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Patterns of Late Quaternary megafaunal extinctions in Europe and northern Asia

With 2 figs

Anthony J. STUART & Adrian M. LISTER

Abstract

This paper summarizes the results so far of our 'Late Quaternary Megafaunal Extinctions' project, focussing on an assessment of latest available dates for selected target species from Europe and northern Asia. Our approach is to directly radiocarbon-date material of extinct megafauna to construct their spatio-temporal histories, and to seek correlations with the environmental and archaeological records with the aim of establishing the cause or causes of extinction. So far we have focussed on *Mammuthus primigenius*, *Coelodonta antiquitatis*, and *Megaloceros giganteus*, and are accumulating data on *Panthera leo/spelaea*, *Crocota crocuta* and *Ursus spelaeus*. Attempts to date *Palaeoloxodon antiquus* and *Stephanorhinus hemitoechus* (from southern Europe) were largely unsuccessful.

The pattern of inferred terminal dates is staggered, with extinctions occurring over ca. 30 millennia, with some species previously thought extinct in the Late Pleistocene – *M. primigenius* and *M. giganteus* – surviving well into the Holocene. All species show dramatic range shifts in response to climatic/vegetational changes, especially the beginning of the Last Glacial Maximum, Late Glacial Interstadial, Allerød, Younger Dryas and Holocene, and there was a general trend of progressive range reduction and fragmentation prior to final extinction. With the possible exceptions of *P. antiquus*, *S. hemitoechus* and *Homo neanderthalensis*, extinctions do not correlate with the appearance of modern humans. However, although most of the observed patterns can be attributed to environmental changes, some features – especially failures to recolonize – suggest human involvement.

Key words: Late Quaternary, megafauna, extinctions, Northern Eurasia, radiocarbon dating

Introduction

We live today in a zoologically impoverished world from which many of the largest and most spectacular large vertebrates (megafauna) have disappeared in the recent geological past. Formerly most of these extinctions were thought to have occurred before the end of the Pleistocene ca. 10 ka (10,000 radiocarbon years BP, ca. 11,600 calendar years), but it is now clear that some megafaunal species, such as woolly mammoth and giant deer, became extinct in the Holocene (VARTANYAN et al. 1993, GUTHRIE 2004, STUART et al. 2004).

As data continue to accumulate, the patterns and processes of Late Quaternary extinctions appear increasingly complex (STUART et al. 2004, BARNOSKY et al. 2004, STUART 2005), while the crucial question of cause or causes remains unresolved. Since Paul S. MARTIN (1967, 1984, MARTIN & STEADMAN 1999) first championed the 'overkill' hypothesis, in which extinctions were attributed

to the impact of human hunters, the subject has generated strong views as to the nature and extent of human involvement in these extinctions (MARTIN & KLEIN 1984, MACPHEE 1999, GRAYSON et al. 2001, BARNOSKY et al. 2004). If true, 'overkill' – in which extinctions are attributed to predation by Stone Age modern humans *Homo sapiens* – can be seen as the beginning of a new episode of 'mass extinction' which continues at an accelerated pace today – the so-called 'Sixth Extinction' (MACPHEE 1999, BENTON 2003). The alternative hypothesis of environmental change necessitates that a unique event or series of climatic events occurred in the Late Pleistocene (SHER 1997, GUTHRIE 1984), as no comparable wave of extinctions had taken place in the previous 0.8 Ma despite a series of major climatic fluctuations (STUART 1991, BARNOSKY et al. 2004). Some, notably SHER (1997), have argued that the last glacial-interglacial cycle was indeed significantly different, because of unprecedented changes in circulation of the Arctic Ocean, and that the resulting

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replacement of arctic steppe-tundra by modern boggy tundra and coniferous forest in the early Holocene caused the extinction of mainland woolly mammoths.

A number of authors (STUART 1991, 1999, BARNOSKY et al. 2004, HAYNES & EISELT 1999) have suggested a combination of 'overkill' and environmental change, in which extinctions resulted from human hunting of megafaunal populations subject to habitat fragmentation and the stress of climatic/vegetational changes.

A further hypothesis, termed 'hyperdisease', involving the spread of diseases to megafaunal species by immigrating humans (MACPHEE & MARX 1997) appears unlikely to have produced the observed timing of extinctions or the body size spectra of the species affected (ALROY 1999, STUART 1999, LYONS et al. 2004).

There is strong evidence that the pattern and timing of Late Pleistocene and Holocene extinctions was very different in each zoogeographical region (STUART 1991, ROBERTS et al. 2001, BARNOSKY et al. 2004, FLANNERY 2005) so that, while also maintaining a global perspective, each region needs to be studied on its own merits. Because many Late Quaternary Extinctions fall within the range of radiocarbon (^{14}C) dating there is enormous potential for resolving the chronology of these extinctions in detail, in marked contrast to the problems of stratigraphic resolution for older extinction episodes (HALLAM & WIGNALL 1997, BENTON 2003). Establishing a reliable chronology for the extinct megafauna of each zoogeographical region is essential for testing these hypotheses. Radiocarbon dating is an especially useful tool for Late Quaternary extinctions that occurred within the reliable chronological range of this method, mainly post-dating ca 35–30,000 ^{14}C years BP, in some cases extending back to ca. 40–50,000 ^{14}C years BP. In this paper dates are given as uncalibrated radiocarbon dates (ka = thousands of radiocarbon years BP), or as calendar dates, including calibrated ^{14}C dates, (cal. ka = thousands of calendar years BP). Many of the radiocarbon determinations collated for this paper are beyond the current limit of the INTCAL04 calibration dataset (REIMER et al. 2004), so here radiocarbon dates have been tentatively compared using the data published by FAIRBANKS et al. (2005). This dataset comprises $^{230}\text{Th}/^{234}\text{U}/^{238}\text{U}$ dates and radiocarbon AMS dates of coral from Barbadian, central and western Pacific locations, which extend back to ca. 55 ka BP.

