LETTERS

New carbon dates link climatic change with human colonization and Pleistocene extinctions

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Drastic ecological restructuring, species redistribution and extinctions mark the Pleistocene–Holocene transition, but an insufficiency of numbers of well-dated large mammal fossils from this transition have impeded progress in understanding the various causative links[1]. Here I add many new radiocarbon dates to those already published on late Pleistocene fossils from Alaska and the Yukon Territory (AK–YT) and show previously unrecognized patterns. Species that survived the Pleistocene, for example, bison (*Bison priscus*, which evolved into *Bison bison*), wapiti (*Cervus canadensis*) and, to a smaller degree, moose (*Alces alces*), began to increase in numbers and continued to do so before and during human colonization and before the regional extinction of horse (*Equus ferus*) and mammoth (*Mammuthus primigenius*). These patterns allow us to reject, at least in AK–YT, some hypotheses of late Pleistocene extinction: 'Blitzkrieg' version of simultaneous human overkill[2], 'keystone' removal[3], and 'palaeo-disease'[4]. Hypotheses of a subtler human impact and/or ecological replacement or displacement are more consistent with the data. The new patterns of dates indicate a radical ecological sorting during a uniquely forage-rich transitional period, affecting all large mammals, including humans.

The gradient from Pleistocene to Holocene covered many millennia, but I show here that in AK–YT the portion of the Pleistocene–Holocene transition (P/HT) most critical for large mammals and their forage occurred from 13,500 to 11,500 radiocarbon years before present (13.5–11.5 kyr BP). The present study focuses on six large mammal species, two that became extinct at the P/HT (mammoth and horse) and four that did not (bison, wapiti, moose and humans). Interior AK–YT is unique in North America for such a study, not only because of its location as a connecting link between the hemispheres but also because many plant and animal species encounter the outer limits of their ecological tolerance at these latitudes, thus often magnifying evidence of climatic–biotic shifts. Fortunately, remains of Pleistocene large mammals are abundant in this region and are exceptionally preserved by permafrost, retaining most of their easy-to-date collagen; indeed, many specimens retain marrow and connective tissue[5].

Although many published dates for fossils of mammoth and horse already existed, these species were so important that I concentrated on them, more than doubling the number of previously published dates for these two species in AK–YT. New dates for moose and wapiti were obtained because of the previous rarity of radiocarbon dates for these species in AK–YT. I did not add to the pool of bison dates because it was well developed by previous work by myself and others[5–7]. For information about humans, I used the accumulated pool of dates from Alaskan archaeological sites[8]. The resulting patterns are illustrated in Fig. 1. Details and dates are provided in Supplementary Information.

An explanation for the unexpected radiocarbon patterns becomes clearer when they are placed in the broader palaeoecological setting (Fig. 2). Fortunately, the character and sequence of the P/HT vegetational changes, lake formation and soil paludification in interior AK–YT have been studied by means of dozens of pollen cores and a wealth of macrofossils[9–11].

In terms of how these date patterns affect extinction theories, neither synchronous extinctions nor demographic morbidity gaps as predicted by the virulent multi-species 'palaeo-disease' hypothesis[4] are apparent in this chronology. Nor do these dates lend support to the 'keystone' hypothesis[3], which proposes that the removal of

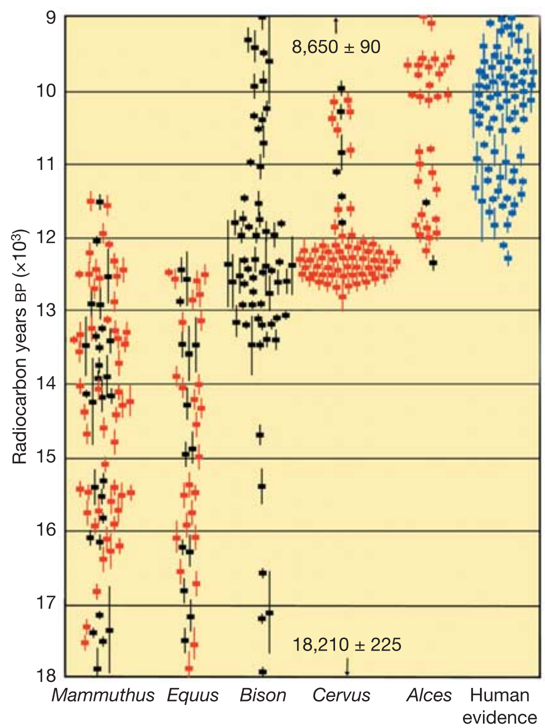

Figure 1 | A plot of radiocarbon dates on AK–YT mammoth, horse, bison, wapiti and moose bones that fall within the 18–9 kyr BP interval, shown alongside dated archaeological material (hearth charcoal mainly) from the same regions[8]. See Supplementary Information for further discussion. Error bars show s.d. Dates from this study are shown in red; other published faunal dates are shown in black, and archaeological dates are blue. The two near-outlier dates listed for wapiti indicate their presence just off the chart. Patterns in this graph are assumed to be a rough indicator of relative abundance and changes with time within each species. A discussion on specimen selection, actual dates and their detailed provenance for all species is provided in Supplementary Information.

