CHAPTER XV

THE FOSSIL MAMMALS OF SPY

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Abstract

The large faunal sample from Spy, a Belgian cave site famous for its Neandertal remains, is for the first time studied in detail. Some 11,600 bones were examined. A wide spectrum of Pleistocene species is present. Horse, cave hyena, mammoth, woolly rhinoceros and reindeer are the primary taxa. Hyena scavenging activities are indicated by the gnawed mammoth and rhinoceros postcranial bones and cervid antlers. Bears used the cave as a hibernation den evidenced by remains of cubs, and of female and male adult bears. Indications of human manipulation (cut marks, ochre traces, worked bone/tooth) occur especially on remains from foxes, mammoth and deer. The age profile of the mammoth is dominated by calves. This selective mortality suggests that they were hunted by prehistoric people. AMS dates range from c. 44,400 BP to c. 25,700 BP. The Spy bone assemblage therefore accumulated through a series of agents over a long period of the Pleniglacial.

INTRODUCTION

This chapter describes and discusses the faunal remains from the Middle and Upper Palaeolithic "fauna-bearing levels" of the Spy cave. The material at our disposal consists of skeletal elements collected at different times by different people (Rougier *et al.*, 2004; Semal *et al.*, this volume: chapter II). So far, the faunal remains from Spy have not been studied in detail. Only species lists have been published with a very short summary of some characteristics of the fauna (Fraipont & Lohest, 1886, 1887; Rucquoy, 1886-1887; de Loë & Rahir, 1911). Therefore, the main objective of the work was the compilation of a complete list of specimens by taxon and skeletal element. As a second goal, we tried to distinguish between the human and carnivore activities based on the analysis of cut-marked, ochre-coloured, worked or gnawed bones. A third aim was to give here a brief review of the most important groups present. A fourth important objective was to analyse the faunal composition of each stratigraphic unit and examine the possible differences between the Middle and Upper Palaeolithic levels.

SITE DESCRIPTION

Spy cave is one of the richest Palaeolithic sites in Belgium. It is located about 18 m above the Orneau (a tributary of the Sambre) in the Meuse Basin (Jungels, 2009). It was first excavated in 1879 (Rucquoy, 1886-1887) and in 1886 two Neandertal skeletons were discovered by M. De Puydt and M. Lohest (Fraipont & Lohest, 1886). Since then, many excavations have been carried out (Rougier *et al.*, 2004). The excavators recognised three main archaeological and "fauna-bearing levels" (Fraipont & Lohest, 1886, 1887; Rucquoy, 1886-1887; de Loë & Rahir, 1911), although each level probably represents a palimpsest. The most important Palaeolithic industries can be assigned to the Gravettian, Aurignacian and Mousterian, including the Lincombian-Ranisian-Jerzmanowician technocomplex (Di Modica *et al.*, this volume: chapter IX; Jungels *et al.*, this volume: chapter X; Flas, this volume: chapter XI; Flas *et al.*, this volume: chapter XII; Pesesse & Flas, this volume: chapter XIII). The presence of Middle Palaeolithic and Upper Palaeolithic artefacts at Spy suggests that both Neandertals and Anatomically Modern Humans (AMH) visited the site.

MATERIAL AND METHODS

The study is based mainly on collections held in the Royal Belgian Institute of Natural Sciences, the Royal Museums of Art and History, the *Université de Liège* and the *Musée Archéologique de Namur*. The variables looked at are the frequency of bones or fragments which could be

identified as skull, tooth or postcranial element, and could be assigned to a taxon. The remains were counted in Number of Identified SPecimens (NISP), Minimum Number of Individuals (MNI) and in relative frequencies. The human manipulation of the bone material was recognised on worked bones (tools, ornaments, other) and by ochre traces and cut marks left on the bones by people manipulating the remains. Carnivore damage traces consist of gnawing traces and indications of gastric acids. The number of cut marked bones, ornaments, bone tools, bones with ochre traces and the number of carnivore damaged bones were expressed in NISP. Measurements, given in mm, were taken according to von den Driesch (1976). Chi-square tests and Fisher's exact tests were undertaken using Graph Pad Instat version 3.00 for Windows 95, Graph Pad Software, San Diego California USA (www.graphpad.com). Linear regressions were calculated with JMP (version 5.1.2). Significance was set at < 0.05.

The age at death of individuals of a number of species was estimated. For the cave hyena remains, we used the papers of Binder & Van Valkenburgh (2000) and Van Horn *et al.* (2003) on age estimations of the extant spotted hyena. The cave hyena (*Crocuta crocuta spelaea*) and spotted hyena (*C. c. crocuta*) are generally regarded as subspecies of the same species based on morphological characteristics of the skull, dentition and postcranial bones (Kurtén, 1957, 1963). Recent analysis of cave hyena coprolites from the Coumère Cave in southern France showed the very close evolutionary relationship between the spotted and the cave hyena. The genetic distance between the mitochondrial genomes of these two hyenas is lower than that documented between different species from the Hyaenidae family and falls in the range of that displayed between sub-species or even different individuals of the same sub-species (Bon *et al.*, 2012). As the cave hyena and recent spotted hyena are closely related, morphological and genetically, we can extrapolate from our knowledge of recent spotted hyenas to draw conclusions about the way of life of cave hyenas. In general, we presume that their life was characterised by similar life strategies. Most of the food (80-95 %) of spotted hyenas is obtained by killing prey (Kruuk, 1972; Cooper, 1990) and they raise their cubs in communal dens (Kruuk, 1972). We assume that cave hyenas showed similar traits. The age at death of individual cave hyenas was estimated using Binder & Van Valkenburgh's (2000) and Van Horn *et al.*'s (2003) papers on estimating the age of extant spotted hyenas. In recent spotted hyenas, the cubs are born with their deciduous incisors and canines erupted. The first deciduous teeth to be replaced are the milk incisors, starting at about six months, followed by the carnassials, the premolars and finally the canines. The permanent dentition is fully erupted between 12 and 14 months (Binder & Van Valkenburgh, 2000; Van Horn *et al.*, 2003).

Several authors reconstructed the age distribution of mammoths by comparing the eruption sequence and wear of their jugal teeth with those of the two modern elephant species (Saunders, 1980; Haynes, 1991; Germonpré *et al.*, 2008). These two modern species are similar in several aspects of their biology and behaviour. Their habits and reproductive cycle probably also apply to the extinct mammoth (Olivier, 1982; Haynes, 1991). Laws (1966) established 30 age classes for the African elephant, using as a basis the progress of eruption and wear of the jugal teeth, and allocated real ages to these groups. To obtain an age distribution for the Spy mammoths, Laws' (1966) technique was used here in an adapted form. The mammoth molars were attributed an "African elephant year" (a.e.y.) age, using the data of G. Craig in Haynes (1991: table A8). These attributions of age facilitate comparisons without implying real absolute ages for the mammoths. We did not use the minimum number of individuals (MNI) to construct the mammoth age profiles (see Lister, 2001 for the Kent's Cavern mammoths). Due to the low number of NISP, each molar is counted, although it is possible that some molars represent other teeth of a tooth row from the same individual.

The age profiles of Spy were compared with the four types of elephant age profiles described by Haynes (199: 216-220). In Haynes' (1991) Type A age profile, young animals (0-12 a.e.y.) predominate and the other age classes are represented in decreasing proportions, as is to be expected in a stable or expanding population (Haynes, 1991: 217). In his Type B age profile, young animals (0-12 a.e.y.) are predominant, greatly outnumbering the mature animals that could have borne them; according to Haynes

Unit	*Attribution*	*Location*	*NISP*	*Ochre %*	*Carnivores trace %*	*AMS*	*Species*
Terrace (*Terrasse*)		Terrace	634	5.0	3.3		
Upper Level (*Niveau supérieur*)	Upper Level (Gravettian)	Terrace	206	1.0	1.0	25,670 +130/-120[a] (GrA-37936)	*Coelodonta antiquitatis*
Terrace red level (*Terrasse niveau rouge*)	Intermediate Level (Aurignacian/ Mousterian)	Terrace	56	3.0	5.4		
Intermediate Level (*Niveau moyen*)	Intermediate Level (Aurignacian/ Mousterian)	Terrace	14	7.1	0.0	29,040 +180/-160[a] (GrA-37934); 36,920 +400/-350[b] (GrA-44546)	*Rangifer tarandus (2x)*
Lower/red Level (*Niveau inférieur/rouge*)	Intermediate Level (Aurignacian/ Mousterian)	Terrace	74	1.4	0.0	34,580 +330/-290[b] (GrA-37932)	*Equus hydruntinus*
Second Level, Upper Mousterian (*Deuxième niveau. Moustérien supérieur*)	Intermediate Level Mousterian)	Terrace	241	0.0	5.0		
Yellow earth (*Terre jaune*)	Lower Level (Mousterian)	Terrace	59	0.0	0.0		
Mousterian in situ (*Moustérien en place*)	Lower Level (Mousterian)	Terrace	5	0.0	0.0		
Third Level, lower hearth (*Troisième niveau foyer inférieur*)	Lower Level (Mousterian)	Terrace	27	0.0	1.0		
Third Level (*Troisième niveau*)	Lower Level (Mousterian)	Terrace	484	0.0	0.4		
Terrace black Level (*Terrasse niveau noir*)	Lower Level (Mousterian)	Terrace	126	0.0	0.0	42,750 +850/-650[b] (Gra-44547); 42,950 +800/-650[b] (GrA-44548)	*Crocuta crocuta; Mammuthus primigenius*
Upper Level of the cave (*Niveau supérieur de la grotte*)	Level α	Inside cave	11	0.0	0.0		
Small chamber to the right (*Petite salle à droite*)		Inside cave	39	2.6	0.0		
Inside of the cave (*Intérieur de la grotte*)		Inside cave	127	1.6	0.0	32,910 +250/-230[b] (GrA-44578)	*Coelodonta antiquitatis*
Third Level, right gallery (*Troisième niveau galerie droite*)	Level γ (Mousterian)	Inside cave	149	0.0	14.8		
Under the stalagmite (*Sous la stalagmite*)		Inside cave	42	0.0	0.0		
Total			*2,294*				

Table 1A. Stratigraphic units as noted by the excavators with age attribution, location, AMS, NISP (Number of Identified Specimens), ochre traces and carnivore traces, based on Fraipont & Lohest (1886, 1887), Rucquoy (1886-1887), de Loë & Rahir (1911), Jungels (2009, personal communication), labels attached to the finds and this work; [a]Semal *et al.* (2009), [b]Semal *et al*. (this volume: chapter XVI).

Species	*Element*	*AMS*	*Human manipulation*
Rangifer tarandus	Metatarsus	26,390 +140/-130[a]	Cut marks, ochre traces
Rangifer tarandus	Metatarsus	34,410 +203/-210[a]	Ochre traces
Ursus arctos	Incisor	34,640 +240/-220[a]	Ochre traces, failed perforation
Mammuthus primigenius	Milk molar	37,010 +440/-380[b]	
Mammuthus primigenius	Milk molar	42,330 +550/-450[a]	
Coelodonta antiquitatis	Premolar	44,350 +650/-500[a]	

Table 1B. AMS dates on mammal remains without stratigraphic context; [a]Semal *et al.* (2009), [b]Semal *et al*. (this volume: chapter XVI).

(1991: 218), the calves must have been killed selectively. In Haynes' (1991) Type C age profile, young animals are rare and prime-aged adults predominate and Haynes' (1991) Type D corresponds to small assemblages containing the bones of few individuals.

The age distribution of the woolly rhinoceros material was based on the stage of dental eruption and wear pattern of the dentition as proposed by Goddard (1970) for the extant *Diceros bicornis*. This author grouped mandibular material of black rhinoceros from Tsavo National Park, Kenya, in 20 age classes, assigning approximate mean ages to each class, based on the eruption sequence and wear pattern of the deciduous and permanent jugal teeth. The development of the teeth is according to Goddard (1970) similar in both the upper and lower jaw, although the maxillary dentition generally develops a little ahead. The eruption sequence and wear pattern in the woolly rhinoceros is comparable to the one of the black rhinoceros (Guérin, 1980). As most of the dental material occurs at Spy as isolated teeth, each identified tooth was assigned to an age class and then the MNI of each class was calculated. For example Class 3 contains six deciduous P^2, one deciduous P^3, seven deciduous P^4 and one M_1; the MNI of this class was counted as 4. The isolated milk teeth were only added up if they were unworn or slightly worn. As proposed by Tong (2001) such teeth can be used as evidence of death at a young age, while heavily worn milk teeth were shed when replaced by the permanent dentition. Each class was attributed a "black rhinoceros year" age (Goddard, 1970: table 4) which does not imply an absolute age but enabled a better visualisation of the age structure of the fossil rhinoceros assemblage.

The age profile of the horse is a combination of the ages of the upper third molars, based on crown height (Levine, 1982; Fernandez & Legendre, 2003), and of deciduous incisors, incisors and P^2, based on their wear (Habermehl, 1961; Levine, 1982).

As unfortunately the exact stratigraphic position of the bulk of the finds is unknown, most of the taxon assemblages were analysed as single entities.