Northern Eurasia is a particularly fruitful region for the study of Late Quaternary extinctions, not only because of the wealth of available archaeological, palaeontological and environmental data, but also because in this region most extinctions occurred well within the range of radiocarbon dating. Building on the large number of radiocarbon dates already available, it is possible to analyse the record to much higher standards and resolution than elsewhere. In contrast to the situation in North America where the arrival of Clovis technology, major environmental change and megafaunal extinction are thought to have been closely coincident and therefore difficult to

unravel (MARTIN & STEADMAN 1999), it has been apparent for some time that in northern Eurasia Late Quaternary extinctions were staggered over a long period (STUART 1991), and recent discoveries have served to strengthen this observation. This situation potentially allows much better discrimination of possible causes.

This paper draws on the results of our first research programme (1999–2002) 'Late Quaternary Megafaunal Extinctions Project' (LQME project), funded by the UK Natural Environment Research Council (NERC), together with some preliminary findings from our second programme (2006–9). The project used both new dates from samples we submitted to the Oxford Radiocarbon Accelerator Unit (ORAU), and dates available in the literature. The principal species investigated are: *Mammuthus primigenius* – woolly mammoth, *Megaloceros giganteus* – giant deer ('Irish elk'), and *Coelodonta antiquitatis* – woolly rhinoceros, *Crocota crocuta* – spotted hyaena, *Panthera spelaea/leo* – lion, and *Ursus spelaeus* – cave bear. Attempts were also made to date apparently late specimens of *Palaeoloxodon antiquus* – straight-tusked elephant, and *Stephanorhinus hemitoechus* – narrow-nosed rhino. Radiocarbon dating of these species met with very limited success, but we have collated and critically assessed available data relevant to their extinction chronology. *Hippopotamus amphibius* and *Crocota crocuta*, although still extant, are considered part of the Late Quaternary extinctions phenomenon from a Eurasian point of view, and the demise of *Homo neanderthalensis* (Neanderthal man) can also be regarded as a part of the Late Quaternary extinctions phenomenon (STEWART 2005); see discussion. Other taxa, including *Equus hydruntinus*, which appears to have survived in the Balkans until ca. 6 cal. ka (SPASSOV & ILIEV 2002) and *Homotherium latidens*, recently claimed to have survived in Europe until ca. 28 ka (ca. 32 cal. ka) (REUMER et al. 2003), are not included in the present study.

Our approach is to obtain radiocarbon dates directly on megafaunal material, thereby minimising problems of stratigraphic control and context. All too often megafaunal material, when dated, proved to be older than its apparent context, probably due to such factors as poor excavation, post-depositional mixing of layers, or the incorporation of older material, e.g. mammoth ivory, collected by humans (STUART 2005). Some AMS (accelerator mass spectrometry) radiocarbon dates produced in the earlier days of the method are now known to be significantly in error. A recent study (JACOBI et al. 2006, HIGHAM et al. 2006), re-dating mammalian fossils using modern techniques (notably ultrafiltration), found that many previous dates were significantly too young, presumably because of inadequate removal of contaminants (see below: *Crocota crocuta*, spotted hyaena).

In our research work, whenever possible the validity of any outstanding or unexpected dates was corroborated through independent dating by another ^{14}C laboratory. Samples of tooth, bone or antler were obtained from Eu-

rope and Siberia, both by visiting relevant museums and also where appropriate by 'mail order' from colleagues, subject to careful checks on the taxonomic identification of the material. Care was taken to ensure correct identification of the dated material by means of diagnostic characters, e.g. with *Megaloceros giganteus* (commonly confused with bovid or red deer material) and *Ursus spelaeus* (confused with brown bear *U. arctos*). In the case of 'mail order' samples, colleagues were asked to provide scaled photographs of the sampled material as a further check on correct identification.

In this paper we focus on the pattern and interpretation of the terminal dates for megafaunal species. Full datasets and discussion of the complex dynamic changes in distributions preceding extinctions will be given elsewhere.

Results

Extinctions before ca. 35 cal. ka

Hippopotamus amphibius, hippopotamus

During the Last Interglacial [Marine Isotope Stage (MIS) 5e] the range of the hippopotamus included Africa and Mediterranean Europe, extending as far north as Britain, but not further east than the Rhine Valley (STUART 1991). However, its suggested survival in Southern Europe significantly post-dating MIS 5e (STUART 1991) cannot be substantiated because of stratigraphical uncertainties and/or misidentifications. For example we re-determined a radio-ulna (in the IPH, Paris), labelled as 'hippopotamus' from the 'Mousterian B' level at Cueva del Castillo, Northern Spain as a large bovid. No samples of hippopotamus were submitted for dating, as none appeared likely to lie within the range of the radiocarbon method. The Pleistocene distribution of hippopotamus and its association at many sites with southern thermophiles such as *Trapa natans* (water chestnut) (STUART 1991) indicates that it was very sensitive to low temperatures. Its disappearance from Europe might therefore relate to the climatic deterioration within MIS 5e ca 122–115 cal. ka (North Greenland Ice Core Project Members 2004), or perhaps later in MIS 5.

Palaeoloxodon antiquus, straight-tusked elephant

In marked contrast to woolly mammoth, which had its maximum range in the cold stages, straight-tusked elephant was widely distributed over most of Western Europe in interglacials, including the Eemian ca. 130–117 cal. ka (Last Interglacial, Marine Isotope Stage 5e) in association with regional temperate and Mediterranean forests (STUART 1991, 2005). With the onset of the Last Cold Stage (equivalent to MIS 5d–2) and the spread of

treeless steppe-tundra vegetation over most of Europe, it apparently withdrew to areas of southern Europe, where areas of relict temperate woodland persisted (TZEDAKIS & BENNETT 1996, VAN ANDEL & TZEDAKIS 1996). Because remains are so few and the age range is close to or beyond the reliable limits of radiocarbon dating, it is difficult to reconstruct the detailed history of the latest *P. antiquus*; and moreover the stratigraphical context of several finds is uncertain. The evidence for Last Cold Stage survival is based mainly on sparse records of *Palaeoloxodon* material from Iberian and Italian cave sequences, in levels with Mousterian artefacts and/or with associated absolute dates (STUART 2005).

