

Neanderthal extinction as part of the faunal change in Europe during Oxygen Isotope Stage 3

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Abstract. The extinction of the Neanderthals has not been widely considered in the light of the palaeoecology of other mammals. Therefore, a palaeoecological and historical biogeographical analysis of a database of European mammalian fossils for the period covering 60-20 thousand calendar years (approximately OIS 3 and covering the time when Neanderthals became extinct) has been conducted that shed light on the ecological conditions of this period. Broadly the larger mammals in this database form historical biogeographical categories including extant ubiquitous, extant northern and montane, extant eastern, extinct northern and extinct southern taxa. Neanderthals appear to belong to the extinct southern grouping which highlights the lack of attention they had received from the perspective of extinct Late Pleistocene Megafaunal elements. The temporal distribution of taxa confirms the decline towards the Last Glacial Maximum of the southern extinct group and further reveals a decrease in the occurrence of many smaller carnivores. The latter may indicate a decrease in carrying capacity as temperatures decreased which is supported by the decrease in occurrence of mammoths on non-archaeological sites and other similar phenomena documented elsewhere. The geographical distribution of the larger mammals of OIS 3 confirms a retreat towards the South and West of Neanderthals similar to that of the straight-tusked elephant *Elephas antiquus* and Merck's rhino *Stephanorhinus kirchbergensis*, both of which also became extinct towards the Last Glacial Maximum. The change in geographical distribution of the European wild ass *Equus hydruntinus* through OIS 3 may be closest to that of the Neanderthals implying similar tolerances. The results of the palaeoecological and palaeobiogeographical study of Neanderthals prompt a reconsideration of their supposed adaptations.

Key words: *Homo neanderthalensis*, megafauna, Late Pleistocene, Last Glacial Maximum.

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I. INTRODUCTION

The Neanderthals are thought by many to be a distinct species of human, *Homo neanderthalensis*, which lived in the western Palaearctic between about 200 and 30 thousand years ago (ka BP). They have been described physically as being generally more robust than modern humans, *H. sapiens*, with many distinct features of the cranium such as the possession of brow ridges, low sloping foreheads and a mandible lacking a chin.

There has been a longstanding debate over the disappearance of Neanderthals from the fossil record. The two main competing theories being either that they evolved into modern Europeans, often called multiregional evolution (e.g. WOLPOFF and CASPARI 1997) or that they went extinct to be replaced by modern humans that had arrived from Africa via the Near East, the Out of Africa theory (e.g. STRINGER and MCKIE 1996). Within the framework of the latter model a number of hypotheses have been proposed including direct and indirect competition from modern humans (MELLARS 1989; MITHEN 1996; KLEIN 2000; PETTITT 1999; LIEBERMAN 1989; BOCQUET-APPEL and DEMARS 2000; CACHEL 1997; PIKE-TAY *et al.* 1999). Another hypothesis regarding their disappearance is that modern humans had no substantial role in the extinction of Neanderthals and that climate change and its effects on the environment was the main cause (FINLAYSON *et al.* 2000a, b; FINLAYSON 2004; STEWART *et al.* 2003b; STEWART 2000, 2004a, b, 2005, 2006; FINLAYSON and CARRIÓN 2007; JIMÉNEZ-ESPEJO *et al.*, in press). Environmental explanations have had relatively little attention which is remarkable considering that Neanderthals are believed to have been hunter-gatherers that would have given them a close relationship with their ecological surroundings. Others have, however, taken the middle ground and argued for a combination of climate and modern human competition (STRINGER and DAVIES 2001; STRINGER *et al.* 2003 and D'ERRICO and SANCHEZ GOÑI 2003). Furthermore, as regards the ecology of Neanderthal extinction, it is noteworthy that this phenomenon has rarely been considered in the light of other Late Pleistocene extinctions. The reverse is also true that the Late Pleistocene extinctions have never been seen in the light of Neanderthal extinctions (cf. STUART 1991).

GUTHRIE (1990a) viewed the Late Pleistocene megafaunal extinctions as part of a Late Pleistocene faunal revolution and stated that too much focus on the extinctions themselves has obscured the fact that other events had taken place. Listed amongst the phenomena which took place during the end of the Pleistocene were rapid evolutionary changes, fractionation of biotic communities and enormous reductions in distributional ranges. More recently SEMKEN *et al.* (1998) concluded that the megafaunas of North America became extinct at the same time as non-analogue [from a modern perspective] mammal associations became reorganised. They further suggested that this was proof that the megafaunal extinctions were at least in part due to climate change rather than the human overkill hypothesis. Similarly, it is my belief that viewing the Neanderthals' extinction as a singular phenomenon has hindered any integration of this event with the complex series of biological changes which took place towards the end of the Pleistocene.

It should be mentioned at this stage that modern human involvement is rejected as a cause of Neanderthal extinction (STEWART 2004a). The reason for this is the lengthy co-occurrence, up to 10 ka BP, of the two species in Europe in areas such as Cantabria (DAVIES 2001a, b). It is realised that a lengthy sympatry in Europe between modern humans and Neanderthals is contested by certain authors (e.g. D'ERRICO *et al.* 1998 and D'ERRICO 1999). These authors appear to reject any early dates for modern humans in Europe on the grounds of poor stratigraphy and dating. However, it is clear that many sites have dates older than 36.5 ka BP and some with more than one absolute dating technique (DAVIES 2001b). A similar dismissal has been made of the late surviving (post 30 ka) Neanderthals in Europe (KLEIN 2000; MELLARS 2006). Some of this resistance may be caused by a genuine concern for the limited nature of the evidence. Others, however, seem set against any significant overlap in the occupation of Europe by two distinct hominin species which may be influenced by the now generally defunct competitive exclusion hypothesis (TATTERSALL 1995; STEWART 2004a). Recently FINLAYSON *et al.* (2006) published evidence for the late survival of Neanderthals in Gibraltar. This further demonstrates that they were contemporary with modern humans in Europe over several millennia. This in turn implies that modern humans are unlikely to have had a significant role in Neanderthal extinction through competition, as is widely believed (e.g. DELSON and HAVARTI 2006).

II. MATERIALS AND METHODS

As part of the Stage Three Project, set up to look at the environment of Oxygen Isotope Stage 3 (*ca.* 60-20 ka BP) (DAVIES *et al.* 2000; VAN ANDEL 2002) and in particular the period during which

the Neanderthal humans were replaced by moderns in Europe, a database of absolutely dated mammalian fossil faunas was constructed. This would, among other objectives, enable the investigation of the ecology of the Neanderthals using a biogeographical approach. It is hoped that this would help yield an explanation for the human transition that occurred from a more ecological perspective and help explain why Neanderthals became extinct. The area of investigation was restricted to Europe although it is realized that the distribution of Neanderthals exceeded that area.

The Database, called the Stage Three Mammalian Faunal database (STEWART *et al.* 2001; STEWART *et al.* 2003a), is made up of existing data from literature published before March 2001 and contains most of the available absolutely dated mammalian faunal sites for Oxygen Isotope Stage 3 from Europe. It is not thought that the data have not changed significantly over the past six years although it is realised that improved results are being achieved using ultrafiltration techniques at the Oxford dating laboratory. Included are approximately 470 dated faunas from nearly 300 sites with just under 2000 radiometric dates between them. Most sites are dated by radiocarbon, whether by conventional or by the Accelerator Mass Spectrometry technique. These dates were calibrated (more properly calendric-age converted) by the method developed by JÖRIS and WENINGER (1996). Also included, however, are thermoluminescence dates (TL), optically-stimulated luminescence dates (OSL), electron spin resonance dates (ESR) and uranium-series dates. Calendric-age converted radiocarbon dates were used in the analysis that follows so that they could be used in combination with the aforementioned dates. Archaeological and palaeontological sites are included in the database and as such the database acts as a complementary resource on the web to the Stage Three Project Archaeological database (DAVIES 2001a).

The data was collected by first making a systematic search for absolute dates, most of which were radiocarbon dates from the two main journals publishing date lists: *Radiocarbon* and *Archaeometry*. The dates are published with information such as their standard deviations (more correctly, standard errors), the grid reference of the site, the horizon and the material dated, as well as a section of variable quality where notes are recorded from the site excavator. The latter may include references that were subsequently followed up. If not, a literature search would often lead to publications regarding the sites' characteristics, including whether there was any fauna identified from any of the dated layers. The search for published faunas was necessarily less systematic as often the locations where sites are published can be obscure. In such cases a broad approach including corresponding with mammalian faunal specialists from various parts of Europe was necessary.

The structure of the database is such that each row represents an absolute date and attached to each date are all the attributes of the layer at each site. Attributes include whether the site is a cave or open air, the archaeological industry if any found in the layer as well as the taxa making up its fauna. Longitudes and latitudes were recorded for each site as digital degrees that would allow analysis using a mapping program.

Listed in the faunas for the sites are about 120 mammalian taxa. In the database the mammals have been arbitrarily divided into large and small mammals (small mammals include all rodents, insectivores and lagomorphs while large mammals comprise carnivores, ungulates and proboscideans). Included as part of the large mammalian faunal field were any human fossils. The human fossils were treated as another mammal fossil in the database. Due to taxonomic identification problems and inconsistencies in practice across scientists a number of pragmatic and generally conservative decisions had to be made. Therefore, *Equus ferus*, *Equus caballus*, *Equus germanicus* and *Equus* sp. were included in *Equus ferus*. Similarly, *Bos* and *Bison* were lumped as *Bos / Bison*, and no attempt was made to distinguish species in the genera *Capra* and *Martes* for the purposes of this paper although they are listed as individual species in the database. Furthermore, only the records that specifically mentioned *Dama dama* rather than *Dama dama/Cervus elaphus* were included. All hyena records were assigned to *Crocuta crocuta* and all lion records were allocated to *Panthera leo*. Unspecified bear records were not included.

For the present purposes only the large mammal taxa were included in the analysis as they are more consistently reported. The greater consistency among larger mammals is due to recovery bias

Table I

Large mammal taxa in the Stage Three Project Mammalian database (STEWART et al. 2001)

| Taxon | | Status | Status Category (see text) |
|--------------------------------------|--------------------------|--|-------------------------------|
| Latin | English | | |
| <i>Alces alces</i> | Elk | Extant | 1a |
| <i>Cervus elaphus</i> | Red deer | Extant | 1a |
| <i>Rangifer tarandus</i> | Reindeer | Extant | 1b |
| <i>Dama dama</i> | Fallow deer | Extant but reintroduced to northern Europe | 2b* |
| <i>Capreolus capreolus</i> | Roe deer | Extant | 1a |
| <i>Megaloceros giganteus</i> | Giant deer | Extinct ^{1, 2} | 2a‡ |
| <i>Bos / Bison</i> | Auroch / Bison | Extinct in Europe | 1a/2a |
| <i>Rupicapra rupicapra</i> | Chamoix | Extant | 1b |
| <i>Capra ibex / pyrenaica</i> | Ibex | Extant | 1b |
| <i>Ovibos moschatus</i> | Musk ox | Extant | 1b |
| <i>Saiga tatarica</i> | Saiga antelope | Extinct in Europe ¹ | 1c |
| <i>Sus scrofa</i> | Wild boar | Extant | 1a |
| <i>Equus ferus</i> | Horse | Extant | 1c |
| <i>Equus hydruntinus</i> | European wild ass | Extinct | § |
| <i>Equus asinus</i> | Donkey | Extant | 1c |
| <i>Equus latipes</i> | Extinct horse | Extinct | ? |
| <i>Stephanorhinus kirchbergensis</i> | Merck's rhino | Extinct ¹ | 2b |
| <i>Stephanorhinus hemitoechus</i> | Narrow-nosed rhino | Extinct in Europe ¹ | 2a/b† |
| <i>Coelodonta antiquitatis</i> | Woolly rhino | Extinct ¹ | 2a |
| <i>Mammuthus primigenius</i> | Mammoth | Extinct ¹ | 2a |
| <i>Elephas antiquus</i> | Straight-tusked elephant | Extinct ¹ | 2b |
| <i>Panthera leo</i> | Lion | Extinct in Europe ¹ | 1c |
| <i>Panthera pardus</i> | Leopard | Extinct in Europe ¹ | 1c |
| <i>Lynx lynx</i> | Lynx | Extant | 1a |
| <i>Lynx pardina</i> | Iberian lynx | Extant | Iberian endemic |
| <i>Felis sylvestris</i> | Wild cat | Extant | 1a |
| <i>Crocota crocota</i> | Spotted hyena | Extinct in Europe ¹ | 1c |
| <i>Canis lupus</i> | Wolf | Extant | 1a |
| <i>Cuon</i> | Dhole | Extant | 1c |
| <i>Vulpes vulpes</i> | Red fox | Extant | 1a |
| <i>Alopex lagopus</i> | Arctic fox | Extant | 1b |
| <i>Ursus arctos</i> | Brown bear | Extant | 1a |
| <i>Ursus spelaea</i> | Cave bear | Extinct ¹ | 2a |
| <i>Meles meles</i> | Badger | Extant | 1a |
| <i>Mustela ermina</i> | Stoat | Extant | 1a |
| <i>Mustela nivalis</i> | Weasle | Extant | 1a |
| <i>Mustela minuta</i> | Least weasle | Extant | 1b |
| <i>Putorius putorius</i> | Polecat | Extant | 1a |
| <i>Martes spp.</i> | Marten | Extant | 1a |
| <i>Gulo gulo</i> | Wolverine | Extant | 1b |
| <i>Lutra lutra</i> | Otter | Extant | 1a |
| <i>Homo neanderthalensis</i> | Neanderthal human | Extinct ³ | 2b |

Notes: Extant / extinct status of taxa has been derived from literature sources. Modern distribution (extant taxa) in Europe comes from MITCHELL-JONES et al. (1999) and STUART (1982). Sources for extinction dates: 1 – STUART (1991); 2 – STUART et al. (2004), 3 – SMITH et al. (1999).