Although most of the material does not have any stratigraphic attribution, some 20 % of the remains are accompanied by a label with a "stratigraphic" unit and could be attributed to the terrace or the cave itself. It is not always clear during which excavation the units were defined. Table 1A lists the units with their localisation (terrace or cave), assignment to one of the three main levels and their archaeological industry, based on Fraipont & Lohest (1886, 1887), Rucquoy (1886-1887), de Loë & Rahir (1911), Jungels (2009; pers. comm.), available AMS dates, NISP and frequency of bones with ochre and carnivore traces. In general, most of the AMS dates indicate that the Upper Level is younger than the Intermediate Level, while the Lower Level is the oldest. However, as shown by the disparate dates of the *niveau moyen*, at least some of the units are mixed (Semal *et al.*, this volume: chapter XVI). This could be due to the fact that the excavations, done more than 100 years ago, were not executed according to the present standards. Furthermore, the units described might very well represent palimpsests. In addition, Rucquoy (1886-1887) mentions that bone material from deeper levels was muddled up inside the Upper Level through bioturbation. A number of finds stored at the Royal Museums of

Art and History in Brussels and excavated by de Loë and Rahir, carry the label *deuxième niveau, Moustérien supérieur*. No published record exists of the attribution of (a part of) this level to the Mousterian, but it was followed below. Table 1B gives the AMS dates on mammalian remains without stratigraphic context.

The fossil assemblages of Spy were compared, when possible, with assemblages from Palaeolithic caves and fluvial sites in Belgium. The Goyet cave lies about 25 km east of Spy. It is situated in a limestone cliff in the Samson Valley, a tributary of the Meuse River. The cave consists of several chambers in which a large number of Middle and Upper Palaeolithic artefacts were discovered along with numerous remains of Ice Age mammals (Dupont, 1871). Five levels were described by Dupont (1871); the upper three levels occurring only in Chamber A. Many of the fossil bones are broken, have cut marks, or display traces of ochre (Germonpré, 1996; Germonpré & Hämäläinen, 2007). The Palaeolithic artefacts date from the Mousterian, Aurignacian, Gravettian, and Magdalenian. Unfortunately, it is not always clear from which level the artefacts and bones originated. Deeper inside the cave, Dupont (1871) distinguished a fourth and fifth level yielding bones from cave bear, cave hyena and cave lion. Trou Magrite is situated about 35 km southeast of Spy and lies in a limestone cliff on the river Lesse, a tributary of the Meuse. This cave delivered, just as Goyet, a long sequence with remains dating from the Mousterian, Aurignacian, Gravettian and Magdalenian. Dupont (1871) excavated the material inside the cave. Recently, new excavations were undertaken on the terrace (Otte & Straus, 1995). The Late Glacial Trou de Chaleux cave is situated in the vicinity of Trou Magrite. One major bone level contained a wealth of Magdalenian artefacts (Dupont, 1871). Hofstade is a fluvial site dating from the Pleniglacial (Germonpré *et al.*, 1993). It is located some 150 km to the west of Spy. It is a natural site, without any traces of human presence. The fauna is dominated by mammoth and woolly rhinoceros (Germonpré, 1993).

Weichselian		*NISP*		*MNI*	
		N	*%*	*N*	*%*
Carnivora					
Vulpes vulpes	≥	15	0.1	1	0.2
Alopex lagopus		60	0.5	10	2.4
Alopex/Vulpes		5			
Canis lupus		95	0.8	9	2.1
Ursus arctos		16	0.1	3	0.7
Ursus spelaeus		488	4.2	18	4.3
Mustela putorius		4		2	0.5
Meles meles	≥	2		1	0.2
Crocuta crocuta spelaea		1,751	15.1	123	29.2
Lynx lynx		2		1	0.2
Panther leo spelaea		4		2	0.5
Carnivora indet.		150	1.3		
Proboscidea					
Mammuthus primigenius		1,178	10.2	23	5.2
Perissodactyla					
Equus ferus		4,499	38.9	144	34.2
Equus hydruntinus		36	0.3	4	1.0
Coelodonta antiquitatis		620	5.4	37	8.8
Artiodactyla					
Sus scrofa	≤	5		1	0.2
Cervus elaphus		198	1.7	4	1.0
Megaloceros giganteus		11	0.1	2	0.5
Rangifer tarandus		392	3.4	14	3.3
Cervidae indet.		61	0.5		
Bos primigenius		26	0.2	7	1.7
Bison priscus		8	0.1	2	0.5
Bos/Bison		434	3.7	10	2.4
Rupicapra rupicapra		3		1	0.2
Capra ibex		6	0.1	1	0.2
Rodentia					
Castor fiber		6	0.1	1	<0.1
Marmotta marmotta		5		1	0.2
Lagomorpha					
Lepus sp.		78	0.7		
Mammalia indet.		1,418	12.2		
Total Weichselian		*11,576*	*100*	*422*	*100*

Holocene		*NISP*	
		N	*%*
Vulpes vulpes	≤	144	31.5
Canis lupus f. familiaris		14	3.1
Meles meles	≤	136	29.8
Felis sylvestris/F.s. f. catus		32	7.0
Sus scrofa f. domestica	≥	32	7.0
Capreolus capreolus		8	1.8
Bos primigenius f. taurus		25	5.5
Ovis/Capra	≥	8	1.8
Artiodactyla indet.	≤	37	8.1
Oryctolagus cuniculus		21	4.6
Total Holocene		*457*	*100*

Table 2. List of Weichselian and Holocene species with their NISP (Number of Identified Specimens) and MNI (Minimum Number of Individuals).

RESULTS

Composition of the total assemblage

The list of species is shown in Table 2. For a number of species it was possible to assign them to the Weichselian or the Holocene. For others that can be present in both periods, minimum / maximum numbers are given. The Ice Age mammalian fauna is composed of almost 11,600 bones, of which 12 % could not be identified (Table 2). Figure 1 displays the frequency diagram of the most important Weichselian species. Horse is the main species in this sample, comprising almost 39 % of all specimens. Cave hyena is a distant second in NISP with about 15 %. Other taxa are present in relatively low frequencies, fluctuating between 10 % (mammoth) and 0.01 % (chamois). Horse and cave hyena dominate again the assemblage based on the MNI with respectively 34 % and 29 % (Figure 1; Table 2).

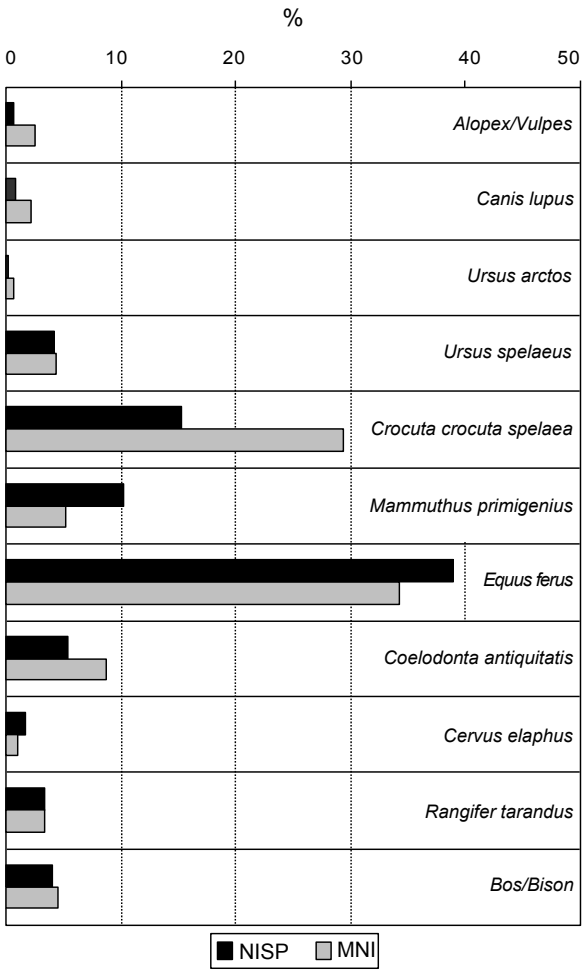


Figure 1. Frequency distribution of the most important Weichselian species present at Spy (NISP: Number of Identified Specimens; MNI: Mininum Number of Individuals).

Skeletal distribution

Table 3 lists the frequency of the three main skeletal parts: skull (including antler and lower jaw), isolated teeth and postcranial bones. Teeth represent the most frequent skeletal part with a NISP of 73 %, postcranial bones have a NISP of 24 % and skull elements amount to a NISP of 3 %. Figure 2 is a ternary plot displaying the frequency of the postcranial material versus the frequency of the isolated teeth and versus the frequency of skull fragments for the most important taxa. Out of this graph three groups of species can be distinguished: Group A: animals with a frequency of at least 90 % teeth (horse, cave hyena, mammoth and rhinoceros); Group B: animals with between 75 % and 50 % teeth (giant deer, cave bear, wolf, red deer, *Bos/Bison*) and finally Group C with animals dominated by postcranial fragments: the reindeer and the foxes.

Taxa	*Skull*	*Teeth*	*Postcranial*	*Total*
Vulpes vulpes				
Total (NISP/MNI)	23/10	39/9	97/6	159/10
cut marks	-	-	1 (1 %)	1 (0.6 %)
ornaments	-	2 (5.1 %)	-	2 (1.2 %)
ochre	-	-	-	-
gnawing traces	-	-	1 (1 %)	1 (0.6 %)
gastric acid	-	-	-	-
Alopex lagopus				
Total (NISP/MNI)	9/4	37/8	14/1	60/8
cut marks	-	-	-	-
ornaments	-	4 (10.8 %)	-	4 (6.7 %)
ochre	-	-	-	-
gnawing traces	-	-	-	-
gastric acid	-	-	-	-
Canis lupus				
Total (NISP/MNI)	9/5	47/7	44/4	100/9
cut marks	-	-	1 (2.3 %)	1 (1 %)
ornaments	-	-	-	-
ochre	-	-	1 (2.3 %)	1 (1 %)
gnawing traces	-	-	-	-
gastric acid	-	-	-	-
Canis familiaris				
Total (NISP/MNI)	3	2	9	14
Ursus arctos				
Total (NISP/MNI)	-	10/2	6/2	16/3
cut marks	-	-	-	-
ornaments	-	2 (20 %)	-	2 (12.5 %)
ochre	-	1 (10 %)	-	1 (6.3 %)
gnawing traces	-	-	1	1 (6.3 %)
gastric acid	-	-	-	-

Ursus spelaeus				
Total (NISP/MNI)	39,909	337/16	145/7	488/18
cut marks	-	-	-	-
ornaments	-	-	-	-
ochre	-	-	1 (0.7 %)	1 (0.2 %)
gnawing traces	-	-	-	-
gastric acid	-	-	-	-
Mustela putorius				
Total (NISP/MNI)	2	-	2	4
Meles meles				
Total (NISP/MNI)	16/6	28/6	94/8	138/8
cut marks	-	-	-	-
ornaments	-	-	-	-
ochre	-	-	-	-
gnawing traces	-	-	1 (1 %)	1 (1.7 %)
gastric acid	-	-	-	-
Crocuta crocuta				
Total (NISP/MNI)	98/20	1,569/123	84/3	1,751/123
cut marks	-	-	-	-
ornaments	-	-	-	-
ochre	-	-	-	-
gnawing traces	7 (7.1 %)	5 (0.3 %)	1 (1.2 %)	13 (0.7 %)
gastric acid	-	3 (0.2 %)	-	3 (0.2 %)
Felis sylvestris/Felis sylvestris format catus				
Total (NISP/MNI)	2	3	27	32
Lynx lynx				
Total (NISP/MNI)	-	-	2/1	2/1
Panthera leo spelaea				
Total (NISP/MNI)	-	4/1	-	4/1
Carnivora indeterminata				
Total (NISP/MNI)	13	73	64	150
cut marks	-	-	-	-
ornaments	-	-	-	-
ochre	-	-	-	-
gnawing traces	-	-	2 (3.1 %)	2 (1.3 %)
gastric acid	-	-	-	-
Mammuthus primigenius				
Total (NISP/MNI)	-	1,108/22	70/3	1,178/22
cut marks	-	-	-	-
ornaments	-	71 (6.4 %)	-	71 (6 %)
tools	-	19 (1.7 %)	-	19 (1.6 %)
worked	-	220 (19.9 %)	-	220 (18.7 %)
ochre	-	145 (13.1 %)	-	145 (12.3 %)
gnawing traces	-	1 (0.1 %)	36 (51.4 %)	37 (3.1 %)
gastric acid	-	-	-	-
Equus ferus				
Total (NISP/MNI)	5/3	4,341/144	153/14	4,499/144
cut marks	-	-	2 (1.3 %)	2 (0.04 %)
ornaments	-	-	-	-
ochre	-	6 (0.1 %)	3 (2.0 %)	9 (0.02 %)
gnawing traces	-	-	42 (27.6 %)	42 (0.9 %)
gastric acid	-	22 (0.5 %)	4 (2.6 %)	26 (0.6 %)
Equus hydruntinus				
Total (NISP/MNI)	-	34/4	2/1	36/4
cut marks	-	-	-	-
ornaments	-	-	-	-
ochre	-	1 (2.9 %)	-	1 (2.8 %)
gnawing traces	-	-	-	-
gastric acid	-	3 (8.8 %)	-	3 (8.3 %)
Coelodonta antiquitatis				
Total (NISP/MNI)	4/2	555/37	61/12	620/37
cut marks	-	-	1 (1.6 %)	1 (0.2 %)
ornaments	-	-	-	-
ochre	-	4 (0.7 %)	-	4 (0.6 %)
gnawing traces	-	-	28 (45.9 %)	28 (4.5 %)
gastric acid	-	-	-	-

