Chukotka Peninsula (Lozhkin et al. 2001). Here, a large series of dates shows mammoths to have been present up to ca 12,000 years ago, and then again between 7700 and 3700 years ago.

This record is remarkable for two reasons. First, the 4300 year gap in the Wrangel mammoth record poses a question that cannot currently be answered. Was the island somehow recolonized at ca 7700 years ago, as Sulerzhitsky and Romanenko (1999) and MacPhee et al. (2002) suggest, or had populations between 12,000 and 7700 years ago fallen so low on the island that they are paleontologically invisible although they were actually present, as Sher (1997) suggests? If they recolonized, then where could they have come from, given that the youngest known mainland date falls at ca. 9700 years ago?

Second, why did the world's most recent mammoths—at far as we know—become extinct at about 3700 years ago? It was initially suggested that mammoths survived here because a Pleistocene-like tundra-steppe survived as well (Vartanyan et al. 1993). However, detailed paleoenvironmental work designed in part to test this hypothesis showed that this was not the case, and that there was no significant climatic or vegetational event at ca 3700 years ago that could account for mammoth extinction on the island. Although there is no evidence that people hunted these animals (Vartanyan et al. 1993), the earliest known archaeological sites on Wrangel are said to date to between 3360 (Ackerman 1984) and 4300 (in Guthrie 2004) years ago. Given the lack of evidence for climatic or vegetational change at this time, this chronology suggests the possibility of a human role in the extinctions. On the

other hand, mammoths are also known to have survived until at least 5700 years ago on St. Paul Island in the Bering Sea. Here, a human-caused extinction is made unlikely by the fact that the island does not appear to have been occupied by people until historic times (Crossen et al. 2005; Guthrie 2004.).

Thus, the construction of a detailed Eurasian mammoth chronology, including an intensive investigation of mammoth history on the Taimyr Peninsula and on Wrangel Island, coupled with equally detailed paleoenvironmental work has built a dynamic history of mammoths for this area. At the same time, it has made certain kinds of explanations for the extinctions far more likely to be correct than others—climate and vegetational change on the northern Siberian mainland, for instance, and perhaps people on Wrangel.

Although the northern Siberian mammoth record is stronger than is available for any other large mammal in this area, it is not the only mammal for which a detailed local history is available. As I mentioned earlier, it was long thought that Eurasian muskoxen became extinct at the end of the Pleistocene. However, we now know that they were present on the Taimyr Peninsula until at least 2700 years ago. They also seem to disappear from this general area at the end of the Pleistocene (the latest date falls at $10,750 \pm 50$ yr BP: MacPhee et al. 2002, Orlova et al. 2004), only to reappear at ca. 3800 yr BP, having recolonized from an unknown location (MacPhee et al. 2002; Kuznetsova et al. 2001; Vereschagin and Baryshnikov 1984). Why this ca 7000 year gap exists is not known.

Studies of this sort have now been replicated in eastern Beringia. Guthrie (2003) has combined an analysis of the chronology of late Pleistocene horse extinction in Alaska with an analysis of the body size of those horses as extinction approached. Of some 300 radiocarbon dates available for *Equus caballus*-like horses from Alaska, none are younger than 12,500 yr BP (on the phylogeny of these horses, see Weinstock et al. 2005). As this date approached, Guthrie (2003) has shown, horses became smaller and smaller, as inferred from the length of the metacarpal (the long bone of the front foot; see Figure 2). As Guthrie (2003) notes, both this decrease and the latest date for Alaskan horses predates the known human arrival in eastern Beringia, which falls at around 11,800 years ago (Hamilton and Goebel 1999; Yesner 2001, and references therein), and occurs at a time of significant climatically-driven landscape change (Guthrie 2003). It was this change, Guthrie (2003) suggests, that drove this particular extinction.

Recent analysis has suggested that the dates for the last Alaskan horses and earliest Alaskan peoples may not be distinguishable with statistical certainty (Solow et al. 2006). In addition, there are earlier, though not fully published, archaeological dates from Alaska (Bever 2006). Even if all this is the case, however, it would not alter a

very important aspect of Guthrie's conclusion: horses were rapidly decreasing in size as extinction approached, a decrease that began long before people are known to have arrived on the scene. Because, as Solow et al. (2006:7352) observe, "such questions can be addressed from, or even settled by, the stratigraphic context of fossil remains", I note that there are no secure stratigraphic associations between late Pleistocene horses and people in Alaska (Grayson and Meltzer 2002).

