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THE EXTINCTION OF LARGE CARNIVORES IN NORTHERN EURASIA

BACKGROUND

In 1876 the eminent biologist Alfred Russell Wallace observed, with remarkable insight: »we live in a zoologically impoverished world from which all the hugest and fiercest and strangest forms have recently disappeared. It is surely a marvellous fact and one that has hardly been sufficiently dwelt upon, this dying out of so many large Mammalia, not in one place only, but over half the land surface of the globe« (Geographical Distribution of Animals, p. 150).

What killed off the mammoths, woolly rhinos, sabre-tooths, giant ground sloths and so many other spectacular giants (»megafauna«), that thrived on all continents (except Antarctica) during the »Ice Age«; some until only a few thousand years ago? »Megafauna« are usually defined as animals with average body weights of 45 kg or more. We tend to think of these extinct giants as almost fantastic »prehistoric monsters«, but as recognized by Wallace these beasts should still be with us if something drastic and extraordinary had not happened. The greatest losses occurred in South America, North America and Australia, but were also severe in northern Eurasia. Only southern Asia and Sub-Saharan Africa suffered very few losses, so that for example rhinos and elephants still occur there at the present day, although now these iconic survivors are seriously threatened by human activities, including hunting and habitat destruction. Was it humans, climate change, a combination of both that were responsible for their extinction – or perhaps something else? The well-established proposed causes are: unsustainable levels of hunting by humans (known as »overkill«); environmental change, or a combination of both. Each of these has its advocates, but there are serious objections to other proposed explanations such as epidemic disease and an asteroid strike.

MEGAFAUNAL EXTINCTIONS IN NORTHERN EURASIA

For hundreds of thousands of years a succession of spectacular large mammals (»megafauna«) roamed northern Eurasia. For example the rich fossil assemblage from West Runton (North Norfolk/GB), about 700 000 years old, includes: a huge mammoth (*Mammuthus trogontherii*); two species of horse; a rhino; wild boar; five species of deer; and a bison. Carnivores include: lion, spotted hyaena, a bear, »European jaguar« (*Panthera gombaszoegensis*) and sabre-tooth (*Homotherium latidens*), in addition to many small vertebrates. Moving 400 000 years forward in time, the large mammals recovered from the main layer at Schöningen (Lkr. Helmstedt/D), about 300 000 years old, include: humans – as shown by stone tools and the famous wooden spears; two species of horse; two species of rhino; wild boar; two kinds of deer; a bison; aurochs; and sabre-tooth (*Homotherium latidens*). Rather older layers at Schöningen yielded remains of additional species: straight-tusked elephant (*Palaeoloxodon antiquus*), lion and cave bear. Long-term changes to the northern Eurasian fauna involved evolution, extinction of some species, and immigration of new ones, but maintaining a broadly similar range of large animals until about 100 000 years ago (Late Quaternary), after which major extinctions – without replacement by other species – began to occur.

In: Nicholas J. Conard · Henning Hassmann · Kurt Felix Hillgruber · Jordi Serangeli · Thomas Terberger (eds), The *Homotherium* Finds from Schöningen 13II-4. Man and Big Cats of the Ice Age. Forschungen zur Urgeschichte aus dem Tagebau von Schöningen 4 (Mainz 2022). DOI: https://doi.org/10.11588/propylaeum.1006.c13524

The Late Quaternary comprises the Last Interglacial (about 130 000-110 000 years ago and rather warmer than today), through the predominantly cold Last Glacial (interrupted by many warmer interstadials), to the temperate Holocene interglacial (postglacial), which began around 11 700 years ago – and in which we still live. The megafauna of the Last Interglacial (Eemian) in northern Eurasia included: straight-tusked (or forest) elephant (*Palaeoloxodon antiquus*); woolly mammoth (*Mammuthus primigenius*); narrow nosed rhino (*Stephanorhinus hemitoechus*); woolly rhinoceros (*Coelodonta antiquitatis*); steppe bison (*Bison priscus*); giant deer (*Megaloceros giganteus*); extinct camel (*Camelus knoblochi*); Neanderthal (*Homo neanderthalensis*); cave lion (*Panthera spelaea*); cave bears (*Ursus spelaeus*, *Ursus ingressus*, *Ursus kudarensis*); and spotted hyaena (*Crocuta crocuta*). All of these went extinct during the Last Glacial, with the exception of woolly mammoth which persisted until 10 700 years (early Holocene) in north-central Siberia, and famously on Wrangel Island (in the Arctic Ocean off north-eastern Siberia) to around 4000 years ago. Spotted hyaena, also disappeared entirely from Eurasia, but still survives today in Africa south of the Sahara.