Sus scrofa/Sus scrofa format domestica				
Total (NISP/MNI)	7	17	13	37
cut marks	-	-	-	-
ornaments	-	-	-	-
ochre	-	-	-	-
gnawing traces	-	-	2 (15.4 %)	2 (5.4 %)
gastric acid	-	-	-	-
Cervus elaphus				
Total (NISP/MNI)	27	103/4	68/3	198/4
cut marks	4 (14.7 %)	-	5 (7.4 %)	9 (4.5 %)
ornaments	-	1 (1 %)	-	1 (0.5 %)
ochre	-	-	12 (17.7 %)	12 (6.1 %)
gnawing traces	11 (40.7 %)	-	1 (1.5 %)	12 (6.1 %)
gastric acid	-	-	-	-
Megaloceros giganteus				
Total (NISP/MNI)	1/1	8/2	2/1	11/2
cut marks	-	-	-	-
ornaments	-	-	-	-
ochre	-	-	-	-
gnawing traces	1/1	-	-	-9.10 %
gastric acid	-	-	-	-
Capreolus capreolus				
Total (NISP/MNI)	-	1	7	8
Rangifer tarandus				
Total (NISP/MNI)	66/5	109/7	217/12	392/14
cut marks	5 (7.6 %)	-	19 (8.8 %)	24 (6.1 %)
ornaments/tool	2 (3.0 %)	2 (1.8 %)	-	4 (1 %)
ochre	-	2 (1.8 %)	70 (32.3 %)	72 (18.4 %)
gnawing traces	5 (7.6 %)	-	3 (1.4 %)	8 (2 %)
gastric acid	-	-	-	-
Cervidae				
Total (NISP/MNI)	12	4	45	61
cut marks	1	-	1 (2.2 %)	2 (3.3 %)
ornaments	-	1	-	1 (1.6 %)
ochre	-	-	11 (24.4 %)	11 (18 %)
gnawing traces	2 (16.7 %)	-	2 (4.3 %)	4 (6.6 %)
gastric acid	-	-	-	-
Bos primigenius				
Total (NISP/MNI)	2/1	13/7	11/5	26/7
cut marks	-	-	2 (18.2 %)	2 (7.7 %)
ornaments	-	-	-	-
ochre	-	-	-	-
gnawing traces	-	-	3 (27.3 %)	3 (11.5 %)
gastric acid	-	-	-	-
Bison priscus				
Total (NISP/MNI)	-	3/2	5/1	8/2
cut marks	-	-	1 (20 %)	1 (12.5 %)
ornaments	-	-	-	-
ochre	-	-	-	-
gnawing traces	-	-	-	-
gastric acid	-	-	-	-
Bos/Bison				
Total (NISP/MNI)	5/1	305/6	124/10	434/10
cut marks	-	-	1 (0.8 %)	1 (0.2 %)
ornaments	-	-	-	-
ochre	1 (20 %)	-	3 (2.4 %)	4 (0.9 %)
gnawing traces	-	-	25 (20.2 %)	25 (5.8 %)
gastric acid	-	-	2 (1.6 %)	2 (0.5 %)
Bos taurus				
Total (NISP/MNI)	3	12	10	25
Rupicapra rupicapra				
Total (NISP/MNI)	1/1	-	2/1	3/1
cut marks	-	-	-	-
ornaments	-	-	-	-
ochre	1 (100 %)	-	2 (100 %)	3 (100 %)
gnawing traces	-	-	-	-
gastric acid	-	-	-	-

Capra ibex				
Total (NISP/MNI)	-	1/1	5/1	6/1
cut marks	-	-	-	-
ornaments	-	-	-	-
ochre	-	-	1 (20 %)	1 (16.7 %)
gnawing traces	-	-	-	-
gastric acid	-	-	-	-
Capra/Ovis				
Total (NISP/MNI)	5	3	-	8
Artiodactyla indeterminata				
Total (NISP/MNI)	-	21	16	37
cut marks	-	-	-	-
ornaments	-	-	-	-
ochre	-	-	3	3
gnawing traces	-	-	1	1
gastric acid	-	-	-	-
Castor fiber				
Total (NISP/MNI)	-	5	-	5
Marmotta marmotta				
Total (NISP/MNI)	2/1	3/1	-	5/1
Lepus species				
Total (NISP/MNI)	11	2	65	78
Oryctolagus cuniculus				
Total (NISP/MNI)	3	-	18	21
Mammalia indeterminata				
Total (NISP/MNI)	7	3	1408	1418
cut marks	-	-	10 (0.7)	10 (0.7 %)
ornaments	-	3	7 (0.5 %)	11 (0.8)
tools	-	-	32 (2.3 %)	32 (2.3 %)
worked	-	-	42 (3 %)	42 (3 %)
ochre	-	-	17 (1.2 %)	17 (1.2 %)
gnawing traces	-	-	163 (11.6 %)	163 (11.5 %)
gastric acid	-	-	57 (4.1 %)	57 (4 %)
burnt	-	-	44 (3.1 %)	44 (3.1 %)

Table 3. (above and previous pages) List of species present with the NISP (Number of Identified Specimens) and MNI (Minimum Number of Individuals) of remains of skull, dentition and postcranial bones and cut marks, ornaments, worked bones, ochre traces, carnivore gnawing traces and gastric acid traces.

Breakage and modifications

The material is in general highly fragmented. Apart from the teeth, the most complete specimens are carpals, tarsals and phalanges. A few of the broken bones are abraded.

The total frequency of the examined human traces amounts to 6 %. Although cut marks occur in low numbers they basically reflect the same pattern as observed on the bones with ochre traces: species with a high number of cut marks also have a high frequency of bones displaying ochre stains and vice versa. The linear fit between the cut marked (including worked bones/teeth) and the ochre stained skeletal elements was calculated based on the $\log_{10}$- transformed NISP counts of each taxon with at least one bone in each category. The regression line obtained is significant ($r^2 = 0.83$, $P = 0.0044$; Figure 3). In addition, horse, the species which dominates the NISP with almost 40 % of the material, displays only 3 % of the total ochre traces, significantly less than expected (Chi-square test, $\chi^2 = 89.31$, $P < 0.0001$). Furthermore, the frequency distribution of all skeletal elements differs drastically from the distribution of the elements with ochre traces (Figure 4). Note that mammoth ivory and tusk fragments were separated from the rest of the dentition. It is interesting that ochre occurs essentially on ivory fragments and distal elements such as metapodials or phalanges, while it is rarely present on the most

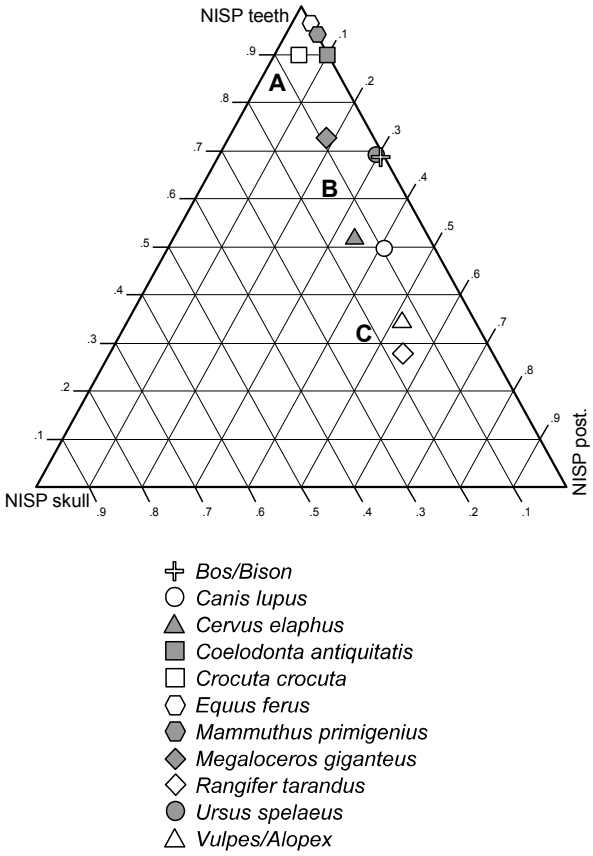


Figure 2. Ternary plot of the frequency distribution of the three main skeletal parts: skull, teeth and postcranial elements of the most important taxa.
A: group dominated by dental remains;
B: group with frequency of dental remains between 75 % and 50 %;
C: group dominated by postcranial remains (post.: postcranial, NISP: Number of Identified Specimens).

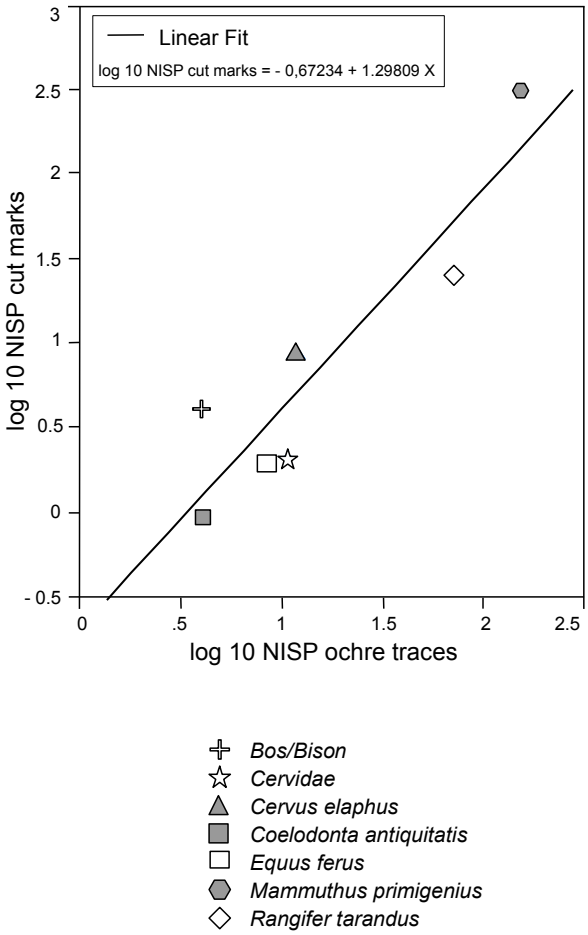


Figure 3. Linear fit of log-10 transformed NISP of bones with cut marks by bones with ochre stains.

frequent element: the dentition (excluding mammoth ivory).

The animals which show the highest frequency of human modifications are the mammoth, the reindeer, the unidentified cervids, the red deer, unidentified artiodactyls and the arctic fox (Table 3). Reindeer has the highest number of ochre coloured bones, followed by unidentified cervids and mammoth. The worked bones include personal ornaments (most often ivory pendants and perforated teeth), tools (especially spear points from reindeer antler, mammoth ivory and bone) and other indications of human manipulation. Mammoth and arctic fox delivered the highest frequencies of ornaments (ivory pendants and perforated teeth). Horse has a very low frequency of human modified bones. The most important species with anthropogenic traces on the skull/antler are the cervids (Table 3). Looking at the dentition it is clear that the three main species with anthropogenic

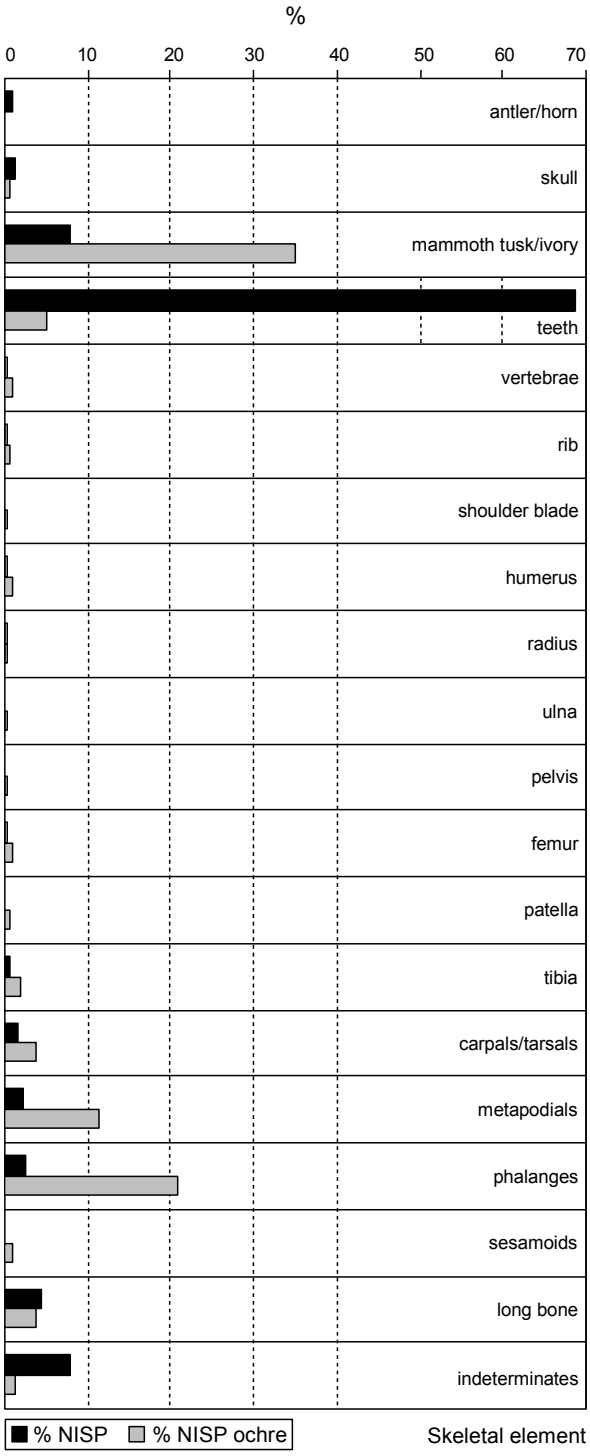


Figure 4. Frequency diagram comparing the NISP of all skeletal elements with the NISP of ochre stained skeletal elements.

traces are arctic fox, mammoth and reindeer. Considering the postcranial elements, reindeer is the most important species with indications of human modifications (SF1), followed by unidentified cervids and red deer (Table 3).