Guthrie (2006) has also presented a raft of new radiocarbon dates for elk (*Cervus elaphus*) and moose (*Alces alces*) in Alaska and compared the histories suggested by these dates to those for mammoth, horse, and bison (Figure 3). The results show that elk appear to have been absent from this area between 18,000 and 13,000 years ago, after which their numbers seem to have increased rapidly. There are also no records for moose between 18,000 and 12,500 years ago. Moose arrive as horses are on their last, shrinking legs, with both moose and elk apparently coming from Asia. The number of dated bison specimens also increased substantially as the end of the Pleistocene neared, but this occurred about 1000 radiocarbon years before horses were lost and about 2000 radiocarbon years before the local extinction of mammoth. The small number of bison reported by Guthrie (2006) between 18,000 and 13,500 yr BP is in line with the demographic history of these animals reconstructed from genetic diversity by Shapiro et al. (2004), although the increase in numbers after this time is not (see Mulligan et al. 2006 and references therein on the possible relationships between population size and mtDNA diversity).

Guthrie (2006) carefully showed that these changes occurred in conjunction with a series of shifts in both climate and vegetation, shifts that readily explain the faunal changes. He also noted that many Pleistocene mammals in Alaska and the Yukon Territory do not seem to have survived the last glacial maximum, ca 18,000 years ago. These earlier losses include the stag-moose, giant beaver, ground sloth (*Megalonyx*), mastodon, stilt-legged horses, and others. Although recognizing a possible role for human predation in the local loss of mammoth, Guthrie (2006) noted that none of this is in accord with the classic Pleistocene overkill model, in which all taxa are lost with great speed at around 11,000 years ago.

Summary

The Eurasian and eastern Beringian analyses that I have reviewed here have in common the fact that they focus on reconstructing the histories of individual taxa, making no assumptions about the chronology of extinction. They also have in common the fact that they found the extinction dates of those taxa to vary in time (Delpech 1999; Guthrie 2003, 2004, 2006) or in time and space (MacPhee et al. 2002; Stuart et al. 2004). Not surprisingly, the

security of the conclusions reached by these studies on the cause or causes of the extinctions depends heavily on the precision of the paleoenvironmental and archaeological records associated with the extinction histories. Detailed archaeological and paleontological records are available for southwestern France and eastern Beringia, allowing Delpéch (1999) and Guthrie (2003, 2006) to attribute the extinctions to climate change. On the northern Siberian mainland, where the paleoenvironmental record is quite strong but the archaeological record far less detailed than in either France or Alaska, the extinctions tend to be attributed to climate change (e.g., Kuzmin et al. 2001; Orlova et al. 2001) or to be considered indecipherable with current data (MacPhee et al. 2002). On Wrangel Island, the extinctions also tend to be considered indecipherable (e.g., Lozhkin et al. 2001), even though the close coincidence of the dates for the first people and last mammoths, coupled with the lack of evidence for environmental change at this time, is certainly intriguing. The lesson would clearly seem to be that the combination of strong individual species histories with detailed archaeological and paleoenvironmental records allows a consensus to be reached on the causes of the extinction of those species.

THE REST OF NORTH AMERICA

During much of the last glacial, eastern Beringia was connected to Eurasia and, from a biogeographic perspective, is perhaps better seen as part of this region than as part of North America. As such, it is certainly possible that all of Eurasia, including “North American Eurasia”, saw asynchronous late Pleistocene mammalian extinctions, but North America south of glacial ice did not.

I have discussed the North American extinctions chronology in many places (e.g., Grayson 1987, 1989, 2001; Grayson and Meltzer 2002, 2003) and will not repeat those discussions here, except to say that, as I noted above, of the 35 genera involved, 16 have been shown to have survived in at least some areas to between 12,000 and 10,000 years ago. Those 16 also tend to be the most frequently reported late Pleistocene North American extinct taxa (Figure 4). This opens the possibility that the lack of dates for the remaining 19 genera is simply a sampling phenomenon—the rarer the taxon was on the landscape at the very end of the Pleistocene, the harder it will be to find latest Pleistocene dates for it (Grayson 2001; Grayson and Meltzer 2002, 2003). However, it is also fully possible that the distribution of abundances shown in Figure 4 is in itself an extinctions chronology—that the greatest number of sites we have is for those animals that happened to have survived until the very end of the Pleistocene. If this is the case, then we have relatively few records for, say, *Eremotherium* and *Aztlanolagus* because they became extinct so much earlier than did the mammoth and the mastodon. In fact, the most recent

radiocarbon date for North American *Eremotherium* falls at $38,860 \pm 1300$ yr BP (Thulman and Webb 2001) and there is no evidence that *Aztlanolagus* survived the last glacial maximum (Grayson and Meltzer 2002). Piecemeal extinction, and thus complex causation, remains a very real possibility for sub-glacial North America.