At present, the best evidence comes from level 18 at Cueva del Castillo, northern Spain (ALTUNA 1972, BERNALDO DE QUIROS 1982, CABRERA-VALDÉS et al. 1996) where *P. antiquus* molars are recorded in association with Aurignacian artefacts, overlying a Mousterian level with ESR dates averaging 70 ± 8 cal. ka. Radiocarbon dates on two deciduous molars (almost certainly from the same individual) of ca. 42.9 and > 47.3 ka (LQME project; STUART 2005), and charcoal dates of ca. 40 ka from the same context, are best regarded as minimum ages. A significantly later record is claimed from Foz do Enxarrique, Portugal, where an unworn upper molar plate from Level C, has associated U-series dates (on horse teeth) of ca. 33–34 cal. ka (BRUGAL & RAPOSO 1999, SOUSA & FIGUEIREDO 2001, STUART 2005). However, this record must be regarded with caution because the single *P. antiquus* specimen was not dated directly and, as is common elsewhere, the possibility of derivation from an older level cannot be ruled out.

Clearly more work and new finds are needed to determine more accurately the extinction chronology of straight-tusked elephant. For the present we can say that it survived well beyond the end of the Last Interglacial in Iberia and Italy, and probably to at least ca. 50 cal. ka in Iberia.

A date of $32,500 \pm 500$ ka on a partial molar from Raalte, the Netherlands (MOL et al. 2005) appears anomalous in that so far there are no other post Eemian records from Central or Northern Europe, and requires further investigation.

Stephanorhinus hemitoechus, 'interglacial' or 'narrow-nosed' rhinoceros

Like *P. antiquus*, *S. hemitoechus* was widespread across Northern Eurasia in the Last Interglacial and retreated to southern Europe in the Last Cold Stage (STUART 1991). Largely because we are again dealing with events close to the reliable limit of radiocarbon dating, the extinction chronology of *S. hemitoechus* is uncertain at present, although there are several cave sequences in southern France, Spain and Portugal where it is recorded, from late Mousterian levels (ALTUNA 1972, BERNALDO DE QUIROS

1982, STUART 1991), suggesting survival to perhaps 42 cal. ka. Putative later records from Aurignacian levels (e.g. Lezetxiki Cave, Northern Spain; ALTUNA 1972) need careful checking as to stratigraphic context, and ideally direct dating. A single tooth is recorded from an Aurignacian level (level 11) in Bacho Kiro Cave, Bulgaria (KOZŁOWSKI 1982) in broad association with a ^{14}C date on charcoal of $37,650 \pm 1450$ (OxA-3183), (cal. $42,542 \pm 1068$).

Samples of *S. hemitoechus* from Cueva del Castillo (see above, *P. antiquus*) submitted for radiocarbon dating (LQME project) gave dates of 42–45 ka – probably minimum ages. Other samples from Spain (Lezetxiki Cave) and Italy (Grotta della Cala, Castelcivita Cave, Sora Cave) contained insufficient collagen for dating.

The extinction of *S. hemitoechus* appears to have occurred well before the Last Glacial Maximum, but a detailed chronology is lacking at present.

Extinctions close to the onset of the Last Glacial Maximum, ca. 26 cal. ka

Crocota crocuta, spotted hyaena

Spotted hyaena, a carnivore and scavenger now confined to Sub-Saharan Africa, was widespread across mid latitude northern Eurasia during the Last Cold Stage (KAHLKE 1994), but did not reach Beringia or the Americas. The limited data available so far from Western Europe and the Urals indicate possible extinction in Europe by ca. 32 cal. ka, broadly corresponding with the onset of the Last Glacial Maximum (fig. 1).

A number of hyaena remains from Britain (JACOBI et al. 2006, HIGHAM et al. 2006), dated some years previously by the Oxford Radiocarbon Accelerator Unit, have been re-dated recently by the same unit using improved pre-treatment methods, especially ultrafiltration. They have demonstrated that several of the previous hyaena dates are erroneously young, due to incomplete removal of consolidants. For example, an earlier date of $22,880 \pm 240$ (OxA-6115) on a tooth from Robin Hood Cave, Derbyshire, England, has been shown to be much too young. Re-dating after preparation using ultrafiltration produced a date of $> 52,800$. JACOBI et al. (2006) regard as suspect even the new date of $23,120 \pm 130$ (OxA-13659) on the re-sampled mandible from Goat's Hole (Paviland), South Wales. In view of these results, the date of $24,000 \pm 300$ (OxA-4234) from Castlepook Cave, Ireland, will be checked by further dating. All of the British hyaena dates appear older than ca. 27 ka.

The youngest reliable dates available so far from continental Europe (LQME project, using ultrafiltration) are from Grotta Paglicci, Italy, $26,120 \pm 330$ (OxA-10523) (cal. $30,841 \pm 153$); and “a cave in the Balkan Range”, Bulgaria, $26,600 \pm 170$ (OxA-11551) (cal. $31,053 \pm 86$).

Claims of survival into the late Glacial and Holocene, e.g. in southern Europe (CARRION et al. 2001) and China (TONG 2004) are the subject of current investigation.

Ursus spelaeus, cave bear

Cave bear is the only extinct megafaunal species that was probably confined to Europe (KAHLKE 1994). It is recorded from both cave and open sites, although most of the remains come from the former – largely representing animals that died in hibernation. In contrast to the omnivorous surviving brown bear *Ursus arctos*, *Ursus spelaeus* appears to have been essentially herbivorous, as shown by cranial and dental morphology and low $\delta^{15}\text{N}$ isotope values of bone collagen (RABEDER et al. 2000, BOCHERENS et al. 1994, PACHER & STUART submitted). The diet very probably included a substantial percentage of high quality herbaceous vegetation, implying that such vegetation was available in the Alps and karst areas of Central Europe, at least in some phases, during the Last Cold Stage before the onset of the Last Glacial Maximum.

