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# Human influence on distribution and extinctions of the late Pleistocene Eurasian megafauna

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## Abstract

Late Pleistocene extinctions are of interest to paleontological and anthropological research. In North America and Australia, human occupation occurred during a short period of time and overexploitation may have led to the extinction of mammalian megafauna. In northern Eurasia megafaunal extinctions are believed to have occurred over a relatively longer period of time, perhaps as a result of changing environmental conditions, but the picture is much less clear. To consider megafaunal extinction in Eurasia, we compare differences in the geographical distribution and commonness of extinct and extant species between paleontological and archaeological localities from the late middle Pleistocene to Holocene. Purely paleontological localities, as well as most extinct species, were distributed north of archaeological sites and of the extant species, suggesting that apart from possible differences in adaptations between humans and other species, humans could also have a detrimental effect on large mammal distribution. However, evidence for human overexploitation applies only to the extinct steppe bison *Bison priscus*. Other human-preferred species survive into the Holocene, including *Rangifer tarandus*, *Equus ferus*, *Capreolus capreolus, Cervus elaphus, Equus hemionus, Saiga tatarica,* and *Sus scrofa*. *Mammuthus primigenius* and *Megaloceros giganteus* were rare in archaeological sites. Carnivores appear little influenced by human presence, although they become rarer in Holocene archaeological sites. Overall, the data are consistent with the conclusion that humans acted as efficient hunters selecting for the most abundant species. Our study supports the idea that the late Pleistocene extinctions were environmentally driven by climatic changes that triggered habitat fragmentation, species range reduction, and population decrease, after which human interference either by direct hunting or via indirect activities probably became critical.
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## Introduction

Humans are often blamed for their imprudent exploitation of the Earth's living resources (Diamond, 2005). A myriad of known and unknown species currently risk extinction because of human activities. The current ineptitude of human societies to adopt an environmentally sustainable lifestyle may trace back to the end of the Pleistocene, when most megafauna vanished in coincidence with the spread of Neolithic people and their advanced tools (Martin, 1973; Barnosky et al., 2004).

In North America, the late Pleistocene megafaunal extinctions were tightly grouped around 10,500–11,000 years ago (kiloannum, ka), a period coinciding with the arrival of humans and with widespread climate change. Consequently, these extinctions are often attributed to humans (Martin, 1973, 1984; Alroy, 2001; Barnosky et al., 2004; Bulte et al., 2006; Pankovic et al., 2006) although evidence is far from conclusive (Graham and Lundelius, 1984; Beck, 1996; Grayson and Meltzer, 2002; Guthrie, 2003, 2006; Grayson, 2006; Solow et al., 2006). The same applies to Australia, where the extinction wave started some 30 ka, following human arrival at 50 ka (Roberts et al., 2001; Johnson, 2002; but see Trueman et al., 2005). In Eurasia, late Pleistocene extinctions were spread over a longer period of time, and human influence is less evident (Stuart et al., 2002,

2004; Stuart, 2005). Consequently, Eurasian megafaunal extinctions have been proposed to result from rapid environmental changes (Kvasov, 1977; Tormidiaro, 1977; Guthrie, 1984; Stuart, 1991; Lister and Sher, 1995; Sher, 1997). At present the largest species in the world have remained only in Africa and, perhaps, in southeastern Asia (Nowak, 1999). Intriguingly, most African megafauna never went extinct although this is the continent on which humans arose (Brook and Bowman, 2002).

Evidence of human species intervention is the keystone to understanding how and to what extent people influenced megafaunal demise. Consequently, most analyses of the late Pleistocene extinction patterns have focused either on surveys of the occurrence and extent of human modification (e.g., bone manipulation, artifacts; Fisher, 1984; Grayson, 2001; Grayson and Meltzer, 2002; Surovell et al., 2005) or on species biological attributes such as reproductive rate (Johnson, 1998; Alroy, 2001; Cardillo and Lister, 2002) or sexual versus nutritional selection pressures (Moen et al., 1999; Pastor and Moen, 2004). Species ecological and/or behavioral responses, such as direct avoidance of predators (i.e., humans) and prey naivety to a novel predator (humans, in this case), often leave few, if any, traces in the fossil record and have been little investigated so far. Here we concentrate on a related attribute, species commonness, to untangle the human influence on the distribution and survival of the late Pleistocene Eurasian large mammals.

We suppose that if humans drove megafauna to rarity and extinction, these species should have been significantly more abundant in human-occupied localities (where human hunters were gathering their remains) than at paleontological sites; such commonness would be an obvious sign of human interest. These species of "human interest" should also have become rarer in time as human presence became more evident. We tested these hypotheses by comparing species commonness and geographic distribution between paleontological and archaeological localities in areas with and without human presence during the late middle and late Pleistocene and Holocene, taking extant species as the control group. We analyzed the temporal trend in commonness patterns looking at the grand scale pattern, not concentrating on any species in particular. We also tried to evaluate possible biases on commonness factor such as species body size or locality environment type. The expectation for the extinct megafauna is to become overrepresented in archaeological sites as human technology improved from paleolithic to neolithic. Otherwise, factors other than direct human exploitation should have driven the demise of Eurasian megafauna.

## Materials and methods

### Locality distribution data

Numerous literature sources and the existing databases: the Neogene of the Old World (NOW, Fortelius, 2007), European Quaternary Mammalia (Pangaea, available online at: http://www.pangaea.de/), the marine oxygen isotope stage 3 project (OIS-3; van Andel, 2002) and the Paleolithic sites of northern Asia (available online at: http://sati.archaeology.nsc.ru/pna/) were incorporated to obtain data on Eurasian localities and species. The dataset comprises the late middle and late Pleistocene as well as the Holocene sites from western and central Europe and the former USSR along with several type localities from eastern Europe and the Mediterranean. However, the main emphasis was made on the former USSR territory because eastern Europe and Siberia were the last stand and key survival area of many species that went extinct at the end of the Weichselian and Holocene. Southeastern Asia (China, India) and Japan were excluded because of controversial taxonomy for many of their species (Chinese), high endemicity (Japanese), or lack of data.

In order to better correlate localities across Eurasia where more detailed temporal divisions are not available, sites were arranged into six age groups: (1) the late middle Pleistocene (or late Early Paleolithic sites, 400–130 ka; here called late MP); (2) Eemian interglacial (or the early Middle Paleolithic or early Mousterian sites, 130–115 ka); (3) early and middle Weichselian Glaciation (or the late Middle Paleolithic or late Mousterian sites along with the early Late Paleolithic or Aurignacian sites, 115–24 ka); (4) late Weichselian or Last Glacial Maximum (LGM) (or the middle Late Paleolithic sites, 24–15 ka); (5) latest late Weichselian or Late Glacial (LG) (or the latest Late Paleolithic or Magdalenian sites, 15–10 ka); and (6) Holocene (or the Mesolithic and Neolithic sites less than 10 ka). Chronostratigraphic correlations were based on marine oxygen isotope record (MIS/OIS) or chronometric dating (radiocarbon, TL, ESR, U-series methods), paleomagnetic polarity and chron correlations, continental mammalian biostratigraphy, along with archaeology (human cultural stages; Shantser, 1982; Stuart, 1991; Kahlke, 1999; van Kolfschoten, 2000; Currant and Jacobi, 2001; Khromov et al., 2001; Vangengeim et al., 2001; Vasil'ev et al., 2002; Sher et al., 2005). The oldest age group consists of the Khazarian and Singilian, which are correlated to the Holsteinian and Saalian sites (Azzaroli et al., 1988; Khromov et al., 2001; Vangengeim et al., 2001). The Eemian interglacial (MIS5e) was excluded from the main analyses because of a possible stratigraphic mixing since only recently have biostratigraphers in western and central Europe begun to discern the Eemian from the earlier interglacial (MIS7) localities, many of which happened to be often mistaken for the Eemian (Schreve and Thomas, 2001).

