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Neanderthals and modern humans in the European landscape during the last glaciation

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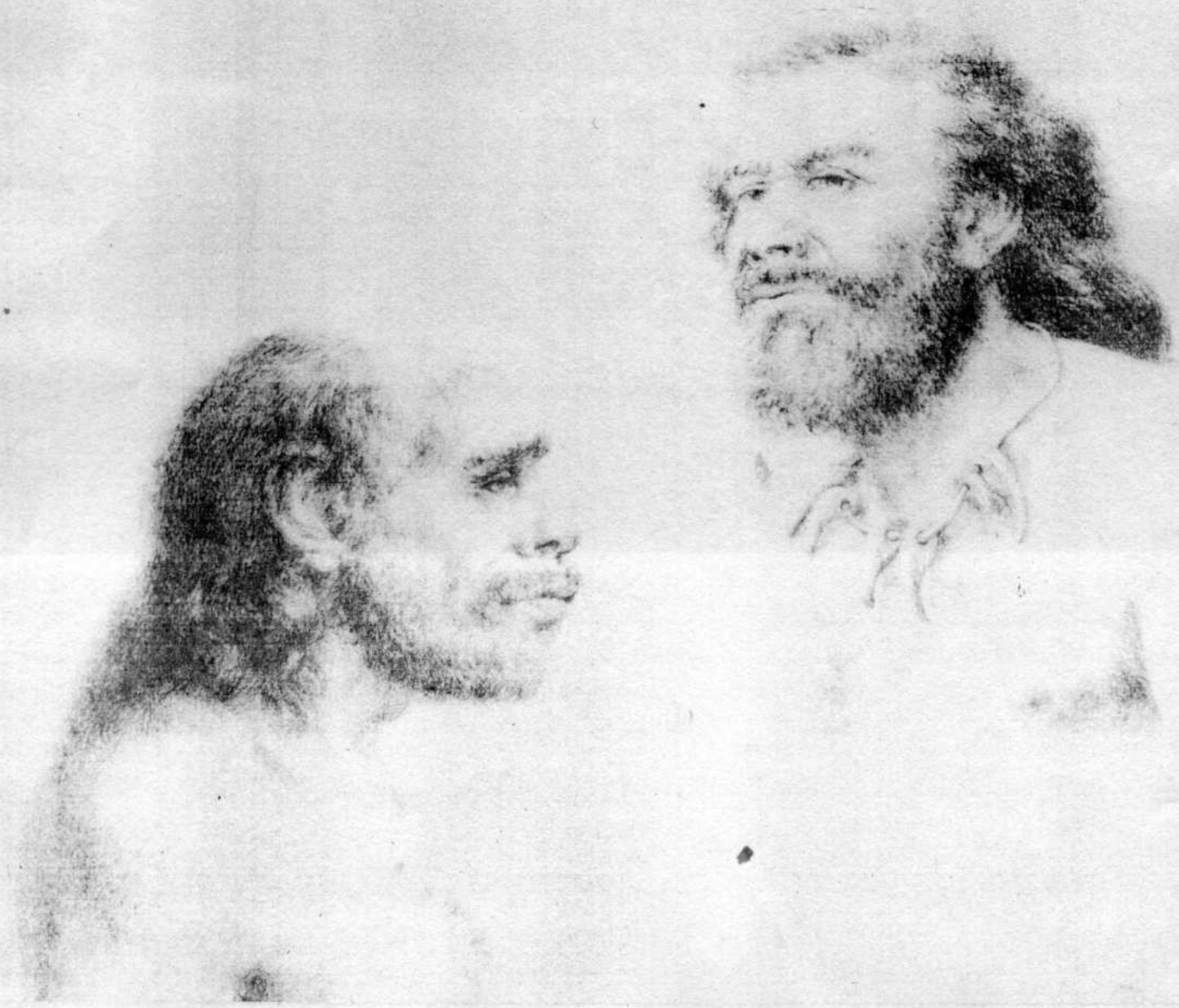

Chapter 12

Neanderthals as Part of the Broader Late Pleistocene Megafaunal Extinctions?

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The fate of the Neanderthals remains controversial despite more than a century of research. Most researchers agree that the Neanderthals disappeared during Oxygen Isotope Stage 3 (OIS-3), but there is no consensus regarding what happened to them (e.g. Aiello 1993; Stringer & Gamble 1993; Stringer & McKie 1996; Krings *et al.* 1997; 1999; Wolpoff & Caspari 1997; Kramer *et al.* 2001; Wolpoff *et al.* 2001). Two models dominate the dispute: the Out of Africa model and the Multiregional Evolution model, both of which have 'extreme' and 'moderate' formulations. The 'extreme' Out of Africa model contends that the Neanderthals were replaced with little or no interbreeding by migrating Anatomically Modern Humans (AMH) whose origins lay in Africa around 150-200 thousand years before present (ka BP) (Stringer & Andrews 1988). The 'extreme' Multiregional Evolution model asserts that the disappearance of the Neanderthals is illusory, and discounts migration of African modern humans as a significant factor in the appearance of the modern humans (Wolpoff 1989). It asserts instead that the Neanderthals simply evolved into the modern humans.