* Fallow deer did not go extinct but was very much reduced in distribution to the Southern and South-eastern Europe by the last glaciation. They were subsequently reintroduced by the Romans to Northern Europe (MITCHELL-JONES et al. 1999). ‡ Giant deer extinct in most areas of Europe by the end of the Pleistocene. However, dates for the early Holocene exist in the Urals (STUART et al. 2004). § *E. hydruntinus* survived the Pleistocene/Holocene boundary but became extinct some time during the earlier Holocene (KAHLKE 1999; BENECKE 1999). † *S. hemitoechus* is traditionally an “interglacial survivor” (STUART 1991) but current analytical questions this.

and possibly a lack of expertise in small mammal identification. The mammals in question are listed in Table I together with their status as either extant or extinct. Most of the large mammals fall into the following historical biogeographical status categories and these categories have been ascribed to the various mammals listed in Table I:

- 1 – Extant taxa. These fall into three categories consisting of:
 - a) Taxa whose distribution remained the same in Europe after the Pleistocene.
 - b) Taxa whose distribution contracted northwards and / or into montane areas in Europe after the Pleistocene.
 - c) Taxa whose distributions contracted eastwards into South-West Asia and Central Asia after the Pleistocene.
- 2 – Extinct taxa. These fall into two categories consisting of:
 - a) Taxa that went extinct at the termination of the Pleistocene.
 - b) Taxa that went extinct at the approach of the Last Glacial Maximum (LGM).

Two of the larger mammals do not fit the above categories. They are the Iberian lynx *Lynx pardina* and the European wild ass *Equus hydruntinus*. The Iberian lynx is the only large mammal that is a peninsular endemic restricted to the Iberian peninsula. There are smaller endemic mammals but they are not discussed in this paper. *Equus hydruntinus*, meanwhile, became extinct during the Holocene (KAHLKE 1999) and so is difficult to categorise.

In order to better understand the Neanderthals as part of this evolving fauna a historical biogeographical approach was taken. This entailed a consideration of the extent to which each taxon or taxonomic grouping in Table I was distributed in Europe and how that may have changed over the time period that approximates to OIS 3. The database included material beyond the end of OIS 3 which is normally agreed to have finished *ca.* 25 ¹⁴C ka BP (radiocarbon kiloyears) or *ca.* 26.5 cal ka BP (calendrical kiloyears), because ending at *ca.* 20 ¹⁴C ka BP or *ca.* 21.4 cal ka BP, coinciding approximately with the start of the LGM, seemed a more reasonable punctuation. Therefore, tables have been drawn up to illustrate any changes that may have taken place between 60 and 20 cal ka BP (Table II-V).

Global temperatures from 60 ka BP through to 20 ka BP have been elucidated through such initiatives as the GRIP and GISP ice core projects in Greenland (e.g. DANSGAARD et al. 1993). This has given us a more detailed view of climate change in the Late Pleistocene than was previously available from the ocean records (e.g. SHACKLETON and OPDYKE 1973) and while there is a net decrease in global temperature during the 60-20 ka episode there appears to have been a larger number of oscillations in those temperatures than previously believed. It has become apparent, however, that despite detailed knowledge of the global climate through this episode and the availability of absolute dates associated with the faunas in the database that correlation of the terrestrial sequence with specific oscillations would be marred by the large standard error on those dates. Furthermore, it has also been discovered that problems exist with the radiocarbon record due to complex plateaus in the dates due to variations in the production of ¹⁴C in the atmosphere through time (JÖRIS and WENINGER 1996). Therefore, the period of time represented by the database was divided into three temporal zones designed to allow comparisons between dated faunas. Any more accurate correlation between terrestrial ¹⁴C dated records and climate records such as attempted by D'ERRICO and SANCHEZ GOÑI 2003 is unrealistic because of the large standard errors associated with such dates. Table VI outlines these three zones that encompass an early, middle and late phase of which the early and late phases can certainly be compared climatically as they represent relatively warmer and colder conditions respectively.

Table II meanwhile gives the percentage number of dates associated with each species in each time zone. The percentages were calculated as parts of the total number of dates associated with each taxon. The use of percentages was necessitated by the problems of multiple dates associated with each faunal horizon. It was felt that it would be wrong to eliminate dates for faunal horizons because the dates represent ages of material making up the deposits from which the faunas derive. There is no *a priori* reason to believe that any one date will best represent the horizon and all of the

Table II

Percentage number of dates associated with large mammal taxa falling in each of the three time zones defined in Table VI

| Taxon | No. of dates | % no. of dates falling per time zone | | | Index of change |
|---|--------------|--------------------------------------|----------|--------|-------------------|
| | | >37 ka | 37-28 ka | <28 ka | |
| All taxa | 1084 | 27.68 | 43.08 | 29.24 | None |
| <i>Alces alces</i> | 46 | 28.26 | 47.83 | 23.91 | None |
| <i>Cervus elaphus</i> | 540 | 28.52 | 40 | 31.48 | None |
| <i>Rangifer tarandus</i> | 733 | 22.92 | 44.61 | 32.47 | None |
| <i>Dama dama</i> | 6 | 16.67 | 66.67 | 16.67 | Increase/Decrease |
| <i>Capreolus capreolus</i> | 224 | 25.89 | 39.29 | 34.82 | None |
| <i>Megaloceros giganteus</i> | 56 | 33.16 | 44.39 | 22.45 | None |
| <i>Bos / Bison</i> | 665 | 29.32 | 44.06 | 26.62 | None |
| <i>Rupicapra rupicapra</i> | 297 | 34.01 | 34.68 | 31.31 | None |
| <i>Capra</i> | 415 | 33.01 | 38.31 | 28.67 | None |
| <i>Ovibos moschatus</i> | 52 | 3.92 | 27.45 | 68.63 | Increase |
| <i>Saiga tatarica</i> | 48 | 47.92 | 35.42 | 12.5 | Decrease |
| <i>Sus scrofa</i> | 203 | 37.25 | 35.78 | 26.96 | None |
| <i>Equus ferus</i> | 605 | 26.45 | 46.12 | 27.44 | None |
| <i>Equus hydruntinus</i> | 102 | 28.43 | 40.2 | 28.43 | None |
| <i>Equus asinus</i> | 11 | 81.82 | 9.09 | 9.09 | Decrease |
| <i>Equus latipes</i> | 55 | 5.45 | 20 | 74.55 | Increase |
| <i>Stephanorhinus kirchbergensis</i> | 15 | 86.67 | 13.33 | 0 | Decrease |
| <i>Stephanorhinus hemitoechus</i> | 24 | 28.57 | 28.57 | 42.86 | None |
| <i>Coelodonta antiquitatis</i> | 313 | 32.59 | 46.96 | 20.45 | None |
| <i>Mammuthus primigenius</i> | 564 | 24.47 | 52.84 | 22.7 | None |
| <i>Elephas antiquus</i> | 24 | 91.67 | 8.33 | 0 | Decrease |
| <i>Panthera leo</i> | 265 | 25.28 | 46.42 | 28.3 | None |
| <i>Pantera pardus</i> | 53 | 60.38 | 32.08 | 7.55 | Decrease |
| <i>Lynx lynx</i> | 94 | 23.4 | 58.15 | 18.09 | Increase/Decrease |
| <i>Lynx pardina</i> | 26 | 53.85 | 34.62 | 11.54 | Decrease |
| <i>Felis sylvestris</i> | 82 | 51.22 | 39.02 | 9.76 | Decrease |
| <i>Crocuta crocuta</i> | 357 | 39.33 | 41.85 | 18.82 | Decrease |
| <i>Canis lupus</i> | 645 | 25.58 | 44.03 | 30.39 | None |
| <i>Cuon</i> | 27 | 25.93 | 29.63 | 44.44 | None |
| <i>Vulpes vulpes</i> | 516 | 37.17 | 24.03 | 22.56 | None |
| <i>Alopex lagopus</i> | 354 | 20.34 | 49.72 | 29.94 | None |
| <i>Ursus arctos</i> | 231 | 31.6 | 40.26 | 28.14 | None |
| <i>Ursus spelaea</i> | 306 | 32.68 | 39.54 | 27.78 | None |
| <i>Meles meles</i> | 52 | 36.54 | 38.46 | 25 | None |
| <i>Mustela ermina</i> | 80 | 55 | 31.25 | 13.75 | Decrease |
| <i>Mustela nivalis</i> | 27 | 53.85 | 42.31 | 3.85 | Decrease |
| <i>Mustela minuta</i> | 6 | 33.33 | 66.67 | 0 | Increase/Decrease |
| <i>Putorius putorius</i> | 49 | 69.39 | 30.61 | 0 | Decrease |
| <i>Martes</i> | 65 | 52.31 | 43.08 | 4.62 | Decrease |
| <i>Gulo gulo</i> | 191 | 16.75 | 51.83 | 31.41 | Increase/Decrease |
| <i>Lutra lutra</i> | 6 | 33.33 | 50 | 16.67 | Increase/Decrease |
| <i>Homo neanderthalensis</i> + Mousterian | 229 | 64.19 | 28.82 | 6.99 | Decrease |

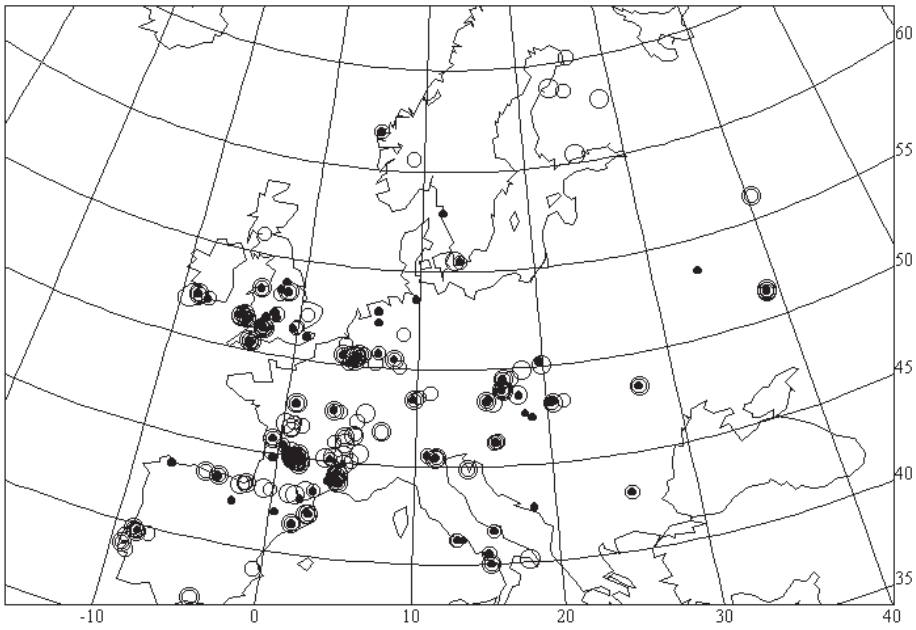


Fig. 1. Map of all absolutely dated sites with large mammal taxa in Europe during OIS 3. Small solid circle – Early time zone; medium circle – Intermediary time zone; large circle – Late time zone.

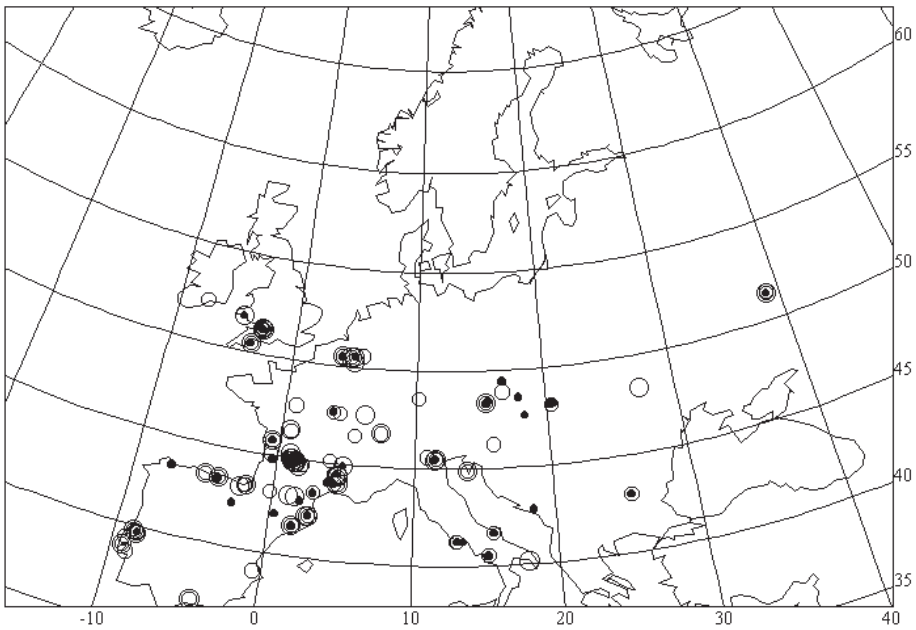


Fig. 2A – *Cervus elaphus*. Example from maps of taxa whose distribution remained the same in Europe after the Pleistocene. Small solid circle – Early time zone; medium circle – Intermediary time zone; large circle – Late time zone.