U. spelaeus probably disappeared from the Alps and adjacent areas – currently the only region for which there is good evidence – by ca. 24,000 ^{14}C years BP (ca. 28 cal. ka) (PACHER & STUART submitted). Climatic cooling and inferred decreased vegetational productivity around the onset of the Last Glacial Maximum were very probably major contributors to its disappearance from this region. There is little evidence so far of direct interaction between cave bears and humans (PACHER 1997, 2002). In collaboration with M. PACHER we are investigating the possibility that cave bear survived significantly later elsewhere, especially in Southern Europe.

Extinctions in the Late Glacial and Holocene, ca. 15–4 cal. ka

Mammuthus primigenius, woolly mammoth

The woolly mammoth has by far the best coverage in terms of ^{14}C dates (SULERZHITSKY 1997, VASIL'CHUK et al. 1997, KUZMIN et al. 2001, MACPHEE et al. 2002, STUART et al. 2002, SHER et al. 2005, STUART 2005). In the middle of the Last Cold Stage, MIS 3 ca. 44–24 cal. ka, woolly mammoths occurred more or less continuously from Western Europe, including Ireland, Britain, Spain and Italy, across Eastern Europe and Siberia to China and Japan, and via Beringia to the northern half of North America (KAHLKE 1994, STUART et al. 2002, AGENBROAD 2005, SHER et al. 2005).

Shortly before ca. 13.8 cal. ka (ca. 12 ka) mammoth disappeared entirely and rather suddenly from Europe and most of northern Asia (fig. 2) (STUART 1991, SHER 1997, STUART et al. 2002, 2004). Significantly, this dramatic event does not correlate with the marked warming and spread of shrub-grassland vegetation over much of Europe, which occurred at the beginning of the Late Glacial Interstadial ca. 15.5–15.0 cal. ka, but does correlate with the major loss of open biomes at the onset of the Allerød (the rather cooler later part of the Late Glacial Interstadial) when boreal birch and pine woodland became widely established (HOEK 2001, LITT et al. 2003).

There is strong evidence (several radiocarbon dates from more than one laboratory) that woolly mammoth populations continued to live in the far north of mainland Siberia on the Taimyr Peninsula for a further two millennia (SHER 1997, SULERZHITSKY 1997, VASIL'CHUK et al. 1997, MACPHEE et al. 2002), in association with persistent open steppe-tundra vegetation (SHER 1997). The latest known dates suggest survival into the earliest Holocene: $9,670 \pm 60$ (GIN-1828) (cal. $11,109 \pm 94$); $9,780 \pm 40$ (GIN-8256) (cal. $11,256 \pm 72$); $9,860 \pm 50$ (GIN-1495) (cal. $11,385 \pm 102$), and $9,920 \pm 60$ (GrA-17350) (cal. $11,503 \pm 128$) (SULERZHITSKY 1997, KUZMIN et al. 2001, MACPHEE et al. 2002, STUART et al. 2002). Possible evidence of mammoth survival post 14 cal. ka in southwest Siberia (ORLOVA et al. 2004) requires further investigation.

Although the data are limited at present, there are strong indications that there was a modest re-expansion of mammoth range ca. 12.6–11.7 cal. ka (ca. 10.5–10.0 ka) from Taimyr into the Yamal/Gydan Peninsulas (northwest Siberia) and thence into northeast Europe (STUART et al. 2002, STUART 2005; fig. 2). This re-immigration to Europe, after an absence of about 1.5 millennia, can be plausibly linked to the renewed cold and open vegetational conditions of the Younger Dryas. The latest records for Europe are from: Zhidikovo peat bog, Cherepovets, north of Moscow (rib from a partial skeleton), $9,760 \pm 40$ (GIN-8885c), $9,810 \pm 100$ (GIN-8676a) (cal. $11,315 \pm 168$), $9,840 \pm 50$ (GIN-8885b) (cal. $11,350 \pm 97$); Purmani, Estonia (molar), $10,100 \pm 100$ (Hela-423) (cal. $11,847 \pm 219$), $10,200 \pm 100$ (Hela-425) (cal. $12,061 \pm 232$) (LÖUGAS et al. 2002, STUART et al. 2002). Since these are similar dates by different laboratories from two distinct sites, the results are probably reliable, but confirmation of each by an independent laboratory is desirable.

The final extinction of mammoth therefore seems to have occurred in mainland Eurasia (both in northeast Europe and northern Siberia) in the very early Holocene (KUZMIN et al. 2001, MACPHEE et al. 2002, STUART et al. 2002). This event occurred soon after, but not coincidentally, with the rapid warming that marks the beginning of the Holocene, and can be plausibly correlated with the loss of the steppe-tundra biome and widespread establishment of temperate and boreal forests in mid latitudes and boggy tundra in the far north (SHER 1997).

However, it seems improbable that habitats suitable for woolly mammoth were entirely eliminated throughout mainland northern Eurasia at this time, especially in view of the Holocene presence of 'steppe-tundra' on Wrangel Island, where an isolated population continued to ca. 4.1 cal. ka (LONG et al. 1994, VARTANYAN et al. 1993, 1995). Recently a mammoth molar from St Paul Island in the Bering Sea off Alaska (Pribilof Islands) has been ^{14}C dated by the Arizona AMS laboratory to $7,908 \pm 100$ (AA26010) (cal. $8,895 \pm 124$) and $8,015 \pm 85$ (AA34501) (cal. $9,013 \pm 89$) (GUTHRIE 2004). These Arizona dates have been independently corroborated (LQME project) by an ORAU date of $8,010 \pm 40$ (OxA-13027) (cal. $9,018 \pm 45$) on the same

specimen. Moreover, three specimens (probably from one individual mammoth) from Qagnax Cave on the same island have produced even younger dates ranging from 5800 ± 80 (Beta 190142) (cal. 6601 ± 97) to 5630 ± 40 (Beta 190141B) (cal. 6404 ± 42) (YESNER et al. 2005).