Within the framework of the Out of Africa model, most explanations for the disappearance of the Neanderthals have focused on their inability to compete effectively with the migrating modern humans (e.g. Mellars 1989; Mithen 1996; Klein 2000). Authors differ regarding the source of the modern human's competitive advantage. For example, some suggest that it was technological (Pettitt 1999), while others contend that it was linguistic (Lieberman 1989), cognitive (Mellars 1989; Mithen 1996; Klein 2000) or demographic (Bocquet-Appel & Demars 2000). But there is widespread agreement that competition with the modern humans was the major or perhaps sole factor in the demise of the Neanderthals. Recently, however, Finlayson *et al.* (2000a,b) have criticized the assumption that the modern humans played a role in the extinction of the Neanderthals. Drawing on the results of a computer simulation study, these authors contend that explanations requiring competitive interactions between the Neanderthals and modern humans are unnecessary. They assert instead that the decline and extinction of the Neanderthals and the growth and dispersal of modern human populations are best explained as independent, climate-linked events. In Finlayson *et al.'s* (2000a) model, Neanderthals and modern humans had been separated ecologically for a long period, and had consequently developed different resource acquisition strategies. The Neanderthals' strategy focused on local exploitation of a variety of resources, whereas the modern humans' strategy was oriented towards long-range hunting of large herbivores. Between 60 and 20 ka BP, deterioration in climatic conditions caused changes in ecology, most notably the expansion of the so-called steppe tundra and its associated fauna, which favoured the resource acquisition strategy of modern humans and made the Neanderthals' resource acquisition strategy ineffective. Accordingly, the size of the modern human population increased leading to their migration from Africa, while the Neanderthal population declined and eventually became extinct around 30 ka.

A further reason for rejecting modern human involvement in Neanderthal extinction is the lengthy co-occurrence, up to 10 ka BP, of the two species in Europe in areas such as Cantabria. This lengthy sympatry between modern humans and Neanderthals is contested by some authors and d'Errico *et al.* (1998) and Zilhao & d'Errico (1999) reject any early dates for modern humans in Europe on the grounds of poor stratigraphy and dating. Klein (2000) dismisses

Table 12.1. *Large mammal taxa in the Stage Three Project Mammalian data base.*[1] *Categories: la) Taxa whose distribution remained the same in Europe after the Pleistocene; lb) Taxa whose distribution contracted northwards and/or into montane areas in Europe after the Pleistocene; lc) Taxa whose distributions contracted eastwards into Southwest Asia and Central Asia after the Pleistocene; 2a) Taxa that went extinct at the termination of the Pleistocene; 2b) Taxa that went extinct at the approach of the Glacial Maximum.*

Taxon no.	Taxon Latin	English	Status	Status category (see text)
2	*Alces alces*	Elk	Extant	lb
3	*Cervus elaphus*	Red deer	Extant	la
4	*Rangifer tarandus*	Reindeer	Extant	lb
5	*Dama dama*	Fallow deer	Extant but reintroduced to northern Europe	2b*
6	*Capreohts capreolus*	Roe deer	Extant	la
7	*Megaloceros giganteus*	Giant deer	Extinct[1]-[2]	2aΦ
8	*Bos 1 Bison*	Auroch/Bison	Effectively extinct in Europe	la/2a
9	*Rupicapra rupicapra*	Chamoix	Extant	lb
10	*Capra ibex/pyrenaica*	Ibex	Extant	lb
11	*Ovibos moschatus*	Musk ox	Extant	lb
12	*Saiga tartarica*	Saiga antelope	Extinct in Europe[1]	lc
13	*Sus scrofa*	Wild boar	Extant	la
14	*Equus ferus*	Horse	Extant	la
15	*Equus hydruntinus*	European wild ass	Extinct[1]	lc§
16	*Equus asinus*	Donkey	Extant	lc**
17	*Equus latipes*	Extinct horse	Extinct	?
18	*Stephanorhinus kirchbergensis*	Merck's rhino	Extinct[1]	2b
19	*Stephanorhinus hemitoechus*	Narrow-nosed rhino	Extinct in Europe[1]	2a/bt
20	*Coelodonta antiquitatis*	Wooly **rhino**	Extinct[1]	2a
21	*Mammuthus primigenius*	Mammoth	Extinct[1]	2a
22	*Elephas antiquus*	Straight-tusked elephant	Extinct[1]	2b
23	*Panthera leo*	Lion	Extinct in Europe[1]	lc
24	*Panihera pardus*	Leopard	Extinct in Europe[1]	lc
25	*Lynx lynx*	Lynx	Extant	la
26	*Lynx pardina*	Iberian lynx	Extant	la Iberian endemic
27	*Felis sylvestris*	Wild cat	Extant	la
28	*Crocuta crocuta*	Spotted hyeana	Extinct in Europe[1]	lc
29	*Canis lupus*	Wolf	Extant	la
30	*Cuon*	Dhole	Extant	lc?
31	*Vulpes vulpes*	Red fox	Extant	la
32	*Alopex lagopus*	Arctic fox	Extant	lb
33	*Ursus arctos*	Brown bear	Extant	la
34	*Ursus spelaca*	Cave bear	Extinct[1]	2a
35	*Meles meles*	Badger	Extant	la
36	*Mustela*	Stoat/Weasel	Extant	la
37	*Putorius putorius*	Polecat	Extant	la
38	*Martcs* spp.	Marten	Extant	la
39	*Gulo gulo*	Wolverine	Extant	lb
40	*Lutra lutra*	Otter	Extant	la
41	*Homo neanderthalensis*	Neanderthal human	Extinct[4]	2b
42	*Homo sapiens*	Modern human	Extant	la