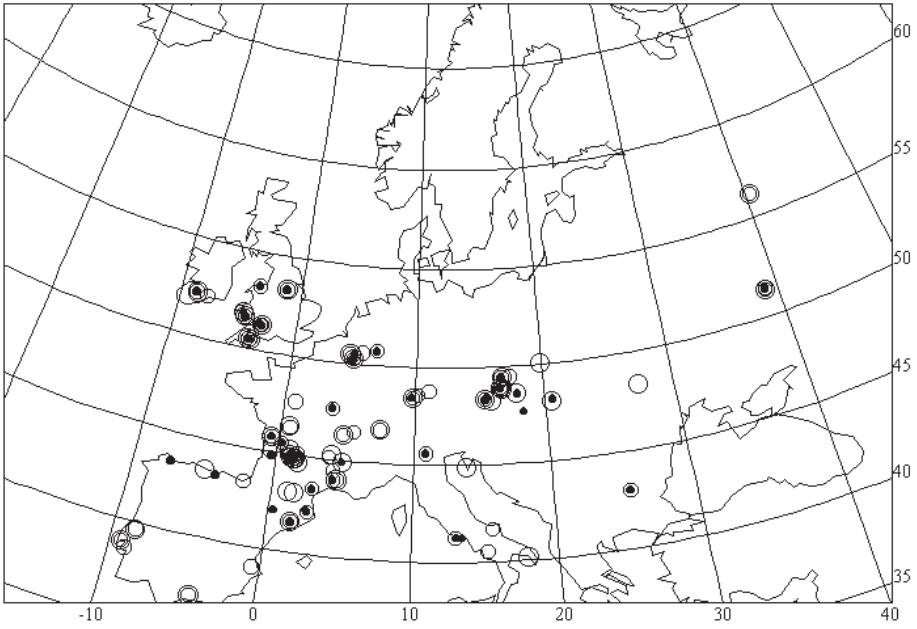


Fig. 2 B – *Canis lupus*. Example from maps of taxa whose distribution remained the same in Europe after the Pleistocene. Small solid circle – Early time zone; medium circle – Intermediary time zone; large circle – Late time zone.

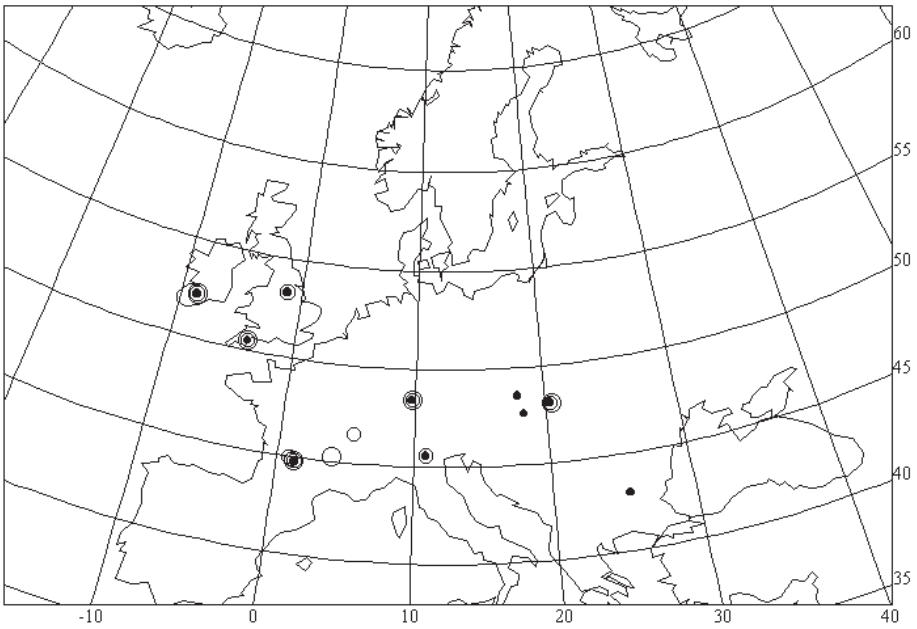


Fig. 2 C – *Mustela ermina*. Example from maps of taxa whose distribution remained the same in Europe after the Pleistocene. Small solid circle – Early time zone; medium circle – Intermediary time zone; large circle – Late time zone.

taxa found as fossils within it. The nature of these clastic deposits with probable multiple occupation by a variety of predators signifies that time depth is likely for each absolutely dated faunal horizon. There seems to be some confusion amongst archaeologists that carbon dates on objects should reflect the age of the depositional event. They do not, they represent the age of the object dated, often a charcoal fragment. This became apparent in criticisms of the chronological sequence at Gorham's Cave in Gibraltar made recently by DELSON and HAVARTI (2006). In the sequence described by FINLAYSON *et al.* (2006) there are reversals in dates up the profile sampled; however, this does not "violate the basic rule of superposition" as suggested by DELSON and HAVARTI (2006) as the dates refer to the objects dated rather than the process of deposition itself. It is to be expected that dated organic objects, or sedimentary particles (STEWART 2003b) such as charcoal fragments, are likely to have been re-deposited. It is of note however, that when such criticisms are made they are not universally applied. On the same basis most, if not all, dates of objects associated with archaeological finds could be rejected. Therefore, the use of a modal or median date during the analysis of the database and certainly any suggestion of a mean were rejected as unrealistic. The use of percentage numbers of dates in each time zone for each taxon does not overcome the problem completely but is preferable to the simple use of raw numbers of dates in each time zone. A further table had to be constructed, however, in order to test the reliability of the results of Table II. This is because the spread of percentages of dates in each time zone associated with many individual taxa was similar to the overall spread of dates associated with all the taxa together, which gave reason for concern. The possibility existed that the overall pattern may be driving the individual patterns. Another possibility is that certain patterns may be dominated by their preferred association with one or other human species because the spread of dates associated with Upper Palaeolithic (modern human) and Middle Palaeolithic (Neanderthal) are not identical (see Table III). There are for instance more than four times as many dates for Upper Palaeolithic sites than Middle Palaeolithic ones (see Table III). Therefore to ascertain the reliability of the results of Table II percentages were calculated for a number of the large mammals but divided into those from Upper Palaeolithic and Middle Palaeolithic sites respectively (Table IV). If the trends in percentages filling each time zone observed in Table II proved to be the same for the Middle Palaeolithic and the Upper Palaeolithic then the trend could be taken to be real rather than a product of their predominant archaeological association. As well as all the mammals that showed a change in percentage through time, four of the most common taxa that showed no change in Table II were also analysed.

Table V meanwhile gives the maximum and minimum latitude for the absolutely dated large mammal taxa in Europe for each of the three time zones described above. In addition to Table V with maximum and minimum latitudes a number of taxa from each of the status categories described above have been mapped for each of the three time zones described in Table VI (see Figs 2-7).

Table III

Breakdown of mammalian database by archaeological association

| Industry | No. | % |
|---|------|-------|
| OIS 3 dates associated with large mammals | 1084 | 100 |
| OIS 3 dates associated with U Pal and large mammals | 586 | 54.06 |
| OIS 3 dates associated with M Pal and large mammals | 135 | 12.45 |
| OIS 3 dates associated with transitional industries and large mammals | 40 | 3.69 |
| OIS 3 dates associated with large mammals and no industry | 323 | 29.8 |

U Pal includes Aurignacian, Gravettian, Solutrean, Magdalenian and unspecified Upper Paleolithic industries; M Pal includes Mousterian and unspecified Middle Palaeolithic industries; transitional industries includes Chatelperronian, Bohunician, Uluzian, Szeletian, Bachokirian and Micoquian.

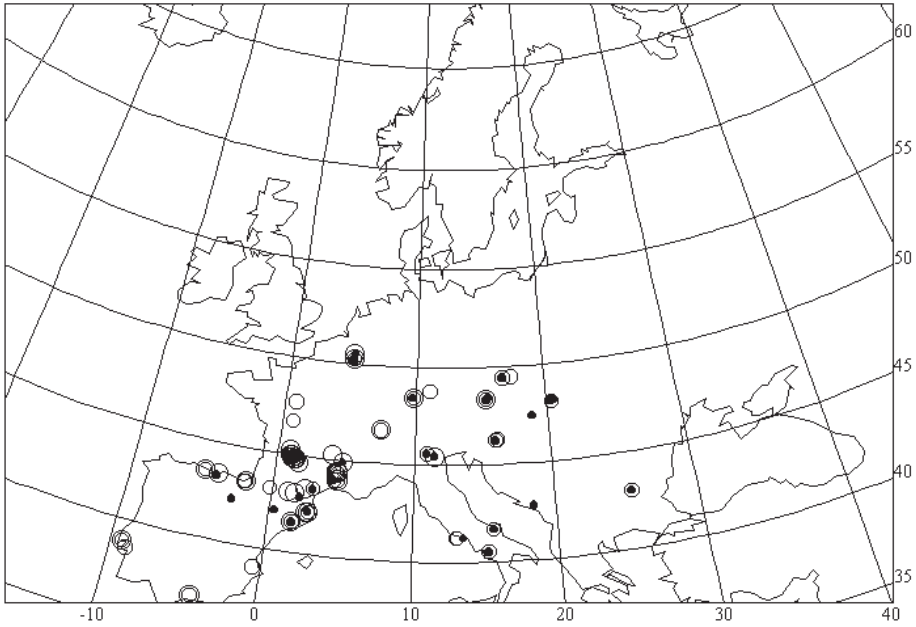


Fig. 3 A – *Capra* spp. Example from maps of taxa whose distribution contracted northwards and / or into montane areas in Europe after the Pleistocene. Small solid circle – Early time zone; medium circle – Intermediary time zone; large circle.

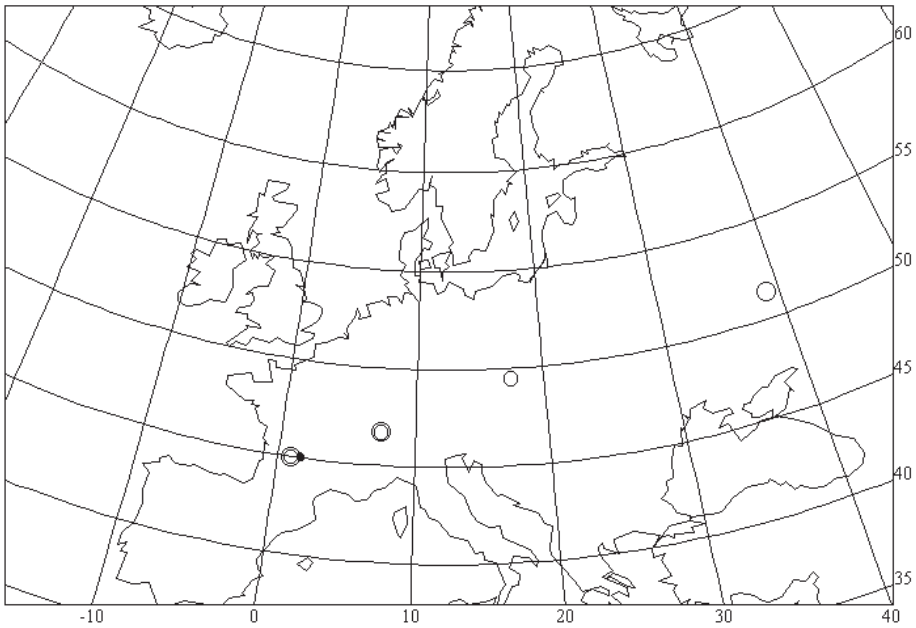


Fig. 3 B – *Oribos moschatus*. Example from maps of taxa whose distribution contracted northwards and / or into montane areas in Europe after the Pleistocene. Small solid circle – Early time zone; medium circle – Intermediary time zone; large circle – Late time zone.

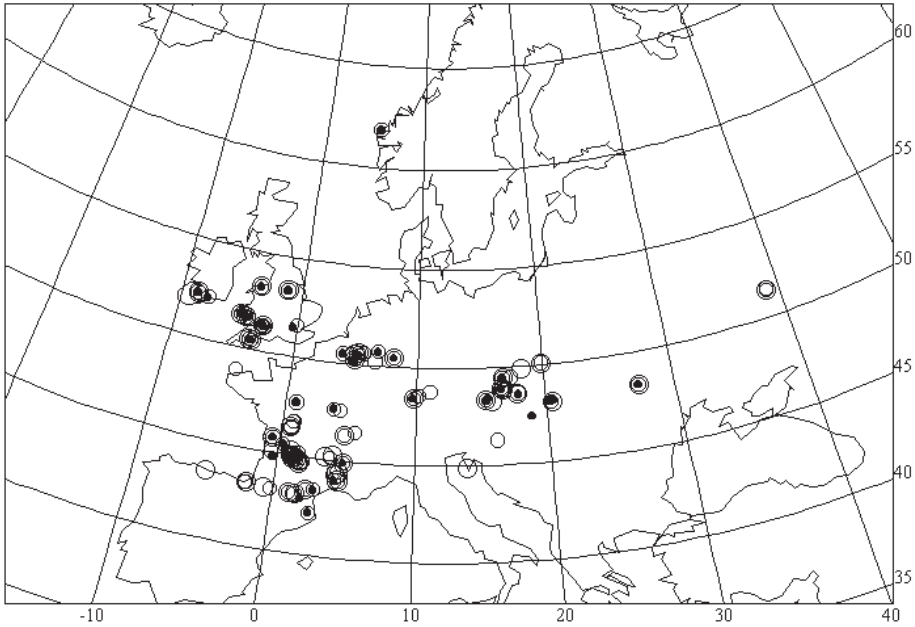


Fig. 3C – *Rangifer tarandus*. Example from maps of taxa whose distribution contracted northwards and / or into montane areas in Europe after the Pleistocene. Small solid circle – Early time zone; medium circle – Intermediary time zone; large circle – Late time zone.