Another category of bone modification is inflicted by carnivores. Here also the traces were compared over the three main skeletal parts (Table 3). The antler fragments of especially red deer show a high frequency of carnivore gnawing (Figure 5a). Also a cast antler of a giant deer was chewed by carnivores (Figure 5b). Few teeth were modified by carnivores (Table 3). Carnivores attacked the postcranial bones of especially mammoth, rhinoceros, horse, large bovids and unidentified mammals as shown by the high frequency of gnawing traces or traces of gastric acids. Also remains of cave hyena display gnawing marks (Table 3).

Description of the most common taxa

Canidae

Two fox species occur at Spy: the red fox (ST1) and the arctic fox (ST2). In a number of cases it is not possible to distinguish between both species. All skeletal parts of the red fox are well represented; most material is from adults although juveniles are also present. A cut mark occurs on an astragalus. A lower canine was partly perforated.

The arctic fox at Spy is represented by nine adult animals, based on the canines, and one juvenile. The most frequent element is the canine (34 upper and lower C) of which four were perforated and used as ornaments (ST2). Also elements from the front and hind paw of at least two individuals are rather well represented. Interesting to note is the presence of one complete

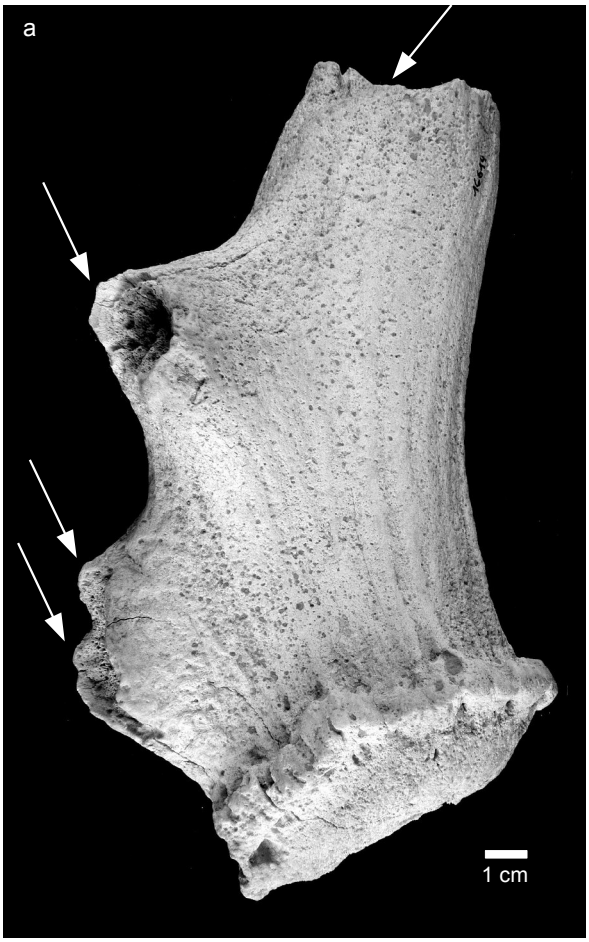


Figure 5a. Gnawing marks on shed red deer antler (16614).



Figure 5b. Gnawing marks on shed giant deer antler (16614).

pathological hind paw; two of the metatarsals were broken previously in life and all metatarsals fused together before the animal died. The remains of a juvenile animal consist of a lower jaw fragment with milk dentition.

We compared the number of perforated and unmodified fox canines in the collections of the Royal Belgian Institute of Natural Sciences (Table 4). We grouped the material from Spy together with fox teeth from Trou Magrite and Goyet level 3 in a Pleniglacial set; another set dating from the Late Glacial includes the teeth from Trou de Chaleux and Goyet levels 1 and 2. If the Palaeolithic people preferred one fox species over the other for making ornaments, the ratio of perforated versus unmodified canines could be distorted so that the preferred fox should have relatively more perforated canines than the other species. No difference could be discerned in the frequencies of the arctic fox or red fox perforated canines compared to the unmodified canines. The Fisher exact test (two-tailed) comparing the number of perforated and unmodified canines of both species is not significant as either for the Pleniglacial (upper canines: P = 1.00, lower canines: P = 0.13), or for the Late Glacial (lower canines: P = 0.39).

Canines	*Perforated*	*Unmodified*	*Total*
Late Glacial			
Alopex lagopus	7	37	44
Vulpes vulpes	1	4	5
Total	*8*	*41*	*49*
Pleniglacial			
Alopex lagopus	15	35	50
Vulpes vulpes	7	20	27
Total	*22*	*55*	*77*

Table 4. Number of perforated and unmodified canines of *Alopex lagopus* and *Vulpes vulpes* from Belgian Late Glacial (Trou de Chaleux, Goyet levels 1 and 2) and Pleniglacial (Spy, Trou Magrite, Goyet level 3) sites.

Large canids are present with a NISP of 100 bones (ST3). As no complete skull is available, it is not possible to identify with certainty if the remains are from Pleistocene wolves or Palaeolithic dogs. A few bones are from juveniles and subadults, but most are from adult canids. Paw elements are rather well represented as are jaws and isolated teeth. A radius displays a cut mark, a metatarsal was gnawed. Fourteen bones are clearly from domestic dogs and probably constitute postglacial intrusive remains (Table 3).

Ursidae

Two bear species are present at Spy: the brown bear (*Ursus arctos*) and the cave bear (*Ursus spelaeus*). The brown bear occurs in low frequencies; only 16 NISP were recognised from this species, consisting of isolated teeth and paw elements (ST4). Based on the wear of the jugal dentition, remains of at least three individuals are present. A metatarsal was gnawed by carnivores.

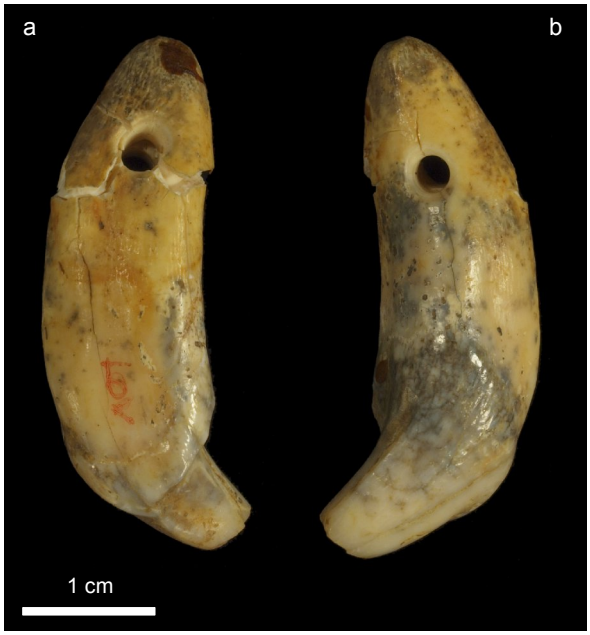


Figure 6. Left (a) and right (b) view of a perforated right third upper incisor of brown bear (Carpentier collection).

A second incisor was manipulated by prehistoric humans: the root displays ochre traces and according to Dewez (unpublished notes), one side of the root shows scraping, and the other side shows scraping with a cup-shaped deepening. This partly perforated tooth has an AMS date of c. 34,600 BP (Semal *et al.*, 2009). A third incisor was perforated (Figure 6).

The NISP of the cave bear amounts to 488; both adult and juvenile remains are included (ST5). The best represented elements are isolated teeth and paw elements. The juvenile material originates from cubs that died in their first winter, based on isolated non resorbed deciduous canines. Second winter cubs lost their deciduous canines inside the cave since a number of canines with a resorbed root were collected. The preponderance of large teeth in the frequency distribution of the crown width of the adult upper canines suggests that male cave bears were more frequent than female cave bears (Figure 7). Two cave bear bones display evidence of human manipulation: a third phalanx shows ochre traces and a cave bear bone was used for making a spear point, based on the specific stable isotope profile of the bone point (Flas *et al.*, this volume: chapter XII; Bocherens *et al.*, this volume: chapter XVII). It has an AMS date of c. 32,800 years BP (Semal *et al.*, 2009).

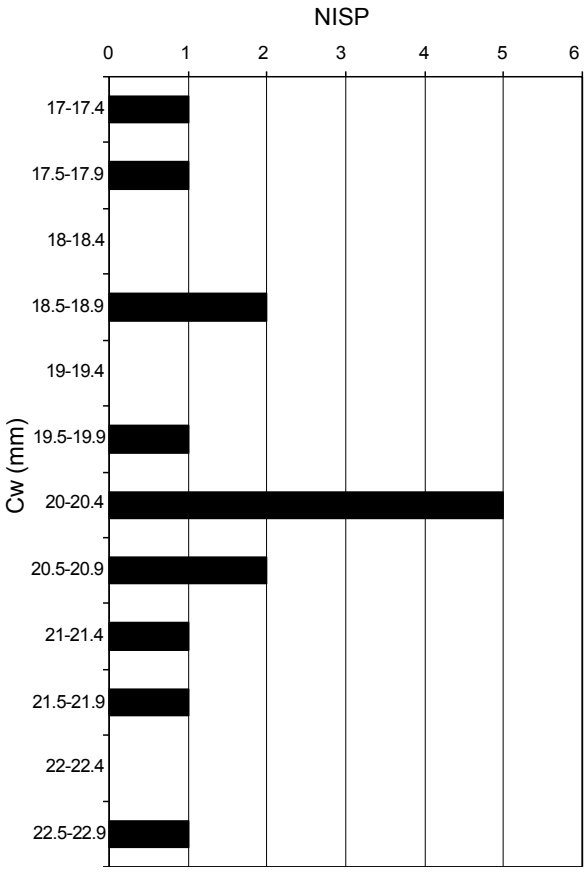


Figure 7. Frequency distribution of the crown width of the upper canines of cave bear.

Crocuta crocuta spelaea

The cave hyena is the most important carnivore at Spy with a NISP of 15 % and a MNI of 29 % (Table 5). The best represented skeletal elements are isolated teeth and lower jaws. Remains from adult animals (MNI: 115) as well as from cubs (MNI: 11) were recovered. Four individuals were at the most six months old when they died, based on the presence of tooth germs of the third upper incisor (*cf.* Binder & Van Valkenburgh, 2000). Nine cubs were younger than 12 months based on the presence of the germ of P_4 (*cf.* Binder & Van Valkenburgh, 2000); two cubs were about one year old based on the presence of erupting carnassials in upper and lower jaws (*cf.* Binder & Van Valkenburgh, 2000). Mean crown length and crown width of the hyena dentitions from Spy is given in Table 6.

Apart from their remains, gnawing traces also testify to the presence of hyenas. Their tooth marks can be recognised on several groups such as cervids, with marks especially on cast antlers; bovids and horse, with marks on the metapodials; and woolly rhinoceros and mammoth, of which long bones in particular were gnawed. Interesting to note is the occurrence of gnawing traces on a number of bones and teeth of cave hyenas, especially on lower jaws (Table 5).

A lower carnassial from the unit *terrasse niveau noir* has an AMS age of c. 42,800 BP (Figure 8; Semal *et al.*, this volume: chapter XVI).