Unfortunately, no analyses comparable to those available for Eurasian or eastern Beringian extinctions exist for this area. This is not because North American archaeologists and paleontologists lack the insight and work ethic of their northern and Eurasian colleagues. Instead, it is at least in part because of the assumption that we know when the extinctions occurred. It is also, however, because we tend to lack the ready sources of data available in these other areas—fossils beautifully preserved in permafrost, bogs, and/or caves (where the presence of bones is routinely due to human hunting and transport). The fact that these sources of chronological information are harder to come by in sub-glacial North America doesn't make the task of studying individual late Pleistocene large mammal species histories impossible, but it does make it harder.

The obvious way to begin the task of building the needed local chronologies is, of course, to date everything that can be dated. There is, however, a different approach to investigating the causes of late Pleistocene extinctions. This approach is worth discussing because, even though it does not meet the need for building individual species histories, it does provide a valuable way of building a general extinction chronology.

Owen Davis (1987) observed that spores of the fungus *Sporormiella* are common in the dung of both domestic and wild large herbivores. They are also to be found in the dung of other animals, including rabbits, but Davis (1987) showed that *Sporormiella* spore frequency in lake sediments increased dramatically in the western United States after the introduction of domestic herbivores. He showed that the spores are abundant in mammoth dung from Bechan Cave, Utah, and that spore frequencies declined significantly at the end of the Pleistocene in a number of western North American settings, most likely as a result of large mammal extinction. Subsequently, Burney et al. (2003) used *Sporormiella* spore abundance to increase our understanding of Holocene mammal extinction in Madagascar.

Robinson et al. (2005) have done exactly the same thing in the lower Hudson River Valley of southeastern New York. They extracted sediment samples from four separate sites that spanned the Pleistocene/Holocene boundary in this area. Of these sites, one had provided the remains of a stag moose directly dated to $12,180 \pm 60$ yr BP; two others had provided mastodon remains, one of which was directly dated to $11,480 \pm 60$ yr BP. For each of

these sites, they extracted information on vegetational change from pollen, *Sporormiella* spore frequency, and charcoal abundances.

Their results are remarkably consistent. In each site, the spores declined as the end of the Pleistocene neared. After that decline set in, charcoal abundance increased, strongly suggesting that local fire frequency increased as well. Robinson and his colleagues infer that as the Pleistocene came to an end here, large mammals dwindled in number and eventually became extinct, a process they suggest took 1,000 years to complete. They see no evidence that this process was caused by vegetational or climate change. Instead, they argue that the arrival of human hunters caused the decline in large mammals (hence the decline in spores), and that this decline in turn increased the amount of natural fuel on the landscape, allowing fire frequency (and hence charcoal) to increase. The increased fire frequency, they suggest, may have been amplified by fires set by people to increase the abundance of new growth on the landscape to attract additional herbivores.

This intriguing argument is bound to be controversial for a number of reasons, the most significant of which involves the chronology of the changes they see. In each site, the decline of dung fungus spores occurred before, and in some cases long before, 12,000 years ago, implying that the cause of local extinction predates that time. The earliest charcoal increase is associated with a date of $13,083 \pm 86$ yr BP, although the first charcoal spike explicitly attributed to human activity falls at 12,600 yr BP with the other charcoal increases following soon thereafter. These dates are a minimum of 1000 years older than the earliest secure evidence for people anywhere in North America south of glacial ice (Meltzer 2004), although the 12,600 yr BP dates does not significantly predate the 12,500 yr BP occupation at Monte Verde, Chile (Dillehay 1997; Meltzer et al. 1997). On the other hand, the ultimate verification of a human presence here at this time can be taken as a necessary but not sufficient prediction of their model, which makes it more testable than some other human-based approaches (Grayson 2006b).

While the approach taken by Robinson et al. (2005) can help build local extinction chronologies, it cannot address other aspects of the need that I have stressed here—to build individual species histories that can be arrayed against precise climatic and archaeological data. This is the case because *Sporormiella* spores cannot be associated with particular members of the late Pleistocene faunal assemblage, even if *Cervalces* and *Mammut* would be good guesses in this setting. All we can know is that one or more large mammals were declining in number across the thousand-year period specified by Robinson et al. (2005). This is no criticism of their work, of course, since this was not at all their goal.

I am aware of no other synoptic attempts to extract detailed late Pleistocene extinction histories in a rich paleoenvironmental context from south of glacial ice in North America. Fisher (1996, 2001, Fisher et al. 2003) has shown that mammoth and mastodon tusks are built in part of laminated structures that grew incrementally on a daily through annual basis. Detailed analysis of these structures can provide information on age, sex, growth rates, age at sexual maturity, and even calving histories for individual animals, as well as detailed mortality profiles for populations of animals. Isotopes extracted from these structures can provide information on diet and temperature at any time during the animal's life. All of this opens the possibility of building detailed mammoth and mastodon demographic histories as the time of their extinction approached. However, while this approach has great potential, there are as of yet no published demographic sequences that help decipher the reasons that either the mastodon or mammoth was lost in North America.