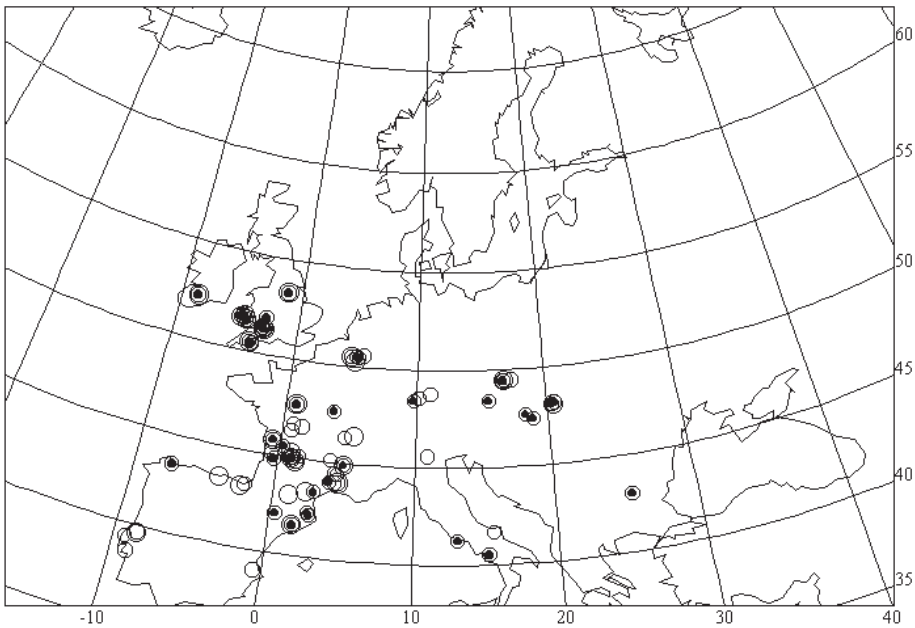


Fig. 4 A – *Crocuta crocuta*. Example from maps of taxa whose distributions contracted eastwards into SW Asia and Central Asia after the Pleistocene. Small solid circle – Early time zone; medium circle – Intermediary time zone; large circle – Late time zone.

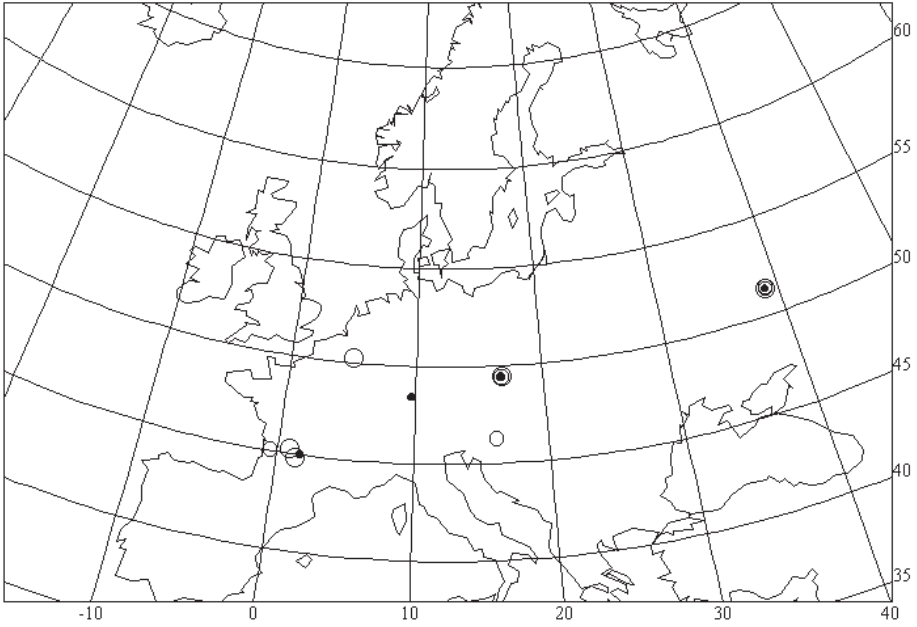


Fig. 4B – *Saiga tatarica*. Example from maps of taxa whose distributions contracted eastwards into SW Asia and Central Asia after the Pleistocene. Small solid circle – Early time zone; medium circle – Intermediary time zone; large circle – Late time zone.

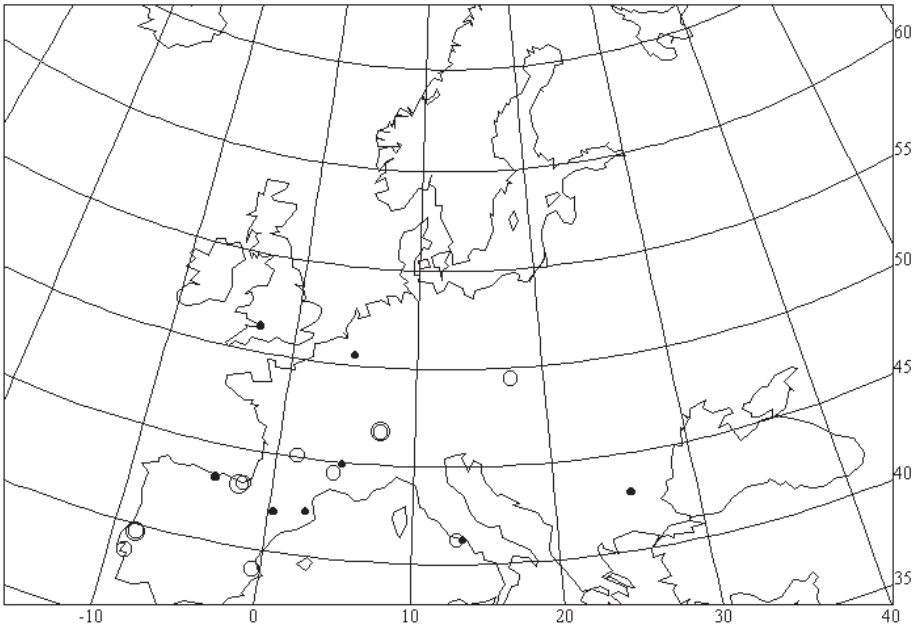


Fig. 4C – *Panthera pardus*. Example from maps of taxa whose distributions contracted eastwards into SW Asia and Central Asia after the Pleistocene. Small solid circle – Early time zone; medium circle – Intermediary time zone; large circle – Late time zone.

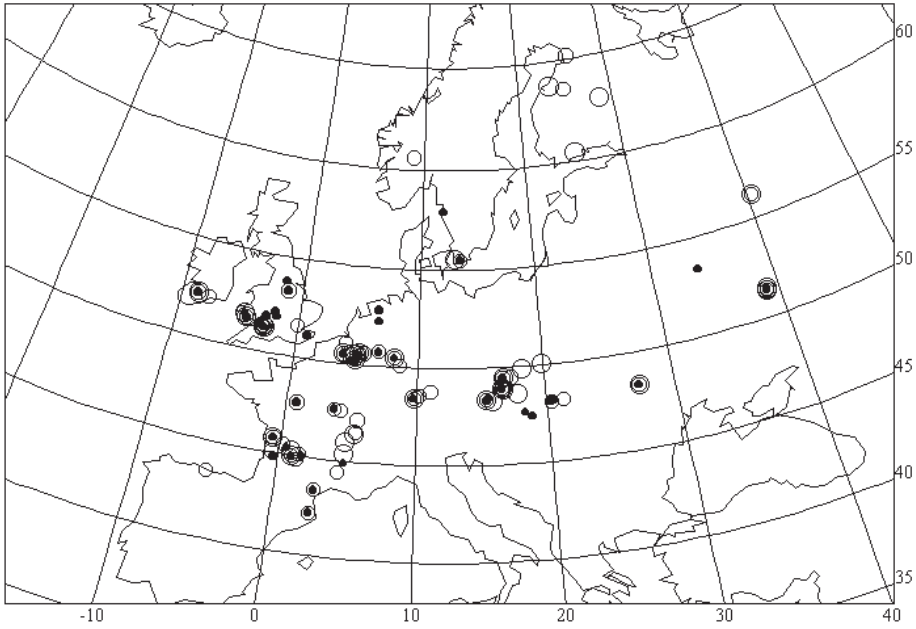


Fig. 5A – *Mammuthus primigenius*. Example from maps of taxa that went extinct at the termination of the Pleistocene. Small solid circle – Early time zone; medium circle – Intermediary time zone; large circle – Late time zone.

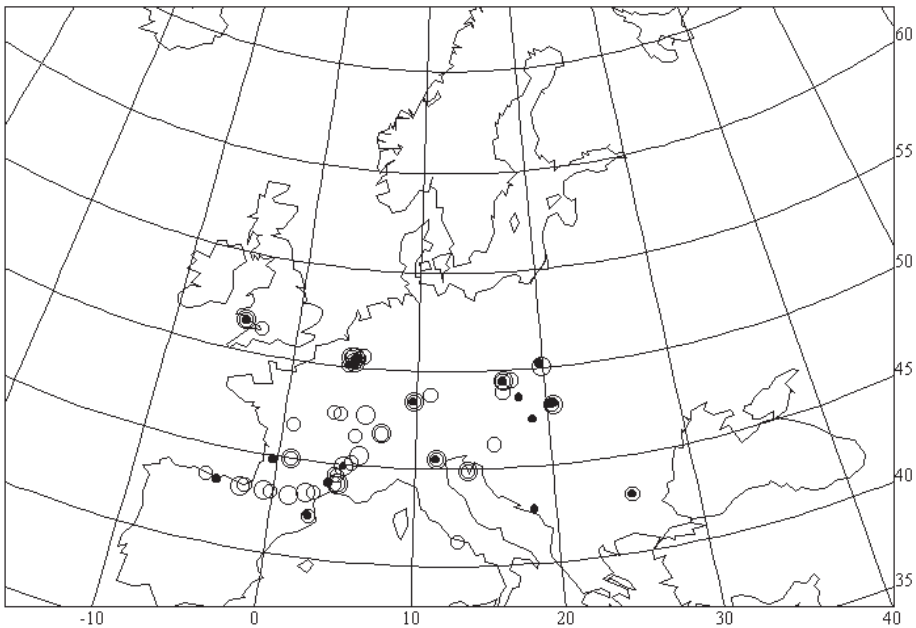


Fig. 5B – *Ursus spelaeus*. Example from maps of taxa that went extinct at the termination of the Pleistocene. Small solid circle – Early time zone; medium circle – Intermediary time zone; large circle – Late time zone.

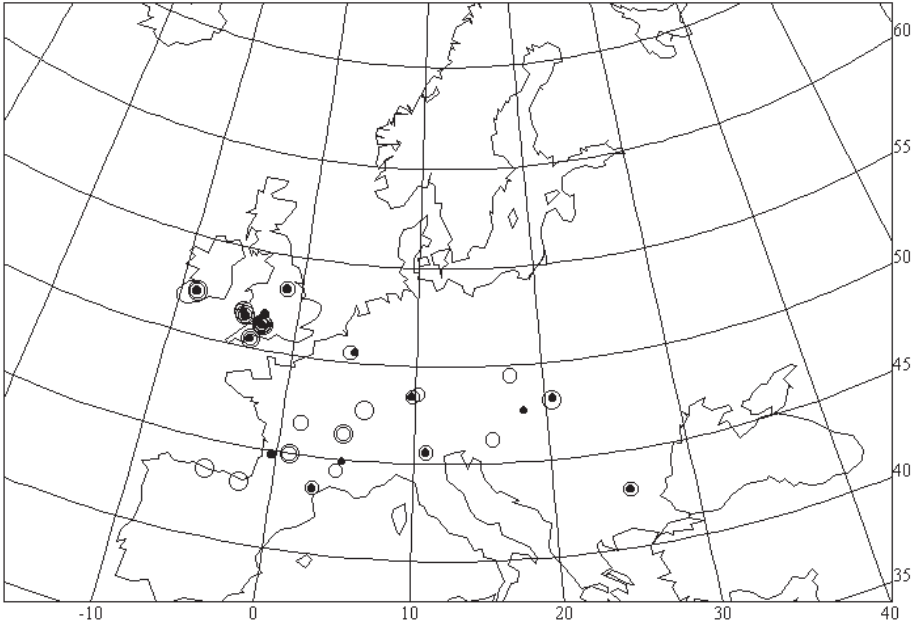


Fig. 5C – *Megaloceros giganteus*. Example from maps of taxa that went extinct at the termination of the Pleistocene. Small solid circle – Early time zone; medium circle – Intermediary time zone; large circle – Late time zone.

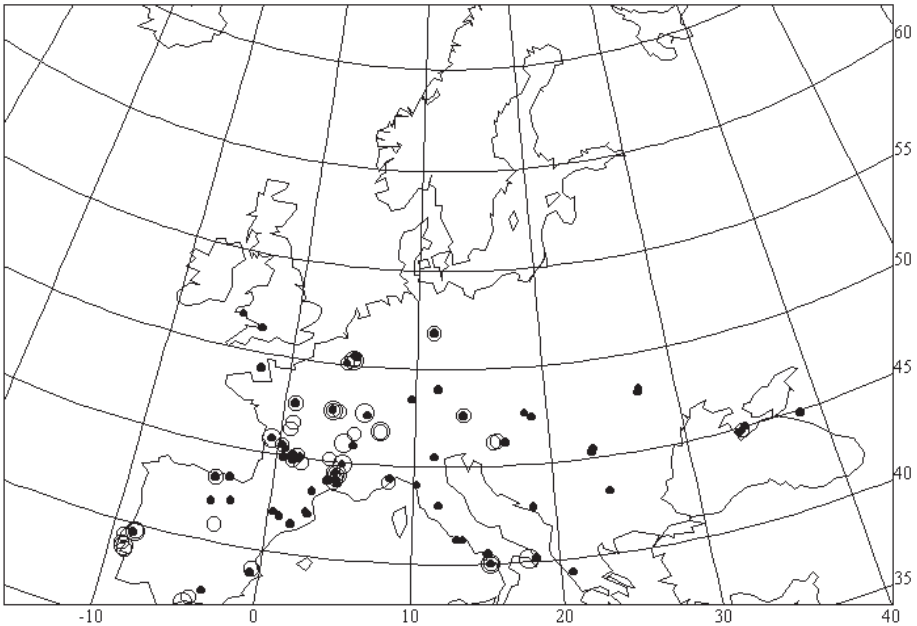


Fig. 6A – *Homo neanderthalensis*. Example from maps of taxa that went extinct at the approach of the LGM. Small solid circle – Early time zone; medium circle – Intermediary time zone; large circle – Late time zone.