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mammoths by humans led to vegetational transformation, which in turn led to a secondary set of extinctions. In this AK–YT chronology, horse extinction seems to have preceded the demise of the proposed keystone species, woolly mammoth, by a calendar millennium[12].

The relevance of this study to the human overkill hypothesis is more complicated. Currently, archaeological visibility of humans in Alaska began soon before 12 kyr BP (Supplementary Information), which just abuts the final dates for horse fossils (Fig. 1). The millennium-wide disjunction of first human dates and terminal mammoth dates indicates that humans could well have had a hand in the gradual extinction of mammoths, but not as in a century-scale 'Blitzkrieg' overkill[2] in which a newly arriving wave of super-efficient human hunters broadly and abruptly devastated local megafaunas. There are two archaeological sites from the period of human–mammoth overlap that contain tusk fragments or tools of ivory[13,14], although that does not necessarily indicate mammoth hunting, much less imply overkill.

Unlike the fossil record in Europe, there is as yet no evidence of humans hunting horses in AK–YT, nor is there in adjacent Siberia. In contrast, there is good evidence from early Alaskan archaeological sites that bison and wapiti were successfully hunted[13–15]. The problem of horse extinction in AK–YT is further compounded by the observation of a decline in horse body size before both human arrival and horse extinction[12]. If humans had a role in horse extinction it occurred on top of other major ecological change that was already well underway. In fact, many species seem to have become extinct in AK–YT well before the period covered by this chart. No AK–YT fossils (see the US–Canadian radiocarbon website in Supplementary Information) of the stilt-legged equids (*Equus* sp.), stag moose (*Cervalces*), camels (*Camelops*), giant beaver (*Castoroides*), ground sloth (*Megalonyx*), extinct musk oxen (*Praeovibos*), mastodon (*Mammut*), short-faced bear (*Arctodus*) and scimitar cat (*Homotherium*) have been recorded after the Last Glacial Maximum (LGM), about 18 kyr BP.

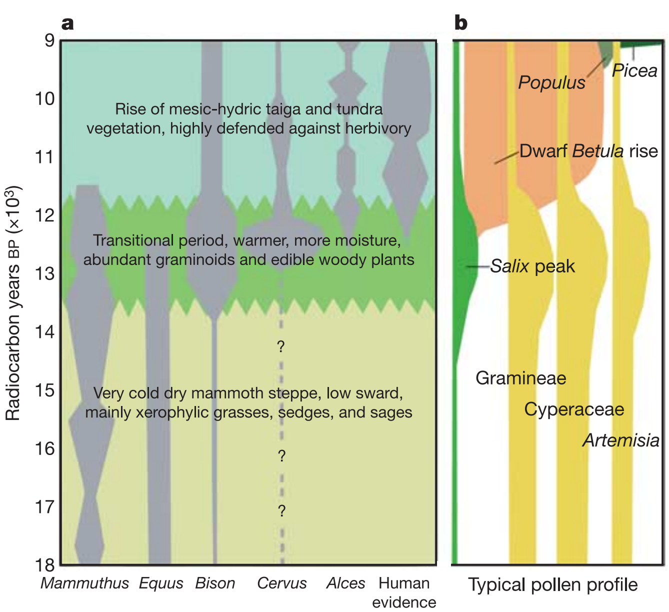

Figure 2 | A visual model linking large mammal date patterns (Fig. 1) to a changing ecological context. **a**, Previous interpretations of the climate–vegetation events are overlain with 'ghost forms' of the large mammal chronology patterns from Fig. 1. The central green band highlights the episode that I refer to as the 'transitional period'. **b**, Generalized pollen influx profiles from several pollen studies in interior AK–YT, using key plant groups[9–11] with emphasis on sites that used the more precise AMS core dating (because conventional radiometric dating of core grab samples generally overestimates time[9]). Patterns from individual pollen cores vary somewhat, yet all have common features; I have smoothed and stressed those regular characters in this generalized graph.

Why were the two grazing specialists, bison and wapiti, absent or rare in AK–YT for five millennia before the transitional period, and how are we to understand their later remarkable boom? We know that conditions in this part of the mammoth steppe during the LGM were extreme. Dune fields, thick loess deposits and the virtual absence of lake sediments indicate arid and windy conditions with a largely treeless, short-grass–sedge–sage sward[5,16]. These conditions of sparse forage and lack of riparian cover and alternate forage might account for the gap in bison and wapiti dates, but I suspect that the competitive advantage of the two caecalid grazing specialists, mammoth and horse, also had a role.