Note: 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 - Gonzalez *et al.* (2000); 3 - Markova *et al.* (1995); 4 - Smith *et al.* (1999).

* Fallow deer not extinct but was very much reduced in distribution to the southern and southeastern Europe by the last glaciation. They were subsequently reintroduced by Romans to Northern Europe (Mitchell-Jones *et al.* 1999).

Φ Giant deer extinct in most areas of Europe by the end of the Pleistocene. However, dates for the early Holocene exist in the Isle on Man and Scotland (Gonzalez *et al.* 2000).

** *Equus asinus* may well be a mistakenly identified taxon as it is generally believed to have arrived from Africa during the Holocene as a domesticate (Musil pers. comm.).

§ *£. hydruntinus* survived the Pleistocene/Holocene boundary but became extinct some time during the Holocene (Benecke 1999).

t *S. hemitoechus* is traditionally an 'interglacial survivor' (Stuart 1991) but current analysis questions this.

the late surviving (post 30 ka BP) Neanderthals in Europe on similar grounds. It is clear, however, that many European early modern human sites have dates that are older than 36.5 ka, and in some cases the dates are based on more than one absolute dating technique (Davies 2001). Likewise, recent dates from Vindija demonstrate that the Neanderthals survived until at least 29 ^{14}C ka BP in some parts of Europe (Smith *et al.* 1999).

It is noteworthy that the debate between those anthropologists and archaeologists who contend that the modern humans played an important role in the demise of the Neanderthals and those who view the Neanderthal's extinction as primarily the consequence of climatic deterioration-induced ecological change parallels the debate in vertebrate palaeontology regarding the Late Pleistocene megafaunal extinctions. In the latter debate two main hypotheses dominate, one involving humans and often called the prehistoric overkill theory (Martin 1967; 1984; Schuster & Schiile 2000), and one where climate is the dominant cause (Graham & Lundelius 1984; Guthrie 1984). The large size of the vertebrates that became extinct with associated relatively small population numbers and slow-breeding strategies is emphasized in both explanations. However, Guthrie (1990) contends that too much focus on the extinctions themselves has obscured the fact that other events had taken place, and that the Late Pleistocene megafaunal extinctions should be seen as part of a Late Pleistocene, climate-driven 'faunal revolution', which involved rapid [micro-] evolutionary changes, fractionation of biotic communities and significant reductions in distributional ranges.

With few exceptions (e.g. Stewart 2000), the disappearance of the Neanderthals has rarely been considered in the light of other Late Pleistocene extinctions, and the Late Pleistocene extinctions have not been viewed in the light of Neanderthal extinctions. Given Guthrie's more holistic perspective (Guthrie 1990) it is clear that such a consideration is overdue. In this paper, we therefore attempt to shed light on the role of climate change and associated ecological developments in the disappearance of the Neanderthals. We do so by analyzing the temporal and geographic distribution of large mammal faunas from European archaeological and palaeontological sites that have been absolutely dated to between 60 and 20 ka BP. This includes an analysis of some of the animals thought to have become extinct during this time frame as well as ones that went extinct after this period and ones that survived until the present.

Materials and methods

In order to investigate the role of climate change and associated ecological developments in the disappearance of the Neanderthals the Stage Three Mammalian Data Base[1] was analyzed in such a way as to test whether there was any synchrony between the demise of Neanderthals and other mammalian ecological occurrences. The data base is described in some detail in Chapter 7 (Stewart *et al.* 2003).

To better understand the Neanderthals as part of the evolving fauna of OIS-3 a historical biogeographical approach was taken. This entailed a consideration of the extent to which each taxon or taxonomic grouping listed in Table 12.1 was distributed in Europe and how that may have changed between 60 and 20 ka BP. Only the large mammal taxa were included in the analysis as they are more consistently reported.

First of all, however, the large mammals were divided into five historical biogeographical categories based on previous knowledge of their extant versus extinct status, what the modern distribution of extant taxa is and when the extinct taxa are believed to have become extinct (for references see Table 12.1):

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 Southwest Asia and central Asia after the Pleistocene.
2. *Extinct taxa.* These fall into two categories consisting of:
   a) taxa that went extinct near the termination of the Pleistocene;
   b) taxa that went extinct at the approach of the LGM.