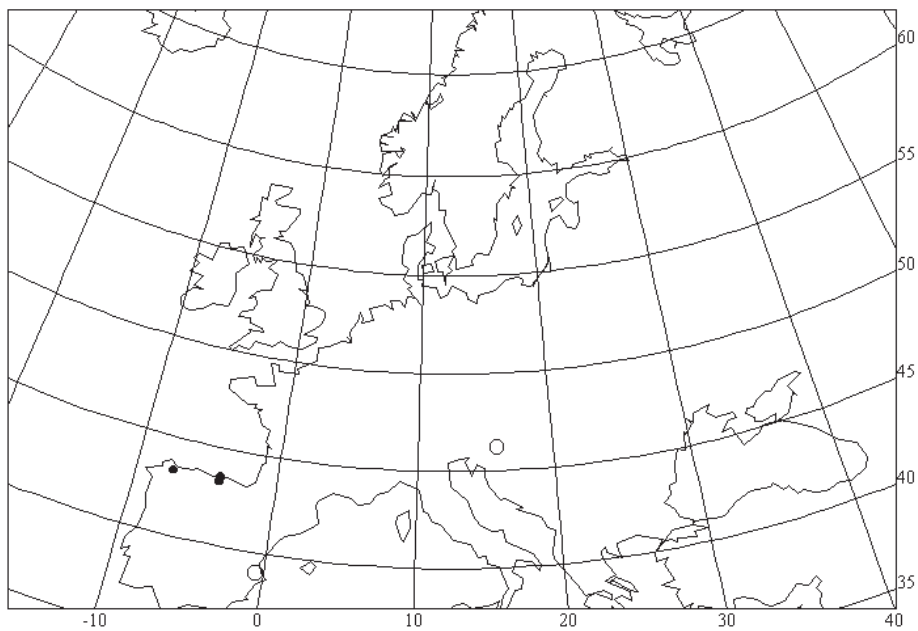


Fig. 6B – *Stephanorhinus kirchbergensis*. Example from maps of taxa that went extinct at the approach of the LGM. Small solid circle – Early time zone; medium circle – Intermediary time zone; large circle – Late time zone.

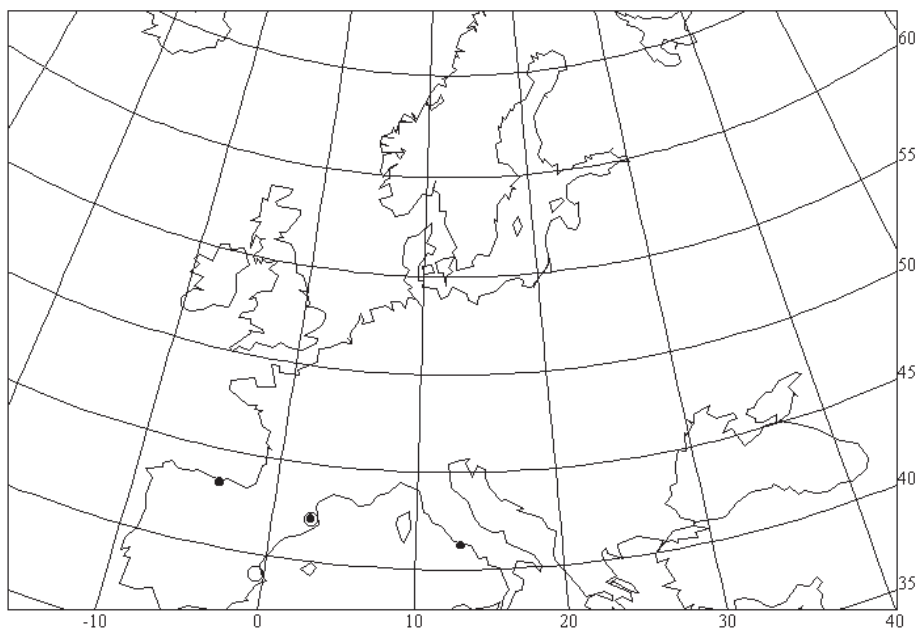


Fig. 6C – *Elephas antiquus*. Example from maps of taxa that went extinct at the approach of the LGM. Small solid circle – Early time zone; medium circle – Intermediary time zone; large circle – Late time zone.

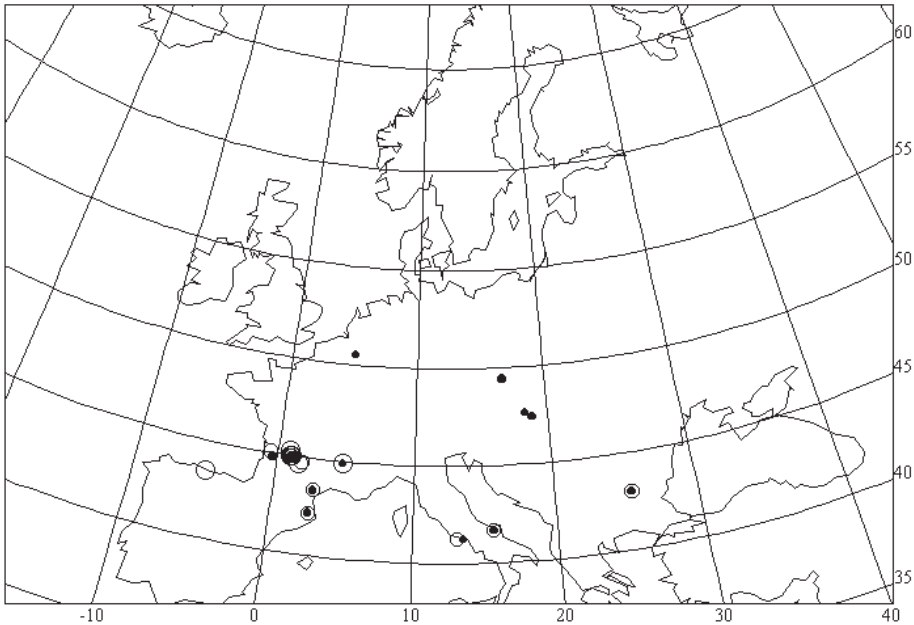


Fig. 7. Map of *Equus hydruntinus* during OIS 3. Small solid circle – Early time zone; medium circle – Intermediary time zone; large circle – Late time zone.

III. RESULTS

From a historical biogeographical point of view the larger mammals in the Stage Three Project database fall into a number of status categories (see above). These categories are first based on whether the taxa are today globally extinct as opposed to extant. Within the extinct category there are two groups including taxa that became extinct towards the LGM before 20 ka BP and ones that became extinct at the end of the Pleistocene or *ca.* 10 ka BP. Within the extant category there are those taxa whose distributions have not significantly changed since the Late Pleistocene as a whole, those whose distributions contracted North or up into more montane regions such as the Alps and taxa whose distributions retreated eastwards and toward South-West Asia.

The two extinction phases described have been known for some time (STUART 1991, 1993 and 1999). However, none of the most important reviews of Pleistocene megafaunal extinctions (STUART 1991; MARTIN and KLEIN 1984) has listed Neanderthals as a large mammal that became extinct at the termination of the Pleistocene in the Palaeartic (Table I). It is also clear that Neanderthals belong in the list of taxa with a body weight greater than 40 Kg that became extinct in the earlier phase called by STUART (1991) the “interglacial survivors” or category 2b (Table I).

If the categories of mammals defined are real then the patterns of their presence/absence in space and time should reflect their different adaptations or at least their environmental tolerances. The opportunity to see if such patterns matched what would be predicted was afforded by the Stage Three Project database (STEWART et al. 2001). Therefore, the temporal distribution of the different taxa was explored by means of an investigation into the percentage number of dates associated with each taxon in the three time zones defined above (Table II). The result of this analysis is that the mammals fall into a number of categories of temporal distribution. The first are those mammals that essentially do not change their occurrence through time and comprise the largest group. The mammals considered not to have changed dramatically have percentages in the 20’s, 30’s or 40’s in each

time zone and hence are approximately evenly spread given a perfect even spread of 33.333...% throughout. The mammals could only approximate an even distribution as the spread of all dates in each time zone was not even (Table II). The spread being 27.68 % for the early time zone, 43.08 % for the intermediary one and 29.24 % for the late zone. The mammals that have a relatively even temporal distribution approximating such percentages are extant taxa whose distribution did not change at the end of the Pleistocene (Table II, 1a), those that retreated north (Table II, 1b) or east (Table II, 1c) and some that became extinct at the end of the Pleistocene (Table II, 2a). The next group are the taxa that decreased significantly over OIS 3 and include ones that became extinct in the first phase of the Late Pleistocene megafaunal extinctions together with an assortment of other mammals. The most important in this category are two of the “interglacial survivors” consisting of *Stephanorhinus kirchbergensis* and *Elephas (Palaeoloxodon) antiquus*. To these one should add the Neanderthal as illustrated by the percentage decrease in Table II which goes from 64.19% to 28.82% and finally to 6.99%. This decrease does not solely represent a decrease in the number of dates associated with Neanderthal fossils as dates associated with Middle Palaeolithic archaeology are also included. This was done to augment the sample of dates for these hominids. It is not surprising that the “interglacial survivors” should decrease in the percentage number of dates associated with them through OIS 3 as they are believed to have become extinct at the end of this time. The result for *Stephanorhinus hemitoechus*, which does not follow this pattern, is unexpected as the species is often said to have become extinct in Europe before the LGM in the first phase of Late Pleistocene extinctions in Europe (STUART 1991). However, the results of the analysis show that if anything they increased slightly in their percentage through time. This may signify that this species survived into the Late Glacial after all. The fact that of the two *Stephanorhinus* species it was the specialist browser *S. kirchbergensis* rather than the grazer *S. hemitoechus* (LOOSE 1975) that became extinct in the early phase may be of significance as the megafaunal grazers of the Late Pleistocene mostly died out at the end of the Pleistocene when the grasslands of the steppe tundra were particularly affected.

Other taxa whose percentages appear to decrease over OIS 3 are more surprising such as the wild cat *Felis sylvestris*, the Iberian lynx *Lynx pardina*, leopard *Panthera pardus*, the spotted hyaena *Crocuta crocuta*, many of the mustelids and the saiga antelope *Saiga tatarica* (Table II). Most of the other large mammal taxa decrease slightly in percentage towards the LGM if we consider the last two time zones and this may be a further reflection of the general environment becoming impoverished. The latter may not be the case, however, as the pattern of decline in percentage numbers of associated dates between the intermediary time zone and the late one mirrors that for all the dates associated with fossil mammals taken together. Although the decline in all dates in itself may reflect a drop in carrying capacity of the environment (Table II).

The only taxon that increased its percentage markedly is the musk ox *Ovibos moschatus* that may be explained by their modern northern distribution (MITCHELL-JONES et al. 1999). Although this result may be unexpected as recent aDNA results on musk ox point to a genetic bottleneck at the LGM which would not normally accompany an expansion of a taxon (MACPHEE et al. 2005). It is also interesting that none of the other taxa that might be considered to be cold adapted, such as the mammoth *Mammuthus primigenius*, show a similar trend and this may be because none was as cold tolerant as the musk ox. The final pattern to note in Table II is that where taxa increased and then decreased. These include the fallow deer *Dama dama*, lynx *Lynx lynx*, least weasel *Mustela minuta*, wolverine *Gulo gulo* and otter *Lutra lutra*. Of these the fallow deer, least weasel and otter can perhaps be disregarded, as the number of dates associated with them is low making it dangerous to draw reliable conclusions from them. However, the lynx and the wolverine appear to have genuinely increased towards the middle time zone followed by a decrease in the later zone. It is just possible that the middle time zone coincides with the greatest spread of forest in Europe in OIS 3 that may have mostly consisted of taiga (conifers). The wolverine and lynx are common in such habitats today (MITCHELL-JONES et al. 1999).