Originally we used a so-called loose temporal locality arrangement, in which a locality with a temporal range was attributed to an age group based on the majority of its temporal range and the description of a locality. In the original "loose" version as "archaeological" we took the sites that were attributed to a human cultural stage or where human artifacts were found. The rest of the localities were treated as "paleontological". Although even when attributed to a cultural stage archaeological sites may contain remains collected by nonhuman related processes or predators, the presence of lithics indicates that humans perhaps exploited some of the remains and it is this latter condition we were seeking.

However, we also used a more conservative approach with a stricter temporal resolution and different interpretation of archaeological versus paleontological sites. In this conservative version we only used directly dated late Paleolithic localities. The earlier archaeological sites were either dated or correlated to the MIS/OIS and Pleistocene/Weichselian stages. An overlap of 1,000 to 3,000 years between age groups may be present in a few of archaeological localities that are considered the latest Late Paleolithic (according to Vasil'ev, 2003), whereas their lower time boundaries are dated to slightly earlier than 15 ka. The rest of the localities have clear-cut boundaries. We also left out sites with a larger age overlap and those in which the dating did not correspond to the archaeological description. A slight bias could exist here toward recognizing an increased human effect during the later periods, because humans could have reworked some bones from earlier periods that were supposed to be either paleontological or archaeological.

In the conservative version, we counted as archaeological (rather than paleontological) any site with any indication of human presence, including those with human skeletal remains but without artifacts or cultural attributes even though it could be argued that such sites might represent carnivore generated accumulations. For that reason it was impossible to determine the exact agent of accumulation in many of our localities from all parts of Eurasia although our dataset consists of localities with a firm indication that faunal remains were accumulated by humans (''kitchen'' remains, camp sites). These latter sites still could have contained scavenged bones of species, which were not actively or passively (using natural traps) hunted in a live form. In general, it is difficult to determine when *Homo* species evolved as the ''hunter'' from the ''hunted upon'' and the predation efficiency of human colonizers is likely to be exaggerated. Thus, we also exaggerated a possible human effect by ascribing to them a selection actually made by other agents, biasing our analysis toward the recognition of human influence.

In sum, the strict conservative database includes 564 Eurasian localities, of which 267 are archaeological and 297 paleontological. We anticipated and obtained strikingly similar results in both approaches, indicating that the patterns we found are robust irrespective of the particular selection criteria we applied. Because of the similarity in the results using both methods, we only show the conservative version below.

*Commonness*

Species commonness is the proportion of sites in which a species was present during a given time period. Commonness is a proxy of abundance of the species remains in a fossil locality or assemblage, because it is likely that within a given region a species abundant in some sites will be present in most of them (Jernvall and Fortelius, 2002, 2004; Raia et al., 2006). It has been shown that the species present in ≥25% of localities (that is, common species) show general evolutionary trends more strongly as they are the ones that make the most use of the available abundant habitats and resources (Jernvall and Fortelius, 2002, 2004), thus, being better adapted to the environment. The rare species, on the other hand, produce the opposite results as the common species and tend only to add noise to the results (Jernvall and Fortelius, 2004; Pushkina, 2006).

Estimates of commonness proved rather robust (Jernvall and Fortelius, 2004), especially when using many localities in a single time period because as proportion (or percentage) commonness is not affected by the actual number of localities. Even a misidentification of several individuals will not significantly change the results. Such a method is strengthened here by using not only a single varying species, but several species belonging to a certain assemblage or group. The differential length of the temporal units we use should not significantly affect the commonness results, especially when the statistical differences between the archaeological and paleontological sites are large.

*Species*

We analyzed the large ungulate and carnivore species in Eurasia during times when the human effect could be observed along with their movement from Europe to Siberia. We chose ungulate species that belonged to the two best known faunal assemblages in Europe and Siberia (*Palaeoloxodon antiquus* interglacial and *Mammuthus primigenius* glacial) and the carnivores that accompanied them in Eurasia during the second half of the Pleistocene and Holocene.

The size of megafauna is not universally defined and some papers do not indicate any explicit size threshold (e.g., Brook and Bowman, 2002; Johnson, 2005; Wroe et al., 2006). Brook and Bowman (2004) interestingly noted that ''…most authors have restricted their discussion of extinct 'megafauna' by reference to some arbitrary body mass threshold, often set at around 45 kg… despite there being no obvious functional basis for this threshold (Owen-Smith, 1988). A point often overlooked is that many medium- and some small-sized mammals also went extinct (Johnson, 2002)…'' We used a body size limit of approximately 7 kg in this study.

We excluded ungulate species known to have had a restricted distribution (e.g., sheep, goats, the antelope, *Spirocerus kiakhtensis*, or the extinct yak, *Bos baikalensis*). And we excluded all domestic species, such as *Bos taurus* or *Canis familiaris*. In the case of horses and pigs, the domesticated forms were not osteologically discriminated from wild forms in all localities. They may be included in some localities. However, no species was used more than once. For instance, if there were *Bison priscus* and *B*. cf. *priscus* in a site list it was counted only once as *B. priscus*.

We divided the species into extinct and extant groups depending on whether the species was currently extant and living in the wild in Eurasia. Contemporary human reintroductions [e.g., *Ovibos* in Eurasia (Kahlke, 1999)] were excluded. The extinct group includes 13 species: the woolly mammoth, *Mammuthus primigenius*; the woolly

rhinoceros, *Coelodonta antiquitatis*; the steppe bison, *Bison priscus*; the musk ox, *Ovibos moschatus*; the straight-tusked elephant, *Palaeoloxodon antiquus*; Merck's rhinoceros, *Stephanorhinus kirchbergensis*; the narrow-nosed rhinoceros, *Stephanorhinus hemitoechus*; the aurochs, *Bos primigenius*; the giant deer or Irish elk, *Megaloceros giganteus*; the Pleistocene ass, *Equus hydruntinus*; cave hyena, *Crocuta crocuta*; cave lion, *Panthera leo*; and cave bear, *Ursus spelaeus*.

We note that although the aurochs was still living in historical times and the giant deer and cave lion survived into the Holocene, we had robust logical grounds to maintain these species in the extinct category despite their presence in our Holocene data. Species become rare before extinction (Jernvall and Fortelius, 2004; Vrba and DeGusta, 2004; Raia et al., 2006) and rare species often do not leave fossilized remains. Hence, as we were dealing with species commonness variation in the presence of humans, the zero commonness data could in fact represent no species present or true extinction, a species doomed to extinction, or a local extinction that could be or not be followed by new access to former habitats. Sorting out among these alternatives is impossible in our data. Yet, considering the aurochs, mammoth, and giant deer as extant or the fallow deer as extinct just because we had the first two (and no fallow deer) in our Holocene data would deny the mere fact that fallow deer are still living while the aurochs, mammoth, and the giant deer are extinct. This would also deny a period of rarity that species pass through prior to extinction. If we did that, we would have supported the illogical conclusion that humans could force a species to extinction by demographic collapse and then neglect extinction as a real consequence of that collapse by assigning them to the category of living species.