Coelodonta antiquitatis, woolly rhinoceros

Although widely regarded as a 'fellow traveller' of the mammoth and similarly adapted to the 'steppe-tundra' biome, judging by the relative scarcity of its remains woolly rhinoceros was less common, and its range was less extensive. It was absent from Ireland and north-central Siberia (KAHLKE 1994) and did not reach North America.

After a contraction of range during part of the Last Glacial Maximum, woolly rhinoceros returned to most areas in the Late Glacial, but failed to recolonize Britain and southern Europe. In collaboration with E. WILLERSER and J. BINLADEN, many more dates on woolly rhinoceros are being done to get a full picture of its latest history, but the youngest available records from Western Europe suggest they had disappeared from this region by ca. 16–14 cal. ka (ca. 13–12 ka), approximately coincident with either the warming at the onset of the Late Glacial Interstadial (ca. 14.5 cal. ka), or with the marked reduction in open habitats at the beginning of the Allerød (ca. 14 cal. ka). So far there are no later dates from Siberia (GARUTT & BOESKOROV 2001, BINLADEN et al. 2007).

The latest available dates include: Lobva Cave, Urals Russia $12,275 \pm 55$ (KIA-5670) (cal. $14,233 \pm 173$); Grotto Kotel, Urals Russia $13,245 \pm 65$ (OxA-10921) (cal. $15,802 \pm 149$); Grotto Pershinsky 1, Urals, Russia $13,575 \pm 65$ (OxA-10928) (cal. $16,262 \pm 159$); Gönnersdorf, Germany $13,610 \pm 80$ (OxA-10201) (cal. $16,311 \pm 173$); and Vauxmarcus, Neuchâtel, Switzerland $13,980 \pm 140$ (ETH-8777) (cal. $16,827 \pm 242$). The suggestion that woolly rhinoceros survived into the early Holocene in the Urals is based on a single conventional ^{14}C date of $9,510 \pm 260$ (IPAE-93, former ^{14}C laboratory, Ekaterinburg) (KOSINTSEV 1999). This date must be regarded with considerable caution in the absence of details of the pre-treatment methods used, or corroborative evidence from this or other sites in the region.

Megaloceros giganteus, giant deer

Formerly widespread across the mid latitudes of Northern Eurasia (KAHLKE 1994, STUART et al. 2004), giant deer apparently vacated most of Europe for much of MIS 2 including the Last Glacial Maximum, possibly surviving in refugia north of the Black Sea and/or in Siberia (STUART et al. 2004). It reappeared, in Northwest Europe only, from ca. 14.7 cal. ka, corresponding to the Late Glacial Interstadial warming and a more productive vegetational pulse (Bølling/Allerød), but this population was subsequently extirpated in the low-productivity Younger Dryas (MOEN et

al. 1999, STUART et al. 2004). The demise of giant deer in Ireland at this time is unequivocally linked to environmental change alone, not overkill, as humans did not colonize this area for another 2.5 millennia (WOODMAN 1985).

Radiocarbon dating at Oxford (LQME project) and Kiel has revealed previously unsuspected survival of giant deer well into the Holocene (STUART et al. 2004). The youngest dates for giant deer known so far are from open sites in Western Siberia, immediately east of the Urals: Kamyshlov Mire, Western Siberia $6,816 \pm 35$ (KIA-5669 – on a rib) (cal. $7,655 \pm 68$), and $6,881 \pm 38$ (OxA-13015 – skull) (cal. $7,728 \pm 72$) from an associated skeleton; Redut, Miass River, Western Siberia $6,968 \pm 33$ (KIA-5668) (cal. $7,826 \pm 70$) and $7,034 \pm 34$ (OxA-13014) (cal. $7,900 \pm 72$), both on a cervical vertebra from an associated skull and vertebrae.

At present the timing of the final extinction of giant deer is uncertain, and is the subject of further work. Its late survival in the Urals/Western Siberia region can be attributed to the persistence there of mixed woodland-grassland environments through the Younger Dryas. Its extirpation from this region, although this might have occurred significantly later than 7.8 cal. ka, could plausibly relate to vegetational changes ca. 9–7.8 cal. ka, in which closed forest occupied the hills, and dry grassland the plains – neither suitable for giant deer (PANOVA 1996, STUART et al. 2004). However, its demise might also relate to the appearance of the Neolithic in this region ca. 9 cal. ka (SERIKOV 2000) with probably increased human populations and environmental modification.

Panthera leo spelaea, cave lion

Today lion is confined to Sub-Saharan Africa and one small area in Northwest India (Gir Forest), but until ca. 200 years ago it occurred also in North Africa, and through Turkey and the Levant to Iran and northern India. Archaeological finds from Neolithic, Bronze Age and Iron Age levels in Bulgaria and Greece indicate Holocene presence of lion in the Balkans until ca. 3 cal. ka (NINOV 1999).

The lion ('cave lion') that was widespread in Eurasia through the Late Pleistocene is now generally regarded as an extinct subspecies *P. leo spelaea*, or even species *Panthera spelaea* (TURNER & ANTÓN 1997, SOTNIKOVA & NIKOLSKIY 2006) and so has the status of an additional extinct megafaunal taxon in the Late Quaternary of Northern Eurasia. The distinctiveness of the Late Pleistocene lion from modern African populations is shown by ancient DNA studies (BURGER et al. 2004) and analysis of cave art (TURNER & ANTÓN 1997). On morphological grounds SPASSOV & ILIEV (1994) regard the Holocene lion material from the Balkans as *P. leo*, which they infer immigrated from Asia Minor early in the Holocene, after the extinction of *P. spelaea*.