However, as mentioned above, the possible bias that may be produced by association of specific archaeological industries with the specific large mammal taxa required a test. This is the reason be-

hind Table IV where the percentage number of dates associated with species showing changes in each time zone was calculated but split into those from either Upper or Middle Palaeolithic archaeology. The results in Table IV confirm that the red deer *Cervus elaphus*, reindeer *Rangifer tarandus*, horse *Equus ferus* and mammoth *Mammuthus primigenius* had percentage patterns for the Middle and Upper Palaeolithic that corresponded to the patterns of all the mammals associated with each in-

Table IV

Percentage number of dates associated with large mammal taxa falling in each of the three time zones but broken down into horizons with Middle Palaeolithic (Neanderthal) and Upper Palaeolithic (modern human) archaeology. Only a proportion of the taxa are shown, mostly ones that showed patterns in Table II

| Taxon | No. of dates | % no. of dates falling per time zone | | | Index of change |
|---|--------------|--------------------------------------|----------|--------|-------------------|
| | | 37 ka | 37-28 ka | <28 ka | |
| All large mammals UP | 933 | 15.11 | 47.37 | 37.51 | Increase/Decrease |
| All large mammals MP | 232 | 65.09 | 27.59 | 7.33 | Decrease |
| <i>Cervus elaphus</i> UP | 317 | 18.61 | 44.16 | 37.22 | Increase/Decrease |
| <i>Cervus elaphus</i> MP | 95 | 57.89 | 31.58 | 10.53 | Decrease |
| <i>Rangifer tarandus</i> UP | 444 | 15.09 | 47.75 | 37.39 | Increase/Decrease |
| <i>Rangifer tarandus</i> MP | 62 | 61.29 | 32.26 | 6.45 | Decrease |
| <i>Equus ferus</i> UP | 355 | 15.49 | 46.76 | 37.75 | Increase/Decrease |
| <i>Equus ferus</i> MP | 98 | 58.16 | 34.69 | 7.14 | Decrease |
| <i>Mammuthus primigenius</i> UP | 310 | 18.39 | 61.61 | 29.68 | Increase/Decrease |
| <i>Mammuthus primigenius</i> MP | 29 | 65.52 | 27.59 | 6.9 | Decrease |
| <i>Ovibos moschatus</i> UP | 20 | 0 | 65 | 35 | Increase/Decrease |
| <i>Ovibos moschatus</i> MP | 4 | 50 | 25 | 25 | Decrease |
| <i>Saiga tatarica</i> UP | 40 | 47.5 | 42.5 | 10 | Decrease |
| <i>Saiga tatarica</i> MP | 2 | 100 | 0 | 0 | Decrease |
| <i>Stephanorhinus kirchbergensis</i> UP | 5 | 100 | 0 | 0 | Decrease |
| <i>Stephanorhinus kirchbergensis</i> MP | 3 | 33.33 | 66.67 | 0 | Increase/Decrease |
| <i>Elephas antiquus</i> UP | 12 | 91.67 | 8.33 | 0 | Decrease |
| <i>Elephas antiquus</i> MP | 6 | 83.33 | 16.67 | 0 | Decrease |
| <i>Pantera pardus</i> UP | 14 | 59.09 | 31.82 | 9.09 | Decrease |
| <i>Pantera pardus</i> MP | 22 | 50 | 42.86 | 7.14 | Decrease |
| <i>Lynx lynx</i> UP | 80 | 15 | 63.75 | 21.25 | Increase/Decrease |
| <i>Lynx lynx</i> MP | 6 | 83.33 | 16.67 | 0 | Decrease |
| <i>Lynx pardina</i> UP | 13 | 61.54 | 23.08 | 15.38 | Decrease |
| <i>Lynx pardina</i> MP | 11 | 45.45 | 45.45 | 9.09 | Decrease |
| <i>Felis sylvestris</i> UP | 40 | 52.5 | 40 | 7.5 | Decrease |
| <i>Felis sylvestris</i> MP | 30 | 48.28 | 34.48 | 17.24 | Decrease |
| <i>Crocuta crocuta</i> UP | 145 | 29.66 | 48.28 | 22.69 | Increase/Decrease |
| <i>Crocuta crocuta</i> MP | 64 | 59.38 | 34.38 | 6.25 | Decrease |
| <i>Mustela ermina</i> UP | 56 | 44.64 | 44.64 | 10.71 | Decrease |
| <i>Mustela ermina</i> MP | 4 | 25 | 75 | 0 | Increase/Decrease |
| <i>Mustela nivalis</i> UP | 59 | 30.51 | 59.32 | 10.17 | Increase/Decrease |
| <i>Mustela nivalis</i> MP | 2 | 50 | 50 | 0 | Decrease |
| <i>Putorius putorius</i> UP | 34 | 73.53 | 26.47 | 0 | Decrease |
| <i>Putorius putorius</i> MP | 4 | 100 | 0 | 0 | Decrease |
| <i>Martes</i> UP | 34 | 61.76 | 32.35 | 5.88 | Decrease |
| <i>Martes</i> MP | 9 | 77.78 | 22.22 | 0 | Decrease |
| <i>Gulo gulo</i> UP | 152 | 19.08 | 61.18 | 19.74 | Increase/Decrease |
| <i>Gulo gulo</i> MP | 2 | 0 | 50 | 50 | Increase |

dustry (Table IV). Of those taxa that showed a decrease through the time zones in Table II the saiga antelope *Saiga tatarica*, the straight-tusked elephant *Elephas antiquus*, the leopard *Panthera pardus*, the Iberian lynx *Lynx pardina*, the wild cat *Felis sylvestris*, the polecat *Putorius putorius* and the martens *Martes* spp. shows a decrease in the percentages from both Upper and Middle Palaeolithic sites (Table IV). The stoat *Mustela ermina* and weasel *M. nivalis* are also confirmed as decreasing through time as the bulk of their finds are from Upper Palaeolithic sites and on these sites they both show a decrease (Table IV). Merck's rhino *Stephanorhinus kirchbergensis* is less convincing in this regard as the numbers are very low, although there is little doubt that the species became extinct before the LGM as no dates are recorded in the last time zone (Table IV). Table IV also revealed that the spotted hyaena *Crocota crocuta* follows the patterns of their industrial associations which could make their pattern in Table II of questionable significance, although they are not found in the Late Glacial in Europe (JACOBI et al 2006). The wolverine *Gulo gulo* and the lynx *Lynx lynx* have patterns of increase/decrease like that of all mammals combined among the dates from Upper Palaeolithic sites, while very few exist from Middle Palaeolithic sites which may remove the significance of these taxa. Finally, the increase in dates associated with musk ox *Ovibos moschatus* cannot be driven by either the Upper or Middle Palaeolithic dates as only the latter shows a decrease and these dates are too few to outbalance the Upper Palaeolithic pattern. Dates associated with musk ox from sites other than those with Upper or Middle Palaeolithic archaeology are dominating it, making the pattern a true representation. The result of the test in Table IV shows that by and large the picture revealed by Table II is substantiated.

A final test of this was conducted on the mammoth data. This is the large mammal with the greatest amount of dates from non-archaeological sites. If the percentage number of dates associated with large mammals was being dominated by the patterns of the archaeological industries, it seemed likely that the only way to find evidence for herbivore reductions through OIS 3 would be from non-archaeological sites. The results are that in the earliest time zone 38.18% of the dates are present, followed by 49.09% in the middle zone and 12.73% in the latest zone. This reduction in dates associated with the mammoth is backed up by recent work directly dating the mammoth remains themselves that show that the species appears to have vanished from much of Europe during the LGM (STUART et al. 2002).

The results of the analysis of the percentages of dates associated with large mammal taxa in each OIS 3 time zone prompted an examination of the geographical distributions of the various taxa. If the results in Table II are associated with climatic and vegetational deterioration through OIS 3, then it is likely that the geographical distribution of these mammals in Europe would have changed. Table V, therefore shows the maximum and minimum latitudes for each taxon in the three time zones of OIS 3. This analysis was expected to be limited in its value as a single date attached to a taxon from a site at an outlying latitude would skew the results dramatically. Table V should be viewed from the perspective of Figure 1 where the distribution of all the OIS 3 sites in Europe with large mammals is shown for each of the OIS 3 time zones together with the major latitude lines. The main observations to be made using Table V are that on the whole very few taxa appear to change either their maximum or minimum latitude. The changes that can be observed are difficult to interpret without knowing more exactly where all the sites are distributed in each time zone. More interesting in Table V are the maximum and minimum latitudes overall, as some species never reach very far north while others never reach far to the south. The taxa, that generally have more northern latitudes, are those such as the mammoth, the reindeer and the arctic fox, which never reached further south than 42°N and approximates with northern Spain, northern Italy and the more northern parts of the Balkans (Figure 1 for latitude lines). Similarly there are those taxa whose distribution never reached further north than 46°N or the latitude of the northern parts of the Dordogne. In addition there are taxa that are distributed throughout Europe such as the red deer, the horse and the wolf. The northern and southern taxa have a latitudinal band of overlap between 42°N and 46°N. This band of overlap encompasses important areas of dense mammalian site occurrence such as the Dordogne and the Rhone Valley. On the basis of this 3 banded latitudinal zones were defined including northern, southern and overlap zones (STEWART 2005).

Table V

Maximum and minimum latitude at which each large mammal taxon is found for each of the three time zones defined in Table IV

| Taxon | No. of dates | Maximum and minimum latitude per time zone | | | Index of change | |
|---|--------------|--|-----------------------|------------------|---------------------|---------------------|
| | | Lat early (37 ka) | Lat middle (37-28 ka) | Lat late (ka) | Lower limit | Upper limit |
| <i>Alces alces</i> | 46 | 43.3409-50.4625 | 43.3409-50.4625 | 43.42-50.4625 | None | None |
| <i>Cervus elaphus</i> | 540 | 36.133-51.7608 | 36.133-52.1 | 36.951-51.7608 | None | None |
| <i>Rangifer tarandus</i> | 733 | 42.161-61.843 | 42.161-61.843 | 43.0104-53.2682 | None | Decrease |
| <i>Dama dama</i> | 6 | 44.891 | 40.495-43.93 | 43.0104 | Decrease/Increase | None |
| <i>Capreolus capreolus</i> | 224 | 40.495-50.488 | 44.85-50.589 | 36.951-48.017 | Increase/Decrease | None |
| <i>Megaloceros giganteus</i> | 56 | 42.944-48.551 | 42.944-49.386 | 43.0104-45.747 | None | Decrease |
| <i>Bos / Bison</i> | 654 | 36.133-53.2869 | 36.133-53.2869 | 36.951-53.2682 | None | None |
| <i>Rupicapra rupicapra</i> | 297 | 40.495-50.488 | 44.85-50.214 | 38.901-50.214 | Increase/Decrease | None |
| <i>Capra ibex / pyrenaica</i> | | 36.133-50.488 | 36.133-50.214 | 36.951-50.483 | None | None |
| <i>Ovibos moschatus</i> | 52 | 44.995 | 44.933-49.449 | 44.933-51.29 | Increase | None |
| <i>Saiga tatarica</i> | 48 | 44.995-51.29 | 45.044-51.3931 | 44.797-51.29 | None | None |
| <i>Sus scrofa</i> | 203 | 40.495-50.488 | 36.133-50.478 | 36.951-50.215 | Decrease | None |
| <i>Equus ferus</i> | 605 | 36.133-53.266 | 36.133-53.266 | 36.951-53.266 | None | None |
| <i>Equus hydruntinus</i> | 102 | 41.219-50.488 | 41.226-45.044 | 43.42-45.2307 | None | Decrease |
| <i>Equus asinus</i> | 11 | 41.539 | 41.539 | 41.539 | None | None |
| <i>Equus latipes</i> | 55 | 51.29 | 51.29 | 51.29 | None | None |
| <i>Stephanorhinus kirchbergensis</i> | 15 | 43.279-43.481 | 46.175 | – | Increase/Extinction | Increase/Extinction |
| <i>Stephanorhinus hemitoechus</i> | 24 | 42.265-44.889 | 38.561-43.95 | 43.95-44.889 | Decrease/Increase | None |
| <i>Coelodonta antiquitatis</i> | 313 | 43.3409-53.354 | 43.107-55.9282 | 44.978-53.266 | None | None |
| <i>Mammuthus primigenius</i> | 548 | 42.161-57.91139 | 42.161-65.122 | 44.933-63.803 | None | Increase |
| <i>Elephas antiquus</i> | 24 | 41.232-43.279 | 38.96-42.161 | – | Decrease/Extinct | None |
| <i>Panthera leo</i> | 265 | 42.944-53.266 | 38.561-53.266 | 44.933-53.266 | Decrease/Increase | None |
| <i>Panthera pardus</i> | 53 | 36.133-51.3236 | 36.133-49.449 | 39.6357 - 46.675 | Increase | Decrease |
| <i>Lynx lynx</i> | 94 | 40.495-48.882 | 44.933-50.478 | 44.933-48.882 | Increase | None |
| <i>Lynx pardina</i> | 26 | 36.133-42.265 | 36.133-42.265 | 38.901-41.539 | None | None |
| <i>Felis sylvestris</i> | 82 | 36.133-51.2908 | 36.133-51.2908 | 38.901-46.675 | None | Decrease |
| <i>Crocota crocota</i> | 357 | 36.133-53.2869 | 36.133-53.2869 | 39.6357-53.266 | Increase | None |
| <i>Canis lupus</i> | 645 | 41.219-53.2643 | 36.133-56.134 | 36.951 – 56.134 | Decrease | Increase |
| <i>Cuon</i> | 27 | 42.944-50.488 | 44.797-46.675 | 43.95-46.675 | None | Decrease |
| <i>Vulpes vulpes</i> | 516 | 41.219-53.2643 | 38.561-53.2643 | 38.901-52.2167 | None | None |
| <i>Alopex lagopus</i> | 354 | 42.851-61.843 | 44.85-61.843 | 44.767-56.134 | Increase | Decrease |
| <i>Ursus arctos</i> | 231 | 40.495-53.2643 | 36.951-53.2645 | 36.951-52.2167 | Decrease | None |
| <i>Ursus spelaea</i> | 306 | 42.161-51.548 | 41.226-51.548 | 43.057-51.548 | None | None |
| <i>Meles meles</i> | 52 | 41.219-50.214 | 43.107-50.478 | 45.2307-50.215 | Increase | None |
| <i>Mustela ermina</i> | 80 | 42.944-53.2643 | 44.767-53.2643 | 44.767-52.2167 | None | None |
| <i>Mustela nivalis</i> | 27 | 40.495-53.354 | 44.997-48.0654 | 44.882 | Increase | Decrease |
| <i>Mustela minuta</i> | 6 | 44.767 | 44.767 | – | None | None |
| <i>Putorius putorius</i> | 49 | 42.944-53.354 | 45.044-53.2643 | – | None | None |
| <i>Martes</i> | 65 | 42.944-48.551 | 42.944-49.386 | 43.0104-45.747 | None | Decrease |
| <i>Gulo gulo</i> | 191 | 45.57-51.559 | 45.567-51.559 | 44.882-51.29 | None | None |
| <i>Lutra lutra</i> | 6 | 42.161-61.843 | 42.161-61.843 | 43.0104 | None | None |
| <i>Homo neanderthalensis + Mousterian</i> | 229 | 34.667-51.828 | 34.667-51.828 | 36.629-50.214 | None | None |

In order to further investigate any geographical change in occurrence of taxa, maps were constructed for all the large mammals in the Stage Three Database. Figures 2 to 7 show a selection of these and show the mapped distributions of a number of taxa taken from each of the status categories described above. Included were a number of taxa that may illustrate any possible changes among those whose distributions did not change at the end of the Pleistocene (Category 1a), the red deer, the wolf and the stoat. None of these appears to change its distributions throughout OIS 3 (Figures 2 A, B and C). All three species are present in all the areas in Europe in which a significant number of mammalian fossil sites are present.

