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Neanderthal Subsistence Behaviours in Europe

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ABSTRACT Ten years of research about the Neanderthal's subsistence behaviour are presented. The study of large mammal bones is now recognized as a means of understanding subsistence behaviour (*sensu lato*), notably by analysing acquisition and processing strategies, as well as patterns of consumption. This paper summarizes the results of an analysis of a corpus of data from several European countries, representing a total of 466 levels corresponding to 323 sites (Patou-Mathis M. 1999a. *Mémoire d'Habilitation à Diriger des Recherches*, submitted to: University Paris I. The countries involved are: France, Belgium, Germany, Poland, the Czech Republic, Slovakia, Hungary, Slovenia, Croatia, Romania, Moldavia, Ukraine and Georgia. The period of study extends from the end of the Middle Pleistocene to the beginning of the Upper Pleistocene, i.e. from isotope stage 8 to stage 3. Three different sources of data are used: bone assemblage studies by the author (reference samples); fully published zooarchaeological studies (reliable samples) and publications containing relatively detailed data about fauna (more problematical samples). The information obtained from these data sources does not have the same degree of precision.

In order to consider the full range of subsistence behaviour exhibited by Neanderthals, faunal analyses are compared to results of the analysis of lithic materials from the target regions. This comparison validates hypotheses about subsistence, site function, settlement territory, and human mobility. Copyright © 2000 John Wiley & Sons, Ltd.

Key words: Europe; Neanderthal; settlement territory; site function; subsistence

Context of the study

In order to understand Neanderthal subsistence behaviour better, the full contexts of faunal assemblages must be considered, including the geographical, topographical, sedimentological, climatic, human and cultural data available.

Geographical background and type of site

The study area extends from northern France to Georgia (Figure 1). Three main geographical zones can be drawn: low level plains; mid-level plateaux and gentle slopes, generally from 200 to 500 m above sea level; and high-level regions, mountains over 500 m above sea level. Topographic relief has influenced local climate, biotopes and, therefore, the choice of settlement area. The distribution of open-air, cave or rock-shelter sites is also dependent on local topography.

The number of sites studied varies from country to country (Table 1, Figure 2). Sites are the most numerous in Germany and Hungary and scarcer in Romania and Slovenia. This is the result of a variety of factors including: archaeological reality, happenstance, the number of publications, or taphonomic processes, particularly climato-edaphic. By correlating the number of settlement levels and the number of sites for each country (see Table 1 and Figure 2), it is apparent that sites were occupied repeatedly in the eastern part of Central Europe and Eastern Europe (where there are apparently fewer sites but more levels per site) versus sites in

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Figure 1. Geographical location of the countries considered in this work (in grey).

Table 1. Number of considered levels by country related to isotopic stages (in per cent); *n* = number of levels

	8	7	6	5e	5d–a	4	3	*n*
France	15.4	23.1	11.5	7.7	11.5	15.4	15.4	26
Belgium	3.1	0	15.6	9.4	28.1	0	43.7	32
Germany	1.6	3.2	19.3	22.6	27.4	16.1	9.7	62
Poland	0	0	6.8	9.1	40.9	20.4	22.7	44
Czech Rep.	0	6.1	12.1	21.2	15.1	9.1	36.4	33
Slovakia	0	0	0	59.4	3.1	0	37.5	32
Hungary	0	0	0	9.8	31.4	23.5	35.3	51
Croatia	0	0	0	34.6	23.1	15.4	26.9	26
Slovenia	0	0	0	12.5	43.7	6.2	37.5	16
Romania	0	0	0	13.6	4.5	27.3	54.5	22
Ukraine	0	0	0	7.1	9.5	23.8	59.5	42
Crimea	0	0	0	0	0	18.7	81.2	32
Georgia	0	0	0	4.2	12.5	22.9	60.4	48

Northwestern Europe and the northwest of Central Europe. All three geographic zones (low, mid, and highlands) were settled. However, the mid-level zone is more settled (except, perhaps, in Ukraine). Cave and open-air sites are almost equally represented in the sample (48.7 and 44.7%, respectively) while rock-shelters are scarcer (8.6%). Open-air settlements are very frequent in France, Ukraine, the Czech Republic and Germany, but are very rare in Georgia,

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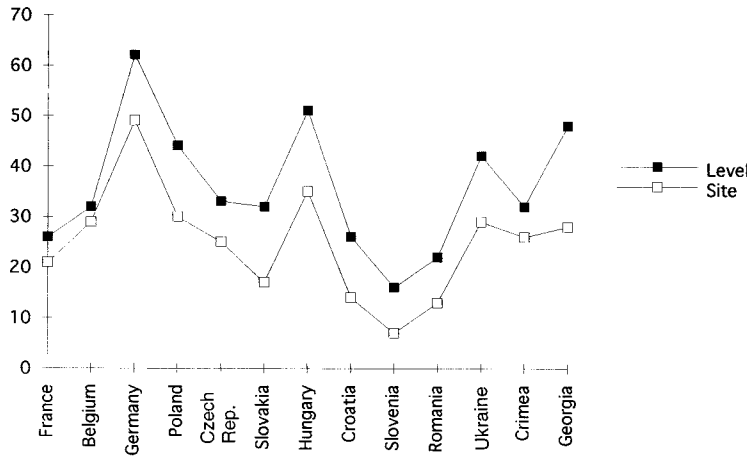

Figure 2. Number of sites and levels considered by country.

Romania, Hungary, and are almost absent in Croatia and Slovenia (Table 2). After the Eemian, cave sites predominate, especially in the First Pleniglacial (Figure 3). Likewise, during the early Glacial (stage 5d–a) and the Interpleniglacial, rock-shelters are somewhat more frequent. Obviously, the type of site is linked to the geography and topography of the region. Furthermore, certain areas must have been particularly sought after during the First Pleniglacial and the cold phases of the Interpleniglacial, because of their cave content and the role of geomorphology also must be considered.

Sedimentary and climatic background

The nature of Upper Pleistocene deposits change over time (through the glacial/interglacial, and cold/temperate climatic oscillations) and between geographic areas. The sedimentary context is mainly either loess and related sediments present at stage 6, 4 and 3 in almost all the studied countries; palaeosoils during warming phases, glacial sediments in the Carpathians, the Slovakian Tatras, and in Silesia, fluvial sediments particularly in France at stage 7 and in Moravia or travertines/limestone in karsts.

Table 2. Number of open-air sites by country, related to isotopic stages

	8	7	6	5e	5d–a	4	3	Total	%
France	2	4	3	2	3	3	4	21	100
Belgium	1	0	5	0	0	0	0	6	20.7
Germany	1	1	9	10	5	4	2	32	65.3
Poland	0	0	2	1	2	1	3	9	30
Czech Rep.	0	2	2	3	0	2	8	17	68
Slovakia	0	0	0	6	1	0	0	7	41.2
Hungary	0	0	0	1	2	0	3	6	17.1
Croatia	0	0	0	0	0	0	0	0	0
Slovenia	0	0	0	0	0	0	0	0	0
Romania	0	0	0	0	0	1	1	2	15.4
Ukraine	0	0	0	2	3	4	12	21	72.4
Crimea	0	0	0	0	0	2	5	7	26.9
Georgia	0	0	0	1	1	2	1	5	3.6
Total	4	7	21	26	17	19	39	133	

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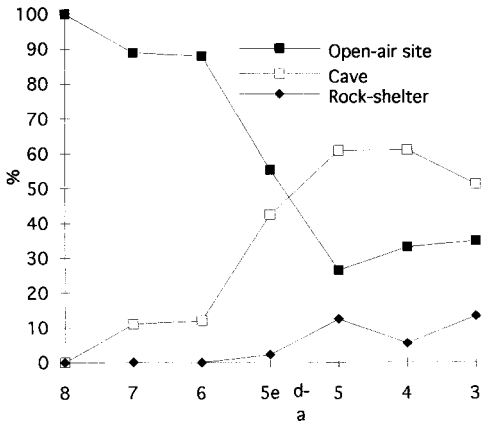

Figure 3. Nature of sites related to isotopic stages (in per cent).