From our accumulating dataset it is clear that, unlike spotted hyaena (see above), cave lion survived into the Late Glacial across wide areas of Europe. The latest dates

(LQME project) are: Zigeuenerfels, Sigmaringen, Germany $12,375 \pm 50$ (OxA-17268) (cal. $14,219 \pm 112$); Abri des Cabones, Ranchot, France $12,565 \pm 50$ (OxA-12021) (cal. $14,853 \pm 101$); Podsemnich Ochotnikov, Urals $13,500 \pm 65$ (OxA-11349) (cal. $16,158 \pm 157$); Grotto Verhnegubahinsky, Urals $13,560 \pm 70$ (OxA-10909) (cal. $16,241 \pm 163$); Grotto Viasher, Urals $13,570 \pm 70$ (OxA-10908) (cal. $16,255 \pm 163$); and Urtiaga, Spain, $13,770 \pm 120$ (OxA-10121) (cal. $16,534 \pm 216$). The published date of $10,670 \pm 160$ (OxA-729) (cal. $12,678 \pm 119$) from Lathum, Netherlands was done early in the life of the Oxford laboratory, and improved pre-treatments are now routinely applied by this laboratory to material in this age range (STUART et al. 2004, HIGHAM et al. 2006, JACOBI et al. 2006). A new determination $44,850 \pm 650$ (OxA-16715) (cal. $48,792 \pm 992$) shows that the specimen is very much older than previously thought.

Discussion

The pattern of Eurasian extinctions, summarised in fig. 1, is based on the evidence currently available, in particular a substantial dataset of radiocarbon dates made directly on megafaunal material. It emphasises the complex, ragged or staggered pattern of extinctions in Northern Eurasian megafauna (STUART 1991, MARTIN & STUART 1995). This pattern contrasts with a claimed much shorter time range for extinctions in North America (MARTIN 1984, MARTIN & STEADMAN 1999).

Potentially significant impacting factors in Europe (see fig. 1) are:

- Cooling trend (with many oscillations) from MIS 5e into the Last Cold Stage.
- Appearance of modern humans in Europe, ca. 40 cal. ka (possibly a little earlier).
- Onset of the Last Glacial Maximum, broadly 26 cal. ka
- Recolonization of Central and Northern Europe by humans, ca. 16 cal. ka (GAMBLE et al. 2004)
- Onset of Late Glacial Interstadial, ca. 14.5 cal. ka
- Spread of trees at onset of Allerød Interstadial, ca. 14 cal. ka.
- Onset of renewed cold of Younger Dryas, ca. 12.7 cal. ka
- Holocene warming and spread of forest, ca. 11.7 cal. ka.

The detailed pattern of megafaunal radiocarbon dates (fig. 2) strongly suggests a close relationship between vegetational changes and the distributional shifts prior to extinction. There are clear correlations between climatic/vegetational changes and major range contractions/expansions in both extinct and extant species. Some of these events may have led directly to extinctions, but certain pieces of evidence suggest that humans could also have been involved, perhaps in more subtle ways than previously recognized (STUART et al. 2004; and below).