RADIOCARBON DATING

Establishing an accurate time scale and dating individual animal specimens is crucial to unravelling what happened to the megafauna. Radiocarbon dating is a powerful tool for accurately dating organic remains as far back as more than 40 000 years ago (exceptionally to around 50 000 years). Fortunately, this time range covers most megafaunal extinctions in most parts of the world, including northern Eurasia. The isotope Carbon 14 (^{14}C, radiocarbon) is constantly being produced in the upper atmosphere and absorbed in the form of carbon dioxide into plant tissues. Animals incorporate radiocarbon, along with the much more plentiful stable isotope Carbon 12 (^{12}C), by eating plants or by eating other animals. The unstable ^{14}C undergoes radioactive decay at a constant known rate, but this is continually replenished while the animal is alive. The »clock« starts at the time of death as new ^{14}C is no longer taken in, so that by accurately measuring the remaining ^{14}C the age of the remains of a plant or animal can be calculated. However, by around 50 000 years ago the remaining amount of radiocarbon is so small that it is impossible to measure accurately, which sets an age limit on dating a sample. Collagen (a protein), extracted from bones, teeth and antlers, is the primary material for radiocarbon dating of megafaunal remains. Charcoal and other material found with megafaunal remains can only give us indirect dates which can be misleading when the degree of association is uncertain. In order to reliably date megafauna we need samples of material from the animal itself. The increasingly wide use of AMS (Accelerator Mass Spectrometry) allows very small samples of half a gram or less to be dated accurately. Of course, it is essential that the sample submitted for dating should be correctly identified to species. However, there is a very important complicating factor that needs to be taken into account. Levels of radiocarbon in the atmosphere have varied significantly in the past, which means that measured radiocarbon dates need to be calibrated against a known time scale in order to convert them to calendar years. All of the dates quoted here have been calibrated.

The extensive and careful application of radiocarbon dating has made it possible to build up a picture of megafaunal extinctions in northern Eurasia. The pattern of extinctions (**fig. 1**) is conspicuously staggered over many thousands of years, with some species disappearing before the Last Glacial Maximum, some much later in the Late Glacial, and others surviving into the Holocene or to the present day. This pattern contrasts with North America where most losses seem to have occurred within the Late Glacial. In northern Eurasia, each megafaunal species exhibits a unique and complex pattern of distributional shifts, culminating in extinction for some species and survival in others.