From the category representing taxa whose distributions contracted northwards and/or into montane areas (Category 1b) I chose the ibex genus, the musk ox and the reindeer (Figs. 3 A, B and C). The musk ox and the reindeer distributions can be seen to be more limited than the ibex to the South, and neither of them make it beyond northern Spain (Figs. 3 B and C). The ibex meanwhile is more restricted to the North and only makes it above the 50°N latitude in the Belgian Ardennes (Fig. 3 A). None of these taxa shows any appreciable change in distribution through OIS 3, neither southwards in the case of reindeer and musk ox, nor onto the very much lower lying areas as the climate deteriorates in that of ibex. The latter is presumably related to the species' adaptation to a mountainous and rocky terrain.

The next category is taxa which disappeared from most of Europe after the end of the Pleistocene towards the East (Category 1c). The spotted hyaena, the saiga antelope and the leopard were chosen from this group (Figs. 4 A, B and C). Of these, only the spotted hyaena is very common and is found in most areas throughout OIS 3. The leopard is fairly rare but is also well distributed, reaching the British Isles, Iberia and the Balkans. The saiga although also more restricted in numbers than the spotted hyaena is probably genuinely not present in more southern areas such as the Iberian, Italian and southern Balkan peninsulas. Again no geographical changes through time can be discerned from the maps of these taxa.

The taxa taken from those that went extinct at the end of the Pleistocene (Category 2a) were the mammoth, the cave bear and the giant deer (Figs. 5 A, B and C). These species have similar distributions and are restricted in the south although the cave bear makes it into central Italy (Fig. 5 B) and may be absent from Ireland. The mammoth is found in Scandinavia in greater numbers than any other mammal in the Stage Three Project Mammalian database. This is, however, more than likely to be because spectacular finds like mammoths are more often found and radiocarbon dated than other mammals, even when from unexpected contexts like glacial till deposits (UKKONEN et al. 1999). There are no apparent changes in the distributions of these mammals through OIS 3 (Figs. 5 A, B and C) and these mammals may have been at their full geographical extent from the beginning to the end of the period although the mammoth eventually became extirpated in Europe during the LGM (STUART et al. 2002).

The final category of mammals are those which are at the heart of the argument being made in this paper and are those which became extinct at the end of OIS 3. They are the straight-tusked elephant, the Merck's rhino and the Neanderthals. As can be seen from Figures 6 A, B and C they all appear to be retreating to the South and some extent to the South and West in the case of the Neanderthals. The straight-tusked elephant and the Merck's rhino are absent by the last time zone while Neanderthals appear to survive, although in fewer numbers. This was recently confirmed by late dates in Gibraltar (FINLAYSON et al. 2006), although these dates are contested (ZILHÃO and PETTITT 2006). The Neanderthals also seem to be retreating into refugia in more northern areas such as the Belgian Ardennes, their most northern haunt at the end of OIS 3. This may be explained by the refugium effect described recently by STEWART and LISTER (2001) and STEWART (2003a). These taxa seem to be contracting towards warmer climes as the climate deteriorates.

One taxon that is difficult to categorise in the status groups defined above is *Equus hydruntinus*, the steppe ass, because it apparently became extinct some time during the Holocene (KAHLKE 1999). However, it may be that the only mammal to show some range contraction to the North accompanying an expansion to the South is *Equus hydruntinus* (Fig. 7). The latter confirms the earlier results of MUSIL (1985). This may be the closest analogue to the Neanderthals we have in terms of evolving zoogeography towards the LGM, except this species appears to have survived into the

Late Glacial in Western Europe and ultimately into the mid-Holocene in northern regions near the Black Sea and elsewhere (MARKOVA *et al.* 1995, KAHLKE 1999). It may be relevant that one of the earliest finds of *E. hydruntinus* is from the Middle Pleistocene Hoxnian (Holsteinian) site of Swanscombe in Southern England (OWEN, pers. comm.). This coincides with the partial hominid skull found at that site which has been claimed to by some to be Neanderthal like (HUBLIN 1998). That is not to say that there is a direct ecological association between Neanderthals and *E. hydruntinus* but it may be that they have similar ecological requirements or tolerances. According to MARKOVA *et al.* (1995) *Equus hydruntinus* were species of the dry steppe and semi-deserts from the more southern regions of northern Eurasia which is similar to the steppe to forest-steppe described as their habitat by MUSIL (1985). It is interesting that they survived longer in the East and seemed more resilient to the cold as MARKOVA *et al.* (1995), unlike MUSIL (1985) found no evidence for their retreat south as the cold of the LGM increased.

IV. DISCUSSION

In a recent review STUART (1999) summarised the main causes that have been hypothesised for the megafaunal extinctions of the Late Pleistocene. These include the hypothesis of overkill by prehistoric human hunters, the climatic change hypothesis, as well as the hyperdisease hypothesis of MACPHEE and MARX (1997) that has few adherents. Crucial to any explanation of the megafaunal extinctions is the chronology of those extinctions. Therefore, terminal dates of species are important in looking for coeval causal phenomena. However, the latest dates for species have been prone to changes as more material is dated by absolute means. For example the giant deer (*Megaloceros giganteus*) has been shown to have survived into the Holocene in the Urals (STUART *et al.* 2004), and more dramatically the Wrangel Island mammoths in Northern Siberia which have been dated to 4000 yrs BP (VARTANYAN *et al.* 1993, 1995; MARTIN and STUART 1995). Both of these species had formerly been believed to become globally extinguished at the end of the Pleistocene *ca.* 10 ka BP.

In Europe the extinctions of mammals over 40 Kg appear from latest associated and direct dates to be anything but synchronous. Two main phases of extinction have been defined (STUART 1991, 1993 and 1999) including the best known later phase during which the apparently cold-adapted species such as mammoth and woolly rhinoceros as well as the more widespread cave bear and, in Europe, the giant deer disappeared in *ca.* 10 ka BP (Table I). The latter two species are well represented in the last interglacial (Eemian/Ipswichian) of Northern Europe so cannot be described as strictly cold-adapted (STUART 1982). The latter is a testament to the fact that climate is not the sole factor in extinction as the effects of climate change on vegetation are also important. In addition to the terminal Pleistocene event there was an earlier phase of extinction in the Late Pleistocene of Europe; this was the time when the “interglacial survivors” vanished. These interglacial survivors were species such as the two rhinos *Stephanorhinus hemitoechus* and *S. kirchbergensis*, and the straight-tusked elephant *Elephas antiquus*, all of which are thought to have perished in Europe by the LGM, *ca.* 20 ka ¹⁴C BP (STUART 1991). The hippopotamus *Hippopotamus amphibius*, another “interglacial survivor”, is not present in OIS 3 (STEWART *et al.* 2001) and probably became extinct in Europe during an earlier part of the last cold stage (STUART 1991), presumably late OIS 5 or OIS 4. The macaque (*Macaca sylvanus*) may also have become extinct at an earlier time because it is also apparently absent from OIS 3 (STEWART *et al.* 2001) although the species’ fossil record is too poor to confirm this (FA 1989). The fallow deer is probably another “interglacial survivor”, which became extinct in much of Europe although it survived into the Holocene in Italy and the Balkans (BENECKE 1999). It was reintroduced into other regions of Europe from these areas in more recent times (LISTER 1984). Interpreting the fossil data for this species is fraught with danger due to the difficulties in distinguishing it from the red deer (LISTER 1996), hence identifications from Italy by STINER (1994) list red deer/fallow deer. This signifies that identifications of fallow deer can never be taken at face value.

Table II shows the percentage number of dates associated with OIS 3 finds of the large mammals, including the “interglacial survivors” described by STUART (1991), in the three time zones defined. While these dates are not on the bones themselves, they give some indication of the proportions of the individuals of these creatures that were living during the three time zones (Table VI). This analysis confirms that *S. kirchbergensis* and *E. antiquus*, although possibly not *S. hemitoechus*, became extinct before the LGM and that in addition the Neanderthal should be added to the list of “interglacial survivors” which became extinct before 20 ka BP. It is of great interest that the Neanderthals, although they were undeniably large mammals (40 Kg) that became extinct between 30 and 20 ka BP, are rarely if ever mentioned in the context of the Late Pleistocene megafaunal extinctions. None of the most important reviews of Pleistocene megafaunal extinctions (STUART 1991; MARTIN and KLEIN 1984) have Neanderthals listed as a large mammal that became extinct at the termination of the Pleistocene in the Palaearctic. The same could be said of *Homo erectus* if their latest dates are to be believed (SWISHER *et al.* 1996). It may be of interest that the latest form of East Asian extinct hominin *Homo floresiensis*, which may have evolved from *H. erectus* and appears to have died out during the Holocene was an island form (BROWN *et al.* 2004). This is true of other late surviving megafaunal populations such as the Wrangel Island mammoths which also became less megafaunal (VARTANYAN *et al.* 1993, 1995).

Table VI

Oxygen Isotope Stage Three Time Zones

| Stage Three Project Foci | Stage 3 Time Zones | Calendric ka Cal. BP | ¹⁴ C ka [BP] | Ice-Core Interstadials | Peat Stratigraphy |
|--------------------------|--------------------|----------------------|-------------------------|------------------------|----------------------|
| – | Late | <28 | <27 | Cold: 4, 3, 2 | Towards cold maximum |
| 30 ka | Intermediary | 28-37 | 27-35 | ? : 5, 6, 7, 8 | “Denekamp” |
| 42 ka | Early | >37 | >35 | Warm: 9, 10, 11, 12 | “Hengelo” |

Note: There is a problem with the corresponding climates of each time zone because the cold event for Stage Three purposes falls in the block of time that also includes the Denekamp interstadial. Therefore we are dealing with climates relative to other time zones i.e. the ‘Intermediary’ time zone will be colder on average than the ‘Early’ one and warmer than the ‘Late’ one.

Extinctions are the most dramatic extreme on a population reduction continuum, whether it is reduction in numbers of individuals and/or geographical range, regardless of the cause of the extinctions. Therefore, to gain an insight into the possible causes of extinctions any evidence of local extinctions (also called extirpations), population numbers reductions or range changes are relevant (as related phenomena). In the case of the earlier phase of Late Pleistocene extinctions there are other animals whose geographical ranges changed and/or that ultimately became locally extinct in Europe. Therefore the result of the analysis in Tables II and IV showing that population reduction may have taken place in taxa such as the leopard, the Iberian lynx, the spotted hyaena, the wild cat, the polecat, the martens, the stoat, the weasel and the saiga antelope are of interest. This appears to represent evidence for a reduction in population density of these animals as LGM was approached. Most of these are carnivores and because they are at the top of the food chain it maybe that their reduction indicates that the carrying capacity of the environment was affected. It may be significant that modern population studies of stoat and weasel show a high correlation between their population

densities and that of their preferred prey species (KING 1990). It may also be that some of these taxa do not particularly favour the extreme cold while others may have relied on arboreal vegetation that may have decreased in abundance towards the LGM. The saiga antelope is unexpected and more difficult to explain although the mammoth retreating from Europe at the LGM (STUART *et al.* 2002), as another grazer, may be an indication that steppe-tundra grasslands were affected.

The Late Pleistocene was characterised by rapid oscillations in temperatures, from ones at or close to those of today, to those of a full glacial within a millennium (DANSGAARD *et al.* 1993). This phenomenon has been claimed to be instrumental in supporting the mosaic vegetation of the Late Pleistocene, which in turn supported the megafauna that became extinct once the climatic oscillations stabilised at the start of the Holocene (LISTER and SHER 1995). This hypothesis was offered as a further explanation of the model of environmentally-driven extinction of GUTHRIE and others (e.g. GUTHRIE 1984a). It seems likely that although it is generally the end of the Late Pleistocene that is considered in the light of a necessity for a high carrying capacity to support the megafauna this would have been an important factor throughout the Late Pleistocene and also have been important to the Stage Three fauna. Therefore, the probable decrease in numbers of occurrences towards the LGM of some of the mammals listed above may indicate that environmental impoverishment occurred at this time as well.

Recently, different characteristics of the faunas of the Late Pleistocene have been linked as being suggestive of a causal mechanism. In North America, a connection has been made between the megafaunal extinctions and the disappearance of the non-analogue faunas characteristic of the period (SEMKEN *et al.* 1998; TANKERSLEY 1999). These non-analogue faunas have been shown to be genuine mixtures of animals alive at the same time and place that today are nowhere found in sympatry. The proof that these were genuine communities rather than palimpsest assemblages came in the form of a series of AMS ^{14}C dates on disparate faunal elements indicative of boreal and more thermophilous conditions (STAFFORD *et al.* 1999). The linking of the phenomena of megafaunal extinction and the disappearance of non-analogue communities would fit very well with the hypothesis put forward by LISTER and SHER (1995) of how the mosaic 'mammoth steppe' habitat was destroyed. In LISTER and SHER's model, the megafauna became extinct due to the breakdown of the diverse mosaic vegetation of Late Pleistocene, leading to replacement by latitudinally-banded vegetation of the Holocene. It may be that the non-analogue communities also relied on the mosaic vegetation of the time and were in fact part of the same phenomenon and so disappeared when it broke down. This would be in addition to the effect of topographically enabled northern refugia described recently (STEWART and LISTER 2001). How the proposed ecological upheaval of diversity loss might have affected the more southern parts of Europe during the earlier episode that Neanderthals became extinct is less clear as most attention has been focused on the northern region during the later phase but similar effects are likely. The change to colder temperatures as the LGM was approached is likely to have had a similar effect to the transition to climax vegetation described for the Late Pleistocene-Holocene boundary.