There are also volcanic deposits in the middle Rhine valley. A climatic cyclic of the Upper Pleistocene affected the different areas of Central Europe at about the same time. The Scandinavian continental ice sheet covered the Great North Plain (except the Rhine) several times during this cycle. Glaciers in the highlands developed during the glacial phases.

The distribution of Middle Palaeolithic settlements seems to be quite independent from the sedimentary context, although many sites occur in karst zones. However, climate has greatly influenced the location of camp settlement. Some areas became deserted during the maximum cooling phases such as the Great Polish Plain. In other areas, only refuge zones with a favourable microclimate maintained a constant human presence.

Chronocultural background (Figure 4)

The earliest Middle Palaeolithic industries seem to have appeared at the end of isotopic stage 9 (e.g. 20″ of Achenheim, France). But they had developed fully by stage 6. Stage 6 occupations are found in Northwestern Europe, France and Belgium, and in Central Europe, Germany, Poland and the Czech Republic (Table 2, Figure 5). During the last Interglacial (Eemian, stage 5e), there were more sites in Central Europe than in Northwestern Europe and Eastern Europe. This phase is unknown in Crimea. Likewise, during the early Glacial (the period contemporary with isotopic stages 5d–5a), Eastern European sites remain scarce. Only from the First Pleniglacial does the number of sites in this area rise (Figure 5). From these observations, it can be suggested that populations moved towards the east during the first part of the last glaciation. The total number of deposits per time period (taking the duration of the period into account) increases from stage 6 to stages 5d–a, 5e, 4 and 3. During these periods, the Neanderthals became more independent from their environment. For example, despite the fact that stage 4 is a rigorous one, the number of deposits increases. The type of site also changes with time. After stage 5e, an increase in the number of cave sites is noted, compared to the previous periods (Figure 3), while rock-shelter deposits are more numerous in the early Glacial and the Interpleniglacial. The last Glacial may have prompted a search for cave shelters.

Human background: the Neanderthals

European Neanderthal populations developed very distinct anatomical features compared to the rest of the Old World. The Neanderthal's specificity and endemism in Europe is apparent as early as the middle of Middle Pleistocene. It seems to result from a geographical isolation (arising from climatic conditions) leading to genetic isolation and regional evolution from an archaic population (Vandermeersch, 1989).

There are numerous Neanderthal remains from the regions studied (Table 3). They are associated with tools of different types, from Middle Palaeolithic to early Upper Palaeolithic transition industries. More than one third of the remains are found in Interpleniglacial levels. The oldest ones date from stage 7, like the human remains from Biache-Saint-Vaast (France) and lower Ehringsdorf (Germany). The most recent ones date to the Hengelo/Les Cottés Interstadial, at Couvin (Belgium). The abundance of Neanderthal fossils in Central Europe

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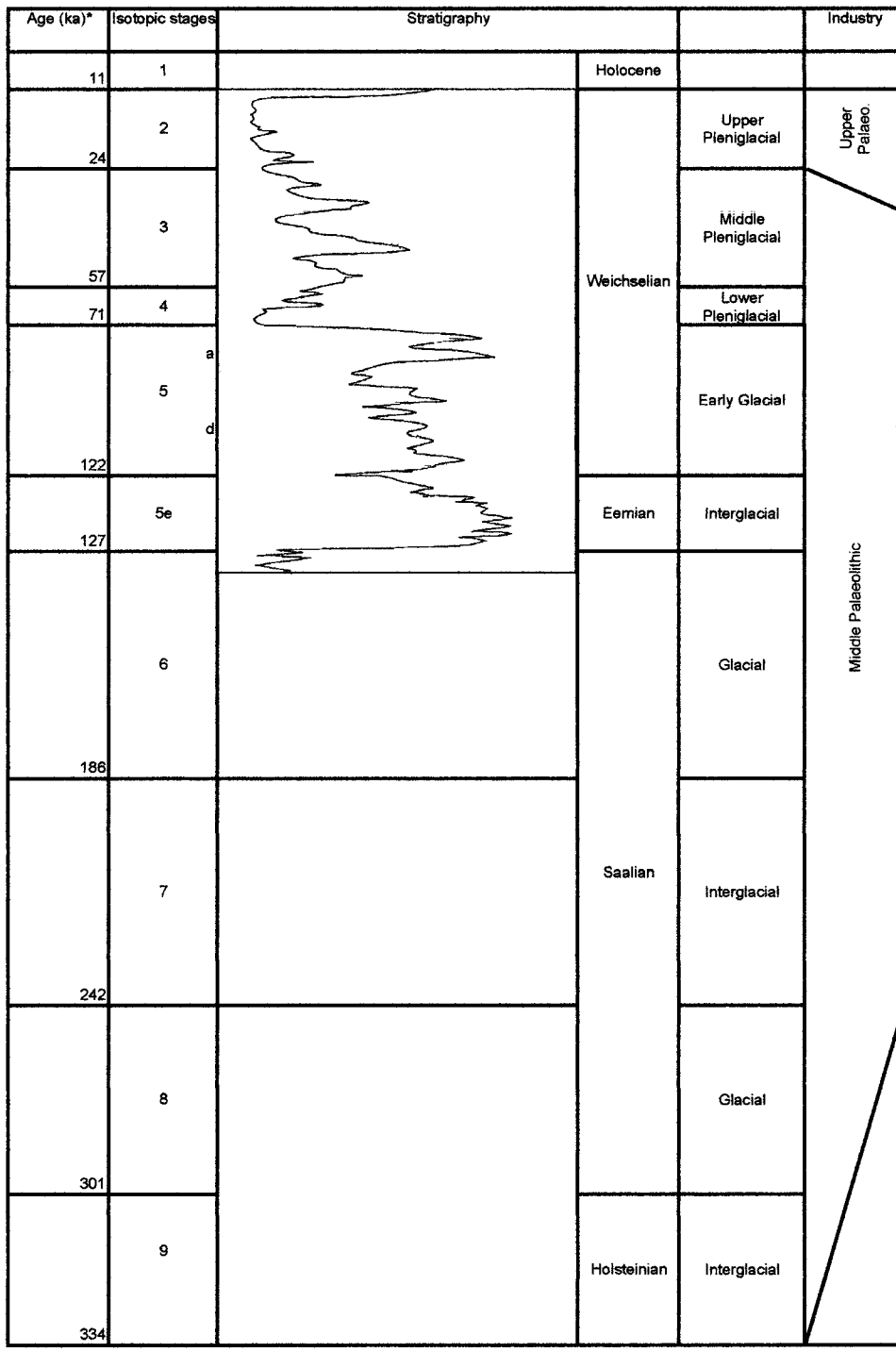

Figure 4. Chronological background of the period considered in this article (after Bassinot *et al.*, 1994).