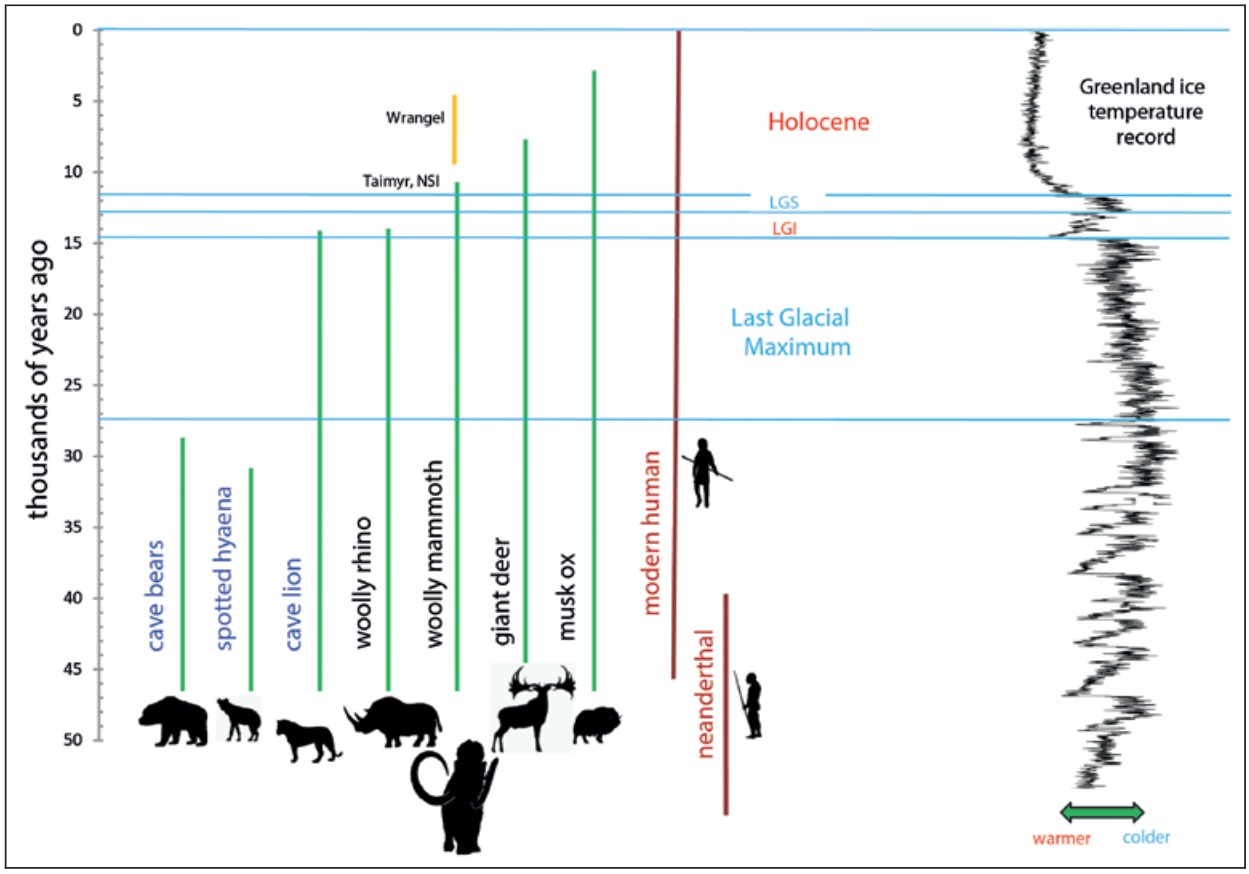

Fig. 1 Chart of extinctions and survivals of representative megafauna during the last 50 000 years in northern Eurasia, based on radiocarbon dates in comparison with the Greenland ice temperature curve. The Last Glacial Maximum was a prolonged cold period; the Holocene a prolonged warm phase in which we still live. Carnivores are lettered in blue. The time ranges of Neanderthals and modern humans are also shown. – LGI: Late Glacial Interstadial (a warm phase); LGS: Late Glacial Stadial (a cold phase); NSI: New Siberian Islands (north-central Siberia); Wrangel: Wrangel Island (north-east Siberia).

LATE QUATERNARY LARGE CARNIVORES

Cave bears (fig. 2)

In the Late Quaternary cave bears (*Ursus spelaeus* and *Ursus ingressus*) were confined to upland areas in western and central Europe, with an isolated population in the Urals. They were absent from northern Europe and also Britain, where only the living brown bear (*Ursus arctos*) occurred. A separate species *Ursus kudarensis* was isolated in the Caucasus. Most tooth wear studies and isotope analyses indicate that cave bears, although belonging to the order *Carnivora*, were largely vegetarian, quite unlike modern brown bears which also eat substantial amounts of animal food. However, isotopic studies indicate that cave bears from Carpathian sites (Romania) enjoyed a broader diet like brown bears today.

The latest of 175 reliable dates (median calibrated years before present) on cave bears (*Ursus spelaeus* and *Ursus ingressus*) are: 28 700 years ago (laboratory number GrA-52632) from Rochedane (dép. Doubs/F); 28 984 years ago (ETH-16879) from Bame aux Pirotas (ct. Jura/CH); and 28 540 years ago (Beta-156100) from Vindija Cave (HR). The latest dates from the Urals indicate that they disappeared from this region around 13 000 years earlier than from central Europe.

Fig. 2 Cave bear skull and mandible (Balkans), total length 50 cm. – (Photo A. J. Stuart).