For the extant group we used the 17 species that survived in the wild in Eurasia until present: reindeer, *Rangifer tarandus*; saiga antelope, *Saiga tatarica*; fallow deer, *Dama dama*; roe deer, *Capreolus capreolus*; European wild boar, *Sus scrofa*; red deer, *Cervus elaphus*; moose, *Alces alces*; horse, *Equus ferus* (including *E. caballus, E. ferus, E. gmelini, E. latipes,* and *E. lenensis* taken as synonyms); kulan, *Equus hemionus*; wolf, *Canis lupus*; red fox, *Vulpes vulpes*; brown bear, *Ursus arctos*; dhole, *Cuon alpinus*; leopard, *Panthera pardus*; Arctic fox, *Alopex lagopus*; and wolverine, *Gulo gulo*.

We tried to eliminate nomenclatural discrepancies as much as possible. Species of horses, bison, and aurochs remain rather enigmatic in their relation to modern species or time of divergence into other species. Certainly, difficulties in species description, especially in discrimination between the numerous species of bison and/or horse and identification of aurochs, may introduce errors into the database; however, this analysis is offered as a broad guide of apparent differences in commonness of extinct and extant species in the sites associated with humans. The case of the horse would be more trivial if the many taxa used to describe its remains are, as many authorities contend, only regional variants of the same species. More detailed systematic analyses may produce more accurate results, although we argue the current results are robust enough to withstand any underlying taxonomic mistakes.

*Tests of possible sampling biases (body size, cave environment) on commonness values*

It is the case that 'natural' commonness could be altered by taphonomic factors that were at play in bone preservation in many of the sites we included in our database. A complete survey of taphonomic biases for each of the 564 localities in our data set is clearly impossible due to lack of information. We would add here that risks imposed by taphonomic factors are usually small in large data sets, given the so-called Portfolio effect (Raia et al., 2005), which we paraphrase as the relative risk associated with any given taphonomic factor is decreased by the number of taphonomic biases present in the dataset, hence by the number of localities included.

Nonetheless, we tested for the effect on commonness values of the two most relevant taphonomic factors: body size and preservation in cave environments. Smaller bones are less resistant to destruction by taphonomic agents because of their higher surface to volume ratio. Consequently, larger species are often overrepresented in fossil sites (Damuth, 1982). To consider whether body size influence commonness, we calculated body size of the extinct species by applying regression equations published in Damuth and MacFadden (1990). The data for a few ''living'' species were not available and we used a compilation of recent mammal body sizes across continents (Smith et al., 2003). The complete lists of data and body sizes can be found in Melore et al. (2007). The regression analysis of body size against commonness was performed on all species together and only on extinct and living species, separately. A significant relationship would suggest that large body sizes bias towards higher commonness, whereas large species cannot be very common (Brown, 1984; Gaston and Blackburn, 2000).

We also analyzed the most pervasive and important effect of cave environments. Caves naturally provided shelters for humans (Rolland, 2004) and other species (most notably the carnivores: cave bear, cave lion, and cave hyena) and were rather unsuitable for the megaherbivores or their bones accumulations. Furthermore, accumulation of bones by carnivore predators in caves could mistakenly increase commonness at human-occupied sites for some species at the expense of others. Similarly, the tendency of humans and some other species to ''frequent'' caves might lead to overestimates of human exploitation on these species. We discerned the layers with and without human artifacts in a locality, where it was possible, according to the latest updated versions of databases and catalogs (e.g., latest publication in Pangaea database; Paunovic et al., 2001). We partitioned our localities into ''cave'' and ''open-air'' categories. Grottos and rock shelters were considered caves. We then performed a χ-test to assess whether archaeological sites included more caves than expected, and then computed commonness to be compared between caves and open air sites with a Wilcoxon test.

Table 1
Species commonness in archaeological and paleontological sites by time period. Body size is given in $\log_{10}$ kg