A large hindgut diverticulum, the caecum, gives today's elephants, horses, rhinos and other caecalids the potential for a rapid gut throughput, allowing them to tolerate high volumes of poor-quality forage[5], although at the cost of more conservative growth and reproduction. Mammoths and horses (and woolly rhinos, *Coleodonta*, in adjacent Siberia) were thus better adapted to quantities of exposure-leached winter graminoids that characterized the mammoth steppe. In addition, winter range is always the bottleneck for northern herbivores[17]. Note that if caecalids are removed from the list of extinct species across northern Eurasia and Beringia, extinctions of large herbivores at the end of the Pleistocene become a minor event.

The first signal of the P/HT appears in AK–YT as a pollen shift arising just before 13.5 kyr BP[9–11,18]. Bison, apparently local although not so abundant, judging from Fig. 1, was the first species to expand at the beginning of the P/HT. Because wapiti fossil dates are completely missing from the 5 kyr before their expansion, we might assume that it reflects their local absence. Lag in wapiti expansion might simply be related to the dynamics of colonization distance. It is possible that wapiti, less dependent than moose on a mesic habitat, colonized from arid northern Eurasia[19], closer to AK–YT. The lateness of AK–YT radiocarbon dates for humans and for moose (an obligate browser), as well as the present pattern of no early dates for humans and moose in adjacent Siberia, suggests that both species might have been colonizing at the same time from more distant mid-continental Asia.

Water-limited cold steppe vegetation apparently responded early in the P/HT to the irregular shift towards slightly more moisture and warmer summer temperatures with an expansion of meadowland graminoids and forbs. Tree willow (*Salix*) also became more abundant[20,21]. Lake histories and pollen cores[9,11,22] across the north show that the trend of increasing temperature and moisture ultimately pushed the adaptive vegetational balance firmly towards the now familiar Holocene lakes, bogs, shrub tundra, forests and low-nutrient acidic soils. This resulted in communities of conservative plants highly defended against herbivory[23] and supporting a small biomass of large mammals[5]. Dwarf birch (*Betula*) (see Fig. 2) is especially toxic[23]. Pivotal species shifts are echoed in the fossil invertebrate record as well[18].

Even though willow is primarily entomophilous, the influx and percentage of willow pollen were often greater during this transitional episode than before or afterwards, ranging up to 20% of the pollen spectra[9,11]. Tree willow macrofossils also appear during this period. The digestible energy content and nutrients of early-growth willow leaves are higher than those of virtually all other northern plants[17,23]. Even though tree willows currently occur at only modest densities, their leaves and stems are a critical part of AK–YT moose diets[17]. Indeed, captive and reintroduced wapiti and bison (which are grazers, but eclectic ones) make heavy use of willows[17].

Despite regional differences, this model of linkage between climate, extinctions and human colonization is generally consistent with data from northern Eurasia[18]. Although the broader question of human impact on large mammals in AK–YT, as in Eurasia, remains somewhat open and must be debated in the context of underlying ecological trends[24,25], it has become increasingly clear that large mammals had a significant impact on humans. Warmer and wetter summers[26], an increasing availability of wood[9], and technological innovation[27] each probably had a role in the human colonization of AK–YT, but archaeological refuse clearly illustrates the crucial role of large mammal (at least bison and wapiti) resources as well as the increasing numbers of migratory waterfowl and salmonids in the Holocene[14]. It cannot be overemphasized that vertebrates, especially large mammals, have historically formed the central resource of northern peoples[28]. These new data indicate that humans might have been not so much riding down the demise of the Pleistocene mammoth steppe as they were being carried into AK–YT on a unique tide of resource abundance created by the P/HT.

METHODS

The collection of specimens for dating, dating potential and an evaluation of the possibility of biases are discussed in Supplementary Information, along with museum acquisition data, site location and provenance. In addition to those listed, I also included for dating six samples of mastodon (*Mammut americana*) and five of stag moose (*Alces latifrons*, which evolved into *Cervalces latifrons*), in case these species were part of the above story, but all 11 samples proved to be infinite or at least at the far outer radiocarbon range. A total of 23 samples of a stilt-legged[29] AK–YT *Equus* species were also submitted for dating; all of them dated to before 30 kyr BP[12]. I chose woolly mammoths and caballoid horses as icons of the open-ground faunas of the mammoth steppe. Moose, a browser, was chosen to represent the Holocene fauna, as this species is particularly well adapted to mesic habitats within boreal forests[17]. The earliest date for moose came from ref. 30. Wapiti and bison were used because preliminary evidence suggested that their fossils were common in Holocene sediments[15] and present in early Holocene archaeological sites[14,15]. Nomenclatural designations are rather straightforward except for bison[7], which was evolving rapidly from the larger *Bison priscus* into the smaller *Bison bison* during the latest Pleistocene. All my samples (red in Fig. 1) were run at the US National Accelerator Mass Spectrometer (AMS) Radiocarbon Laboratory at Tucson, Arizona, using their conventional pretreatment[12].

Received 2 September 2005; accepted 25 January 2006.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

Acknowledgements I thank curators R. Tedford, R. Gangfloff, R. Harington and R. Purdy for dating access to museum collections, and M. L. Guthrie, F. Dean and D. Murray for suggestions that improved the manuscript. I also thank the NSF and the Tucson AMS laboratory.

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