Spotted hyaena (fig. 3)

In the Last Glacial spotted hyaenas ranged from Iberia and the British Isles, eastwards across central and southern Europe, to European Russia, southern Siberia, and the Pacific coast in the Russian Far East. They were entirely absent north of 58 degrees latitude. Spotted hyaenas in Africa at the present day are active pack (clan) hunters of large ungulates up to the size of wildebeest and zebra, as well as scavengers of their carcasses. The powerful jaws and massive teeth have evolved for specialized bone crushing, thus allowing the maximum nutrition to be extracted from a carcass. Likely prey species in Last Glacial northern Eurasia include adult and juvenile horse, reindeer, red deer, giant deer (*Megaloceros giganteus*), extinct bison (*Bison priscus*), aurochs (*Bos primigenius*) and wild boar. No doubt hyaenas would have disputed »kills« with humans.

On the basis of 99 dates, spotted hyaena is last recorded at 30 813 years ago (OxA-10523) from Paglicci Cave (prov. Foggia/I), and 31 433 years ago (GrA-2812) from Goyet Cave (prov. Namur/B). The latest dates from central Europe to the Russian Far East are more than 9000 years older. The available evidence indicates that spotted hyaena disappeared from northern Eurasia probably in response to the onset of the Last Glacial Maximum, due to cooling climate and also reduction of its herbivore prey abundance driven by deteriorating vegetational productivity. Spotted hyaenas probably disappeared from central Europe and eastwards about 40 000 years ago, but persisted substantially later – to about 31 000 years ago – in north-western and southern Europe where the climate remained milder for longer.

Fig. 3 Partial left mandible of spotted hyaena (Urals, Russia). – (Photo A. J. Stuart). – Scale 1:2.

Fig. 4 Cave lion right mandible (Lena River, north-eastern Siberia). – (Photo A. J. Stuart). – Scale 1:2.

Cave lion (fig. 4)

During the Late Quaternary the cave lion, *Panthera spelaea* (an extinct species distinct from modern lions) was widespread across northern Eurasia to north-eastern Siberia and was able to cross the Bering region into north-western North America (Alaska and the Yukon). Cave lions were rather larger than modern lions and probably could have tackled larger prey. In northern Eurasia the likely prey species would have included horse, reindeer, giant deer, red deer, musk ox, extinct bison, and occasionally young woolly rhino and young mammoth.
The latest of 140 dates that we have for cave lion are: 14 378 years ago (OxA-17268) from Zigeunerfels Cave (Lkr. Sigmaringen/D; **fig. 5**); 14 141 years ago (AA-41882) from Le Closeau (dép. Seine-et-Marne/F); and 14 640 years ago (OxA-12901) from the Lena River in north-eastern Siberia. Younger dates from Alaska suggest that they persisted about 900 years later in that region. This evidence indicates that cave lion extinction occurred within the Late Glacial period throughout Eurasia by about 14 000 years ago, very likely in response to a warming climate accompanied by the spread of trees and shrubs. Perhaps there was also a reduction in numbers of available prey, although nearly all its potential prey species survived much later. There is no indication that they survived anywhere into the Holocene (i. e. later than 11 700 years ago).

Fig. 5 Cave lion upper canine tooth (Zigeunerfels Cave, southern Germany). – (Photo W. von Koenigswald). – Scale 1:2.

Sabre-tooth

The single radiocarbon-dated find of sabre-tooth (*Homotherium latidens*), based on a mandible trawled from the North Sea, is discussed elsewhere in this publication. My view is that we need more evidence to demonstrate its presence in Europe during the Last Glacial. Otherwise the latest record is much older – from Schöningen at around 300 000 years ago.

LARGE CARNIVORES AND PALAEOLITHIC HUMANS

The presence of formidable large carnivores throughout the Quaternary no doubt posed a constant danger to humans as well as disputing their kills, although in turn humans very likely stole carnivore kills when the opportunity arose. As has been suggested, the 300 000-year-old Schöningen spears are likely to have been used in defence against predators, including sabre-tooths, lions and hyaenas, as well as for hunting large game.