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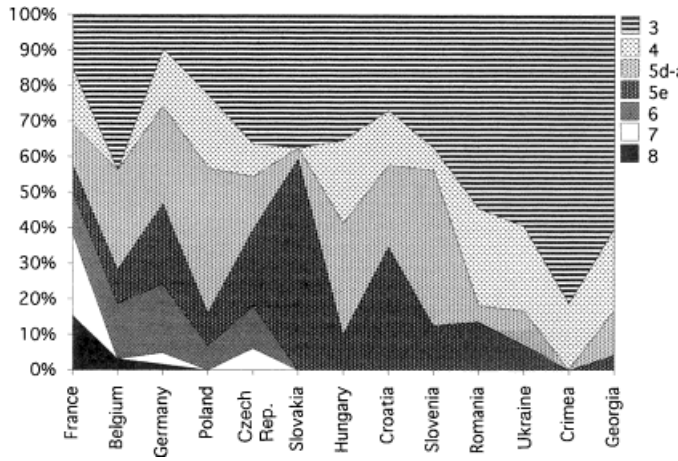

Figure 5. Variation of the number of sites, related to isotopic stages, by country.

during warmer phases, in particular the last Interglacial (Eemian), may reflect either a discontinuous population in Central and Eastern Europe, or a taphonomic phenomenon. A few human remains have been discovered in 'transition industry' levels. For example, in layer G1 (Olchevian industry) of Vindija cave, in Croatia where the Neanderthal attribution is still

Table 3. Sites which have delivered human remains attributed to Neanderthals (Mousterian)

Sites	Region	Country	Type	Industry	Period
Biache-Saint-Vaast	Pas-de-Calais	France	Open air	M. Ferrassie	7c
Trou de la Naulette	Namur	Belgium	Cave	Hors stratigraphy	5e
Spy	Namur	Belgium	Cave	'Charentien' Mousterian	3
Goyet cave IV	Namur	Belgium	Cave	M. Quina	End 3
Engis cave II	Liège	Belgium	Cave	M. Typique	3
Scladina	Namur	Belgium	Cave	Nonanthropic level	5d–a, 4, 3
Fonds-de-Forêt, cave 1	Liège	Belgium	Cave	M. Quina	3
Couvin	Namur	Belgium	Cave	M. w foliate points	End 3
Salzgitter-Lebenstedt	Basse-Saxe	Germany	Open air	Micoquian affinities	4
Lower Ehringsdorf	Thuringe	Germany	Open air	Taubachian/Micro-M.	7a
Taubach	Thuringe	Germany	Open air	Taubachian	5e, a
Stadel VIII	Bade-Wurtemburg	Germany	Cave	Moustérian	?a
Sipka (level III)	Moravia	Czech R.	Cave	Moustérian	5d–a
Svéduv stul	Moravia	Czech R.	Cave	M. Typique	5d–a
Kulna (level 7a)	Moravia	Czech R.	Cave	Micoquian	3a
Ganovce		Slovakia	Open air	Taubachian	End 5e, a
Sala		Slovakia	Open air	Hors stratigraphy	5e?
Subalyuk	Bükk Mountains	Hungary	Cave	M. Ferrassie?	3
Széléta Supérieur	Bükk Mountains	Hungary	Cave	Evolved Szélétian	3
Remete felsö (level 4)	Transdanube	Hungary	Cave	Jankovichian	3a
Krapina		Croatia	Cave	Moustérian	5e, a
Vindija (level G3)		Croatia	Cave	Moustérian	3a
Vindija (couche G1)		Croatia	Cave	Olchévian	3a
Zaskalnaya V	Crimea	Ukraine	Cave	Ak-Kaya	3
Zaskalnaya VI	Crimea	Ukraine	Cave	Ak-Kaya	3
Kiik Koba	Crimea	Ukraine	Cave	Kiik-Koba	4?
Cuckhvati	Colchide	Georgia	Cave	Moustérian	5d–a
Sakajia (levels 3B, 3D)	Colchide	Georgia	Cave	Moustérian	4a
Ortvala	Colchide	Georgia	Cave	Moustérian	3a
Lower Djruchula	Colchide	Georgia	Cave	Moustérian	4 or 3a
Barakaev	N Caucasus	Georgia	Cave	Micro-Moustérian	3?a
Mezmaï (level 3)	N Caucasus	Georgia	Cave	M. w Micoquian affinities	3

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Table 4. Main industries related to isotopic stages (in per cent); n = number of levels

Industry	8	7	6	5e	5d–a	4	3	*n*
Jungacheulean and Epi-Acheulean	0	25	50	16.6	0	0	0	12
Taubachian and Micro-Mousterian	0	2.9	0	85.3	11.8	0	0	34
Micoquian complex	1.4	0	1.4	9.8	30.9	23.9	30.9	71
Moustérien complex	0.7	2.2	5.4	9.4	20.8	17.5	43.8	274
Industries w foliate points	0	0	0	6.2	31.2	50	12.5	16
Transitional industries	0	0	0	0	0	0	100	24

controversial, (Wolpoff *et al.*, 1981; Smith & Ahern, 1994). In Hungary, they occur in layer 4 of Remete Felsö cave (Jankovichian industry) and in the upper level of Széléta cave (Szélétian industry). The 'regional continuity hypothesis', which assumes that the Neanderthals evolved into anatomically modern humans, relies on the Central European Neanderthals (Sipka, Kulna, Krapina, Vindija) who show less morphological specialization (Smith, 1982).

Though there are quite a lot of human remains that are considered as Neanderthals, they are often only represented by a few isolated anatomical elements. Burials are rare in Central and Eastern Europe. Two skeletons discovered at Spy, in Belgium, proved not to derive from a burial context. Simple graves have been discovered at Kiik-Koba in Crimea. Their rarity does not mean that the Neanderthals did not bury their dead. They may have buried the dead outside their camps.

The presence of cutmarks on broken human bones discovered at Krapina, in Croatia, has given rise to much debate, sometimes controversial (Patou-Mathis, 1997c). Some specialists support an anthropophagous practice (Smith, 1976; Ullrich, 1982). Other authors dismiss this hypothesis (Trinkaus, 1985; Russel, 1987). Following (Patou-Mathis, *ibid.*) the analyses of the bones from layers 3 and 4 of Krapina, which contain most of the human remains, suggest that the Krapina Neanderthals practised cannibalism, although whether for food or ritual purposes could not be ascertained. The small number of animal bones found in these layers supports a hypothesis of ritual cannibalism. Indeed, it is difficult to imagine that the people at Krapina would have exclusively consumed human flesh. However, the age of the archaeological excavations leads us to be careful when interpretating these data.

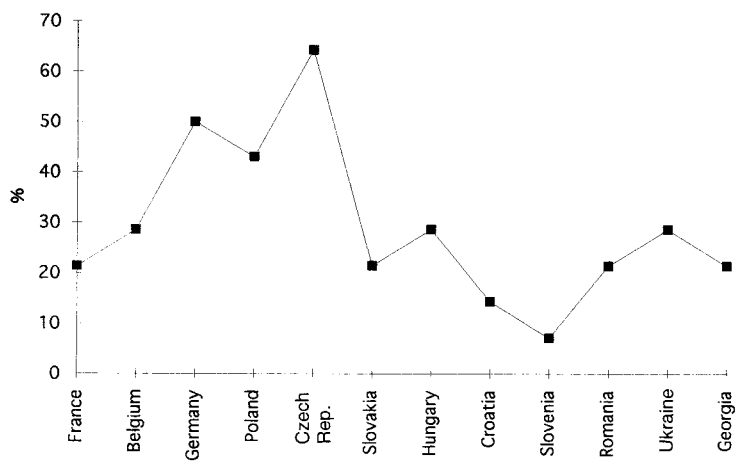

Figure 6. Variation of the number of industries by country (in per cent).