Table 12.1 gives the categories for each of the 41 large mammalian taxa (including the Neanderthals and modern humans) in the data base. The categories created suggested differences in tolerances of the mammals to prevailing environmental conditions and hence led one to expect different responses to the changing environments of OIS-3.

The temporal resolution of the analysis was guided by two factors regarding the practical potential of making meaningful comparisons between the absolutely dated mammalian faunas and the global

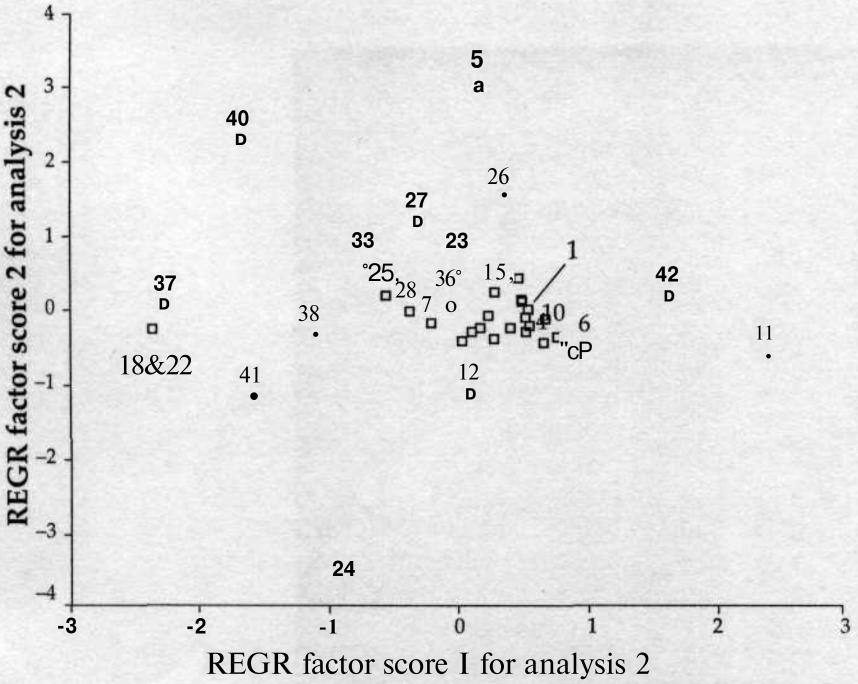

Figure 12.1. *Principal component analysis of the percentage frequency analysis through time. The numbers corresponding with each taxon are listed in Table 12.1. No. 1 represents all taxa taken together.*

climate signature. The first involved the precision of the dates in relation to the amplitude of the climatic cycles during OIS-3, while the second simply involved the problems of turning the ^{14}C dates into calendrical years. Three time zones were defined, 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.

The analysis of the faunal data had two separate parts. These were:

1. analysis of taxon frequency of occurrence in the three time periods;
2. analysis of taxon geographic distribution.

The analysis of the taxon frequency of occurrence in each of the three time periods was done by calculating the percentage number of dated faunas with a taxon in each time zone as part of the total number of dated faunas with the taxon. These percentage data were subjected to Principal Components Analysis (PCA) with and without arcsine transformation (Sokal & Rohl 1995) (Fig. 12.1).

A further analysis had to be designed, however, in order to test the reliability of the results of the percentage analysis. This is because the spread of percentages of dated faunas in each time zone 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. This was also problematic as the length of each time zone was not equal (Early = 23 ka BP, Middle = 9 ka BP, Late = 8 ka BP) although it was hoped that the disproportionate length of the early time zone would be countered by the comparatively lack of dates falling within it. Another possibility is that their preferred association with one or other human species may dominate patterns, because the number of dates associated with Upper Palaeolithic (modern human) and Middle Palaeolithic (Neanderthal) are not identical (Table 12.2). There are, for instance, about twice as many dated faunas from Upper Palaeolithic sites than Middle Palaeolithic ones (Table 12.2). Therefore to ascertain the reliability of the results of the initial analysis percentages were calculated for the large mammals, but divided into those from Upper Palaeolithic and Middle Palaeolithic sites respectively (Table 12.3). If the trends in percentages filling each time zone observed in the undifferentiated analysis 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.

The analysis of taxon geographic distribution was achieved in two ways. First, the maximum and minimum latitude for the absolutely dated large mammal taxa in Europe for each of the three time zones were calculated. Then all the large mammal taxa were mapped for each of the time zones to better investigate any changes in geographical distribution through time.

A final part of the geographical analysis was an investigation into the percentage number of dated faunas associated with the Neanderthals or the Middle Palaeolithic that fall into the latitudinal and longitudinal bands represented on the maps. These bands are 5° deep for the latitude and 10° wide for the longitude. The results of this analysis are shown in Table 12.4.