Mammuthus primigenius

Mammoth is the third most frequent species at Spy with a NISP of 10 %. No skull, lower jaw fragment nor short, compact bones, such as carpals, tarsals, metacarpals, metatarsals and phalanges, from mammoth could be identified. The best represented elements are teeth, including both tusks and jugal teeth. A large number of ivory fragments and ivory ornaments and tools are present. Ochre traces occur only on ivory fragments (Table 7; ST2, SF3). None of the molars or of the postcranial bones display ochre. Around 310 ivory fragments are worked, including ornaments (pearls, pendants, rods) and tools (Khlopachev, this volume: chapter XIV). Molars and molar fragments amount to 231 specimens. One

	Adult		*Juvenile*		*Total*		*Gnawing traces*	*Gastric traces*
	NISP	MNIe	NISP	MNIe	NISP	MNIe	NISP	NISP
Maxilla	19	5	2	2	21	7	1	
Mandible	75	18	2	2	77	20	6	
di			11		11			
dp^3			4	2	4	2		
dp^4			1	1	1	1		
dp_2			2	1	2	1		
dp_3			5	3	5	3		
dp_4			9	5	9	5		
Deciduous teeth			4	3	4	3		
I^1	37	21			37	21		
I_1	18	10			18	10		
I^2	36	19	1	1	37	20		
I_2	36	18			36	18		
I^3	116	60	6	4	122	64		
I_3	21	12	1	1	22	13		
C^1	106	56	2	1	108	57	2	1
C_1	231	115	11	8	242	123	2	
C indet.	93		7		100			
P^1	15	8			15	8		
P^2	9	6	5	3	14	9		
P^3	93	51	14	8	107	59	1	
P^4	112	66	14	9	126	75		
P_2	58	26	3	2	61	28		
P_3	118	64	2	2	120	66		2
P_4	108	63	10	5	118	68		
M_1	150	78	11	6	161	84		
Teeth indet.	84		5		89			
Vertebrae - thoracic	1	1			1	1		
Ulna	1	1			1	1		
Radius	1	1			1	1		
MC II	5	3			5	3		
MC IV	2	2			2	2		
MC V	4	3			4	3		
Tibia	1	1			1	1		
Carpals/tarsals	15				15			
Metapodials	6				6			
Phalanges I	39	3			39	3	1	
Phalanges II	8	1			8	1		
Phalanges III	1	1			1	1		
Total NISP/MNI	*1,619*	*115*	*132*	*11*	*1,751*	*123*	*13*	*3*

Table 5. *Crocuta crocuta.* List of material: NISP = Number of Identified Specimens; MNI = Minimum Number of Individuals; MNIe = Minimum Number of Individuals per skeletal element.

milk molar has an AMS age of c. 42,300 BP (Semal *et al.*, 2009). A molar fragment of a subadult from the unit *terrasse niveau noir* has an AMS age of c. 43,000 BP. The AMS date of another milk molar is much younger with an age of c. 37,000 BP (Table 1A-1B; Semal *et al.*, this volume: chapter XVI). The stratigraphic position of most of the teeth is not clear, although a number were found in the *deuxième niveau Moustérien supérieur*. The postcranial bones are much fragmented and most of the bones were found isolated. However, four associated thoracic vertebrae are from one individual. Gnawing traces by cave hyenas occur on 53 % of the post-

	Mean	*Standard deviation*	*Number of specimens*
P^{1} cl	7.48	0.61	9
P^{1} cw	7.28	0.68	7
P^{2} cl	17.58		2
P^{2} cw	12.57		2
P^{3} cl	24.01	1.42	29
P^{3} cw	17.68	1.23	28
P^{4} cl	41.61	1.94	55
P^{4} cw	22.32	1.20	51
P_{2} cl	16.25	0.64	12
P_{2} cw	12.50	0.75	5
P_{3} cl	22.39	0.78	19
P_{3} cw	16.21	1.07	19
P_{4} cl	23.97	0.87	31
P_{4} cw	14.99	0.63	32
M_{1} cl	32.41	1.42	60
M_{1} cw	14.10	0.59	64

Table 6. Crown length (cl) and crown width (cw) of permanent premolars and molars from *Crocuta crocuta spelaea*.

cranial bones (Table 7). The frequency distribution of the skeletal elements from the unit Second level, Upper Mousterian is also given in Table 7. This unit yielded only molars, one ivory fragment and two shoulder blade fragments.



Figure 8. Lower carnassial of cave hyena (13534).

Fifty-six isolated complete or fragmented molars recovered from Spy permitted an exact identification and could be attributed a Laws' (1966) age class. These molars were given an age in a.e.y., based on the data of G. Craig in Haynes (1991: table A8; Table 3). Complete molars and large fragments of teeth from upper and lower jaws were included. These remains, which comprise material from all horizons and material without stratigraphic attribution, were used to construct an age profile based on the NISP. The age profile of the total mammoth assemblage is dominated by remains of mammoth calves in the age group 0 to 12 a.e.y. with 74 %

	Total		*Ochre*	*Worked*	*Gnawing traces*
	NISP	MNIe	NISP	NISP	NISP
I^{2}	13	5	2		1
Ivory	864		143	310	
M1	4	1			
M^{2}	5	4			
M_{2}	6	4			
M2	25				
M^{3}	5	5			
M3	14	4			
M^{4}	4	4			
M_{4}	3	1			
M4	7				
M_{5}	3	3			
M5	5				
M^{6}	2	2			
M6	3				
Molar indet.	145				
Rib	1	1			
Vertebrae					
cervical	2	1			1
thoracic	11	2			
lumbar	1	1			
Scapula	4	2			2
Humerus	2	1			2
Pelvis	3	1			2
Femur	5	2			1
Long bone	41				28
Total NISP/MNI	*1178*	*22*	*145*	*310*	*37*

Table 7. *Mammuthus primigenius*. List of material (worked: ornaments, tools, worked fragments; NISP = Number of Identified Specimens; MNI = Minimum Number of Individuals; MNIe = Minimum Number of Individuals per skeletal element).

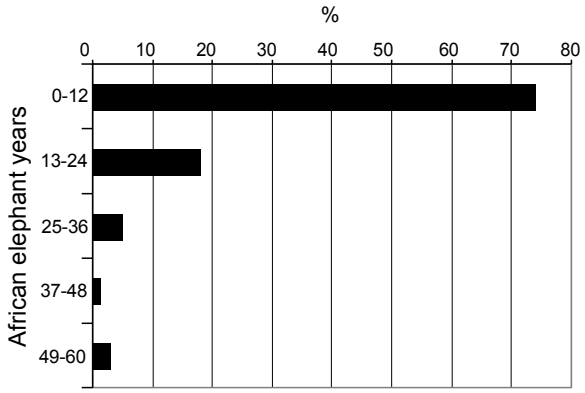


Figure 9. Age distribution of all mammoth molars of the total Spy assemblage (a.e.y.: African elephant years, NISP: Number of Identified Specimens).

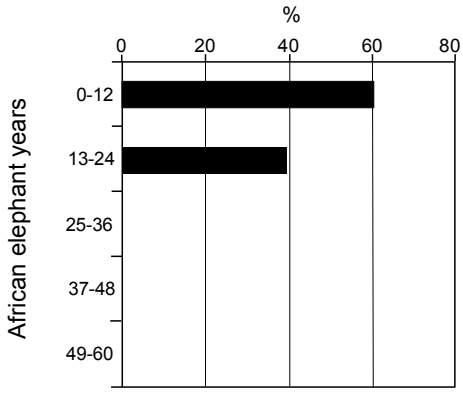


Figure 11. Age distribution of the NISP of the mammoth molars of the *deuxième niveau, Moustérien supérieur* (NISP: Number of Identified Specimens).

(Figure 9). Furthermore, most of the remains are molars in Laws' (1966) age classes I to VII (ST6). The calves from these age classes were between 0 and 5 a.e.y. when they died (Figure 10). Dental material from the next age group (13-24 a.e.y.) is much less represented with 18 % of the NISP. The next age groups each contain less than 5 % of the mammoth dentition (Figure 9; ST6). The total age profile resembles most Haynes' (1991) Type B age profile. A second age profile was constructed on the basis of the 14 molars from the stratigraphic unit Second level, Upper Mousterian. Again, the profile is based on the NISP only. The Mousterian profile is also dominated by remains from young individuals (Figure 11; ST7). The age group 0-12 a.e.y. contains 61 % of the remains, all of which are second molars (M2) in Laws' (1966) class III and are from calves that died when they were between 1 and 2 a.e.y. The next age group (13-24 a.e.y.) of this profile contains 39 % of the remains. There are no remains from mammoths older than 24 a.e.y. The age pro-



Figure 10. Lower second molar (16640) of a mammoth calf (*Université de Liège* collection).

	Mean	*Standard deviation*	*Number of specimens*
P^2 cl	30.81	1.63	12
P^2 cw	32.48	2.81	10
P^3 cl	34.93	2.96	6
P^3 cw	40.48	2.98	5
P^4 cl	40.92	0.72	3
P^4 cw	47.60	2.63	7
M^1 cl	50.65	6.66	8
M^1 cw	50.78	5.94	8
M^2 cl	54.31	6.78	9
M^2 cw	54.09	3.60	9
M^3 cl	56.37	3.95	11
M^3 cw	49.76	4.46	10
P_2 cl	23.62	3.31	8
P_2 cw	15.09	2.38	8
P_3 cl	31.43	4.22	8
P_3 cw	21.44	3.40	10
P_4 cl	37.43	3.05	16
P_4 cw	26.49	4.29	15
M_1 cl	44.10	2.45	12
M_1 cw	28.92	1.37	12
M_2 cl	48.26	3.04	15
M_2 cw	30.04	1.61	14
M_3 cl	51.70	1.57	12
M_3 cw	30.14	1.32	14

Table 8. Crown length (cl) and crown width (cw) in mm of permanent premolars and molars from *Coelodonta antiquitatis.*

file of the Mousterian unit resembles Haynes' (1991) Type B age profile as well as Haynes' (1991) Type A age profile, with a marked absence of older age classes.

Coelodonta antiquitatis

The woolly rhinoceros is represented with about 5 % of the NISP and 8 % of the MNI of the total material from Spy. The remains are dominated by dental material (89.5 %; ST8). A detailed age attribution of the teeth was carried out based on Goddard's (1970) age classes (ST9). A large MNI was obtained, making the woolly rhinoceros the third most frequent species in MNI. The measurements of the premolars and molars are given in Table 8.

A humerus fragment shows a cut mark. Three teeth display ochre traces, and they are from at least two individuals: a fragmented crown with little wear, a deciduous P^3 (c. 2 b.r.y.) and a P^2 with



Figure 12. Gnawing traces on distal half of woolly rhinoceros humerus (16604).

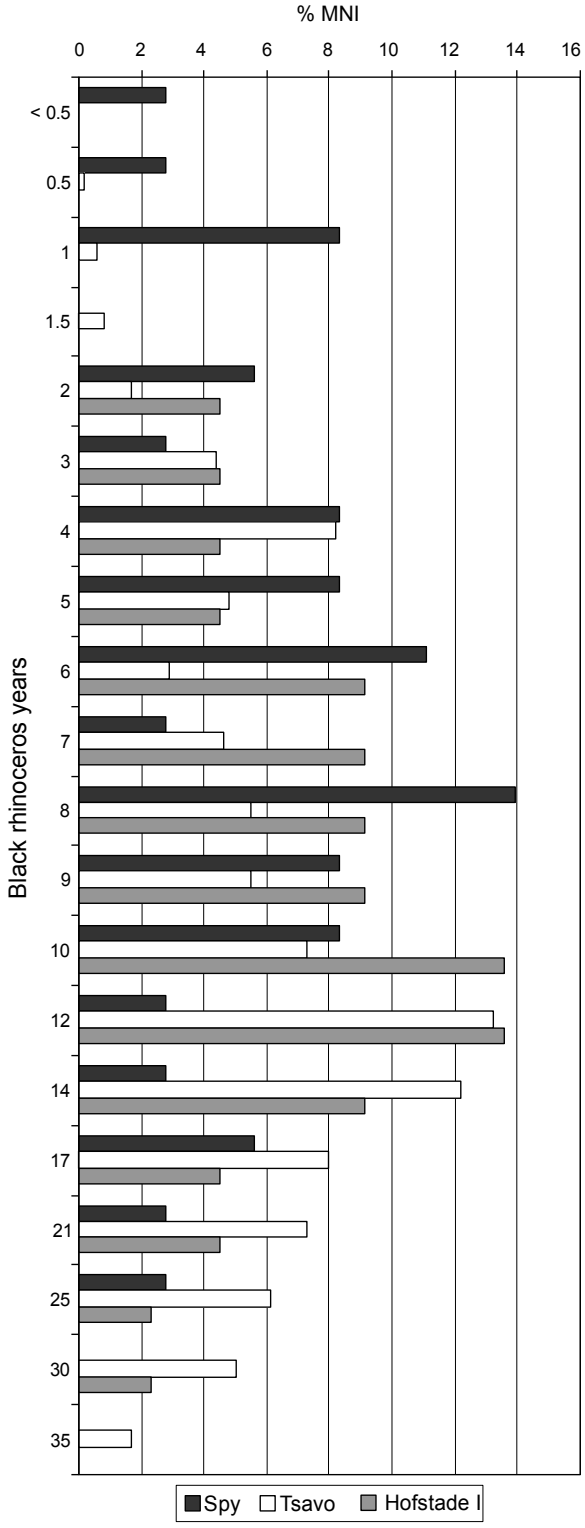


Figure 13. Age distribution of the jugal dentition of woolly rhinoceros compared with the distribution of the woolly rhinoceros from Hofstade I (Germonpré, 2003) and the extant black rhinoceros from Tsavo, Kenya (Goddard, 1970); MNI: Mininum Number of Individuals.