Finally, there are the exquisite individual chronologies available for Harrington's mountain goat (*Oreamnos harringtoni*; because the genus still occurs in North America, this extinct species does not appear on Table 1) and Shasta ground sloth. Radiocarbon dates on *O. harringtoni* horn sheaths and dung pellets show this animal to have become extinct in the Grand Canyon (Arizona) area very close to 11,000 years ago (Mead and Agenbroad 1992; Mead et al. 1986; Mead et al. 2003). Detailed analysis of the plant remains found in goat dung pellets from this same area, coupled with strong knowledge of the nature of Pleistocene vegetational change here, provides no support for the argument that the local extinction of this animal was due to such change (Mead and Lawler 1994; Mead et al. 1986;). Mead and Lawler (1994) observe, however, this does not rule out other climate-based accounts of their extinction. In addition, as Mead et al. (2003:82) note, the loss of Harrington's mountain goat at ca. 11,000 yr BP in the Grand Canyon may simply "record a final demise as the culmination of a very long process."

The Shasta ground sloth was also lost from the Grand Canyon at about the same time, and there is strong evidence that it also lasted until ca. 11,000 years ago in western Texas and southern New Mexico (Long and Martin 1974; Martin et al. 1985). As with Harrington's mountain goat, analyses of plants found in Shasta ground sloth dung do not support vegetational change as the cause of extinction in these areas (e.g., Hansen 1978; Martin et al. 1961; Thompson et al. 1980; see Kopfe et al. 2007 for a similar situation with the shrub ox *Euceratherium*). What we do not know, however, is whether these late populations reflect the last flicker in the fading history of this species or instead one part of a discrete and synchronous extinction event (Mead et al. 2003).

These regional chronologies thus tell us a great deal about two terminal Pleistocene extinctions in the southwestern United States, yet lack the broader context that might help avoid continuing debates over the causes of the extinctions. One could not, for instance, correctly infer the date of the Eurasian extinction of the muskox from its disappearance in France 19,000 years ago.

In short, while we have strong chronologies for some taxa in some places in sub-glacial North America, we do not have the kinds of meticulous, broad-scale chronologies that are becoming available for substantial parts of Eurasia and eastern Beringia. In addition, while we have synoptic studies available for particular places, like the lower Hudson Valley, nowhere do we have multi-taxon chronological sequences that can be arrayed against detailed archaeological and paleoenvironmental histories as we do for elsewhere in the Northern Hemisphere. It is not coincidental that there continues to be contentious debate over the causes of the North American extinctions, but only subdued and cautious ones for the Eurasian losses.

CONCLUSIONS

The debate over the causes of Pleistocene extinctions has led to a vastly increased understanding of the past. In Eurasia, that increase has been so dramatic that the debate itself hardly exists anymore.

In North America, the situation is distinctly different. This is not to say that we haven't learned a remarkable amount about the past because of the debate, since we have. For instance, we now have superb local extinction chronologies for Harrington's mountain goat and Shasta ground sloth in the northern Southwest. We have improved means of assessing the nature of extinct mammal remains from possible archaeological contexts (e.g., Grayson and Meltzer 2002; Haynes and Stanford 1984). We have new approaches to understanding the past, including the use of *Sporomiella* spores as an indicator of large mammal abundance, and DNA-based approaches to identifying the contents of the dung of extinct mammals (e.g., Poinar et al. 1998; Stokstad 1998). What we don't have, however, is any indication that resolution of the debate is close. This, I think it fair to say, is because we have been going about seeking the answers in the wrong way.

American paleobotanists and vertebrate paleontologists began to enter the Gleasonian world of biotic individualism decades ago. Today, it is fully agreed that understanding the histories of assemblages of plants and animals requires that we understand the history of each species on its own. In Eurasia, there is little debate over the causes of the extinctions precisely because such individual histories are available for the animals involved, and because those accounts can often be arrayed against detailed climatic, vegetational, and archaeological histories.

Nothing comparable has been established for the now-extinct Pleistocene mammals for North America south of glacial ice. Remarkable progress has been made for plant (e.g., Spaulding 1990; Van Devender 1990; Webb et al. 1998, 2004) and small mammal (e.g., Grayson 2000, 2006a; Stafford et al. 1999) species histories in this area, but not for the animals at the heart of the argument.

We now have conceptual, empirical, and historical reasons to think that the North American debate will not be resolved until those individual species histories have been constructed. The conceptual reason is provided by the fact that Gleasonian approaches to the past have done so much to increase our understanding of biotic history in general. The empirical reason is provided by the Eurasian example, in which individual species histories have led to satisfactory explanations for the extinctions in so many cases. The historical reason is provided by the fact that the North American debate has gone on for so long and shows no indication of ending given current scientific approaches to the issues involved. There is, however, every reason to think that it will succumb to the same empirical assault that has tamed the European version, even if the explanatory outcome turns out to be different.