Table 12.2. *Breakdown of mammalian data base by archaeological association. Percentage number of dated faunas associated with each broad archaeological industry.*

Industry	No.	%
OIS-3 dated assemblages with large mammals	468	100
OIS-3 dated assemblages with Upper Palaeolithic industries and large mammals	224	47.86
OIS-3 dated assemblages with Middle Palaeolithic industries and large mammals	107	22.86
OIS-3 dated assemblages with transitional industry and large mammals	24	4.94
OIS-3 dated assemblages with large mammals and no industry	90	19.23
OIS-3 dated assemblages with large mammals and undefined industry	23	4.91

Upper Palaeolithic includes Aurignacian, Gravettian, Solutréan, Magdalenian and unspecified Upper Palaeolithic industries; Middle Palaeolithic includes Mousterian and unspecified Middle Palaeolithic industries; transitional industries includes Châtelperronian, Bohunician, Uluzzian, Szeletian, Bachokirian and Micoquian.

Table 12.3. *Percentage number of dated assemblages with large mammal taxa falling in each of the three time zones but broken down into from horizons with Middle Palaeolithic (Neanderthal) and Upper Palaeolithic (modern human) archaeology.*

Taxon	**No. of dated faunas with taxon**	**% no. of dated faunas with taxon per time** zone					
		>37ka		37-28 ka		<28ka	
		MP	UP	MP	UP	MP	UP
All taxa	322	48.19	19.24686	39.75904	43.51464	12.04819	37.23849
Alces alces	15	50	23.07692	50	46.15385	0	30.76923
Cervus elaphus	186	50	20	37.5	43.84615	12.5	36.15385
Rangifer tarandus	204	52.5	17.68293	42.5	40.85366	5	41.46341
Dama dama	10	66.66667	0	33.33333	75	0	25
Capreolus capreolus	71	7.692308	15.51724	61.53846	41.37931	30.76923	43.10345
Megaloceros giganteus	32	63.63636	9.52381	27.27273	61.90476	9.090909	28.57143
Bos1Bison	219	56.14035	20.98765	40.35088	44.44444	3.508772	34.5679
Rupicapra rupicapra	125	46.875	19.35484	34.375	41.93548	18.75	38.70968
Capra	149	45.45455	20.68966	36.36364	42.24138	18.18182	37.06897
Ovibos moschatus	7	33.33333	0	33.33333	50	33.33333	50
Saiga tartarica	15	100	35.71429	0	42.85714	0	21.42857
Sus scrofa	81	50	22.80702	25	49.12281	25	28.07018
Equus ferus	201	51.85185	17.68707	40.74074	42.17687	7.407407	40.13605
Equus hydruntimts	52	70	11.90476	20	47.61905	10	40.47619
Equus asinus	3	None	33.33333	None	33.33333	None	33.33333
Equus latipes	4	None	50	None	50	None	0
Stephanorhinus kirchbergensis	5	25	100	50	0	25	0
Stephanorhinus hemitoechus	9	50	0	50	33.33333	0	66.66667
Coelodonta antiquitatis	67	62.5	21.56863	31.25	45.09804	6.25	33.33333
Mammuthus primigenius	111	55	20.87912	35	46.15385	10	32.96703
Elephas antiquus	5	50	66.66667	50	33.33333	0	0
Panthera leo	54	46.15385	21.95122	46.15385	51.21951	7.692308	26.82927
Panthera pardus	14	70	50	10	25	20	25
Lynx lynx	20	66.66667	23.52941	33.33333	52.94118	0	23.52941
Lynx pardina	13	28.57143	16.66667	57.14286	50	14.28571	33.33333
Felis sylvestris	32	26.66667	35.29412	53.33333	47.05882	20	17.64706
Crocuta crocuta	94	57.14286	23.72881	37.14286	52.54237	5.714286	23.72881
Canis lupus	148	42.85714	22.12389	45.71429	43.36283	11.42857	34.51327
Cuon	10	40	0	40	60	20	40
Vulpes vulpes	156	45.45455	17.88618	42.42424	43.90244	12.12121	38.21138
Alopex lagopus	87	46.15385	20.27027	30.76923	48.64865	23.07692	31.08108
Ursus arctos	42	41.17647	32	47.05882	56	11.76471	12
Ursus spelaea	96	51.72414	23.8806	37.93103	46.26866	10.34483	29.85075
Meles meles	27	66.66667	19.04762	16.66667	47.61905	16.66667	33.33333
Mustek	28	33.33333	24	66.66667	48	0	28
Putorius putorius	11	100	44.44444	0	55.55556	0	0
Martes	14	50	30	50	60	0	10
Gulo gulo	36	0	29.41176	50	47.05882	50	23.52941
Lutra lutra	3	0	50	100	50	0	0

Table 12.4. *Percentage number of dated assemblages with Neanderthals or the Middle Palaeolithic found in latitudinal and longitudinal hands in the three time OIS-3 time zones.*

Latitude	35-40	40-45	45-50	50-55
Early	7.87	29.21	57.3	5.62
Middle	15.38	30.77	48.08	5.77
Late	17.65	29.41	47.06	5.88

Longitude	-10-0	0-10	10-20	20-30	30-40	40-50
Early	17.98	44.94	21.35	8.99	4.49	2.25
Middle	21.15	53.85	15.38	3.85	1.92	3.85
Late	29.41	52.94	11.76	5.88	0	0

Results

The two-part analysis of the OIS-3 large mammal fossil data was designed to distinguish any changes in temporal distribution of taxon frequency and any changes of geographical range of the large mammalian taxa of OIS-3.