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Cultural background

Lithic industries or technocomplexes

The Middle Palaeolithic lithic industries in the study region are quite diverse (Table 4). This variability seems more important in Central Europe (Figure 6). Moustérian and Micoquian industries appear as early as stage 6, the Micoquian being mainly present in Central Europe. These two technocomplexes, chiefly discovered in the mid-level zone (on plateaux, especially the Moustérian), persist until the Interpleniglacial. Jungacheulean and Epi-acheulean industries are present from stage 7 to stage 5e. The Krumlovian (Czech Republic) is only present during the Eemian. The Babonyian (Hungary) is only present in the early Glacial. The Taubachien and/or Micro-Moustérian, present in stage 7, do not persist beyond the end of the early Glacial. These industries are mainly found in Central Europe, in low-level areas on plains. The leaf-shaped point industries are particularly abundant during the First Pleniglacial, and the 'transition' industries date to the Interpleniglacial, chiefly in mid-level areas in Central Europe. The Jankovichian (Hungary), which is mainly associated with mid-level, crater or plateau sites in Northwestern Europe or western Central Europe, appears during the last Interglacial and disappears at the end of stage 4.

It is worth noting that many of these industries are tied to specific site types, independent of climate. The majority of the Jungacheulean or Epi-acheulean are open-air sites (85%), as are the Taubachian (82%), the Krumlovian (mainly surface collections), the Bohunician, and the 'transition facies' sites, except for the Ranisien–Jerzmanowicien which seems to be linked to cave sites. The Moustérian and Micoquian complexes show a high adaptability; 65% of the former occur in caves, and 76% of the latter are either cave (45%) or rock-shelter occupations (31%).

Bone industry

A well-defined bone industry does not really exist during the study period. Only a few rare tools can attest the Neanderthal's ability to work bone. However, artefacts called retouchers have been discovered from many sites. Cervid antler collection is attested, but the reason for this practise remains controversial: were they unshaped tools, pick, pickaxes, or fences? It seems clear that animal bones were used as tools, and shaped for a non-food purpose. However, although technically capable of making bone tools, Neanderthals were uninterested in doing so for reasons which still remain unclear.

Subsistence behaviour

The study of bone materials provides evidence for strategies of game acquisition and processing, as well as evidence for the non-food use of animal products. Two levels of analysis are used: one coarse-grained, based on the presence/absence of species; the other a more precise, quantitative approach to the data. For each geographical area, period, climate and associated industry, we have established the following for the various taxa encountered: their diversity, frequency, relative abundance and relationship with the biotopes (Patou-Mathis, 1999a).

The presence of large predators, such as cave hyena, in many sites requires us to take their presence/absence into account at all sites. The frequency of occurrence of cave hyena varies with time (Figure 7). It is proportionally more abundant during the early Glacial (63.6% of the studied sites) and rarer during the Eemian (17.8%). Though its presence is often recorded from sites, the caves were rarely used as dens (12 sites only were also den sites; Figure 7). Whatever the period considered, the presence of large carnivores notably cave hyena, correlates with an increase in the number of herbivore species present (Figure 8). This shows why a preliminary taphonomic study of the assemblages is needed before palaeoethnographic analysis can proceed.

From the early glacial to the end of the Interpleniglacial, the following faunal association is the best represented: red deer (*Cervus elaphus*); horse (*Equus* sp.); wooly rhinoceros (*Coelodonta antiquitatis*); mammoth (*Mammuthus primigenius*); reindeer (*Rangifer tarandus*) and bison (*Bison priscus*). These are mainly large species

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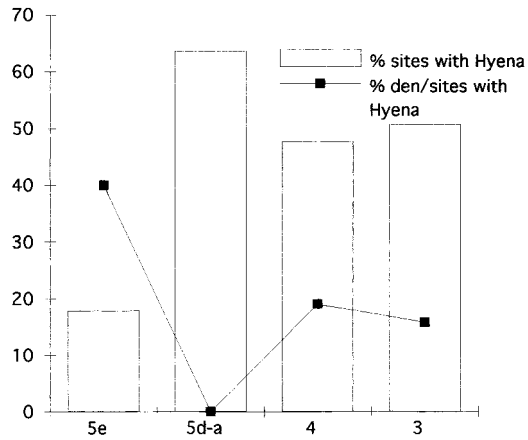

Figure 7. Variation of the frequency of the cave Hyena related to isotopic stages (in per cent).

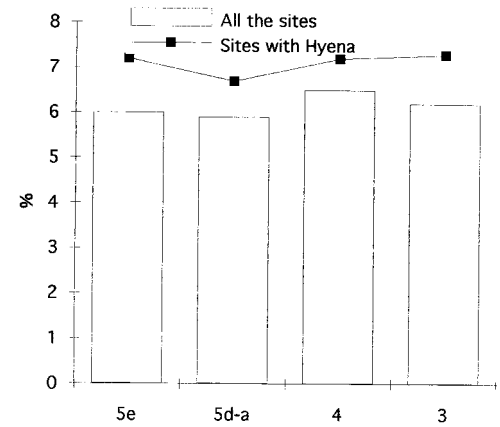

Figure 8. Comparison between the average numbers of herbivore taxa in all sites and of the cave Hyena in those where it appear, related to isotopic stages (in per cent).

typical of steppic or grassland (open) environments, and they live under quite cold climates and migrate seasonally. Only during the Eemian period are the forest taxa better represented. The hippopotamus (*Hippopotamus* sp.) disappears from the faunal spectra during stage 6, *Paleoxondonta antiquus* disappears during stages 5d–a and the Merck's rhinoceros (*Dicerorhinus mercki*) drops out at stage 4 (Table 5). Reindeer (*R. tarandus*) appears at stage 6, ibex and chamois (*Capra ibex* and *Capreolus capreolus*) at stage 5e, musk-ox (*Ovibos moschatus*) and saiga antelope (*Saiga tatarica*) stages 5d–a, and mouflon at stage 4 (Table 5).

There is a predominance of assemblages dominated by single (primary) species, or by a cohort of two or three species in some levels (Table 6). The species numbering at least twice the number of remains of the next most abundant taxa is the 'primary' prey species, the other taxa are termed 'secondary'. Horse is the Neanderthal's preferred game except in Eastern Europe. In some levels, the abundance of megafauna, such as woolly rhinoceros and mammoth, raises a question about the mode of acquisition: i.e. hunting or scavenging. Globally, the number of levels where a single species dominates decreases from stage 5e to stage 3. The single-taxon dominated assemblages occur in cave or rock-shelters (61.5%). They are also more numerous during the temperate fluctuations. Specialized hunting appears quite frequent, therefore, especially in Western Europe and in the northern part of Central Europe (Germany and Poland), as early as stage 7. Between six and eight species tend to be the focus of these specialized hunts, chiefly horse (in particular from the early Glacial), and, to a smaller extent, mammoth, red deer, bison, ibex, Merck's rhinoceros (especially during the Eemian) and reindeer. These dominant species are mainly large, gregarious, and migratory. They are also, except for the red deer and Merck's rhinoceros, typical of cold climates and open environments. In some deposits from Eastern Europe, hunting seems 'over-specialized' (more than 90% of the bone remains belong to a single taxon), with either *Equus hydruntinus* or the saiga antelope dominating such assemblages in Crimea, while ibex dominates in the Caucasus.

The main species exploited by humans can be divided according to ecological groups belonging to: steep and rocky ground, forest, semi-open forest edge and open environments. It is noted (Table 7 and Figure 9) that, from stage 5e to stage 4, all these biotopes are exploited. Open environment species predominate, however, except during stages 7 and 5e.