Another phenomenon that seems to have accompanied these various biogeographical changes during the end of the Late Pleistocene is a reduction in the body size of a number of species, including both mammals (KURTÉN 1968; LISTER 1987; GUTHRIE 1984b) and birds (STEWART 1999). A traditional explanation for the body size changes has been that they are due to Bergmann's Rule, where warm blooded vertebrates are larger in relatively colder climates in order to conserve heat (e.g. DAVIS 1981). This attractive hypothesis has however received criticism and is probably no longer be the consensus view among Quaternary palaeontologists. More recently GUTHRIE (1984b, 1990b) and GEIST (1986) have ascribed the changes in body size to a change in the length and quality of the growing season, which was in turn affected by climate change. This difference in growing season supported the highly productive 'mammoth-steppe' or 'steppe-tundra' that was first described by GUTHRIE as a mosaic flora with a high diversity.

Many of the animals that were larger during the late Pleistocene in general may have formed distinct populations that became extinct with the demise of the steppe-tundra rather than evolving into modern forms. This would signify that there might have been many more extinctions at the local level in the Late Pleistocene than often indicated. Vanished populations and subspecies whose individuals were more robust than modern equivalents living in Europe today were red deer (hence *Strongyloceros spelaeus* OWEN 1846) (LISTER 1987), brown bear *Ursus arctos* (KURTÉN 1968), mole *Talpa europaea magna*, a hamster *Cricetus cricetus major* and water vole *Arvicola terrestris antiquus* (STORCH 1974) amongst mammals, and willow grouse *Lagopus lagopus* and ptarmigan *L. mutus* (STEWART 1999), woodcock *Scolopax rusticola magnus* and ruff *Philomachus pugnax rhy-paeicus* (POTAPOVA 1990) amongst birds. Animals no longer in Europe today were also larger than modern counterparts such as the spotted hyaena and the lion of the time, both of which have at times been described as distinct species or subspecies, the so called cave lion and cave hyaena. Of these the lion has been shown using aDNA to be an extinct Pleistocene clade (BURGER *et al.* 2004). The richer environment of the Late Pleistocene may have sustained the greater relative robusticity and body size seen in many of these animals. It also seems that some of these population level extinctions took place during the earlier phase towards the LGM. Recently ancient DNA studies by BARNES *et al.* (2002) on brown bear, SHAPIRO *et al.* (2004) on bison and by MACPHEE *et al.* (2005) on musk ox have confirmed that genotypic diversity in a number of extant mammals became reduced across the LGM. It has also been claimed that no geographic patterning existed in brown bear, cave bear, spotted hyena and Neanderthals before the LGM (HOFREITER *et al.* 2004) which may seem unlikely but if correct could imply that the LGM carved out the phylogeographic patterns identified today in extant taxa like the brown bear.

An argument against this explanation is that all the factors I have discussed, such as disappearance of the rich Late Pleistocene mosaic vegetation or the disappearance of more robust populations of modern taxa, were not necessarily synchronous with the extinction of the Neanderthals. However, I contend that the phenomena should not be dealt with in isolation from each other. The environmental changes that affected the earlier Late Pleistocene extinctions, including the Neanderthals, contributed to the eventual disappearance of the steppe-tundra and all the later Late Pleistocene animals that relied upon it. The transition from Late Pleistocene to the Holocene may also have been similar to the changes that took place earlier at the approach of the LGM. Certainly we have evidence for a reduction in carrying capacity through OIS 3 in the form of a decrease in small carnivore occurrences as well as a decrease of mammoth numbers on non-archaeological sites towards the LGM (see above). The steppe-tundra appears to have reached a peak during the earlier part of OIS 3 and had deteriorated by the start of OIS 2, at the end of which it was replaced by the latitudinally banded vegetation zones of the Holocene still seen today. Therefore, the terminal Late Pleistocene extinctions may have been caused by the combination of the LGM together with the eventual warming and stabilising of the climate at the onset of the Holocene. It seems likely that other relatively large climate oscillations such as the Dryas events and other stadials may also have contributed.

The geographical and temporal patterns of occurrence of Neanderthals through OIS 3 prompt a re-examination of their environmental adaptations. Various authors (COON 1962, TRINKAUS 1981) have explained the body form of Neanderthals, in particular the limb proportions (the so-called crural and brachial indices), as being cold-adapted when compared to anatomically modern humans (*H. sapiens*). TRINKAUS has described Neanderthals as cold adapted although he conceded that locomotion may have played a part (TRINKAUS 1981). The reason given for this was that Neanderthals conform to ALLEN'S Rule (ALLEN 1877), which states that populations of animals within a species living in cold environments will on average have shorter distal extremities than those living in warmer climates. TRINKAUS (1981) further explained the phenomenon as being due to the fact that the more distal parts of a limb will receive reduced amounts of nutrients and growth hormones because this is a general physiological response of warm-blooded vertebrates to low temperature environments. The first point regarding this explanation is that if Neanderthals are a different species from modern humans then thermoregulatory ecogeographic rules are not applicable, as the lat-

ter can only be applied to intraspecific variability (MAYR 1970). The next point is that the geographical and temporal distribution of the last-dated Neanderthals does not match that of any of the primarily cold-adapted mammals in OIS 3. The primarily cold-adapted mammals that became extinct did so at the termination of the Pleistocene at a later time than the Neanderthals. The cold-adapted mammals as a whole, such as the extinct mammoth and extant species like the reindeer and the arctic fox, did not retreat from the north as the climate cooled like the Neanderthals. Their distributions did not appear to change through this time (Fig. 5 A, B and C). Other taxa like the ibex and chamoix retreated into montane areas as climates warmed in the Holocene although they do not show any appreciable change during OIS 3 (Fig. 3 A). It is crucial to consider the geographical distribution of taxa if they are to be deemed cold-adapted in their ecomorphological limb proportions. Our knowledge of ecomorphology has been derived through an understanding of the geographical distributions of organisms in the first instance. An explanation needs to be given for the anomaly that the distribution of Neanderthals retreats southwards as global temperatures decrease. Therefore to view Neanderthal body proportions as purely due to cold adaptation without reference to geographical distribution is to ignore the way in which ecogeographic rules were originally identified and may therefore be premature.

Another puzzle regarding Neanderthal body proportions is why modern humans, who were living in similar climates in Northern Europe, had body proportions that would seem to be warm-adapted. This has led TRINKAUS and others (TRINKAUS 1981; HOLLIDAY 1997) to suggest that despite their interpretation that body proportions have a large genetic component and that modern humans probably had a greater ability to protect themselves from the thermal stresses of Late Pleistocene winters than had Neanderthals. The fact that modern humans were comparative newcomers to Europe may also be important as their more “southern” body proportions could thus be preserved. Another important perspective regarding limb proportions is of course locomotion because the primary role of limbs is locomotion and not thermoregulation (STEWART 2005). Limb proportions will only be affected by climate if all other natural selective pressures are effectively neutral. It is difficult to see thermoregulation as being important enough to counter the selection for effective locomotion. Recently I speculated that locomotion is indeed the factor behind the Neanderthal body proportions and that they may have been proficient sprinters to accommodate their proposed encounter hunting (STEWART 2005) although many others have alluded to locomotor explanations (e.g. TRINKAUS 1981).

Robusticity is a feature of the Neanderthal skeleton that was noted early on in their study (TRINKAUS 1983). This robusticity is to be found in many of the bones of the Neanderthal post-cranium. In the ribs and vertebrae this has been explained as probably related to the hypertrophy of the shoulders and back, which in turn has been explained as due to the use of the front teeth in holding objects (TRINKAUS 1983). In the upper and lower limbs robusticity is primarily due to the greater development of muscle scars. It would appear that Neanderthals were stronger with greater endurance than modern humans as reflected by their more massive bones (TRINKAUS 1983). Due to the positive correlation between body size (mass) and robusticity, it is surprising that Neanderthal robusticity has not been more strongly linked to increased body size conforming to Bergmann’s Rule. Neanderthal robusticity would then, albeit with a similar question mark, have the same explanation as their limb proportions. However, while Bergmann’s Rule is a more traditional explanation for body size differences in warm-blooded animals during the Pleistocene (e.g. DAVIS 1981; see above) many palaeontologists now favour explanations involving a richer environment than that of Europe today (e.g. see above). However, it is not unlikely that all the robust characters reflect the powerful bodies of proficient sprinters.

The Neanderthal nose and associated anatomical features have been described as being distinct from those of modern humans and have been interpreted as an adaptation to cold and dry climate (COON 1962; FRANCISCUS and TRINKAUS 1988; SCHWARTZ and TATTERSALL 1996). These differences have not been accepted unanimously, although claims have been made that *a priori* beliefs regarding taxonomic affinities of Neanderthals may be guiding workers’ willingness to recognise differences (LAITMAN *et al.* 1996). LAITMAN has, however, praised efforts to look at the adaptive

significance of morphology rather than simply to blindly give it taxonomic meaning (HOLDEN 1999). It appears that a growing number of features may be collectively described as defining a unique Neanderthal upper respiratory tract complex *bauplan*, including differences in the eustachian tubes and sinuses and even the inner ear (HOLDEN 1999). The significance of the unique characters such as the large external nose and paranasal sinuses is that Neanderthals relied more heavily on nasal rather than oral respiration. Furthermore, the larger paranasal sinuses were probably an adaptation to warming and humidifying cold and dry air (SCHWARTZ and TATTERSALL 1996; LAITMAN *et al.* 1996; COON 1962; FRANCISCUS and TRINKAUS 1988; WOLPOFF 1968). The medial projections or swellings described by SCHWARTZ and TATTERSALL (1996) may well have provided additional surface area for mucus and ciliated membranes to humidify and warm incoming air. However, regardless of this claim it has not been demonstrated that variation in the Neanderthal upper respiratory tract mirrored differences in temperature and humidity across the Neanderthal geographic range (LAITMAN *et al.* 1996). The same is true for the other proposed adaptations to climate, such as the brachial and crural indices. If all these features are truly adaptations to the environment, there may be differences between Neanderthal populations in different climatic regimes across their range. If Neanderthal home ranges are as small as suggested by work on lithic raw materials (MELLARS 1996), there should also be greater variation in Neanderthals than in modern humans, whose ranges were larger. This is because the more sedentary a population of animals the more opportunity there should be for variation due to a lack of interbreeding with other populations. It should be said, however, that differences between regions in the ecomorphology have not been demonstrated in many other mammals during OIS 3. The only example known to the author is the difference shown between OIS 3 reindeer populations from south-west France and southern Germany (WEINSTOCK 2000). The German reindeer were statistically larger than the French population although no specific reason were given other than the comment that environments, as seen from the accompanying mammals, “must have been very different indeed” (WEINSTOCK 2000).

Other animals with adaptations for breathing cold and/or dry air in Eurasia today may be said to be steppic- or continental-adapted. Continental-adapted would signify cold winters and relatively warm summers. This may explain the similarity in pattern of the southwards retreat of the Neanderthals to that of *E. hydruntinus* that seems to have been a steppic element of the late Quaternary fauna (Fig. 7). If we consider that the period during which Neanderthals evolved and lived was probably largely more continental than the present day, then this might make sense. Indeed, from a modern perspective, the animals which formed part of the Late Pleistocene biota were northern “cold-adapted” taxa and “eastern continental” taxa. Some of these animals were colder-continental adapted, while Neanderthals were presumably warmer-continental adapted species, based on their geographical distribution through time. Neanderthals seem to have been better-suited to the Mediterranean during the Late Pleistocene than to the more northern parts of Europe.

V. CONCLUSION

If we regard the Neanderthals as a Pleistocene large and robust member of the genus *Homo*, then they, in addition to other larger vertebrates, were adapted to the rich mosaic biota of the latter parts of the Pleistocene (STEWART 2005). They may not have been specifically adapted to the “mammoth-steppe” like many of the megafaunal elements of more northern latitudes usually discussed in this context. However, it may be that the European vegetation was generally richer in carrying capacity. What is being argued here is that the greater robusticity and size of Neanderthals may have relied on the richer environment of the Late Pleistocene, much as did the larger and more robust individuals of other taxa. This does not negate the behavioural explanation of Neanderthals robusticity including their possible greater turn of speed, but does cause one to question any simplistic thermoregulatory explanation.

Neanderthals appear to be a European endemic species and they evolved on the western fringes of the Eurasian landmass during the Middle Pleistocene, presumably from an African ancestor that

may have been *Homo heidelbergensis* (HUBLIN 1998). The period during which they evolved seems to have been dominated by continental phases of climate during which the Atlantic Ocean was influencing the European landmass to a far lesser extent than it is today. In relation to today's climate Western Europe was more continental but in relation to more central parts of Eurasia at that time it must have been relatively oceanic. Therefore, it may be that the *Homo heidelbergensis* / Neanderthal lineage became particularly well-adapted to the western fringes of the Eurasian landmass which we could term Western Palaeartic continental-adapted rather than simply continental-adapted. The south-western fringes of the Palaeartic were probably richer in forested habitats which require some rainfall and it has been shown that Neanderthals appear to prefer closed rather than open vegetation (STEWART 2004). The latter would in turn correlate with encounter hunting and their proposed sprinting capabilities (STEWART 2005).

Finally, the extinction of Neanderthals is often blamed on competition with modern humans although this should not be taken as fact (STEWART 2004). The gene-pool bottlenecking events within various mammalian species demonstrated to have taken place towards the LGM have not been blamed on modern humans colonisation events around the world and neither can the similar extinction in diversity that has become apparent from the oldest Neanderthal aDNA (ORLANDO et al. 2006). The latter study was an analysis of 100,000 year old Neanderthal mtDNA from Belgium showing genetic variation before the penultimate period of extreme cold (OIS 4) which was not present towards the end of Neanderthal existence. This variation appears to have disappeared by OIS 3 and implies that climate caused a bottleneck in the Neanderthals long before the modern humans arrived in Europe. This in turn suggests that there may be no need to blame our own species for the final demise of the Neanderthals.

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