The percentages derived from the number of dated faunas with each taxon in the three time zones defined were then subjected to principle component analysis (PCA). Figure 12.1 presents the two principal components extracted from the percentage data in the PCA. Principal component 1 (PCI) accounted for 59.4 per cent of the variance in the data set, and PC2 for 40.6 per cent. The PCA results shown in Figure 12.1 have a PCI which describes the relationship between the early and late time zones of OIS-3. As PCI increases so the percentage for the early time zone decreases while the late time zone increases. PC2, on the other hand, describes the middle time zone percentage in relation to the early and late time zones. As PC2 increases so the middle time zone percentage increases while the early and late time zones decrease. Together, Figure 12.1 and Table 12.3 indicate that there are three main patterns of temporal distribution among the percentage data. The first, are those mammals that do not appear to change their occurrence through time and comprise the largest group. These mammals can only approximate an even spread though time. This is because the percentage occurrence of all mammals in this study shows a 'humped' distribution through time, with 29.29 per cent in the early zone, 41.21 per cent for the middle one and 29.5 per cent for the late zone. The mammals falling in this first cluster include extant taxa whose distribution did not change at the end of the Pleistocene, those that retreated north or east and some that became extinct around the end of the Pleistocene. They include herbivorous taxa such as reindeer *Rangifer tarandus,* horse *Equus ferus* and mammoth *Mammuthus primigenius* as well as carnivorous mammals including wolf *Canis lupus,* red fox *Vulpes vulpes* and arctic fox *Alopex lagopus.* These taxa can be seen to cluster around the point representing all taxa in Figure 12.1 and have a relatively 'humped' distribution, although this may be a function of the humped data set.

The second group includes the taxa that decreased significantly over OIS-3 and includes those that became extinct in the first phase of the Late Pleistocene megafaunal extinctions together with an assortment of other mammals. This group includes mostly carnivores like the leopard *Panthera pardus,* the polecat *Putorius putorius* and the martens *Martes* spp., larger herbivores such as *Stephanorhinus kirchbergensis, Elephas (Palaeoloxodon) antiquus* as well as the Neanderthal. In Figure 12.1 they fall to the left of the main central cluster, signifying that they have low percentage values for the late time zone relative to the early zone. Among these the carnivores are all extant whils the herbivores and Neanderthals are now extinct or absent from Europe. Most important in this category are two of the 'interglacial survivors'; a term first used by Stuart (1991), i.e. *Stephanorhinus kirchbergensis* and *Elephas (Palaeoloxodon) antiquus.* These last two species belong to the group in Figure 12.1 plotting furthest in the negative for PCI (Nos. 18 and 22 respectively) to have values of 0 per cent in the last time zone which distinguishes them from the cluster with Neanderthals that falls to around 10 per cent (No. 42). It appears, however, that one should add the Neanderthals to the extinct group as illustrated by their percentage decrease which goes from 56.6 per cent to 32.7 per cent and finally to 10.69 per cent. This decrease is not solely because the decrease in the number of sites with Neanderthal fossils, as dates associated with Middle Palaeolithic archaeology are also included which 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 towards the end of this time. The temporal frequency pattern for *Stephanorhinus hemitoechus* was unexpected as the species is often said to have become extinct in Europe during the first phase of megafaunal extinctions (Stuart 1991). The results of the analysis, however, show that they appreciably increase in 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 were particularly affected.

The other taxa whose percentages appear to decrease over OIS-3 are more surprising, such as the leopard *Panthera pardus,* the otter *Lutra lutra,* the polecat *Putorius putorius* and the martens *Maries* spp. It should be pointed out that carnivores form the major group that have a negative deviation relative to the pattern for all other mammalian taxa. There is also a slight decrease in all large mammal taxa towards the LGM, if we consider the two later time zones and that may be a further reflection of general environmental impoverishment. The latter may not be the case, however, as the pattern of decline in percentage numbers of sites between the intermediary time zone and the late one mirrors that for all the sites with fossil mammals taken together.

The only taxa that reliably increased their percentages markedly are the musk ox *Ovibos moschatus* and the modern humans *Homo sapiens.* The increase in percentage in the musk ox may be explained by their modern northern distribution and tolerance of cold temperatures (Mitchell-Jones *et al.* 1999). In Figure 12.1 these taxa have the highest values for PCI. It is 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 were as cold tolerant as the musk ox. The final pattern to note is where taxa increased and then decreased. These include the fallow deer *Dama dama,* and the otter *Lutra lutra* can perhaps be disregarded, as the number of sites with these species is low, making it dangerous to draw reliable conclusions from them.