| Species | Late middle Pleistocene | | Eemian | | Early and middle Weichselian | | Late Glacial Maximum | | Late Glacial | | Holocene | | status | mass |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | paleo | archaeo | paleo | archaeo | paleo | archaeo | paleo | archaeo | paleo | archaeo | paleo | archaeo | | |
| *Alces alces* | 0.04 | 0.07 | 0.17 | 0.17 | 0.1 | 0.19 | 0.05 | 0.06 | 0.04 | 0.25 | 0.27 | 0.29 | living | 5.585 |
| *Alopex lagopus* | 0.01 | 0 | 0.04 | 0 | 0.11 | 0.21 | 0.14 | 0.45 | 0.11 | 0.23 | 0 | 0.03 | living | 3.798 |
| *Bison priscus* | 0.45 | 0.21 | 0.57 | 0.33 | 0.37 | 0.53 | 0.18 | 0.52 | 0.11 | 0.67 | 0.05 | 0.04 | extinct | 5.837 |
| *Bos primigenius* | 0.09 | 0.43 | 0.28 | 0.67 | 0.08 | 0.18 | 0 | 0.09 | 0.04 | 0.08 | 0.02 | 0.13 | extinct | 6.021 |
| *Canis lupus* | 0.1 | 0.57 | 0.3 | 0.67 | 0.23 | 0.66 | 0.27 | 0.45 | 0.11 | 0.43 | 0.32 | 0.32 | living | 4.568 |
| *Capreolus capreolus* | 0.02 | 0.64 | 0.26 | 1 | 0.11 | 0.27 | 0.05 | 0.09 | 0.04 | 0.28 | 0.37 | 0.56 | living | 4.364 |
| *Cervus elaphus* | 0.4 | 1 | 0.55 | 1 | 0.28 | 0.75 | 0.09 | 0.39 | 0.15 | 0.54 | 0.32 | 0.74 | living | 5.272 |
| *Coelodonta antiquitatis* | 0.19 | 0.07 | 0.21 | 0 | 0.37 | 0.52 | 0.27 | 0.55 | 0.11 | 0.13 | 0 | 0 | extinct | 6.429 |
| *Crocuta crocuta* | 0.09 | 0.29 | 0.26 | 0.33 | 0.21 | 0.47 | 0.14 | 0.09 | 0 | 0.03 | 0 | 0 | extinct | 5.009 |
| *Cuon alpinus* | 0.04 | 0.07 | 0 | 0 | 0 | 0.13 | 0 | 0 | 0 | 0 | 0.02 | 0.04 | living | 4.106 |
| *Dama dama* | 0.11 | 0.14 | 0.26 | 1 | 0.04 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | living | 4.813 |
| *Equus ferus* | 0.49 | 0.36 | 0.17 | 0.33 | 0.34 | 0.62 | 0.55 | 0.61 | 0.15 | 0.64 | 0.2 | 0.5 | living | 5.699 |
| *Equus hydruntinus* | 0.02 | 0.21 | 0.04 | 0.33 | 0.04 | 0.15 | 0 | 0.09 | 0 | 0.02 | 0 | 0 | extinct | 5.362 |
| *Equus hemionus* | 0.02 | 0 | 0.02 | 0 | 0.03 | 0.15 | 0 | 0.24 | 0 | 0.21 | 0.05 | 0.12 | living | 5.322 |
| *Gulo gulo* | 0.02 | 0 | 0 | 0 | 0.07 | 0.2 | 0.14 | 0.24 | 0.07 | 0.18 | 0.15 | 0.06 | living | 4.29 |
| *Lynx lynx* | 0 | 0.14 | 0 | 0.17 | 0.07 | 0.19 | 0 | 0.03 | 0.07 | 0.03 | 0.12 | 0.03 | living | 4.254 |
| *Mammuthus primigenius* | 0.15 | 0.07 | 0.34 | 0 | 0.69 | 0.49 | 0.73 | 0.67 | 0.67 | 0.33 | 0.1 | 0 | extinct | 6.632 |
| *Megaloceros giganteus* | 0.13 | 0.29 | 0.43 | 0.67 | 0.15 | 0.22 | 0 | 0 | 0.11 | 0.02 | 0.07 | 0.01 | extinct | 5.589 |
| *Ovibos moschatus* | 0.02 | 0 | 0.02 | 0 | 0.25 | 0.05 | 0.32 | 0.06 | 0.11 | 0.05 | 0.05 | 0 | extinct | 5.496 |
| *Paleoloxodon antiquus* | 0.13 | 0.5 | 0.45 | 0.83 | 0.04 | 0.04 | 0 | 0 | 0 | 0 | 0 | 0 | extinct | 6.678 |
| *Panthera leo* | 0.29 | 0.5 | 0.32 | 0.67 | 0.27 | 0.35 | 0.14 | 0.09 | 0.07 | 0.1 | 0 | 0.01 | extinct | 5.262 |
| *Panthera pardus* | 0.01 | 0.5 | 0.02 | 0.67 | 0.03 | 0.13 | 0 | 0 | 0 | 0 | 0.05 | 0.04 | living | 4.778 |
| *Rangifer tarandus* | 0.11 | 0.14 | 0.15 | 0 | 0.34 | 0.47 | 0.23 | 0.64 | 0.22 | 0.59 | 0.05 | 0.09 | living | 4.935 |
| *Saiga tatarica* | 0.07 | 0 | 0.02 | 0 | 0.01 | 0.22 | 0 | 0.18 | 0 | 0.13 | 0 | 0.07 | living | 4.462 |
| *Stephanorhinus kirchbergensis* | 0.15 | 0.29 | 0.36 | 1 | 0.04 | 0.07 | 0 | 0 | 0 | 0 | 0 | 0 | extinct | 6.341 |
| *Stephanorhinus hemitoechus* | 0.04 | 0.21 | 0.21 | 0.33 | 0.03 | 0.01 | 0 | 0 | 0 | 0 | 0 | 0 | extinct | 6.429 |
| *Sus scrofa* | 0.07 | 0.29 | 0.21 | 0.83 | 0.1 | 0.16 | 0.05 | 0.09 | 0.07 | 0.08 | 0.24 | 0.69 | living | 5.069 |
| *Ursus arctos* | 0.04 | 0.43 | 0.23 | 0.33 | 0.18 | 0.38 | 0.05 | 0.27 | 0.07 | 0.26 | 0.44 | 0.34 | living | 5.223 |
| *Ursus spelaeus* | 0.04 | 0.36 | 0.17 | 0.67 | 0.23 | 0.44 | 0.14 | 0.09 | 0.07 | 0.07 | 0.02 | 0.06 | extinct | 5.439 |
| *Vulpes vulpes* | 0.13 | 0.5 | 0.17 | 0.33 | 0.2 | 0.52 | 0.09 | 0.24 | 0.11 | 0.21 | 0.34 | 0.44 | living | 3.778 |

*Testing for human influence on commonness values*

The northernmost human-occupied sites in our data reached 51°N during the late MP, 52.87°N during the Eemian (early middle Palaeolithic or early Mousterian), 58.3°N during the early and middle Weichselian (late Middle Paleolithic or late Mousterian and early Late Paleolithic), 60.35°N during the LGM (middle Late Paleolithic), 70.43°N during the Late Glacial (latest Late Paleolithic), and 65.07°N during the Holocene (Mesolithic and Neolithic). Many other species resided far north of humans (see below). Theoretically, it is possible that the northern ''human free'' areas acted as a refuge to species ''trying to avoid'' human overexploitation in the south, or for those already extirpated there (as suggested by Surovell et al., 2005, for proboscideans). To consider the importance of these northern areas as potential refugia for large mammal species, we calculated species commonness both within and beyond the northernmost limit of human occupation, regardless of whether they occurred in archaeological or paleontologial sites, and then compared the extinct and extant species groups, using a nonparametric (Mann-Whitney) test. For these following analyses we used only five time periods, excluding the 130–115 ka as mentioned earlier because of the extremely low frequency of archaeological sites.

Many late Pleistocene species of the cold-adapted *Mammuthus primigenius* assemblage or the mammoth steppe roamed mostly northward of human settlements. However, the use of northern refugia was by no means the only way to avoid people for species were able to tolerate very cold conditions typical of northern latitudes. Human-free areas were also available within human ranges (Stewart and Lister, 2001; Surovell et al., 2005). Thus, we calculated species commonness separately in archaeological and paleontological sites to test if and which species were abundant in human-occupied sites (Table 1). We also computed a ''human preference'' (HP) or human association factor for each time period by calculating the difference in commonness between archaeological and paleontological sites for each species. Any strong association between humans and currently extinct species (indicated by higher than expected commonness in archaeological sites or higher HPs) may depend on human selection and exploitation of these animals; yet, it could also depend on geographical distribution and a possible habitat selection of the latter. An obvious bias would occur when comparing species with different geographic ranges than humans, because latitudinal differences in commonness within a species range can be substantial since species abundance, and, hence, commonness is expected to decrease toward the periphery of its range (Lawton, 1993; Brown et al., 1995; Blackburn et al., 1999). Accordingly, we corrected for the species distribution effects by taking the difference in mid-latitude range point between the focal species and humans in each age group. These differences in latitude were regressed against the differences in HP (commonness) using a least squares regression analysis. HP residuals were then compared between living and extinct species for each time period by a Mann-Whitney test. If humans effectively altered commonness patterns of extinct species via hunting, HP residuals of extinct species should

be significantly higher (i.e., they should be more common than expected in archaeological sites). The opposite result (i.e., living species being more common than expected in archaeological sites) would not support the influence of humans on megafaunal extinction. Apart from geographical distribution, habitat selection could similarly bias the HP residuals. Thus, it is important to take into account if human-associated species (i.e., species with high HP residuals) were present in the same habitats as humans. If they were not, then the interpretation that their abundance in archaeological sites was caused by human selection on them would be strengthened.