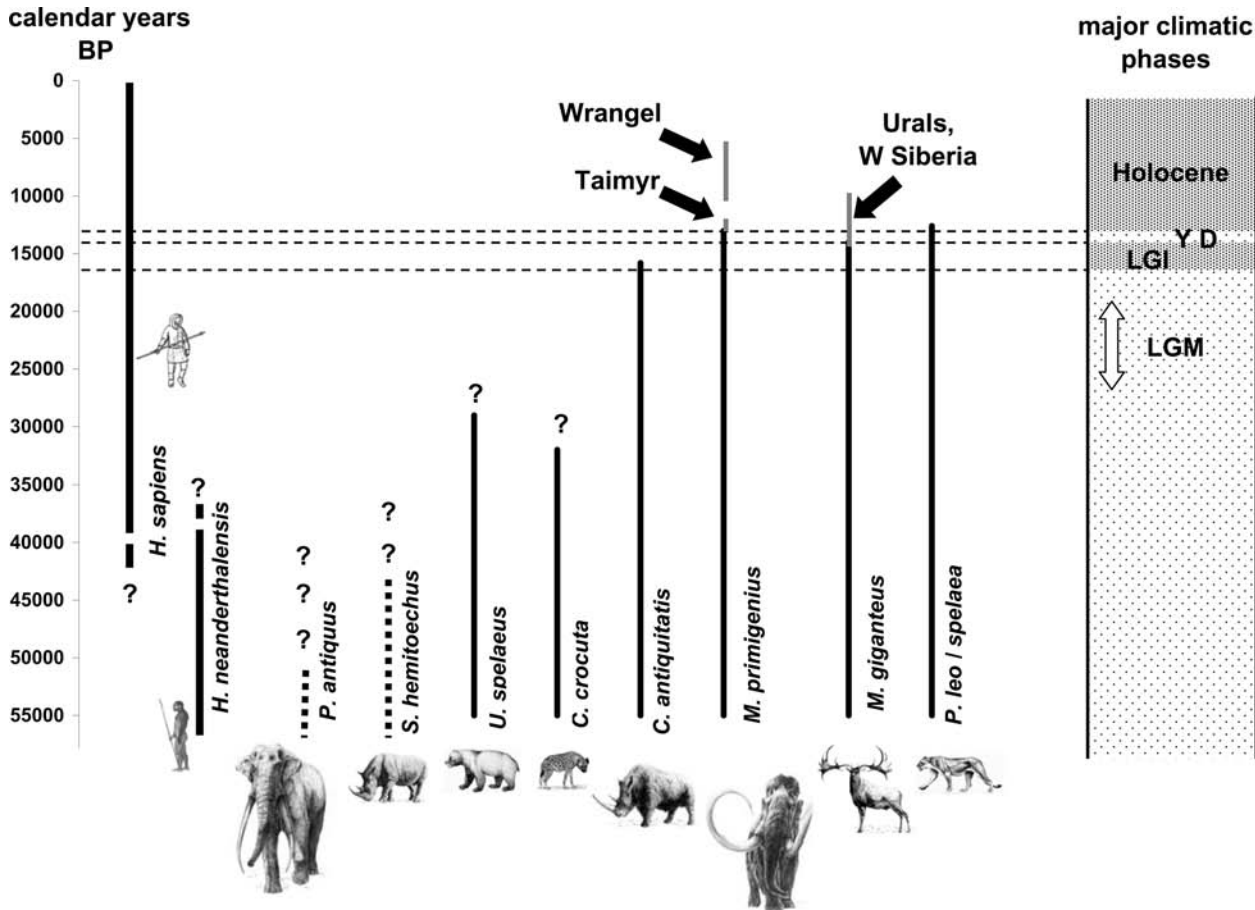


Fig. 1: Summary chart showing current interpretation of the chronology of extinction for megafaunal species in Europe and Northern Asia. Solid lines: species present on the basis of direct radiocarbon dates. Grey lines: last occurrences in limited regions (refugia). Dashed lines: occurrence inferred from limited absolute dating, archaeological association or stratigraphy. Question marks: dates that are poorly evidenced. Note that lines implying continuous presence summarise data for the entire species' range, within which there were complex patterns of regional appearances and disappearances (STUART et al. 2004, STUART & LISTER in preparation.). NB. *P. antiquus* and *S. hemitoechus* probably occurred only in Southern Europe over the time range shown. LGM: Last Glacial Maximum; LGI: Late Glacial Interstadial; YD: Younger Dryas.

The extinction of *Palaeoloxodon antiquus* and *Stephanorhinus hemitoechus* in their southern refugia could be attributed to the overall cooling, and consequent decline of woodland habitats, in the early and middle part of the Last Cold Stage, broadly 75–30 cal. ka. Alternatively, their demise could be related to the appearance of modern humans *Homo sapiens*, now thought to have immigrated to Europe ca. 40 cal. ka or possibly a little earlier (STRINGER 2006) (fig. 1). On the basis of the unsatisfactory dating evidence currently available for these species (see above), we cannot distinguish between these possibilities. The extinction of Neanderthals *Homo neanderthalensis* ca. 35 cal. ka has also been blamed on climatic deterioration (STEWART 2005), or alternatively on competition from, or even active persecution by, modern humans (STRAUS 2005). The available evidence suggests that there was an overlap between the two species of perhaps 5 millennia in Europe (STRINGER 2006) (fig. 1). Others estimate a longer overlap, e.g. ca. 12 ka (FINLAYSON 2005). On present data, the disappearance

of Neanderthals does not obviously correspond with any major climatic event, but follows the arrival of modern humans, with a significant lag between the appearance of one species of *Homo* and the demise of the other. However, it has also been argued that the combination of rapid climatic fluctuations and the arrival of modern humans were factors in Neanderthal extinction (STRINGER et al. 2003)

The Last Glacial Maximum saw the disappearance of most megafauna (extinct and extant) from much of Europe, for variable durations probably related to the ecology of each species (STUART et al. 2004). Humans also vacated most of northern and Central Europe for much of this time (GAMBLE et al. 2004). The limited data available so far indicate probable extinction of spotted hyaena (in Northern Eurasia) and cave bear at the onset of the Last Glacial Maximum before ca. 25 cal. ka. In contrast, cave lion was widespread in the Late Glacial and survived until at least ca. 14.5 cal. ka. Further work is needed, including many more dates, to investigate possible explanations for