It became apparent, however, that a possible bias may have occurred due to the association of specific archaeological industries with specific large mammal taxa. This is the reason behind Table 12.3 where the percentage number of dated assemblages with species showing changes in each time zone was calculated, but divided into those from either Upper or Middle Palaeolithic archaeological sites. The results in Table 12.3 confirm that taxa such as the red deer *Cervus elaplius,* reindeer *Rangifer tarandus,* horse *Equus* ***fonts*** and mammoth *Mammuthus primigenius* had percentage patterns for the Middle and Upper Palaeolithic that correspond reasonably well with the patterns of all the mammals associated with each industry (Table 12.3). Of those taxa that showed a decrease through the time zones in the archaeologically undifferentiated analysis the extinct rhino *Stephanorhinus kirchbirgensis,* the straight-tusked elephant *Elephas antiquus,* the otter *Lutra lutra,* the polecat *Putorius putorius* and the martens *Martes* spp. show the same pattern in the percentages from Upper Palaeolithic as Middle Palaeolithic sites (Table 12.3). It should be added, however, that the percentage number of faunas with wild cat *Felis sylvestris* and brown bear showed a marked decrease towards the LGM on Upper Palaeolithic sites suggesting that they too suffered a decline with time. Finally, the increase in dated faunas with musk ox *Ovibos moschatus* cannot be proved. The result of the test in Table 12.3 shows that, by and large, the picture revealed by the archaeologically undifferentiated analysis was substantiated.

If the results of the temporal distribution analysis in Figure 12.1 and Table 12.3 are associated with climatic and vegetational deterioration through OIS-3, it is likely that the geographical distribution of these mammals in Europe would have changed. Therefore the maximum and minimum latitudes for each taxon in the three time zones of OIS-3 were calculated. The main observations to be made from this analysis was 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. The most interesting observation to be made from the maximum and minimum latitudes over-all is that some species never reach very far north while others never reach far to the south. The taxa which generally have more northern latitudes are those such as the mammoth *M. primigenius,* the reindeer *R. tarandus* and the arctic fox *A. lagopus* which never reached further south than 42° and approximates with northern Spain, northern Italy and the more northern parts of the Balkans (see Fig. 12.2 for latitude lines). These taxa are ones that belong in category lb, extant taxa whose ranges today are northern and montane (although the montane species ibex *Copra* spp. and chamoix *Rupicapra* do not follow this geographical pattern) and ones from category 2a, taxa that became extinct at the end of the Pleistocene. Then there are those taxa whose distribution never reached further north of 46° or the latitude of the northern parts of the Dordogne. These include the three 'interglacial survivors', *Stephanorhinus kirchbergensis, S. hemitoechus* and *Elephas antiquus* as well as the endemic Iberian lynx **Lynx** *pardina* and the fallow deer *Dama dama.* Finally, there are taxa that

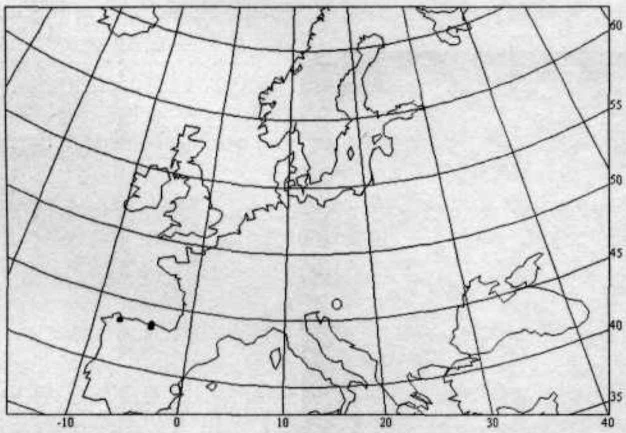

Figure 12.2. *Map of taxon* Stephanorhinus kirchbirgensis *that went extinct at the approach of the Late Glacial Maximum. Small solid circle - Early time zone; medium circle - Intermediate time zone; large circle - Late time zone.*

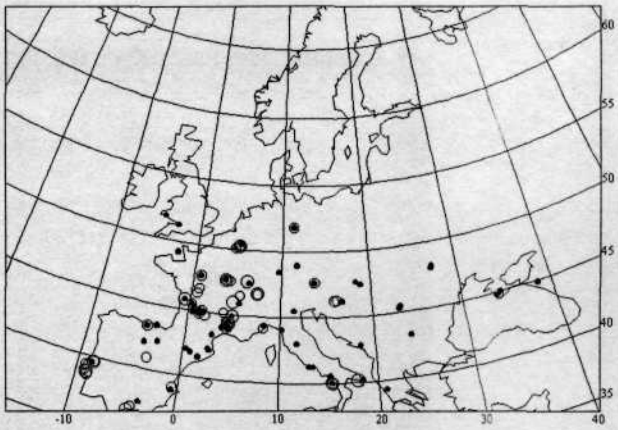

Figure 12.3. *Map of taxon* Homo neanderthalensis *that went extinct at the approach of the Late Glacial Maximum. Small solid circle - Early time zone; medium circle - Intermediate time zone; large circle - Late time zone.*

are distributed throughout Europe such as the red deer *C. elaphus;* the horse *E. ferus* and the wolf *Canis lupus,* all taxa that fall within category 1a. The northern and southern taxa have a latitudinal band of overlap between 42° and 46°. This band of overlap encompasses important areas of dense mammalian fossil and archaeological site occurrence such as the Dordogne and the Rhone Valley (Davies *et al.* in press).