The steep/rocky ground taxa are well represented during stages 3 and 5d–a, but they do not dominate during stages 7 and 6. This latter result is linked to the fact that sites from the old phase of Middle Palaeolithic are not located in this biotope. These observations confirm that

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Table 5. Representation of herbivore taxa related to isotopic stages (in per cent)

	7	6	5c	5d–a	4	3
Hippopotamus sp.	28.5	0	0	0	0	0
Palaeoloxodon antiquus	71.5	0	22.5	0	0	0
Mammuthus primigenius	0	60	22.5	51	58	62
Coelodonta antiquitatis	14.5	80	26	52.5	64.5	56
Dicerorhinus mercki	86	0	39	11.5	9	2.5
Dicerorhinus hemitoechus	51.5	0	3.5	3.5	0	0
Equus (*caballus*)	100	100	61.5	72.5	69.5	66
Equus hydruntinus	51.5	30	16.5	15	24	29
Bison priscus	28.5	50	34.5	44.5	51	64.5
Bos primigenius	43	20	19.5	26.5	15.5	16.5
Cervus elaphus	100	80	81.5	64	78	67.5
Rangifer tarandus	0	70	10	47.5	52.5	52
Megaloceros giganteus	71.5	40	29	46	42.5	39.5
Alces alces	14.5	0	19.5	11.5	13.5	5
Dama dama	14.5	0	26	6.5	2.5	0
Capreolus capreolus	71.5	0	35.5	23	18	16.5
Ovis sp.	0	0	0	0	11.5	11
Capra ibex	0	0	19.5	33	33.5	30
Rupicapra rupicapra	0	0	6.5	24.5	29	20.5
Saiga tatarica	0	0	0	5	20	26.5
Ovibos moschatus	0	0	0	3.5	2.5	2.5
Sus scrofa	43	10	26	15	24.5	28

Table 6. Number of levels where one, two or three species are dominant, related to isotopic stages (in per cent)

Dominance	7	6	5e	5d–a	4	3
One species	28.6	36.4	50	46	36	30.8
Two species	28.6	20	9.5	23	16	24.7
Three species	14.3	20	9.5	11.5	22	9.2
One, two or three species	71.5	76.5	69	80.5	74	62.5

open environment species were preferentially hunted.

Hunting strategies

After determining which species comprised the Neanderthal's subsistence base (that is, which taxa were dominant, or 'primary') and, by implication, the proportional representation of so-called secondary species as well as patterns of game exploitation according to the environment, we can deal with the Neanderthal's hunting strategies. As direct evidence of hunting techniques during the Middle Palaeolithic is rare, zooarchaeological studies are the main way to look for it. Quantitative and qualitative faunalanalyses, together with eco-ethological data about game and environment, provide us with the data with which to develop hypotheses. Published zooarchaeological studies for 34 deposits for which we are given precise information, combined with the previous results of the above study enable us to bring to the fore the acquisition strategies implemented by Middle Palaeolithic people in Europe. The reference deposits used in this research come from a corpus of data which the author previously compiled (Patou-Mathis, 1999a).

The Neanderthals selectively hunted two or three primary species as early as stage 7. Specialized hunts seem to decrease from the Eemian to the end of the Interpleniglacial. They are more frequent in Western Europe, in Germany and Poland than anywhere else in Europe, and tend to be represented in cave and rock-shelter sites, which are often used as hunting stations. For this latter type and for the hyperspecialized hunt, the site function is the deciding factor killing (for example, killing and/or butchering

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Table 7. Relative percentages of different biotopes, depending on herbivore taxa, related to isotopic stages

Environment	7	6	5e	5d–a	4	3
Forested	60	0	36.3	18.2	25	23.1
Semi-open	20	16.7	18.2	18.2	16.6	0
Open	20	83.3	36.3	45.5	50	53.8
Broken relief	0	0	9.1	18.2	8.3	23.1

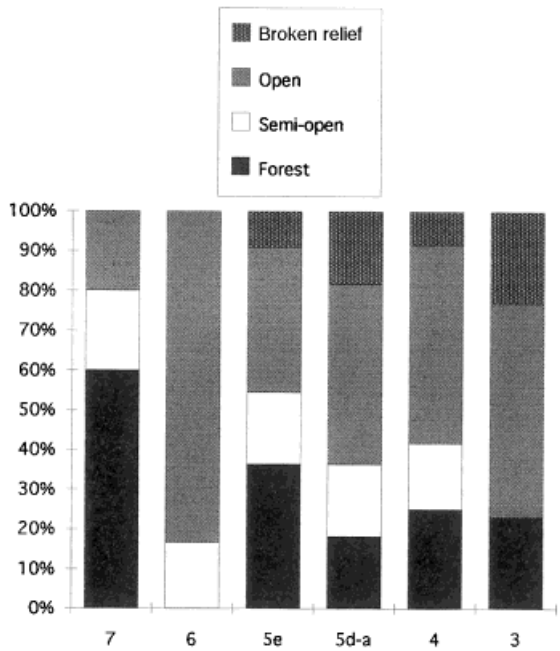

Figure 9. Relative percentages of different biotopes related to isotopic stages.

sites). Less specialized assemblages, based on small game, or hyperspecialized single-taxa ones are clearly not as common.

Neanderthals practised selective hunting according to the age and/or sex of prey as early as stage 7. For very big species, like the rhinoceros, very young or old individuals were selected. Gravid females were also hunted. Mature adults of large species, such as the horse and bison, are also sometimes hunted. This shows a certain skill in hunting.

The Neanderthals were apparently not constrained by the size or weight of the animal. On the contrary, as mentioned above, large species were often preferentially chosen. However, this criterion was an important factor in carcass transport decisions. In most cases, large prey was dismembered at the kill location, and carried to camp in pieces.

As early as the old phase of the Middle Palaeolithic, hunting of herds was frequently practised by the Neanderthals. However, they also hunted lone animals as early as stage 7. Once again, the hunting skills of these prehistoric people are apparent. Migrating species are hunted seasonally (Auguste, 1995). The Neanderthals even sometimes set up their camps on the migration routes of these animals (Locht & Patou-Mathis, 1998). But more sedentary prey were also hunted during this period.

The hunting of rarer species (rarity is defined based on the ratio of expected species rank/observed species rank) testifies to the independence of the Neanderthals from their environment. It also testifies especially to the existence of choices based on their hunting skill and/or cultural choices, and not only on the availability of prey in their environment.

At some sites, two different killing seasons are noted in some levels, either for one single species, e.g. horse at Unchesberg, site 1, layer B, (Conard, 1992, 1998) or reindeer at Kulna (Valoch, 1988), or for different species (for example, at Biache-Saint-Vaast, and at Tönchesberg, site 1, layer A (*op. cit.*). Two hypotheses may be proposed for this pattern. Either people lived in the site during the whole year, and practised selective hunts according to the season; or they occupied sites during two different season and the archaeological levels are palimpsests if this is the case). Indeed, sites are often repeatedly occupied, making the season(s) of occupation difficult to determine. Hunting occurs during every season, however, reindeer seems to have been preferentially hunted during spring and autumn (their migration times), and the sedentary species were hunted more in winter. Once again, this practise seems to be independent from the region, chronological period, climate, environment or the associated industry. The rarity of sites where evidence of seasonal hunting is identified is probably the result of a lack of full archaeozoological analysis. Where these analyses exist, seasonal hunting is systematically brought to the fore. If this were confirmed, the hypothesized high mobility of the

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Neanderthals would also be confirmed (Geneste, 1989).

In summary, therefore, the Neanderthals sometimes selected their game according to the animal's age, sex and ethology. Likewise, they hunted some species according to the season. Furthermore, during the whole Middle Palaeolithic, the Neanderthals collected pieces from fresh complete carcasses that predators and scavengers had not damaged (quick access to animals probably 'naturally' dead), as well as from carcasses ravaged by other carnivores (late access, low meat-value elements) — especially in the case of big species such as proboscideans and rhinoceros. However, the discovery of Lehringen testifies to the Neanderthal's active participation in obtaining these big species (Thieme & Veil, 1985).