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TABLE 1

The extinct late Pleistocene mammals of North America. Genera marked with an asterisk live on elsewhere; those in bold are also known from Eurasia (after Grayson and Meltzer 2002).

Order and Family	Genus	Common Name
Cingulata		
Pampatheriidae	<i>Pampatherium</i>	Southern Pampathere
	<i>Holmesina</i>	Northern Pampathere
Glyptodontidae	<i>Glyptotherium</i>	Simpson's Glyptodont
Pilosa		
Megalonychidae	<i>Megalonyx</i>	Jefferson's Ground Sloth
Megatheriidae	<i>Eremotherium</i>	Rusconi's Ground Sloth
	<i>Nothrotheriops</i>	Shasta Ground Sloth
Mylodontidae	<i>Paramylodon</i>	Harlan's Ground Sloth
Carnivora		
Mustelidae	<i>Brachyprotoma</i>	Short-faced Skunk
Canidae	<i>Cuon</i> *	Dhole
Ursidae	<i>Tremarctos</i> *	Florida Cave Bear
	<i>Arctodus</i>	Giant Short-faced Bear
Felidae	<i>Smilodon</i>	Sabertooth
	<i>Homotherium</i>	Scimitar Cat
	<i>Miracinonyx</i>	American Cheetah
Rodentia		
Castoridae	<i>Castoroides</i>	Giant Beaver
Hydrochaeridae	<i>Hydrochaerus</i> *	Holmes's Capybara
	<i>Neochoerus</i>	Pinckney's Capybara
Lagomorpha		

Leporidae	<i>Aztilanolagus</i>	Aztlan Rabbit
Perissodactyla		
Equidae	<i>Equus*</i>	Horses
Tapiridae	<i>Tapirus*</i>	Tapirs
Artiodactyla		
Tayassuidae	<i>Mylohyus</i>	Long-nosed Peccary
	<i>Platygonus</i>	Flat-headed Peccary
Camelidae	<i>Camelops</i>	Yesterday's Camel
	<i>Hemiauchenia</i>	Large-headed Llama
	<i>Palaeolama</i>	Stout-legged Llama
Cervidae	<i>Navahoceros</i>	Mountain Deer
	<i>Cervalces</i>	Stag-Moose
Antilocapridae	<i>Capromeryx</i>	Diminutive Pronghorn
	<i>Tetrameryx</i>	Shuler's Pronghorn
	<i>Stockoceros</i>	Pronghorns
Bovidae	<i>Saiga*</i>	Saiga
	<i>Euceratherium</i>	Shrub Ox
	<i>Bootherium</i>	Harlan's Musk Ox
Proboscidea		
Mammutidae	<i>Mammut</i>	American Mastodon
Elephantidae	<i>Mammuthus</i>	Mammoths

TABLE 2

Extinct late Pleistocene mammalian genera with radiocarbon dates < 12,000 C-14 yr BP and illustrative sites

Genus	Illustrative Site	References
<i>Arctodus</i>	Sheridan Cave, OH	Bills and McDonald 1998; Tankersley 1997; Tankersley et al. 2001
<i>Bootherium</i>	Wally's Beach, AB	Kooyman et al. 2001
<i>Camelops</i>	Casper, WY	Frison 2000
<i>Castoroides</i>	Dutchess Quarry Caves, NY	Steadman et al. 1997
<i>Cervalces</i>	Kendallville, IN	Farlow and McClain 1996
<i>Equus</i>	Rancho La Brea, CA	Marcus and Berger 1984
<i>Euceratherium</i>	Falcon Hill, NV	Dansie and Jerrems 2005; Kropf et al. 2007
<i>Mammut</i>	Pleasant Lake, MI	Fisher 1984
<i>Mammuthus</i>	Dent, CO	Stafford et al. 1991
<i>Megalonyx</i>	Little River Rapids, FL	Muniz 1998; Webb, Hemmings, and Muniz 1998
<i>Mylohyus</i>	Sheriden Cave, OH	Redmond and Tankersley 2005
<i>Nothrotheriops</i>	Muav Caves, AZ	Long and Martin 1974; Mead and Agenbroad 1992
<i>Palaeolama</i>	Woody Long, MO	Graham 1992, pers. comm.; Grayson 1991
<i>Platygonus</i>	Sheriden Cave, OH	Bills and McDonald 1998; Tankersley 1997; Tankersley et al. 2001
<i>Smilodon</i>	Rancho La Brea, CA	Marcus and Berger 1984
<i>Tapirus</i>	Lehner, AZ	Haury et al. 1959; Haynes 1992