## Results

*Archaeological versus paleontological sites*

The number of human-occupied sites increases considerably from the late MP into the Weichselian and Holocene. The temporal shifts in mean latitudinal distribution demonstrate that localities bearing signs of human intervention are continuously situated southward of the localities with purely paleontological associations [ANOVA effect of age group $F_{5,552} = 21.98$, $p < 0.001$; effect of human presence $F_{1,552} = 109.58$, $p < 0.001$; the effect of interaction between age group and human presence $F_{5,552} = 3.51$, $p = 0.004$ (Fig. 1)]. This suggests that earlier in time and prior to human northward spread, purely paleontological localities would be situated
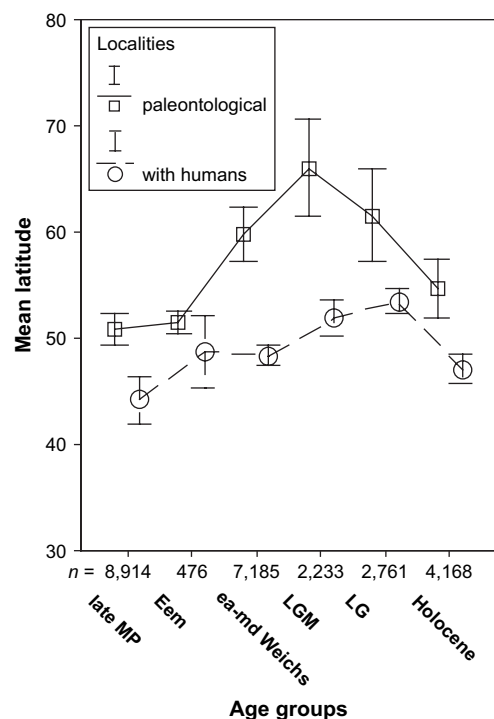


Fig. 1. Temporal changes in mean latitudinal distribution in archaeological and paleontological localities. Error bars represent 95% confidence limits. Age group are defined in Methods (some abbreviations: late MP, late middle Pleistocene; Eem, Eemian; ea-md Weichs, early and middle Weichselian glaciation).

Table 2
Results of regression of body size versus total commonness by time period

| Age group | Status | Intercept | Slope | $r^2$ | F | p |
|---|---|---|---|---|---|---|
| Late MP | extinct | 0.032077 | 0.000785 | 0.000233 | 0.002568 | 0.960496 |
| | living | −0.09715 | 0.027049 | 0.189786 | 3.513629 | 0.080475 |
| Eemian | extinct | −0.04209 | 0.014371 | 0.125931 | 1.584816 | 0.234129 |
| | living | −0.04793 | 0.015703 | 0.144577 | 2.535185 | 0.132184 |
| Early and middle Weichselian | extinct | 0.049699 | −0.00258 | 0.0034 | 0.03753 | 0.849922 |
| | living | −0.01361 | 0.009773 | 0.063682 | 1.020206 | 0.328487 |
| Last Glacial Maximum | extinct | −0.07935 | 0.019122 | 0.0673 | 0.793717 | 0.392049 |
| | living | −0.02285 | 0.011927 | 0.0406 | 0.634773 | 0.438039 |
| Late Glacial | extinct | 0.002889 | 0.003824 | 0.004616 | 0.05101 | 0.825457 |
| | living | −0.05572 | 0.020115 | 0.114641 | 1.942272 | 0.183728 |
| Holocene | extinct | 0.029179 | −0.00381 | 0.07437 | 0.883797 | 0.36735 |
| | living | −0.06766 | 0.025638 | 0.089894 | 1.481594 | 0.242329 |

northwards of sites associated with humans. At all times, some wild species were better adapted to cold conditions than were humans and humans were occupying the southern end of the spectrum of other species' occupation.

In general, the human-occupied localities show a tendency to shift to the north during the Weichselian or the late Paleolithic (ANOVA $F_{5,261} = 18.71$, $p < 0.001$). Post-hoc Tukey differences between age groups indicate that the most significant
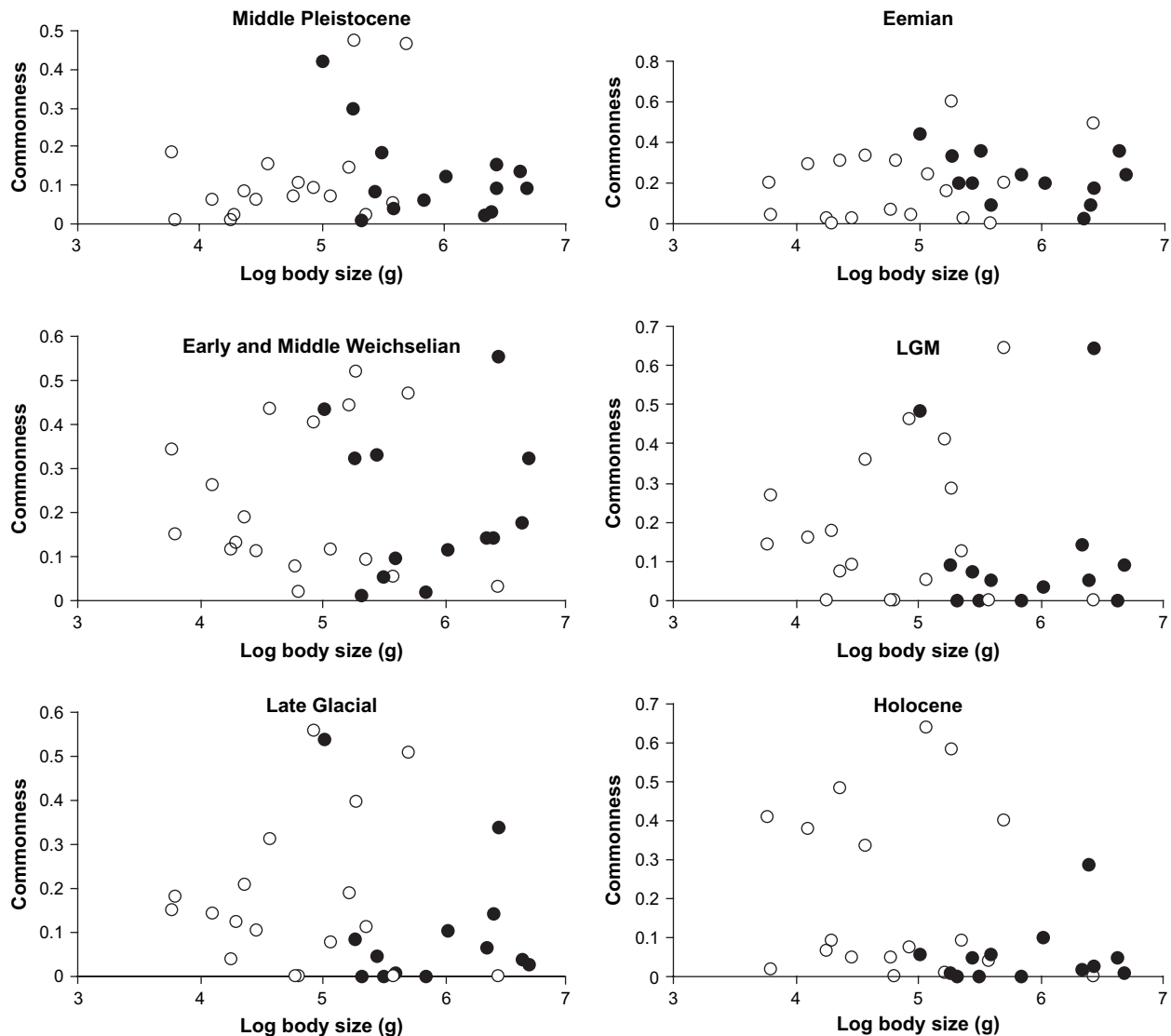


Fig. 2. Species body size plotted versus commonness. Extinct species are represented by solid circles. Living species are represented by open circles. The difference in body size between extinct and extant species is highly significant (Mann and Whitney U = 18.000; p < 0.0001).