	Total		*Cut marks*	*Gnawing traces*	*Gastric traces*	*Ochre*
	NISP	MNIe	NISP	NISP	NISP	NISP
Maxilla	3	3				
Mandible	2	2				
Deciduous teeth	91				1	
I^1	52	23				
I_1	87	44				
I^2	53	29				1
I_2	71	36			2	
I^3	33	18				
I_3	65	33			1	
I indet.	104				8	
C	39	10				
P^2	281	140			1	1
P_2	151	124			1	
M^3	283	140				
M_3	242	120			1	1
P3/M2	2,628				4	3
P/M indet.	161				3	
Vertebrae						
atlas	1	1				
Humerus	1	1		1		
Ulna	1	1				
Radius	4	2				
Carpals	10			1		1
MC	20	8		7		
Femur	2	1		1		
Tibia	11	5	1	5		
Tarsals						
astragalus	19	14		4	4	
calcaneum	1					
other	8					
MT	19	9		6		1
Metapodials	12			4		
Metapodials lat.	15	7	1	3		
Sesamoids	4					
Phalanges I	11			4		
Phalanges II	12			6		
Phalanges III	2					1
Total NISP/MNI	*4,499*	*144*	*2*	*42*	*26*	*9*

Table 9. *Equus ferus*. List of material: NISP = Number of Identified Specimens; MNI = Minimum Number of Individuals; MNIe = Minimum Number of Individuals per skeletal element.

very slight wear (c. 4 b.r.y.; SF4). This P^2 has an AMS age of c. 32,900 BP (Semal *et al.*, this volume: chapter XVI). A milk molar from a calf less than six months old has an AMS age of c. 44,400 BP (Semal *et al.*, 2009). A third AMS date on a P_4 from a rhinoceros of about six b.r.y. gave an age of c. 25,700 BP (Semal *et al.*, 2009).

A large number of long bones show gnawing traces of large carnivores (Figure 12), including the cut-marked humerus, produced most probably by cave hyenas. Furthermore, two deciduous P^2 display traces from gastric acids: one with little wear (c. 1 b.r.y.) and one with heavy wear (c. 2 b.r.y.).

In the age distribution, a first peak can be observed at the age of one year (Figure 13; ST9). A second peak is reached at an age between six to nine b.r.y. Animals older than 25 b.r.y. are lacking. The Spy material is compared with the woolly rhinoceros from the Pleniglacial fluvial site of Hofstade I located some 150 km to the west of Spy (Germonpré, 1989, 1993). At Hofstade I, the age profile is dominated by remains of animals of about 10 - 12 b.r.y. The black rhinoceros that died from 1958 to 1968 in Tsavo National Park, Kenya, are also included in the graph. The Tsavo profile shows a bimodal distribution with a subadult peak (animals of around four b.r.y.) and an adult peak with animals in the 12 - 14 b.r.y. range (Goddard, 1970).

Equus ferus

Horse is the best represented species as well in NISP (39 %) as in MNI (34 %). Teeth are the dominant skeletal element with 95 % of the NISP (Table 9). The horse belongs to Group A. The most frequent tooth is the third molar (M3) with a NISP of 525 (upper and lower com-

	Gl	*Ll*	*Bp*	*Bd*
MC				
Carpentier collection	218.0	209.0	51.2	50.0
Université de Liège, (Spy IV 2b - 4364)	225.0	215.0	53.1	48.9
MT				
Carpentier collection	271.0	266.0	53.0	54.3
Carpentier collection	270.5	265.0	51.1	50.4
MRAH (*deuxième réserve*)	275.0	269.0	55.6	58.5
MRAH (*deuxième réserve*)	266.0	260.0	51.0	51.8

Table 10. *Equus ferus*. Measurements on metacarpi (MC) and metatarsi (MT); Gl: greatest length; Ll: lateral length; Bp: proximal width; Bd: distal width.

bined). This is in contrast with the low frequency of the canine with a total NISP of 39 (upper and lower C combined). The ratio MNIC/MNIM3 is about 1/14. The total MNI is 144, based on the M^3, germs of the P^2, deciduous incisors and permanent incisors. Some 22 teeth display traces of gastric acid. Gnawing marks occur on 27 % of the postcranial bones. Evidence of human manipulation occurs on teeth and postcranial bones. Six teeth (0.14 % of the teeth NISP) and three postcranial elements (2 % of the postcranial bones NISP) present ochre traces. A tibia and an accessory metacarpal show cut marks (1.3 % of the postcranial bones NISP). Based on the length of six complete cannon bones, the Spy horses can be estimated to have been of moderate size (Table 10). The Kiesewalter index gives a shoulder height ranging between 134 cm and 143 cm with a mean of 140 cm (*cf.* von den Driesch & Boessneck, 1974). An AMS date on a jugal tooth from the unit *Moustérien en place* gave an age of c. 32,800 BP. However, the parameters of the yield and carbon content of this date indicate a poor quality of the collagen, so this date is questionable (Semal *et al.*, this volume: chapter XVI).

The large number of teeth permits to reconstruct an age profile. The profile is based on the complete Spy horse assemblage, without taking into account the stratigraphic position of the finds, since in most cases this is not known. It is dominated by animals in the age range of six to twelve years (Figure 14; ST10). Juveniles are most probably underrepresented. The Spy profile is com-

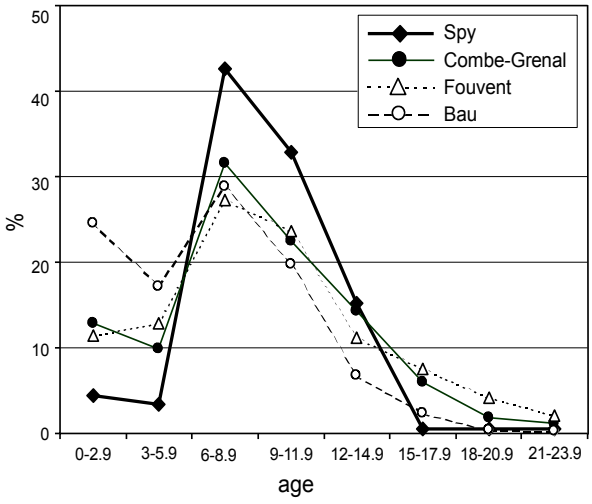


Figure 14. Age distribution of the dentition of the horses from Spy, Combe-Grenal, Fouvent and Bau de l'Aubesier (Fernandez *et al.*, 2006).



Figure 15. Gnawing marks on a cast antler of a male reindeer (16615).

pared with that of two Neandertal sites (Bau de l'Aubesier and Combe-Grenal) and one cave hyena den site (Fouvent) described in Fernandez *et al.* (2006). These three profiles are also dominated by groups with an age between six and twelve years.

	Adult		*Subadult*		*Juvenile*		*Total*		*Ochre*	*Cut/worked*	*Carnivores traces*
	NISP	*MNIe*	*NISP*	*MNIe*	*NISP*	*MNIe*	*NISP*	*MNIe*	*NISP*	*NISP*	*NISP*
Antler	56	5					56	5		6	6
Skull	2	2					2	2			
Mandible	6	2			2	2	8	4			
dp^4	3	2					3	2			
P^2	4	1					4	1			
P_2	2	1					2	1			
P^3	5	3					5	3			
P_3	2	1					2	1			
P^4	4	3					4	3			
P_4	6	4					6	4			
M^1	2	1					2	1			
M_1	2	1					2	1	1		
M^2	5	2					5	2			
M^3	1	1					1	1	1		
M_3	10	6			1	1	11	7	1		
Teeth indet.	62						62		1		
Rib	1	1					1	1	1		
Scapula	1	1	1	1			2	2	1		
Humerus	1	1					1	1		1	
Radius	3	2					3	2			
Carpals	2	2					2	2			
MC	9	2	1	1			10	3	1	3	3
Femur	6	2					6	2	3		
Patella	3	2					3	2			
Tibia	7	2	2	1			9	3	1	1	
Tarsals							0				
astragalus	12	6					12	6			
calcaneum	5	4					5	4	1		
other	9	2					9	2	3		
MT	19	5	1	1			20	6	9	4	
Metapodials	13		3				16		10		
Sesamoids	1	1					1	1			
Phalanges I	43	9	5	2	1	1	49	12	13	3	
Phalanges I acc.	1	1					1	1			
Phalanges II	32	7	1	1			33	8	8	6	
Phalanges II lat.	8						8		6	2	
Phalanges III	16	4					16	4	6		
Phalanges III lat.	9						9		7		
Phalanges - other	1						1				
Total NISP/MNI	*374*	*9*	*14*	*2*	*4*	*3*	*392*	*14*	*77*	*26*	*9*

Table 11. *Rangifer tarandus.*
List of material: Cut/worked = cut marked and worked bones; NISP = Number of Identified Specimens; MNI = Minimum Number of Individuals; MNIe = Minimum Number of Individuals per skeletal element.

Rangifer tarandus

The reindeer belongs to Group C and is characterised by a large frequency of postcranial bones (Table 11). It is represented with a NISP of 392 and a MNI of 14. A total of 56 antler fragments were identified. Six fragments are tools. Eleven are cast antler fragments. One of these was of an adult male (Figure 15); the others are from females and/or young animals.

On six of the cast antlers, gnawing marks occur: the tines have been removed by carnivores. Two antler fragments are still attached to the skull; they are also from a young or female individual. Two lower jaws contain milk dentition only.

Teeth are also quite numerous. The best represented postcranial elements are the phalanges (Table 11). The first phalanx corresponds to 20.3 %, the second phalanx to 18.4 % and the third phalanx to 11.5 % of the number of the postcranial bones. Interesting to note is the high frequency of postcranial bones with signs of human manipulation (Table 11). Red pigment traces occur on 32 % of the postcranial material (Figure 18; SF1), especially on the distal elements (phalanges, metapodials, carpals and tarsals). Cut marks are present on 9 % of the postcranial bones (Tables 3 & 11; Figures 16-17). They occur on the distal part of a humerus, a tibia and metapodials, on some tarsalia, and on a large number of the phalanges (Table 11). The postcranial material is highly fragmented. All long bones and metapodials are broken. 60 % of the first phalanges, 16 % of the second phalanges and 13 % of the third phalanges are broken. Gnawing traces occur on 14 % of the postcranial bones.

Four AMS dates on reindeer remains are available: c. 26,400 BP on a metatarsus fragment with cut marks and ochre traces; c. 29,000 BP on a phalanx from the unit *niveau moyen*; c. 34,400 BP on a metatarsus fragment with ochre traces and c. 36,900 BP on a cut-marked metacarpus fragment also from the unit *niveau moyen* (Semal *et al.*, 2009, this volume: chapter XVI).

- *Large Bovids*

Large bovids occur with a NISP of 468. Of these a small percentage could be assigned to *Bos primigenius* (6 %; ST11) and *Bison priscus* (2 %; ST12). In both the aurochs and the steppe bison, the metacarpi display cut marks. The



Figure 16. a: Cut marks on a distal humerus (10042) of reindeer, identified as the Hd-5 cut mark (Binford, 1987) produced during dismembering; b: Detail of the cut marks on the distal humerus (10042) of reindeer.

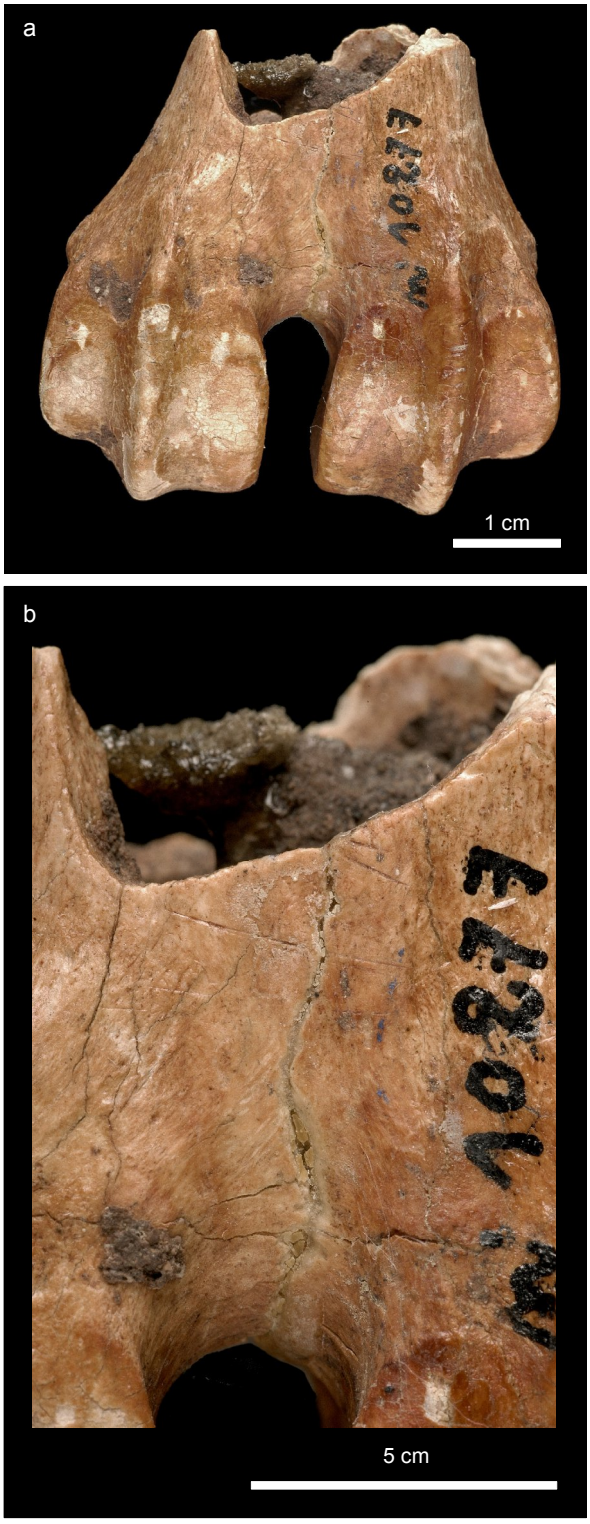


Figure 17. a: Cut marks on the distal fragment of a reindeer metatarsus (10277);
b: Detail of the cut marks on the distal fragment of a reindeer metatarsus (10277);
c: Cut marks on a first phalanx (16595) of a reindeer.

bulk of the material could not be further identified as *Bison priscus/Bos primigenius* (ST13). Large bovids constitute in total 9 % of the complete Spy assemblage (Table 2). The large bovids belong to Group B. Teeth and postcranial elements are more or less equally represented. Red pigment traces are present on 4 % of the postcranial elements, while carnivore traces occur on about 24 % of the postcranial. In addition to the aurochs and bison cut-marked metacarpi, a third phalanx displays also cut marks, bringing the total frequency of cut-marked bovid postcranial bones to 3 %.