TABLE 3

The extinct late Pleistocene mammals of northern Eurasia (*sensu* Koch and Barnosky 2006; from Koch and Barnosky 2006; Reumer et al. 2003; Stuart 1991, 1999; Vereshchagin and Baryshnikov 1984). Genera marked with an asterisk live on elsewhere; those in bold are also known from North America; *Bison priscus* is ancestral to *Bison bonasus*

Order and Family	Genus	Common Name
Carnivora		
Hyaenidae	<i>Crocota*</i>	Spotted Hyena
Felidae	<i>Homotherium</i>	Scimitar Cat
Perissodactyla		
Rhinocerotidae	<i>Coelodonta</i>	Woolly Rhinoceros
	<i>Stephanorhinus</i>	Rhinoceros
Artiodactyla		
Hippopotamidae	<i>Hippopotamus*</i>	Hippopotamus
Cervidae	<i>Megaloceros</i>	Giant Deer
	<i>Cervalces</i>	Stag-Moose
Bovidae	<i>Spirocerus</i>	Spiral-horned Antelope
	<i>Ovibos*</i>	Muskox
Proboscidea		
Elephantidae	<i>Palaeoloxodon</i>	Straight-Tusked Elephant
	<i>Mammuthus</i>	Mammoths
Species level losses:		
	<i>Panthera leo (spelaea)</i>	Lion
	<i>Ursus spelaeus</i>	Cave Bear
	<i>Bison priscus*</i>	Extinct bison

TABLE 4

The late Pleistocene (<40,000 yr bp) larger mammals of southwestern France (Delpech 1983, 1999; Grayson and Delpech 2006; terminology follows Guérin and Patou-Mathis 1996). Extinct taxa indicated by †; late Pleistocene extirpations in bold (*Bison priscus* is ancestral to *B. bonasus*; *Capra ibex* and *C. pyrenaica* are not routinely distinguishable from fragmentary material)

Order/Family	Genus/Species	Common Name
Carnivora		
Canidae	<i>Canis lupus</i>	Wolf
Felidae	<i>Panthera spelaea</i> †	Cave Lion
Hyaenidae	<i>Crocuta crocuta spelaea</i> †	Spotted Hyena
Ursidae	<i>Ursus arctos</i>	Brown Bear
	<i>Ursus spelaeus</i> †	Cave Bear
Perissodactyla		
Equidae	<i>Equus caballus</i>	Horse
	<i>Equus hydruntinus</i> †	Wild Ass
Rhinocerotidae	<i>Coelodonta antiquitatis</i> †	Woolly Rhino
Artiodactyla		
Suidae	<i>Sus scrofa</i>	Wild Boar
Cervidae	<i>Alces</i> sp.	Moose
	<i>Capreolus capreolus</i>	Roe Deer
	<i>Cervus elaphus</i>	Red Deer
	<i>Megaloceros giganteus</i> †	Giant Deer
Bovidae	<i>Bison priscus</i> †/ <i>B. bonasus</i>	Bison
	<i>Bos primigenius</i>	Aurochs
	<i>Capra ibex</i> / <i>C. pyrenaica</i>	Ibex
	<i>Ovibos moschatus</i>	Muskox
	<i>Rangifer tarandus</i>	Reindeer
	<i>Rupicapra rupicapra</i>	Chamois
	<i>Saiga tatarica</i>	Saiga
Proboscidea		
Elephantidae	<i>Mammuthus primigenius</i> †	Woolly Mammoth

Figure Captions:

Figure 1. The histories of selected late Pleistocene mammals in the lower elevations of the Aquitaine region, southwestern France (after Delpech 1999; Delpech 2007 pers. comm.).

Figure 2. Radiocarbon dates and metacarpal lengths for Alaskan *Equus caballus*-like horses (after Guthrie 2003).

Figure 3. Radiocarbon dates for selected late Pleistocene and early Holocene Alaskan large mammals (after Guthrie 2006).

Figure 4. Extinct late Pleistocene genera with secure radiocarbon dates that fall between 12,000 and 10,000 yr BP (see Table 4). The height of the bars scales to the number of stratigraphically distinct occurrences of each genus (after Grayson and Meltzer 2002).

Figure 1. The histories of selected late Pleistocene mammals in the lower elevations of the Aquitaine region, southwestern France (after Delpech 1999; Delpech 2007 pers. comm.)