Table 3
Number and type of fossil assemblage and site type by time period

| Age group | Locality type | Assemblage type | | Total |
|---|---|---|---|---|
| | | paleontological | archaeological | |
| Late middle | open-air site | 61 | 6 | 67 |
| Pleistocene | cave | 18 | 8 | 26 |
| | unknown | 10 | 0 | 10 |
| Eemian | open-air site | 25 | 4 | 29 |
| | cave | 11 | 2 | 13 |
| | unknown | 11 | 0 | 11 |
| Early and middle | open-air site | 49 | 30 | 79 |
| Weichselian | cave | 19 | 52 | 71 |
| | unknown | 3 | 3 | 6 |
| Last Glacial | open-air site | 17 | 27 | 44 |
| Maximum | cave | 5 | 4 | 9 |
| | unknown | 0 | 2 | 2 |
| Late Glacial | open-air site | 18 | 50 | 68 |
| | cave | 7 | 9 | 16 |
| | unknown | 2 | 2 | 4 |
| Holocene | open-air site | 19 | 27 | 46 |
| | cave | 19 | 33 | 52 |
| | unknown | 3 | 8 | 11 |

northward shifts occurred between the late middle Pleistocene and Weichselian ($p = 0.026$) and between the early and middle Weichselian and LGM ($p = 0.004$). The shift between the LGM and LG is not significant. The southward Holocene trend possibly occurs due to a paucity of northern sites in our dataset in this epoch.

### Analysis of potential biases

Body size did not exert a significant effect on species commonness (Table 2). The relationship was nonsignificant in spite of the extreme commonness of the woolly mammoth during the early and middle Weichselian or LGM. We anticipate here that the woolly mammoth shows the least association with humans (see below), and consequently, its high commonness is further evidence that its scarce association with humans is probably genuine. Most extinct megafauna were significantly larger than their living counterparts (Fig. 2). Thus, we point out that if the effect of body size on commonness was indeed larger than with our interpretation, it should have favored the presence of large, extinct species in association with people.

The human association with caves is significant ($\chi$ test, $\chi = 48.87$, df = 5, p < 0.001; Table 3). Interestingly, this association between humans and caves is very strong during

the early and middle Weichselian. Differences in commonness between caves and open sites are not pronounced (Table 4). Wilcoxon tests indicate living species to be more common than expected in caves in all time periods, but significantly so only during early and middle Weichselian. The same does not apply to extinct species (Table 4). This discrepancy should have increased the association of living species with people, at least for the early and middle Weichselian period.

### Human interference

All extinct species were much more common north of the human geographic range limit than they were within it. This difference is especially apparent since the early and middle Weichselian (Table 5). On the contrary, living species were always more common within than beyond the human range. Differences between extinct and living species are generally nonsignificant both within and beyond human range, except for the obvious rarity of extinct species during the Holocene period. This commonness pattern is probably explained by the better adaptation of majority of extinct species to cold conditions as mentioned earlier, although it is also consistent with human overexploitation (Table 5). Except for the late MP and the early and middle Weichselian, latitudinal differences in distribution between humans and other large mammals were poor predictors of the difference in commonness between archaeological and paleontological sites, especially in the more recent periods (Table 6).

The analysis of HP residuals indicates that the differences between the extinct and living species are significant during the Weichselian glaciation. Yet, contrary to the hypothesis of human-induced extinction, Mann-Whitney U tests performed on the HP residuals indicate that the species with the highest relative commonness in archaeological sites (high HP residuals) are extant taxa (Tables 7 and 8), except for the extinct steppe bison *Bison priscus*.

Contrary to the surviving late Pleistocene cold-adapted reindeer and saiga that were strongly associated with humans, the extinct cold-adapted ungulate species (woolly mammoth, woolly rhino, musk ox) were extremely rare in human-occupied sites, as expected by their distribution. The commonness of extinct warm-adapted species (straight-tusked elephant, hippopotamus, Merck's and narrow-nosed rhinoceri, giant deer, aurochs) is very similar with and without humans, again indicating little human influence on them.

Table 4
Results of Wilcoxon tests performed to compare species commonness between caves and open air sites. Positive signs indicate that commonness was higher in caves

| Age group | Extinct | | | Living | | |
|---|---|---|---|---|---|---|
| | Z | p | sign of difference | Z | p | sign of difference |
| Late MP | −1.57339 | 0.115629 | − | −1.49136 | 0.135867 | + |
| Early and middle Weichselian | −0.62757 | 0.530285 | + | −2.17177 | 0.029873 | + |
| LGM | −0.1777 | 0.858955 | − | −0.38437 | 0.700703 | + |
| Late Glacial | −0.05096 | 0.959354 | + | −0.84748 | 0.396726 | + |
| Holocene | 0 | 1 | − | −0.84748 | 0.396726 | + |

Table 5
Commonness of extant and extinct species within and beyond human geographic range

| Age group | 400–130 ky ago | 115–24 ky BP | 24–15 ky BP | 15–10 ky BP | Holocene |
|---|---|---|---|---|---|
| *Commonness (site occupancy) outside human range* | | | | | |
| Extinct | 0.132 | 0.212 | 0.142 | 0.156 | 0.112 |
| Living | 0.057 | 0.055 | 0.052 | 0.026 | 0.039 |
| p = | *0.869083* | *0.650058* | *0.650058* | *0.156925* | *0.001473* |
| | | | | | |
| *Commonness (site occupancy) within human range* | | | | | |
| Extinct | 0.152 | 0.270 | 0.197 | 0.128 | 0.032 |
| Living | 0.168 | 0.281 | 0.237 | 0.221 | 0.232 |
| p = | *0.015382* | *0.680075* | *0.772946* | *0.408285* | *0.591685* |
| | | | | | |
| *Species mid-range point (in degrees of latitude, range in parentheses)* | | | | | |
| Extinct | 49.3 | 51.9 | 56.0 | 55.2 | 52.1 |
| | (70–39.0) | (76–38.1) | (75.5–40.1) | (75.3–39.4) | (74.5–40.3) |
| Living | 46.7 | 49.3 | 53.3 | 53.0 | 48.5 |
| | (68.0–39.0) | (74.5–8.1) | (75.3–40.1) | (70.5–39.4) | (74.5–40.2) |
| p = | *0.1* | *0.2* | *0.4* | *0.2* | *0.1* |

The commonness of the extinct carnivores declined at a similar rate in both paleontological and archaeological sites. Among the surviving carnivores in the human-occupied sites, the commonness of the brown bear and red fox declined during the Weichselian (especially LGM and LG), but the commonness of the arctic fox increased during the late Weichselian (LGM). The wolves were very abundant throughout all stages. The carnivores' HP residuals were very close to zero for most of the late middle to late Pleistocene. Yet, the carnivores become rarer in the Holocene archaeological sites, perhaps, indicating that humans become increasingly able to keep them out of their sites (Table 9).