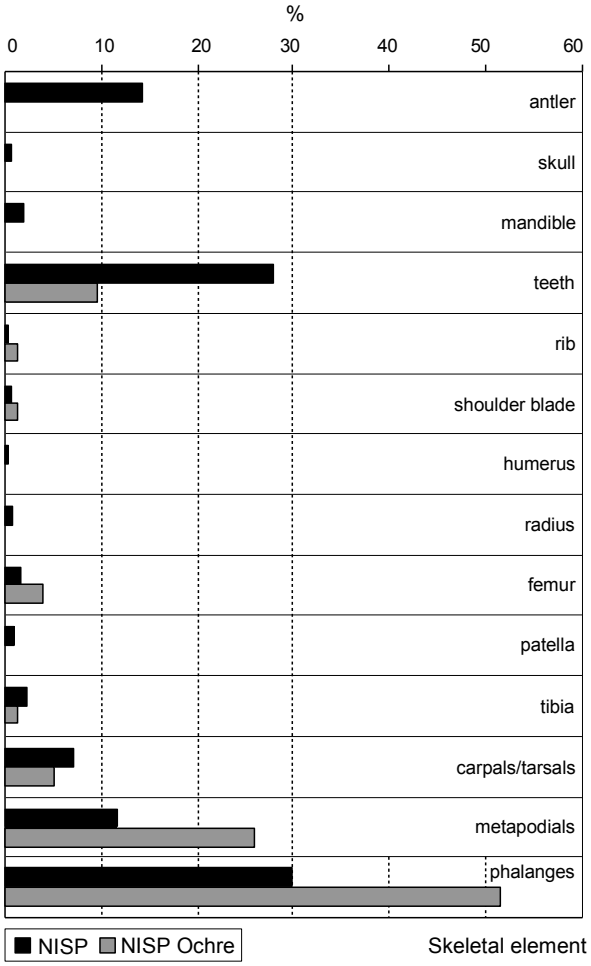


Figure 18. Comparison of the frequency distributions of the NISP of the skeletal elements with the NISP of ochre stained skeletal elements from reindeer (NISP: Number of Identified Specimens).

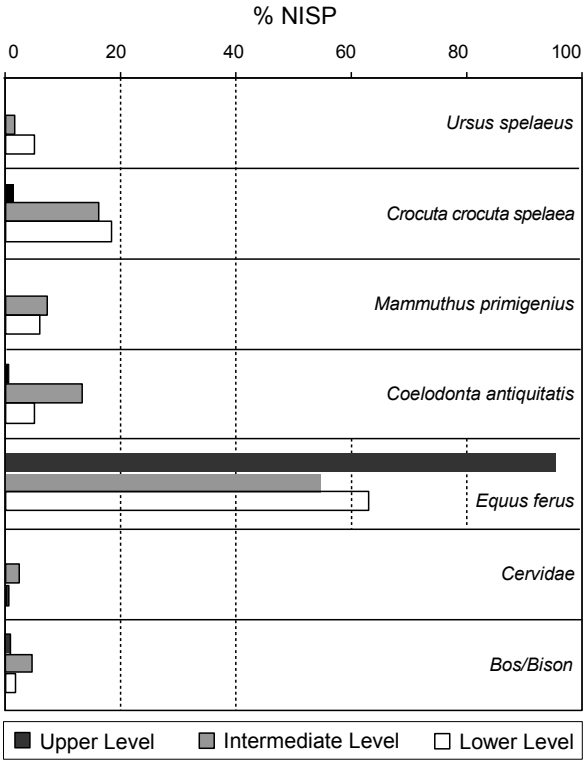


Figure 19. Comparison of the frequency distributions of the NISP of the most important species in the three assemblages dating from the Gravettian (Upper Level), Aurignacian/Mousterian (Indermediate Level) and Mousterian (Lower Level) (NISP: Number of Identified Specimens).

Composition of the units

The species distribution of the stratigraphic units is given in ST14 and Figure 19. Cut-marked bones are very rare in these units. Since a good correlation exists for the species present between ochre-marked and worked bones (see above), ochre is taken here as an indicator of the human manipulation on the mammalian remains.

Species frequencies are generally similar on the terrace and inside the cave. However, horse is better represented (Chi-square $\chi^2 = 63.2$, $P < 0.0001$) on the terrace (52 % NISP) than inside the cave (20 % NISP), while cave hyena is more frequent (Chi-square $\chi^2 = 23.07$, $P < 0.0001$) inside the cave (29 % NISP) than on the terrace (17 % NISP). Teeth are better represented (Chi-square $\chi^2 = 77.04$, $P < 0.0001$) on the terrace (82 %) than inside the cave (61 %), while post-cranial bones are more frequent (Chi-square $\chi^2 = 73.52$, $P < 0.0001$) inside the cave (36 % NISP) than on the terrace (17 %). When comparing evidence of human influence on the terrace to the cave, a number of differences are obvious. On the terrace, many groups display ochre traces: unidentified carnivores, mammoth, horse, hydruntine horse, red deer, reindeer, unidentified cervids, and *Bos/Bison*. Inside the cave the bones of only four groups show ochre traces: woolly rhinoceros, horse, reindeer, and unidentified mammals. The frequency of bones with ochre traces on the terrace (1.9 %) and inside the cave (1.4 %) is low. Carnivore traces are significantly more frequent (Chi-square $\chi^2 = 17.92$, $P < 0.0001$) inside the cave (6 %) than on the terrace (2 %). On the terrace, mammoth, rhino-

ceros, horse, large bovids and unidentified mammalian bones show evidence of carnivore damage. Inside the cave, apart from the foregoing animals, some cervid bones were also gnawed by carnivores.

In the following we detail the composition of each stratigraphic unit on the terrace as well as inside the cave (Table 1A; ST14). Details on the AMS dates can be found in Table 1A and in Semal *et al.* (this volume: chapter XVI). First the units of the terrace are treated. In all units, except unit *niveau moyen*, where horse is lacking, horse is the best represented species.

The *terrasse* unit is the richest unit on the terrace and contains material from both the Upper and Middle Palaeolithic. Ochre traces occur on 5 % of the bones and carnivore traces on 3 %. Reindeer is, after horse and hyena, the third best represented species. Almost 70 % of its remains display ochre traces. Ochre is lacking on the bones of horse and hyena from this unit.

The Upper Level contains the unit *niveau supérieur*. Only two carnivore damaged bones occur. Two horse remains (from *Equus ferus* and *Equus hydruntinus*) show ochre stains. Cervids are lacking all together. A rhinoceros tooth has an AMS age of c. 25,700 BP.

The Intermediate level includes the units *terrasse niveau rouge*, *niveau inférieur ou rouge*, *deuxième niveau moustérien supérieur*, and *niveau moyen*. They contain a mixture of Aurignacian, Lincombian-Ranisian-Jerzmanowician and Mousterian material. In *terrasse niveau rouge*, three horse remains display ochre traces. In the *niveau inférieur ou rouge*, cervids are present in low frequencies. An ochre-stained jugal tooth of *Equus hydruntinus* has an AMS age of c. 34,600 BP. The *niveau moyen* contains only 14 specimens, reindeer is best represented. The two AMS dates on reindeer bones from this unit are very scattered: c. 29,000 BP and c. 36,900 BP. In the *deuxième niveau, Moustérien supérieur*, mammoth and rhinoceros are rather well represented.

The Lower Level consists of the units *terre jaune, terrasse niveau noir*, *troisième niveau*, *niveau moustérien en place* and *troisième niveau foyer inférieur*. These units did not deliver bones with red pigment traces. The *terrasse niveau noir* and *troisième niveau* are dominated by horse and hyena remains. Two AMS dates on a mammoth tooth and a hyena tooth from the former unit are very similar (c. 42,900 BP). In the *troisième niveau foyer inférieur*, horse and mammoth are the most important species. The *niveau moustérien en place* has a NISP of only 5 specimens of both horse species. An AMS date on a jugal tooth resulted in an age of c. 32,800 BP, but the quality of the collagen is probably not good enough. So this date can be rejected (see also Semal *et al.*, this volume: chapter XVI).

Inside the cave, horse is also the dominant species of all units, except for unit *petite salle à droite* and *niveau supérieur de la grotte* where cave hyena has the highest frequency. The assemblage *petite salle à droite* did yield one ochre coloured tooth from a horse. Carnivore damaged bones are absent. The "Interior of the cave" has 1.6 % of ochre coloured bones, but no carnivore damaged bones. A rhinoceros premolar with ochre traces from this unit has an age of c. 32,900 BP (Table 1A; Semal *et al.*, this volume: chapter XVI). The "Mousterian" unit *troisième niveau, galerie de droite* contains the highest frequency of bones with carnivore gnawing traces with 15 % of the bones damaged. This unit also yielded the highest frequency of cave bear material. Ochre traces are absent.

Figure 19 shows the frequencies of the most important taxa. Interesting to note is the increase of the horse remains and the decrease of hyena and rhinoceros material from the Lower Level over the Intermediate Level to the Upper Level.

DISCUSSION

The faunal assemblage of Spy is very large. Unfortunately, the bulk of the material was not assigned to a stratigraphic level, which hinders a detailed interpretation of the faunal remains.

Based on the small assemblages that could be assigned to a stratigraphic unit on the terrace or inside the cave it is clear that carnivores were more active inside the cave than on the ter-

race. Carnivore traces are significantly more present inside the cave. Also the remains of cave hyena occur more frequently inside the cave. The large number of individuals and the presence of remains from hyena cubs demonstrate that the Spy cave was used as a communal den probably during recurrent occupations.

On the terrace, the Upper Level has a thickness of 80 cm to 100 cm (De Puydt & Lohest, 1886). The artefacts can in general be attributed to the Gravettian (Dewez, 1981; Pirson *et al.*, this volume: chapter VI). A rhinoceros premolar from this level has an AMS age of about 25,700 BP (Semal *et al.*, 2009). This Upper Level contains only one stratigraphic unit: the *niveau supérieur* (Table 1A). The horse is the dominant species of this level with 95.6 % of the NISP, the second best represented species is the cave hyena. Ochre stains occur on 1 % of the bones, and carnivore damaged bones are limited to 1 % of the remains.

The Intermediate Level or red level has a thickness of 5 to 30 cm (De Puydt & Lohest, 1886). Its artefacts belong to the Aurignacian, Lincombian-Ranisian-Jerzmanowician and/or Mousterian. According to Fraipont & Lohest (1886, 1887), this level yielded a large part of the bone and ivory implements and ornaments. The ivory ornaments and tools from Spy were fabricated during the Aurignacian and the Gravettian (Otte, 1979; Khlopachev, this volume: chapter XIV). Ochre traces occur on many of the ivory implements. AMH are known to have used red ochre for several reasons (e.g. Germonpré & Hämäläinen, 2007). Recently, Soressi & d'Errico (2007) concluded that Neandertals used mainly black pigments and rarely red ochre. Given that Neandertals apparently did not use red ochre on a regular basis, the presence of red ochre at Spy is most likely to be related to the presence of AMH. This is confirmed by the fact that at Spy none of the units from the Lower Level that is attributed to the Middle Palaeolithic contain ochre-stained bones (Table 1).

An ochre-stained tooth from *Equus hydruntinus*, discovered in unit *niveau inférieur ou rouge*, has an AMS age of c. 34,600 BP (Table 1A; Semal *et al.*, this volume: chapter XVI). A reindeer phalanx found in the *niveau moyen* has an AMS age of about 29,000 BP, another reindeer bone from this same unit delivered an AMS age of c. 36,900 BP, pointing to a certain amount of mixing between this unit and the older bone levels or to imprecise excavations (Semal *et al.*, this volume: chapter XVI). When the limited number of bones from the Aurignacian/Mousterian units (*terrasse niveau rouge*; *niveau inférieur ou rouge*; *niveau moyen*; *deuxième niveau, moustérien supérieur*) is grouped, the horse is the dominant species with about 55 % of the NISP, the cave hyena is second with about 16 % and the third species is the woolly rhinoceros with 13 %. Ochre stains occur on 1.3 % of the bones. Ochre-stained ornaments, which partly derive from this level, are not included in this calculation since their exact stratigraphic attribution is unknown. So the frequency of ochre-stained remains from this level could be higher. Carnivores damaged about 3 % of the mammalian bones.