Food processing

The different ways of preparing meat influences bone preservation. The animal provides a variety of resources, alimentary or not. By thoroughly studying the butchery marks (their repetition, orientation and localization on the bone, the length, width and depth of the trauma observed; the morphology and morphometry of the percussion impacts) we can discover the main technical steps of the processing of game (Patou-Mathis, 1997a,b). But, for a good analysis of these marks, the agent responsible for the observed trauma (the taphonomic filter) must be identified. Butchery activities must be differentiated from other modifications made to bones resulting from bacteria or animals. Furthermore, in most butchery contexts, the spatial organization of the bone remains is not contingent and can be linked to processing techniques (Locht & Patou-Mathis, 1998).

Underlining the treatment of various prey is very important in order to understand subsistence because it is a strong cultural index (Noe-Nygaard, 1977). As early as stage 7, Middle Palaeolithic people have almost systematically picked up meat, fat and long bone marrow. The processing of game can be understood as a series of steps (or 'chaîne opératoire'), logically linked according to the animal's anatomy and to the relative availability of prey; (Patou-Mathis, 1995–1996, 1996, 1999a). The associated industry does not seem to be correlated with the processing. Further more, the Neanderthals knew how to manage shortage, especially during the Pleniglacial, by adapting their game acquisition and processing strategies. For example, they set their camps up at favourable spots, selecting prey, maximally exploiting them and probably practising time-limited 'storage' (seasonal reserves, Locht & Patou-Mathis, *ibid.*). Direct evidence of cooking remains are rare. Only indirect evidence testifies to the utilization of fire to cook meat, or even to smoke it, for example, at Beauvais (Locht & Patou-Mathis, *ibid.*).

Non-food use of bone and antler

From stage 7, there is evidence that Neanderthals killed animals not only for their meat and fat, but also for their skin. Ligaments and tendons were also harvested (Patou-Mathis, 1997d). The fur from some carnivores, such as brown bear, wolf, and fox, may have been the main motivation for hunting these taxa, for example, at Mutzig I (Patou-Mathis, 1997d). Bones have also been used as fuel, tools, containers, work supports (chopping 'block', such as the innominate of a young Merck's rhinoceros discovered at Krapina, Croatia, Patou-Mathis, 1997c) and maybe as an artistic medium (engraved and painted mammoth scapula at Molodova I, layer 2, in Ukraine, Leroi-Gourhan, 1988) and possibly as an architectural material, particularly in open-air sites (Paunescu, 1989).

During the Pleniglacial and the Interpleniglacial, Neanderthals used bone as fuel, at Beauvais, at Le Trou du Diable and Engilhoul (Belgium; Ulrix-Closset, 1975) and at Kabasi V (Crimea; Burke, 1999). They made choices among the bone material at their disposal, presumably preferring elements best adapted to alternate uses.

As already mentioned, there is very little in the way of bone or antler industry in the Middle Palaeolithic — it really developed only in the Upper Palaeolithic. However, a few examples testify to the use of bone for making

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scrapers and points. Retouched bone fragments have been found in Germany, Belgium, Hungary, the Czech Republic, Romania, Ukraine and Georgia. Red deer antler accumulations, without any apparent signs of use, occur at Tönchesberg 2B in Germany (Conard, 1998). The carving of large ungulate innominates to preserve the cotyloid cavity, which could be used as a 'pot', is attested in Belgium (Ulrix-Closset, *ibid*.). The Lovas site, in Hungary, is particularly interesting. Discovered in 1951, the site consists of two natural cavities filled with 'limonite' and haematite, containing graves with more than one hundred bone and Moose antler tools (Dobosi & Voros, 1978). About 150 kg of pigment are estimated to have been extracted from the site, which may be a single archaeological layer (Gabori-Csank, 1993). Besides bones and moose antlers used as 'picks', a cylindrical bone spear point, with a double-bevelled base, and a polished awl (made from a moose metatarsal), have also been identified (Gabori-Csank, *ibid*.). But, a few sites aside, Middle Palaeolithic bone 'tools' consist mainly of retouchers.

The Neanderthals probably used large bones, in particular those of mammoth, as dwelling frames. This appears in the areas where rock-shelters are rare on the great plains, in earlier times (as soon as stage 6), particularly when climatic conditions were harsh. There are few grounds for suggesting that these pachyderms would have been hunted, however. Bones would more likely be taken from carcasses already in an advanced state of decay or even already fossilized.

Site function

We know that prehistoric people chose their sites according to different factors: view, water proximity, availability of wood, game or lithic availability, biotope diversity, protection, aspect and available area. In some prehistoric deposits (caves in particular), it is difficult to differentiate between occupations and to determine their duration, however. Knowing the mode of subsistence allows us to attempt this.

By the Middle Palaeolithic, there is considerable variability among the open-air sites. Several types of site have been defined: base camps, Biache-Saint-Vaast in France (Auguste, 1995); transit or seasonal camps, Mutzig in France (Patou-Mathis, 1997d); hunting stations, Sclayn in Belgium (Patou-Mathis, 1998) and Beauvais-La Justice in France (Locht & Patou-Mathis, 1998); killing (or 'scavenging') and butchering sites, Zwolen in Poland (Gautier, 1989), Lehringen in Germany (Thieme & Veil, 1985) and Kabazi II in Crimea (Patou-Mathis, 1999b); lithic extraction sites, Boritov V in the Czech Republic (Valoch, 1996), and pigment extraction mines such as Lovas in Hungary (Dobosi & Voros, 1978).

The presence of shelter (especially from the First Pleniglacial) and microenvironments, with a favourable climate and varied biotopes are all factors which played a big part in the choice of site location. With some exceptions, the proximity of lithic deposits does not seem to have been a deciding factor. The diversity of site types underlines how well the Neanderthals knew the available resources in their environment and managed them according to their needs. Furthermore, the relative rarity of base camps, compared to temporary camps, confirms the hypothesis of logistical mobility (Binford, 1980).

Intra-site spatial organization

Few actual dwellings are found during the Middle Paleolithic. It is true that many deposits of the time are caves or rock-shelters, and this could provide a partial explanation of this fact. Domestic space seems to be relatively organized during the more recent stages of the Middle Palaeolithic, however. Zones with specific activities such as cutting, butchering and cooking, have been identified during excavation or using spatial analyses, for example, at Biache-Saint-Vaast and at Beauvais in France, at Tönchesberg 2B in Germany and at Kulna in the Czech Republic. Lithic reduction areas have been identified at various sites, such as at Betalov Spodmol in Slovenia (Montet-White, 1996). At Kiik-Koba rock-shelter in Crimea (Chabaï *et al*.,

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1995), five excavated pits correspond to storage pits, according to the excavators, possibly for meat stores.

Other built structures are rare, except for evidence of hearths, mostly poorly constructed but attested by the presence of burned bones and stones, ashes, charcoal or bone charcoal. These occur, for example, at Beauvais in France, (Locht & Patou-Mathis, 1998); at Le Trou du Diable and at Sclayn (layer 5) in Belgium (Patou-Mathis, 1998); Töchensberg 2B and Wallertheim A in Germany (Conard, 1992, 1998); at Piekary II, Skaratki and Raj (layer 4) in Poland (Kozlowski & Kozlowski, 1996), at Krapina in Croatia (Patou-Mathis, 1997c) and at Kabazi V in Crimea (Burke, 1999). The rare contructed hearths are simple pits, like in Belgium at Engihoul (2nd level) and at Le Trou du Diable; at Becov I in the Czech Republic (Valoch, 1996); at Parska Golobina (layer 6), Divje Babe I (layers 5 and 6) and Betalov Spodmol (layer 12-III-B) in Slovenia (Montet-White, 1996) and at Ripiceni Izvor in Romania (Paunescu, 1989). At Engihoul (1st level) in Belgium, the bottom which was 2 m^2 wide was covered with 'psammit' tablets (Ulrix-Closset, 1975). In Sipka cave, in the Czech Republic, a Neanderthal child's mandible was discovered mixed with charcoal, in an ash layer next to a hearth (Valoch, 1996). At the Krakow-Zwierzyniec site, in Poland, four hearths were located around a mammoth molar with a cupola-like oven above them. The excavators suggest that this structure was used for smoking meat (Kozlowski & Kozlowski, 1996).