The commonness in the extinct species is quite similar in paleontological and archaeological sites within human ranges, suggesting that humans did not intentionally avoid bringing bones of the large species (that represent the extinct category) back to their site (Table 10).

## Discussion

### Human distribution

Long before 100,000 years ago, humans coexisted with the megafauna without causing any extinction. In western Europe, there is archaeological evidence of human occupation as early as about 800,000 years ago (Carbonell et al., 1995; Bermúdez de Castro et al., 1997; Finlayson, 2004, 2005). The Acheulean cultures are known from the Caucasus from about 583,000 years ago (Baryshnikov, 1987; Molodkov, 2001). Humans were present in northern Eurasia (Eurasian Plains) at about 45,000–40,000 years ago (Finlayson, 2005; Anikovich et al., 2007). Anatomically modern humans inhabited western Europe at about 34,000–36, 000 years ago (Smith et al., 1999; Paunovic et al., 2001; Trinkaus et al., 2003) or 31,000 years ago (Finlayson and Carrión, 2007). The earliest modern human occupation or early Late Paleolithic occupation for southern Siberia is recorded at 43–39,000 yrs ago and they appear to have occupied all of northern Asia by 13,000 yr ago (Vasil'ev et al., 2002).

The difference in distribution between humans and other species suggests that humans were rather warm-loving species, considering their place of origin in tropical Africa and the late survival of archaic hominins in Southeast Asia (Finlayson, 2004, 2005). The majority of the large mammals that survived the late Pleistocene were also adapted to temperate environments. Nevertheless, humans dispersed northwards from the late MP to the Weichselian (Praslov, 1984; this study). During the LGM humans moved northwards along the main Siberian rivers, perhaps, fleeing from the deserted steppes in the south (Madeyska, 1992).

Much evidence exists on human/animal interactions in a broad sense. Various mammoth products dated to 20–14,000 yr BP are known from many countries; including Ukraine, Poland, and the Czech Republic (Pidoplichko, 1998; Péan, 2001). However, the evidence for hunting and/or scavenging may be much older as humans could also collect the bones of already long dead animals (Vereshchagin and Baryshnikov, 1984; Vasil'ev, 2003). In this case, not all species from the archaeological sites are necessarily dated to the corresponding cultural stage and, thus, may increase the bias towards human influence. Therefore, it is all the more striking to find no or little effect of human exploitation in our study.

### Biases due to cave sites and body size

Large body size did not translate into artificially high commonness values. This structure of the commonness/body size plot is very similar to the abundance/body size

Table 6
Results of the least-squares regression of HP factor (commonness differences between archaeological and paleontological sites) against differences in mid-latitude geographical range between large mammal species and humans by time period

| Time period | Intercept | Slope | $r^2$ | Significance |
|---|---|---|---|---|
| Late MP | 0.012 | −0.04 | 0.283 | 0.003 |
| Early and middle Weichselian | 0.04 | −0.04 | 0.448 | 0.001 |
| LGM | −0.001 | −0.003 | 0.122 | 0.061 |
| LG | −0.001 | −0.002 | 0.012 | 0.268 |
| Holocene | 0.005 | −0.001 | 0.051 | 0.153 |

Table 7
Comparison of HP residuals between extinct and living species

| Age group | Status | $n$ | Mean rank | Mann-Whitney U | Z | p |
|---|---|---|---|---|---|---|
| Late MP | extinct | 13 | 15.154 | 106 | −0.188 | 0.851 |
|  | living | 17 | 15.765 |  |  |  |
|  | total | 30 |  |  |  |  |
| Early and middle Weichselian | extinct | 13 | 11.462 | 58 | −2.197 | 0.028 |
|  | living | 17 | 18.588 |  |  |  |
|  | total | 30 |  |  |  |  |
| LGM | extinct | 9 | 9.000 | 36 | −1.503 | 0.133 |
|  | living | 13 | 13.231 |  |  |  |
|  | total | 22 |  |  |  |  |
| Late Glacial | extinct | 10 | 10.300 | 48 | −1.288 | 0.198 |
|  | living | 14 | 14.071 |  |  |  |
|  | total | 24 |  |  |  |  |
| Holocene | extinct | 8 | 13.125 | 51 | −0.581 | 0.561 |
|  | living | 15 | 11.400 |  |  |  |
|  | total | 23 |  |  |  |  |

plot in the macroecological literature (cf. Brown and Maurer, 1987; Gaston and Blackburn, 2000). Similarly, the significant association of humans and cave environment only during the early and middle Weichselian or the late Middle Paleolithic (late Mousterian) and the early Late Paleolithic does not entail relevant alteration of commonness of human-associated fauna.

Intriguingly, this is consistent with the evidence that regular cave occupation begins during the later Acheulean and becomes frequent during the Middle and Late Paleolithic (Rolland, 2004). Only during the late Paleolithic did humans probably start to dominate open landscapes considering vast territories of northern Eurasia given that the majority of the Late Paleolithic sites in Siberia, for example, are open-air sites on river terraces or not very high mountains (Derevianko et al., 1997; Reinhart-Waller, 2000; Goebel, 1999). Beauval et al. (2005) suggest that mobility becomes an important component of the middle Late Paleolithic hunter-gatherer adaptation across Europe.

However, according to our analysis, species commonness was not significantly different between caves and open air sites. Abundance of extant large mammals in caves seems little influenced by human activity (see below). Instead, it seems to reflect the preference of these species for warmer habitats and their smaller body size. Indeed, the penchant of extant species for caves becomes nonsignificant in the LGM and, especially, Late Glacial and Holocene, when most megafauna had already vanished and climate became warmer. The

significant "preferences" of humans and extant species for caves during the early and middle Weichselian certainly can indicate that humans rarely brought megamammal bones home to caves.

Intuitively, the relative rarity of remains of extinct species in many archaeological sites could simply reflect a situation in which remains of these heavy animals were seldom brought back to any human site. Yet, the extinct large mammals were equally rare in paleontological sites at similar latitudes. This latter observation indicates that the rarity of extinct species within human ranges (and not just in archaeological sites) was a real ecological phenomenon, and strongly argues against the notion that humans were responsible for their demise. Our data suggest that if a direct avoidance of humans by these species via gathering in northern areas was possible, it was not due to human overexploitation in the south.

The association between extant species and humans was particularly strong in middle-sized species like deer (reindeer, roe deer, red deer), horse (horse, kulan), saiga, and, during the Holocene, the wild boar. Although this association is partially driven by some proclivity to inhabit caves or be collected there by carnivore predators it holds for open-air sites as well, and for some extant species (e.g., saiga, reindeer, and moose), which were extremely rare in caves. Wolves are extremely common at archaeological sites which may indicate the long association between "man and his dog" and a confirmed domestication of a Paleolithic dog known from Eurasia (Reinhart-Waller, 2000).

The exploitation of similar habitats was not responsible for the strong human association with some species in our study. Indeed, those most heavily-exploited by humans include species of different habitat; forest species, such as red deer and wild boar (although both can be met outside forests), and typical steppe inhabitants, such as reindeer, horse, and steppe bison. In addition, typical steppe species appear both among the human-preferred (bison, horse, reindeer) and the human-avoided (woolly mammoth, musk ox) categories.