Modern humans arrived in Europe about 45 000 years ago, via the Middle East, replacing the Neanderthals, who preceded them within a few thousand years. However, by far, the majority of extinctions in northern Eurasia, including the large carnivores, occurred much later – which is inconsistent with »overkill«. The evidence that we have so far favoured the idea that carnivore extinctions were driven by climatic and/or vegetational changes. However, the possible role of humans, especially in reducing remaining populations to the point of extinction, has yet to be satisfactorily explored.

There are many artistic depictions of cave lions, including the beautiful multiple painted images from Chauvet Cave (dép. Ardèche/F) and the enigmatic lion-headed human figure (carved out of mammoth tusk) from Hohlenstein Stadel (Alb-Donau-Kreis/D). Although lions were clearly prominent in the minds of Upper Palaeolithic people, there is no evidence that they were hunted. So far, depictions of cave bears, with their distinctive domed foreheads, are known only from Chauvet Cave. However, numerous cut marks on cave bear bones from the cave sites Casamène (dép. Doubs/F) and Hohle Fels (Alb-Donau-Kreis/D) clearly show that their carcasses were exploited by humans, although direct evidence suggesting that they were hunted by people is extremely scarce. The only example known so far is from Hohle Fels Cave, where a bear thoracic vertebra (either cave bear or brown bear) was found with a small triangular fragment of *Hornstein* embedded in it; perhaps broken off a much larger projectile point. In the case of hyaenas, there are no convincing representations from any site and so far no evidence has been found to suggest that any were killed by humans.

CONCLUDING REMARKS

So radiocarbon dates (as well as stratigraphic evidence) from many localities show a large difference between the histories of cave bears and spotted hyaena on the one hand and cave lion on the other. Cave lion survived into the Late Glacial period about 14 000 years ago, whereas cave bears and spotted hyaena disappeared around 13 000 years earlier, before the beginning of the Last Glacial Maximum about 27 500 years ago. Significantly, there is no evidence whatsoever that the extinction of large carnivores resulted from the extinction of their herbivore prey. It should be pointed out that for each species the actual time of extinction is likely to be a little later than the youngest available date. Further advances in our understanding of megafaunal extinctions will involve obtaining many more radiocarbon dates as well as the increasingly important developments in isotope chemistry and ancient DNA.

ACKNOWLEDGEMENTS

I am most grateful for the opportunity to attend the excellent and stimulating workshop at the Paläon Museum in June 2015. Especial thanks are due to my principal collaborator Adrian Lister and the UK Natural Environment Research Council who have funded our research.

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SUMMARY / ZUSAMMENFASSUNG

The Extinction of Large Carnivores in Northern Eurasia

During the Late Quaternary northern Eurasia supported a range of large mammals (megafauna) that are now extinct or extirpated from the region. These include cave bears (*Ursus spelaeus* and *Ursus ingressus*), spotted hyaena (*Crocuta crocuta*) (still lives in Africa), cave lion (*Panthera spelaea*), and possibly also a sabre-tooth cat (*Homotherium latidens*). Radiocarbon dates made directly on megafaunal remains allow us to estimate when each disappeared. The dates quoted here have all been calibrated, that is converted into calendar years. Cave bears and hyaenas had all disappeared before the Last Glacial Maximum 27 500 years ago, whereas cave lion survived much longer until about 14 000 years ago.

Das Aussterben der großen Fleischfresser in Nordeurasien

Während des späten Quartärs gab es in Nordeurasien eine Reihe von großen Säugetieren (Megafauna), die heute ausgestorben oder in der Region ausgerottet sind. Dazu gehören Höhlenbären (*Ursus spelaeus* und *Ursus ingressus*), Tüpfelhyänen (*Crocuta crocuta*) (diese leben heute noch in Afrika), Höhlenlöwen (*Panthera spelaea*) und möglicherweise auch eine Säbelzahnkatzenart (*Homotherium latidens*). Anhand von ^{14}C-Daten, die direkt an den Überresten der Megafauna vorgenommen wurden, lässt sich abschätzen, wann diese verschwunden sind. Die hier angegebenen Daten wurden alle kalibriert, d. h. in Kalenderjahre umgerechnet. Höhlenbären und Hyänen waren bereits vor dem letzten glazialen Maximum vor 27 500 Jahren verschwunden, während der Höhlenlöwe noch bis vor etwa 14 000 Jahren überlebte.