A few dwelling structures have been discovered, for example, at the Mutzig site (Bas-Rhin, France, Patou-Mathis, 1997d) and in Raj cave (layer 6) in Poland (Kozlowski & Kozlowski, 1996). The oldest dwelling structure, dating from stage 7, seems to be the open-air site Becov I (level A-III C6) in the Czech Republic (Valoch, 1996). More recent structures have been discovered at Ariendorf in Germany (Bosinski *et al.*, 1983), at Dzierzyslaw (site 1), in Poland (Kozlowski & Kozlowski, 1996). Open-air sites, from stage 4 and 3, such as Ripiceni Izvor (levels I, IV and V) in Romania (Paunescu, 1989), Ketrosy (2nd accumulation), Molodova I (layers 4 and 2) and Molodova V (layer 12) in Ukraine (Anissutkine, 1990), offer proof of how bones, (in particular the mammoth bones) were used as tent frames.

Territory and mobility

The following hypotheses are advanced. The Neanderthals organised themselves into hunting territories containing sources of both meat and lithic resources. As early as stage 7 of the Middle Palaeolithic, territories were differentially settled according to their biotope and topography, and this trend increased during the more recent phases of this period. Whole groups or parties of a few hunters, moved according to season, choosing to camp in places known to provide food since fauna of local origin is consumed. Hunters were very mobile in these territories and many sites were temporary camps or hunting stations, for example, at Jankovichian and Szeletian sites along the Rhine. Furthermore, the Neanderthals intercepted migrating game as at Beauvais). The existence of high mobility within a wide territory that is itself socially defined, is supported by studies of lithic material (Féblot-Augustins, 1997). This type of mobility corresponds to the definition of logistical organization (Binford, 1980). This is supported by the existence of some multiple-occupation base camps and a network of specialized camps, such as temporary seasonal camps and hunting stations. Movements appear multidirectional, in a radial or star pattern (Féblot-Augustins, *ibid.*). However, for unknown reasons (possibly because of local resource shortages), groups seem to have changed their territory. During the early Glacial and especially during the first Pleniglacial, quite important population movements are noted in Eastern Europe (Figure 5).

Conclusion

By the first stages of the Middle Palaeolithic, Prehistoric people had mastered diverse techniques for acquiring meat. Very few sites show evidence of opportunistic hunting only; the exclusive consumption of small game and

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'scavenged' remains does not exist during the Middle Palaeolithic in the study regions. While Neanderthals practised different synergetic modes, they preferentially hunted two or three species, or specialized in a single species. In many cases, hunted species are large or medium sized, gregarious, migratory and inhabit open grassland or steppe regions. In the case of specialized hunting, the species chosen were abundant around the site, which typically consisted of a hunting station or temporary camp.

Moreover, this degree of hunting specialization seems more frequent during temperate phases or maximum cold phases. Animals are often selectively killed according to their age, sex, size and ethology. This is a testament to the hunting skills of Neanderthals. Species rare in the environment, smaller and less 'profitable' species, or those difficult to hunt are sometimes preferred. This may indicate that cultural traditions also influenced the choice of prey.

Due to their rudimentary weaponry, the Neanderthals had to elaborate their hunting strategies. Very early on, selecting the appropriate fit between prey and predation strategy (choice of hunting method and/or weapon) will have been a real survival issue. However, faunal assemblages with identical species composition are associated with different tools. Furthermore, the adaptation of subsistence strategies according to the environment or climate is not clearly testified. The Neanderthals exploited all available biotopes, irrespective of the climatic period; this testifies to their independence from the environment. Particular geomorphological features, such as sinkholes, precipices, box canyons or swamps have favoured the development of certain meat acquisition strategies, however. Natural traps were probable sources of rhinoceros and mammoth, either hunted or, more likely, scavenged.

Proof of 'scavenging' by Neanderthals has been clearly established, in particular from big species. Although it is more frequent in modern humans, this behaviour is not an indicator of primitiveness, nor is it a chronological indicator. The Neanderthals knew how to manage the 'shortage' periods (climatic crises), by modifying their game acquisition and treatment strategies. Indeed, during these periods, the faunal spectrum is more diversified, both sexes, including gravid females, and all ages are represented with a relative lack of young individuals, however, whose meat is too lean. Seasonality is not so marked, animals can originate far from the place of consumption and bone is very fragmentary, testifying to heavy exploitation of carcasses.

Neanderthals clearly considered animals as sets of resource, both food and non-food. The animal was skinned, dismembered, disarticulated and filleted according to processing behaviours similar to those documented for the Upper Palaeolithic. The harvesting of skin, tendons, and bones is testified as early as the old phase of the Middle Palaeolithic. Contrary to what is noticed in the Upper Palaeolithic, however, the collection and use of antler and bone for tool making is less frequent. Wood may have been used instead of bone, as testified by use-wear analyses.

The Neanderthals settled their territory mainly according to the presence of game. Territories become more organized over time during the Middle Palaeolithic. Neanderthals appear to have been very mobile, adopting a logistical and multidirectional type of mobility. Seasonal hunting and recurring patterns of site occupation underlines the mobility of the Neanderthal's settlement systems in large hunting territories. They would set up numerous temporary camps and many sites correspond to temporary hunting stations. Plateaux and nearby slopes as well as caves are clearly favourable microenvironments, during cold phases, when they are preferentially chosen camp sites. Even if traces of dwellings and built hearths are rare, the organization of domestic space appears very early on.

Meat supplying does not uniformly evolve over time, rather, different acquisition strategies appear simultaneously. The Neanderthals subsistence behaviour seems to be relatively independent from geography, climate, biotope and associated industry. But the striking point, compared to previous periods, is the development of hunting, which leads to real disruptions in social organization. Hunting requires theoretical and practical knowledge, experience and teaching; it builds traditions, creates memory, and structures society by particularly increasing social

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cohesion and co-operation. Implementing strategies, planning and managing the daily diet requires complex thinking, cognitive abilities, and social organization, all of which the Neanderthals apparently knew how to acquire and develop. This original synthesis of data from many sites, distributed in a wide geographical area, gaining a better knowledge of the European Neanderthal's subsistence behaviour. The behavioural hypotheses, based upon the zooarchaeological analysis, will hopefully be tested against data resulting from other fields.

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References

Anissutkine NK. 1990. Le Moustérien du Sud-Ouest de l'URSS. Paris. *L'Anthropologie* **94**(4): 713–738.

Auguste P. 1995. Cadres biostratigraphique et paléoécologique du peuplement humain de la France septentrionale durant le Pléistocéne. Apports de l'étude paléontologique des grands mamifères de Biache-Saint-Vaast (Pas-de-Calais). Thèse de 3ème cycle du MNHN, 2 vol. de text, Paris, 724 p.

Bassinot FC, *et al*. 1994. The astronomical theory of climate and the age of the Brunhes–Matuyama magnetic reversal. *EPSL* **126**: 91–108.

Binford LR. 1980. Willow smoke and dog's tails: hunter–gatherer settlement system and archaeological site formation. *American Antiquity* **45**: 1–17.

Bosinski G, Brunnacker K, Turner E. 1983. Ein siedlungsbefund des FrŸhen Mittelpalõlithikums von Ariendorf, Kr Neuwied. *Archõlogisches Korrespondenzblatt* **13**: 157–169.

Burke A. 1999. Kabazi V: faunal exploitation at a Middle Paleolithic rockshelter in Western Crimea. In *The Middle Paleolithic of Western Crimea*, vol. 2, Chabaï VP, Monigal K (eds). ERAUL 87: Liège; 29–39.