The tendency of commonness either to increase or to decrease is consistent between archaeological and paleontological sites for most extinct megafauna (this study; Grayson and Meltzer, 2002). A "peaked" trajectory in which species are initially relatively uncommon, then increase in commonness, and then become less common prior to extinction is consistent with the "natural" course for the species through time (Raia et al., 2006) and casts further doubts on the hypothesis that humans doomed these megafauna to extinction.

Table 8
Herbivore species with the three highest and lowest HP residuals by time period

|  | Late middle Pleistocene | Early and middle Weichselian | LGM | Late Glacial | Holocene |
|---|---|---|---|---|---|
| high | *Capreolus capreolus* | *Cervus elaphus* | *Rangifer tarandus* | *Bison priscus* | *Sus scrofa* |
|  | *Ovibos moschatus* | *Saiga tatarica* | *Equus hemionus* | *Equus ferus* | *Cervus elaphus* |
|  | *Bos primigenius* | *Equus ferus* | *Bison priscus* | *Equus hemionus* | *Equus ferus* |
| HP*res* |  |  |  |  |  |
| low | *Bison priscus* | *Dama dama* | *Ovibos moschatus* | *Coelodonta antiqutatis* | *Capreolus capreolus* |
|  | *Equus ferus* | *Stephanorhinus hemitoecus* | *Equus ferus* | *Megaloceros giganteus* | *Megaloceros giganteus* |
|  | *Dama dama* | *Mammuthus primigenius* | *Mammuthus primigenius* | *Mammuthus primigenius* | *Alces alces* |

Table 9
Differences in HP residuals between herbivores and carnivores by time period

|  |  | Late MP | Early and middle Weichselian | LGM | Late Glacial | Holocene |
|---|---|---|---|---|---|---|
| Mann-Whitney U |  | 85 | 75 | 52 | 49 | 17 |
| Mean | Carnivore | 17.273 | 18.182 | 12.000 | 10.444 | 7.200 |
| Rank | Herbivore | 14.474 | 13.947 | 11.214 | 13.733 | 15.692 |
| Asymp. Sig. (2-tailed) |  | 0.401 | 0.204 | 0.785 | 0.270 | 0.003 |
| Exact Sig. [2*(1-tailed Sig.)] |  | 0.420 | 0.216 | 0.815 | 0.290 | 0.002 |

Only the data for the extinct steppe bison may indicate a disproportionate selection by humans although more sufficient and recently updated data are needed. The bison becomes more common in archaeological sites with time but declines in paleontological sites. Shapiro et al. (2004) showed that the bison's genetic decline in Beringia started at 37,000 years ago. However, a genetic bottleneck does not always lead to extinction. A good example in medium-sized mammals are muskoxen that survived in North America despite suffering a great loss of genetic diversity at the Pleistocene-Holocene boundary that leaves them with very low genetic variability (MacPhee et al., 2005). Other extant cold-adapted species may reflect this drastic change in ecological conditions in their genetic history. A study of the Late Paleolithic sites in the Baikal and Altai regions indicated that the bison's commonness increased significantly from the late middle Weichselian (30−24 ka) to the LGM (Pushkina, 2006), while humans were present in southern Siberia slightly prior to 37,000 years ago (Vasil'ev et al., 2002; Shapiro et al., 2004).

In our study too the extinction of the steppe bison appears to be related to humans. Human subsistence activities in Siberia heavily relied on bison, reindeer, and horse during the Late Paleolithic (Vasil'ev, 2003). The commonness of the extinct bison and surviving ungulate species (reindeer, horse, saiga, and red deer) in archaeological sites strongly indicates their intensive utilization by humans, especially during the Weichselian glaciation or the late Middle and Late Paleolithic. This can be related to increased population density (archaeological sites outnumber paleontological sites for the first time during the early and middle Weichselian) and to improving hunting technologies, such as the appearance of the microblade-producing populations of highly mobile hunters across Siberia after the LGM who concentrated on a single prey species of large or medium size (Goebel, 2002). The microblade technology appeared with the exploitation of smaller less gregarious species probably because the big game species were disappearing (Tankersley and Kuzmin, 1998). Overall, it appears that humans were generalized, albeit effective, predators and efficiently concentrated on the most abundant prey species, most of which survive today.

Mesolithic hunting was similar to Paleolithic hunting (Reinhart-Waller, 2000), but the range of hunted species was reduced for the Mesolithic hunters (Tankersley and Kuzmin, 1998). However, agriculture and domestication that appeared during the Mesolithic could increase the pressure on exploitable animals, on one hand, and relieve the extinction pressure of some species, on the other. In our case, almost all heavily-exploited species that survived were either forest inhabitants or domesticated. The reindeer was domesticated around 5,000 years ago (Beringia series, 1992), and the horse rather late around 4−3,000 years ago (Reinhart-Waller, 2000; Bunzel-Drüke, 2001). The steppe bison gave rise to the two extant species: *Bison bonasus* and *Bison bison* (Ricciuti, 1973). In striking contrast to domestication and long coexistence of ungulates and people in Eurasia, prey naivety to humans has been claimed to be relevant to the late Pleistocene faunal extinction on other continents and later on islands (Burney and Flannery, 2005).

In summary, the evidence we found argues against the possibility that humans caused the late Pleistocene megafaunal extinctions of Eurasia. In northern Eurasia extinctions at the Pleistocene-Holocene boundary coincided with a rapid vegetation shift towards more humid and closed conditions (Guthrie, 1984, 1995; Sher, 1997). Highly productive grasslands or steppe-tundra, that occupied vast territories in northern Eurasia during the late Pleistocene, disappeared in the Holocene giving space to zonal vegetation, tundra in the north, and boreal forest or taiga in the south (Guthrie, 1984). Consistently, typically forest taxa such as the moose, red deer, roe deer, and wild boar, spread after the Weichselian glaciation. Likely, this extensive environmental change (and the vanishing of ''mammoth-steppe'' in particular) was the most important determinant of megafaunal extinction.

## Conclusions

The relative commonnes of the large mammals of Eurasia were influenced by human activity to some extent. People became increasingly able to hunt abundant prey species, many of which, however, are still living. Humans became able to exclude large carnivores from their sites or defend their homes. By the latest Late Paleolithic populations of large mammals of the ''mammoth-steppe'' were already suffering from the deterioration and contraction to the north of their preferred habitat, while humans appeared to show little interest in the now-

Table 10
Paired comparisons of extinct species commonness between archaeological and paleontological sites, limited to sites located within human geographic range

|  | Middle Pleistocene | Early and middle Weichselian | LGM | Late Glacial | Holocene |
|---|---|---|---|---|---|
| Z | −0.319 | −0.339 | −0.276 | −0.143 | −0.052 |
| p | 0.750 | 0.734 | 0.783 | 0.886 | 0.958 |

extinct species, even when a conservative archaeological approach was used that should have favored finding human influence on extinct fauna. Only the extinct steppe bison appears to have been negatively influenced by humans. Our findings are mainly consistent with the climatic explanation of the late Pleistocene extinctions in Eurasia.

## Acknowledgements

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