In order to further investigate any geographical change in occurrence of taxa, maps were constructed for all the large mammals in the Stage Three Data Base. The results show that the red deer *Cervus elaphus* (Category 1a), the reindeer *Rangifer tarandus* (Category 1b) and the saiga *Saiga tatarica* (Category 1c) do not appear to change their distributions through OIS-3.

There are also extinct taxa such as the mammoth (Category 2a) whose distribution is restricted in the south, although it is found in Scandinavia in greater numbers than any other mammal in the Stage Three Project Mammalian Data Base. There are no apparent changes in the distributions of the mammoth through OIS-3 although recent evidence shows that they were absent from Europe during the LGM (Stuart *et al.* 2002).

The final category of mammals contains those which are at the heart of the main argument 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 12.2 and 12.3 they all appear either to be retreating or to have retreated to the south and to some extent to the west and south 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. 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 & Lister (2001). These taxa seem to be contracting towards warmer climes as the climate deteriorates.

Table 12.4 was constructed to better test the southwards and westwards retreat of Neanderthals through OIS-3. It shows the percentage number of dated assemblages with Neanderthals or their Middle Palaeolithic industries in each latitudinal and longitudinal band. The results for the longitude are clearer than those for the latitude as there is a clear and progressive retreat from the east towards the west through the three time zones (Chapter 4: van Andel *et al.* 2003). The latitude analysis shows that while there is a clear northward decline with fewer sites in the north the Neanderthals manage to persist in specific areas to the last time zone. This could be explained by the northern refugium effect described above. There is some indication that the Neanderthals retreated south as the 35°^10° latitudinal band can be seen to increase though time at the expense of the 45°-50° band.

Conclusion

The larger mammals in the Stage Three Project Data Base were classified at the outset into a number of historical biogeographical categories. These categories are first based on whether the taxa are globally extinct today as opposed to extant. Within the extinct category there are two groups including taxa that became extinct towards the Glacial Maximum earlier than c 20 ka BP, and ones that became extinct around the end of the Pleistocene *c* 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 Southwest Asia. These large mammals were then subjected to two analyses to further investigate their temporal and geographical patterns during OIS-3. This led to the following main conclusions:

1. The Neanderthals are most similar to the 'interglacial survivors' in terms of their frequency and geographic distributions throughout Oxygen Isotope Stage 3.
2. The results of the analysis also suggest that the biomass declined towards the LGM.

As we hope we have demonstrated there is much merit in viewing the extinction of the Neanderthals from the perspective of an evolving biosphere with particular emphasis on their fellow mammals. An *a-priori* classification of the large mammals of OIS-3 immediately suggests that the Neanderthals belong with the megafauna that became extinct in the first part of the Late Pleistocene extinction event, known as the extinction of the 'interglacial survivors'. Historical biogeographical analyses conducted further reveal that Neanderthals decrease in numbers towards the LGM and retreat westwards and possibly southwards throughout OIS-3 (for practical purposes in this paper between 60 and 20 ka BP). This conclusion appears to support a case for the extinction of the Neanderthals, *Elephas antiquus* and *Stephanorhinus kirchbergensis* as a result of the increasingly cold global temperatures. The analysis of the other mammals yielded the unexpected result that many of the carnivores, in particular, were decreasing in numbers towards the LGM. This is further supported by evidence that the mammoth was doing likewise (Stuart *et al.* 2002), suggesting a general decrease in the environment's carrying capacity at this time. The latter adds a further layer of complexity to the argument regarding the extinction of the 'interglacial survivors', including the Neanderthals, as it may be that it was not simply cold temperatures that were to blame but a series'of ecological repercussions caused by the increasing cold of the LGM.

It should be stated that it may not be necessary to invoke a role for modern humans in the demise of the Neanderthal and that a solely climatically driven extinction mechanism may be sufficient. Neanderthals appear to be a European endemic species that 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 the 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 would term Western Eurasian continental-adapted rather than simply continental-adapted. These requisite conditions began to unravel towards the LGM, immediately before the rest of the animals that had become adapted to such dominant conditions became extinct or retreated to their present ranges at the end of the Pleistocene.

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Note

1. Stewart, J.R., M. van Kolfschoten, A. Markova & R. Musil, 2001. *Stage Three Project Mammalian Data Base.* http://www.esc.esc.cam.ac.uk/oistage3/Details/Homepage.html.

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