Chabaï V, Marks AE, Yevtushenko A. 1995. Views of the Crimea Middle Paleolithic past and present. *Liège, Préhistoire Européenne* **7**: 59–80.

Conard N. 1992. *Tönchesberg and its position in the Paleolithic prehistory of Northern Europe*. Rõmisch-Germanisches Zentralmuseum, Band 20: Bonn; 176.

Conard N. 1998. Middle Paleolithic settlement in the Rhineland. In *Actes du XIIème Congrès IUSPP*, Forli, Septembre 1996, Vol. 6, Tome I; 255–268.

Dobosi V, Voros I. 1978. Data to an evaluation of finds assemblage of the Palaeolithic mine at Lovas. *Folia arch*. **XXX**.

Féblot-Augustins J. 1997. *La circulation des matières premières au Paléolithique*, vol. 2. ERAUL 75: Liège; 275.

Gabori-Csank V. 1993. *Le Jankovichien: une civilisation paléolithique en Hongrie*. ERAUL 53: Liège; 198.

Gautier A. 1989. Preliminary notes on the fauna of the middle Palaeolithic site at Zwolen (Poland). Liége. In *L'Homme de Néandertal. La Subsistance*, vol. 6, Otte M (ed.). ERAUL 33: Liège; 69–73.

Geneste J-M. 1989. Economie des ressources lithiques dans le Moustèrien du Sud-Ouest de la France. In *L'Homme de Néandertal. La Subsistance*, vol. 6, Otte M (ed.). ERAUL 33: Liège; 75–97.

Kozlowski JK, Kozlowski SK. 1996. Le Paléolithique en Pologne. In *Collection L'Homme des origines, Série Préhistoire d'Europe*, vol. 2, Jérôme Millon (ed.). Grenoble; 239.

Leroi-Gourhan A (sous la dir. de). 1988. *Dictionnaire de la Préhistoire*. PUF Ed.: Paris; 1222.

Locht J-L, Patou-Mathis M. 1998. Activité spécifiques pratiquées par les Néandertaliens: le site de 'La Justice', Beauvais (Oise, France). In *Actes du XIIème Congrès IUSPP*, Forli, Septembre 1996, Vol. 2; 165–187.

Montet-White A. 1996. Le Paléolithique en ancienne Yougoslavie. In *Collection L'Homme des origines, Série Préhistoire d'Europe*, vol. 4, Jérôme Millon (ed.). Grenoble; 268.

Noe-Nygaard N. 1977. Butchering and marrow fracturing as a taphonomic factor in archaeological deposits. *Paleobiology* **3**: 218–237.

Patou-Mathis M. 1995–1996. Stress biologiques et comportements de subsistance au Paléolithique moyen et au Paléolithique supérieur en Europe. In *Nature et Culture*. Actes du Colloque International de Liège, Décembre 1993, Etude et Recherche archéologique de l'Université de Liège, 68; 445–452.

Patou-Mathis M. 1996. Techniques d'acquisition et de traitement des grands mammifères par les Néandertaliens européens: exemples de 'chaînes opératoires. Actes du Colloque: Reduction processes for the European mousterian, Rome, Mai 1995. *Rome, Quaternaria nova* **VI**: 187–203.

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Patou-Mathis M. 1997a. Etude de la fracturation des os longs de Renne; méthode et résultats: le niveau Magdalénien 'archaïque' de la grotte Tournal à Bize (Aude). In *Proceeding of 1993 Bone Modification Conference*, Hot Springs, South Dakota, USA, The Eighth International Meeting of Working Group 1 on Bone Modification (M. Patou-Mathis Resp). Augustana College, Sioux Falls, SD, Hannus LA, Rossum L, Winham RP (eds). Occasional Publication No. 1, Archeology Laboratory; 195–219.

Patou-Mathis M. 1997b. Les marques de boucherie au Paléolithique. *Toulouse, Revue de Médecine Vétérinaire* **148**(12): 959–968.

Patou-Mathis M. 1997c. Analyses taphonomique et palethnographique du matériel osseux de Krapina (Croatie): nouvelles données sur la faune et les restes humains. *Liège, Préhistoire Européenne* **10**: 63–90.

Patou-Mathis M. 1997d. Les grands mammifères de la couche 5 de Mutzig I (Bas-Rhin). La subsistance au Paléolithique moyen en Alsace, Actes du 7éme Congrès ICAZ, Constance, 1994, Paris. *Anthropozoologica* **25–26**: 363–374.

Patou-Mathis M. 1998. Les espèces chassées et consommées par l'Homme en C5. In *La Grotte Scladina: L'Archiologie*, vol. 2. ERAUL 79: Liège; 297–310.

Patou-Mathis M. 1999a. Mémoire d'Habilitation à Diriger des Recherches, Université Paris I, in press.

Patou-Mathis M. 1999b. Archeozoologie analysis of the middle Paleolithic fauna from selected levels of Kabazi II. In *The Middle Paleolithic of Western Crimea*, vol. 2, Chabaï VP, Monigal K (eds). ERAUL 87: Liège; 41–74.

Paunescu A. 1989. Structures d'habitat moustériennes mises auj our dans l'établissement de Ripiceni-Izvor (Roumanie) et quelques considérations concernant le type d'habitat Paléolithique moyen de l'Est des Carpates. In *L'Homme de Néandertal: La Subsistance*, vol. 6, Otte M (ed.). ERAUL 33: Liège; 127–143.

Russel MD. 1987. Mortuary practices at the Krapina Neandertal site. *American Journal of Physical Anthropology* **72**: 381–397.

Smith FH. 1976. The Neandertal remains from Krapina: a descriptive and comparative study. In *Report of Investigations*, vol. 15. University of Tennessee: Knoxville; 329.

Smith FH. 1982. Upper Pleistocene Hominid evolution in South-Central Europe a review of evidence and an analysis of trends. *Current Anthropology* **23**: 667–703.

Smith FH, Ahern JC. 1994. Brief communication: additional cranial remains from Vindija Cave, Croatia. *American Journal of Physical Anthropology* **93**: 275–285.

Thieme H, Veil S. 1985. Neue untersuchungen zum eemzeitlichen Elefanten Jagdplatz Lehringen, Ldkr. Verden. *Die Kunde NF* **36**: 11–58.

Trinkaus E. 1985. Cannibalism and burial at Krapina. *Journal of Human Evolution* **14**: 203–216.

Ullrich H. 1982. Zur frage des kannibalismus beine Neandertales von Krapina. *Glasnih Antrepolaskog Drustva Jugoslavije* **15**: 7–15.

Ulrix-Closset M. 1975. Le Paléolithique moyen dans le Bassin mosan en Belgique. *[Publications exceptionnelles*, vol. 3. Bibliothèque de la Fac. de Philo. et Lettres de l'Univ. de Liège]: Liège; 214.

Valoch K. 1988. Le Taubachien et le Micoquien de la grotte de Kulna en Moravie (Tchécoslovaquie). In *L'Homme de Néandertal: La Technique*, vol. 4, Otte M (ed.). ERAUL 31: Liège; 205–217.

Valoch K. 1996. *Le Paléolithique en Tchéquie et en Slovaquie*, Collection L'Homme des origines, série Préhistoire d'Europe,. Jérôme Millon Ed.: Grenoble; 328.

Vandermeersch B. 1989. L'extinction des Neandertaliens. In *L'Homme de Néandertal: L'extinction*, vol. 7, Otte M (ed.). ERAUL 34: Liège; 11–21.

Wolpoff MH, Smith FH, Malez M, Radovcic J, Rukavina D. 1981. Upper Pleistocene human remains from Vindija Cave, Croatia. *American Journal of Physical Anthropology* **54**: 499–545.

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