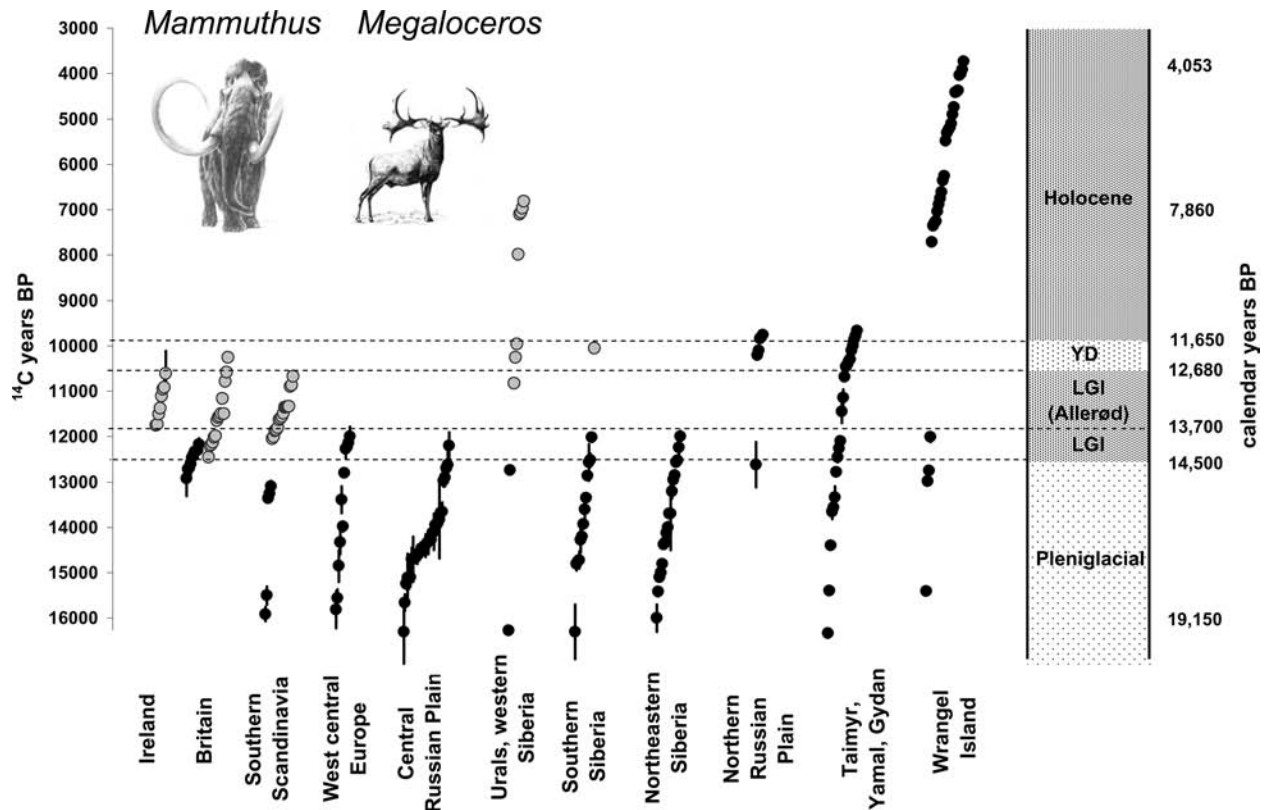


Fig. 2: Chart of radiocarbon dates less than 16 ka (ca. 19 cal. ka) made directly on material of woolly mammoth *Mammuthus primigenius* (black discs) and giant deer *Megaloceros giganteus* (grey discs) for Europe and selected areas of Siberia (modified from STUART et al. 2004). (For clarity northern Germany is grouped with southern Scandinavia). LGI: Late Glacial Interstadial; YD: Younger Dryas. Note contrasting patterns related to differences in ecology between these two species (see text). Mammoth dates for most of Europe and Siberia terminate ca. 12 ka (ca. 14 cal. ka) (Allerød), but mammoths survived into the early Holocene in mainland North Siberia (Taimyr etc), and much later on Wrangel Island (MACPHEE et al. 2002, STUART et al. 2002, STUART 2005, SHER et al. 2005, LONG et al. 1994). Outlying mammoth dates ca. 10 ka (ca. 11.7 cal. ka) in Northeast Europe, probably represent a brief Younger Dryas repopulation from Northern Siberia. After a long absence during the Last Glacial Maximum, giant deer reappeared (in Northwest Europe only) ca. 12.5 ka (ca. 14.7 cal. ka) (Britain) with most dates ca. 12–10.6 ka (ca. 14–12.6 cal. ka). Giant deer disappeared from most of Europe at the Younger Dryas, but survived into the Holocene in the Urals/West Siberia region.

these patterns. Intriguingly, on available evidence, mammoth, woolly rhinoceros and giant deer failed to return to Southern Europe after the Last Glacial Maximum, perhaps because humans continued to occupy these regions in relatively high population densities through this period, thus inhibiting recolonization by these megafaunal species (STUART et al. 2004). If such a relationship can be demonstrated by further work, it would have important implications for understanding the role of humans in megafaunal extinction.

The extinction of woolly rhinoceros may relate to the warming at the onset of the Late Glacial Interstadial ca. 14.5 cal. ka, although the timing of the extinction is unclear (see above). Another possibility is that it may have become extinct ca. 14 cal. ka, coincident with major loss of the steppe-tundra biome with the onset of the Allerød (see below). The Late Glacial Interstadial also broadly correlates with the return of both giant deer and humans to Northwest Europe. Interestingly, the hu-

man recolonization occurred a little in advance of the climatic amelioration (GAMBLE et al. 2004). The onset of the Allerød phase of the Late Glacial Interstadial (ca. 14 cal. ka), accompanied by widespread replacement of former open habitats by forests, had a profound effect on the megafauna. Mammoth withdrew apparently rapidly from most of its range, and was then largely restricted to north-central Siberia (Taimyr Peninsula) where open steppe-tundra persisted. In contrast giant deer evidently flourished (in North West Europe) during the Allerød (fig. 2), and human populations in Europe also appear to have increased (GAMBLE et al. 2004).

The renewed cold of the Younger Dryas ca. 12.7 cal. ka saw the extirpation of giant deer from Western Europe. Data from Eastern Europe and most of Siberia are lacking at present, but we now know that it survived through the Younger Dryas and into the Holocene in the southern Urals and adjacent west Siberia (STUART et al. 2004). In marked contrast to the retreat of giant deer, at the same

time mammoth underwent limited re-expansion from its North Siberian refugium into North East Europe, presumably in response to the renewed spread of open herb-rich vegetation (fig. 2; STUART et al. 2002, STUART 2005).

The final major climatic and vegetational event, the Holocene warming ca. 11.7 cal. ka and extensive spread of broad-leafed and conifer forests across northern Eurasia, broadly coincides with the disappearance of the last known mainland mammoths (Taimyr) (figs 1, 2), although several dates suggest that there was a lag of several hundred years, perhaps reflecting a lag between climate change and vegetational response from dry steppe tundra to boggy modern tundra (SHER 1997, MACPHEE et al. 2002). At the same time many extant species formerly co-existing and widespread in the Last Cold Stage, such as reindeer, arctic fox, horses and lemmings, retreated either to the tundra or to the steppe as the steppe tundra biome almost disappeared.

Most of those megafaunal species that did survive into the Holocene seem to have undergone range fragmentation and reduction, before finally becoming extinct at different times (figs 1, 2). Such a pattern, not correlated with any marked climatic event (in contrast to the Last Cold Stage), implies anthropogenic involvement.

There remain many unanswered questions on the pattern and causes of the range shifts, and their significance for the final extinction of megafaunal species. For example, why did giant deer recolonize only northwest Europe during the Late Glacial Interstadial? Why did it subsequently survive only in limited refugia during the Holocene? The identification of refugia, and of events within them, is clearly critical for determining causes of extinction. The possible role of humans in limiting the natural expansion of these species, and in precipitating the demise of refugial populations, also requires further investigation, both in Europe and northern Asia.

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