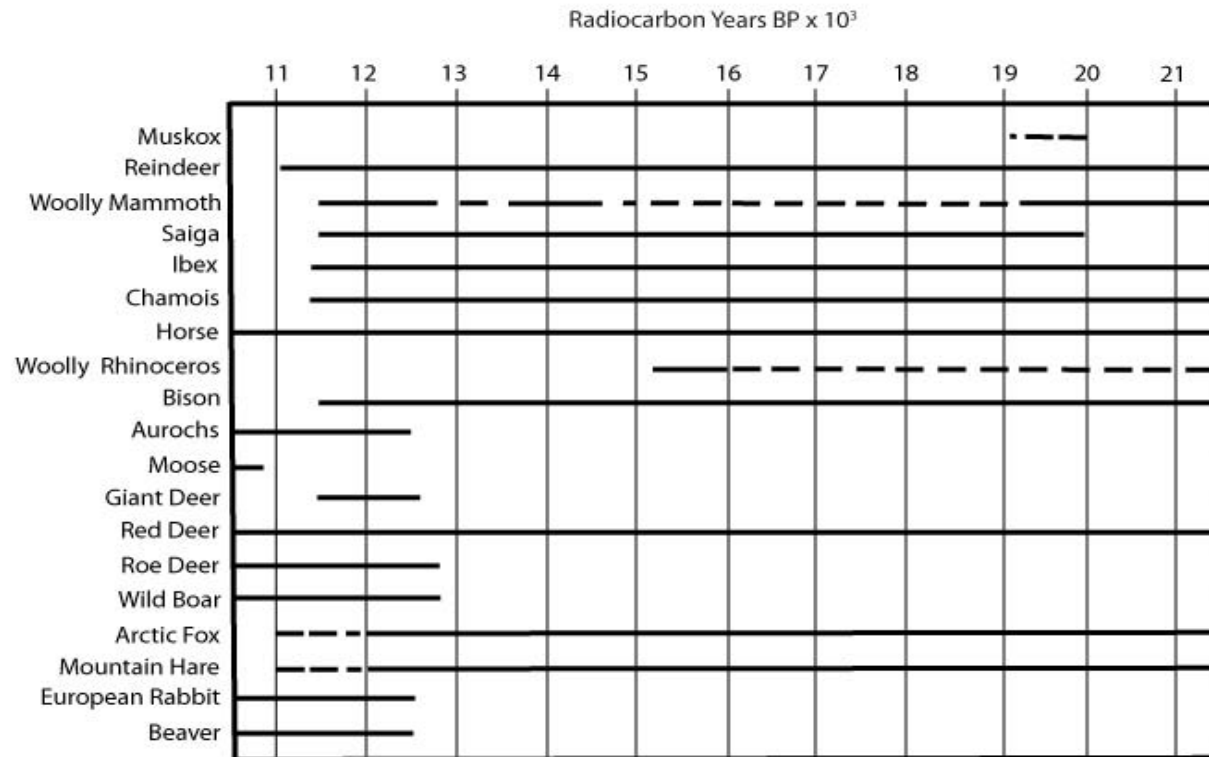


Figure 2. Radiocarbon dates and metacarpal lengths for Alaskan *Equus caballus*-like horses (after Guthrie 2003).

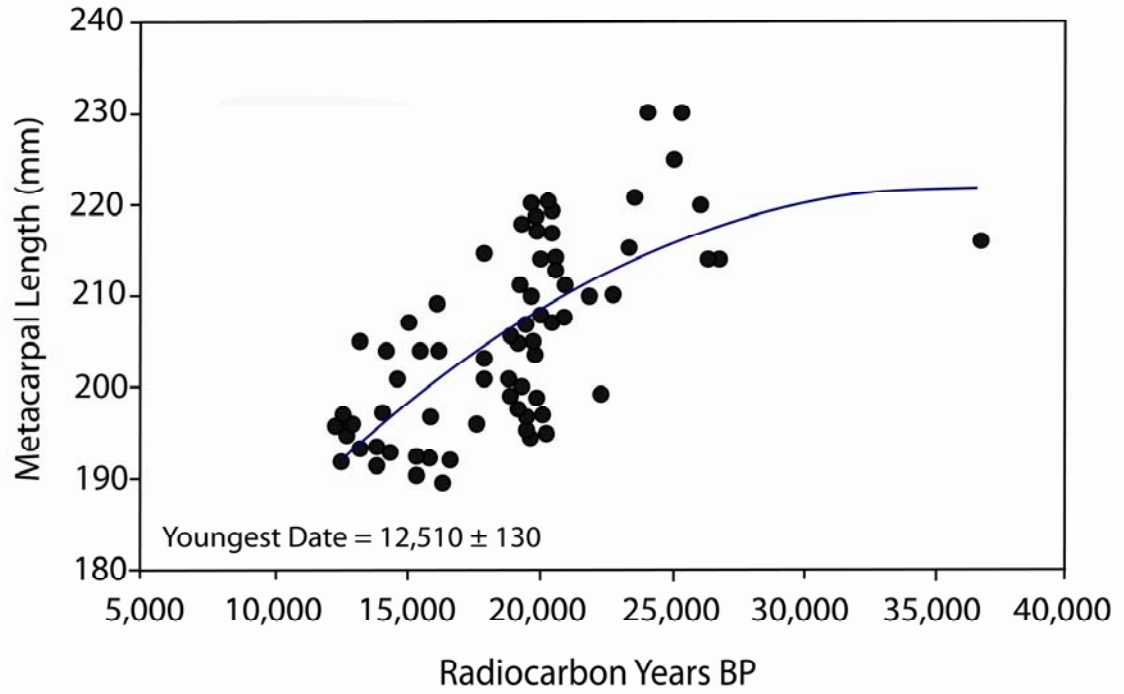


Figure 3. Radiocarbon dates for selected late Pleistocene and early Holocene Alaskan large mammals (after Guthrie 2006)

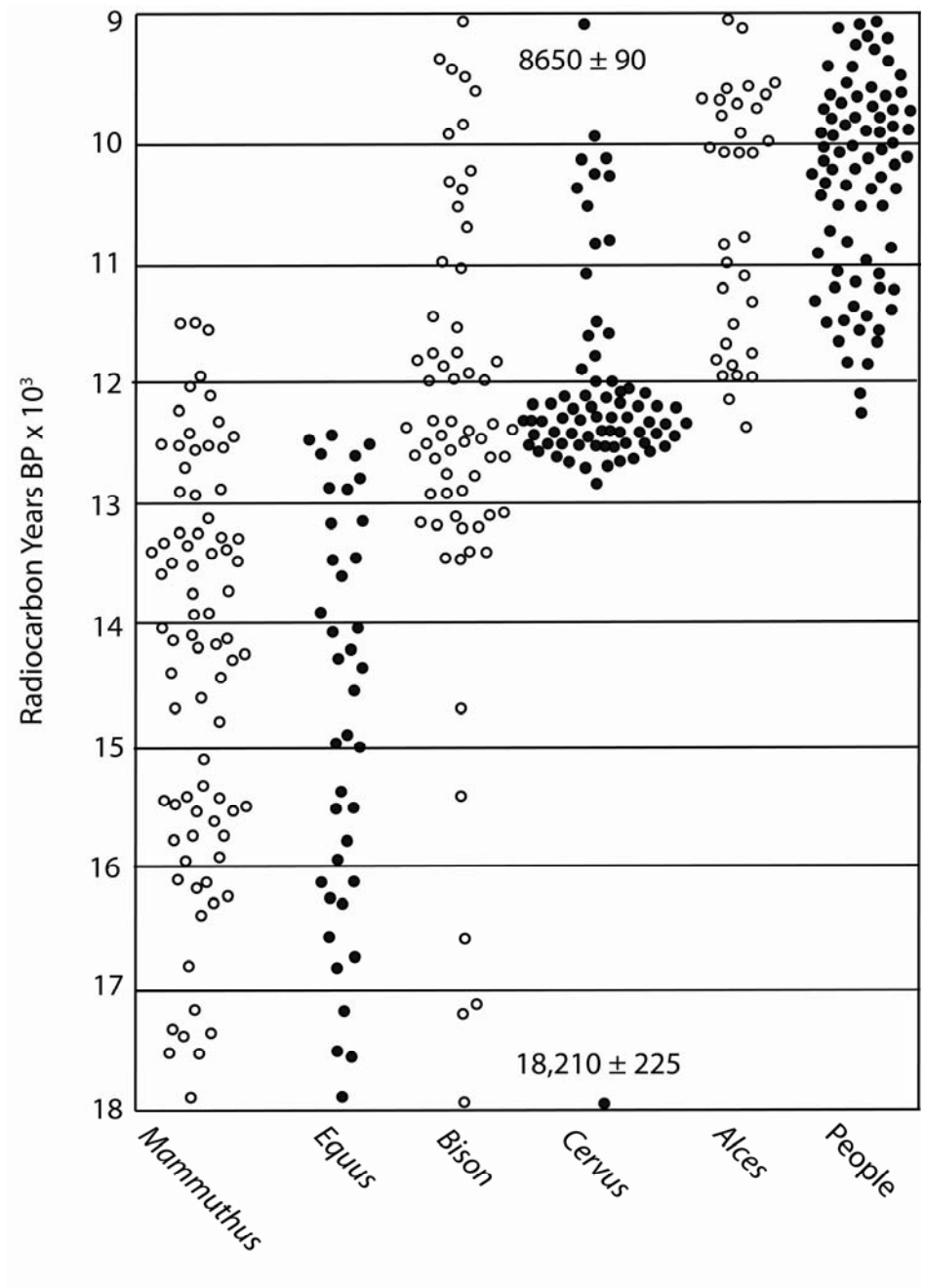


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