The Lower Level is a few cm to 1 m thick and is composed of a yellow clay lying above a dark brown clayey horizon. In the Lower Level, remains from horse are the most abundant, remains from woolly rhinoceros, bovids, mammoth and hyena are abundant, remains from red deer, badger and cave bear are rare, and reindeer remains are very rare. The following stratigraphic notes are associated with this level: *terre jaune, Moustérien en place, troisième niveau foyer inférieur, troisième niveau et terrasse niveau noir*. The adult Neandertal bones were found at the top of the brown, blackish horizon. It is not entirely clear whether they were found inside the dark brown horizon or inside the yellow clay above the brown horizon, although they were found under the Intermediate Level. They have AMS ages of about 36,000 BP. However, on the basis of the AMS dates of two bones from the dark horizon (*terrasse niveau noir*), which are around 43,000 BP (Table 1), the Neandertal skeletons are too young to be contemporaneous with the faunal remains from the black horizon; it seems that the skeletons could have originated from the yellow clay, i.e. from the upper part of the Lower Level. One mammoth milk molar, without stratigraphic provenance, has an AMS age of 37,010 +440/-380 BP (GrA-37933). Its AMS age suggests that it is more or less contemporaneous with the adult

Neandertals. The two comparable AMS dates of c. 43,000 BP from the unit *terrasse niveau noir* (Table 1A) are from a molar fragment of a subadult mammoth and a carnassial tooth of a hyena. A mammoth milk molar without stratigraphic attribution has an AMS age of 42,330 +550/-450 BP (GrA-32616); its AMS age suggests that it could be contemporaneous with the animals found in the *terrasse niveau noir*. The artefacts from the Lower Level are all described as Mousterian. There are no bone or ivory tools in this horizon. The horse accounts for 63.5 % of the bones to which we had access and that are from the Lower Level. The hyena is also well represented with 18 % of the NISP. The mammoth is present with 6 % of the NISP. Bones damaged by carnivores account for 1 % of the NISP. No ochre traces occur on bones or stone tools from this level. The fact that red pigment traces on bone material are absent from the supposedly Mousterian units can possibly confirm their attribution to the Middle Palaeolithic. Two comparable dates are available for the unit *terrasse niveau noir* (c. 42,800 BP and c. 43,000 BP). Interesting to note is the AMS date of c. 36,900 BP of a cut-marked reindeer bone from the small unit *niveau moyen* that contains both early Upper Palaeolithic and Middle Palaeolithic material. This date is comparable to the AMS dates of the Neandertal skeletons (Semal *et al.*, 2009).

Inside the cave, the dated rhinoceros premolar with ochre traces from the unit *Intérieur de la grotte* has an AMS age of c. 32,900 BP, suggesting an early Upper Palaeolithic presence. The "Mousterian" unit did not yield ochre.

The stratigraphic units with artefacts dating from the Middle or Upper Palaeolithic and the range of AMS dates on remains manipulated by humans suggest that both Neandertal and Anatomically Modern Humans (AMH) visited intermittently the site.

In the assemblages, combining all Pleistocene finds, the frequency distribution of the different skeletal parts of a number of species seems to be biased. In Group A including horse, cave hyena, rhinoceros and mammoth, teeth are the best represented part. Enamel is the hardest skeletal tissue and dentine, softer than enamel, is still harder than compact bone (Lyman, 1994). Teeth preserve therefore in general quite well. Postcranial horse bones were heavily utilised by cave hyenas. The same can be concluded for the woolly rhinoceros. The low frequency of hyena postcranial body parts can maybe be explained by destruction of the remains through cannibalism. The high frequency of mammoth dentition is to be expected. In other Belgian caves as well, mammoths are essentially represented by tusk fragments, worked ivory and jugal teeth. Group B contains species with more or less equal frequencies of dentition and postcranial parts. This group includes the bears, wolf, large bovids, giant and red deer. In Group C, the postcranial remains dominate, although teeth are still frequent. The mammals in this group are reindeer, and the foxes. It is possible that during the excavations the small isolated teeth of these species were somewhat overlooked. Mineral densities of the skeletal elements can furthermore not be invoked to explain the frequency distribution of the reindeer remains. The elements with the highest bone mineral densities (excluding teeth) for deer are the carpals/tarsals, metacarpals/metatarsals, and tibia (Lyman, 1994). The mineral densities of the phalanges score about the lowest among the skeletal elements of deer (Lyman, 1994). Nevertheless, reindeer phalanges are at Spy the best represented elements of the postcranial material. As a conclusion we can say that, generally speaking, the skeletal element distribution is biased at Spy.

At Spy, human activities are clearly signalled by the occurrences of worked, cut marked and ochre stained bones. A significant correlation exists between the frequency of cut marked bones and worked teeth *vs*. red-ochre stained bones compared by taxon (Figure 3). Also, the frequency of ochre stained remains of the preponderant species, the horse, is much lower than expected. In addition, the most frequent skeletal element, the dentition, displays few ochre traces (Figure 4). If the ochre colouring of bones was caused by contact with ochre containing sediment or by the accidental covering with spilt ochre, an *ad random* distribution of red pigment adhering to the different skeletal elements could be expected. This is clearly not the case at Spy. Based on the above, the presence of the ochre traces cannot be explained by a contamination by coloured sediment or contact with spilt ochre, while human involvement obviously is a better explanation.

Therefore we conclude that most of the ochre staining of the bones is the result of an intentional process by prehistoric people and not due to contamination with spilt ochre or contact with ochre containing sediments.

The appearance of the first AMH in Africa coincides with the recurrent evidence of the use of objects and/or acts in the "symbolic" realm (Clark *et al.*, 2003; Henshilwood *et al.*, 2004; Vanhaeren *et al.*, 2006; Barham & Mitchell, 2008). The use of red ochre has been established in Southern Africa from the Middle Stone Age on (McBrearty & Brooks, 2000; Henshilwood *et al.*, 2002; Watts, 2002). Middle Stone Age people preferred red colorant to yellow or brown (Watts, 2002; d'Errico, 2003). Detailed analyses of Middle Stone Age ochre assemblages have shown that the ochre nodules with the reddest hues and most saturated nuances ("blood red") were preferentially used. This permits to conclude that ochre was mainly used as pigment and that a utilitarian use was limited. Furthermore, a regular pigment use can be considered as supporting colour symbolism (Henshilwood *et al.*, 2009; Watts, 2009). Not only AMH are known to have used pigment, there is some evidence that also Neandertals utilised it. Recently, Zilhão *et al.* (2010) reported a few ochre-stained perforated marine shells in two Middle Palaeolithic Iberian sites. Bordes (1952) excavated in the cave of Pech de l'Azé, France, hundreds of blocks of colorants, mainly manganese, in a Mousterian of Acheulean Tradition context and considered that the Mousterian people employed the blocks for body paint or for colouring animal skins. The numerous manganese blocks of Pech de l'Azé show clear traces of utilisation, while the few red and yellow ochre blocks do not. Furthermore, other European sites attributed to a Mousterian of Acheulean Tradition or Charentian-type Mousterian yielded manganese dioxides (Soressi & d'Errico, 2007). These latter authors conclude that Neandertals used mostly black pigments, only rarely ochre. Since Neandertals apparently did not utilise red ochre on a regular basis, the presence of red ochre at Spy is most likely related to the presence of AMH. Indeed, at Spy, none of the lower units, attributed to the Mousterian, delivered ochre-stained bones (Table 1A; ST14). The oldest unquestionable remains of AMH in Europe, found at the Peştera cu Oase, have an AMS age of about 35,000 BP; unfortunately, they are not associated with an archaeological industry (Trinkaus *et al.*, 2003). According to Jöris & Street (2008), the Aurignacian seems to emerge at the same time over Europe around 35,000 BP. The utilisation of ochre in figurative art can be placed at about this time. Red ochre paintings including a schematic human head adorned with horns from the Fumane cave in Italy are believed to be about 35,500 years old. This age attribution is based on the dating of charcoals in the Early Aurignacian unit A2 which contains ochre of the same type as was used in the red paintings (Broglio *et al.*, 2009). Furthermore, at Isturitz cave (Southern France) recent AMS dates of cut-marked bones, from a layer sandwiched between a unit attributed to the Proto-Aurignacian and containing numerous artefacts belonging to the "symbolic" realm and a unit attributed to the Early Aurignacian, place the transition/switch between the Proto-Aurignacian and the Early Aurignacian at c. 37,200 BP (Szmidt *et al.*, 2010b). Moreover, closer to Spy, the Proto-Aurignacian site of Trou de la Mère Clochette in North-Eastern France yielded split-based organic points of which one is dated at c. 35,500 BP (Szmidt *et al.*, 2010a). Also at Spy there is evidence for the presence of the Proto-Aurignacian and the Early Aurignacian based on the occurrence of Dufour bladelets and split-based points (Flas *et al.*, this volume: chapter XII). Human remains associated with the Aurignacian are sparse and often restricted to teeth. A recent detailed analysis of isolated dental remains from more than 30 Aurignacian sites points to AMH as the makers of the Aurignacian (Bailey *et al.*, 2009). The oldest indication of the utilisation of red pigment at Spy – and in Belgium – dates from around 34,500 BP. Ochre stained elements from three different species delivered the following AMS dates: c. 34,600 BP for a bear incisor with a "failed" perforation; c. 34,600 BP for a hydruntine horse tooth discovered in the Intermediate Level; and c. 34,400 BP for a broken reindeer metatarsus (Semal *et al.*, 2009, this volume: chapter XVI; Tables 1A-1B). These AMS dates are in agreement with the presence of the Aurignacian associated with the occurrence of AMH in Europe. At Spy, a next phase of pigment utilisation occurred at c. 32,900 BP, based on the AMS date of an ochre-stained rhinoceros premolar, a date that is similar to the AMS date of the Aurignacian spear point carved out of a cave bear bone (Semal *et al.*,

this volume: chapter XVI; Bocherens *et al.*, this volume: chapter XVII). Finally, a third phase of ochre utilisation at Spy seems to have taken place around 26,000 BP (Table 1A).

Unfortunately, the presence of ochre traces on mammalian bones dating from the Upper Palaeolithic has been rarely treated in the literature. Exceptions are the discussion of red ochre associated with human burials, the presence of ochre on personal ornaments, and the occurrence of ochre on bones in Belgian Upper Palaeolithic caves. In Europe, red ochre is a traditional element in the ceremonial human burials from the Gravettian (Djindjian *et al.*, 1999; Mussi, 2000). Human burials with ochre date in the West from c. 29,000 – 28,000 BP ("Red Lady of Paviland": Jacobi & Higham, 2008), in Central Europe from c. 26,600 BP (Triple burial from Dolní Věstonice: Formicola *et al.*, 2001; the infant burials at Krems-Wachtberg: Einwögerer *et al.*, 2006); and further to the east from c. 24,000 BP (Double child burial of Sunghir 2 and 3: Formicola & Buzhilov, 2004). Red ochre is also typically associated with Magdalenian burials (Sacchi, 2003). Ochre was also used as a metallic abrasive to obtain lustre on ivory beads dating from the Aurignacian (White, 1997). At Spy, about 5 % of the ivory ornaments display ochre traces (SF2, SF3). This is the frequency after the cleaning of the ornaments; initially the frequency could have been higher. Regarding the presence of red ochre on skeletal elements of all taxa combined, it is notable that at Spy the most frequent body parts with ochre traces are paw elements, while teeth with ochre marks are underrepresented. Mammoth ivory fragments, many with ochre stains, are separated from the dentition of other mammals (Figure 4). This same pattern was also discovered in other Belgian caves, where the same type of bear bones with ochre traces suggests the existence of Upper Palaeolithic bear rituals (Germonpré & Hämäläinen, 2007). At Spy, the most important taxa associated with ochre are: reindeer, unidentified cervids, mammoth and red deer. Interesting to note is that with the mammoth, ochre occurs solely on ivory, not on other skeletal elements. The following carnivores also display a few elements with ochre traces: red fox, wolf, cave bear and brown bear (Table 3).

Based on the general overview of the frequency of the traces (Table 3), we conclude that prehistoric humans dealt especially with the cervids, mammoths and foxes. There is a difference between the cervids, the mammoths and the foxes in that in the cervids, the postcranial bones show most of the traces of human manipulation, while for the mammoths and foxes mainly the teeth show evidence of human actions. There is no significant difference in the ratios of the perforated to unmodified arctic fox canines and red fox canines during the Pleniglacial and the Late Glacial in the Belgian material (Table 4). This suggests that the Upper Palaeolithic people did not have a preference for either fox species. Although red foxes were, without doubt, more rarely encountered in the Weichselian landscape of the region than the arctic fox, the Palaeolithic people seemingly did use fox canines as ornaments in the proportions the species were captured. The presence of paw elements suggests that the arctic foxes were taken for their pelt as well, probably in winter. A pup died in early summer, based on the lower jaw with milk dentition. The red fox skeletal elements are more evenly distributed than the arctic fox material. This could mean that the foxes were also using the Spy cave as a den. According to White (1997) and Vanhaeren (2002), perforated fox canines predominate in Northern Europe during the Aurignacian among pierced teeth used as personal adornment.

The cave bears used the Spy cave as a den, as shown by the presence of first and second winter cubs together with female cave bears. At Goyet, the mean crown width of the male canines is above 20 mm, while that of the mean width of the female canines is less than 19 mm (Germonpré, 2004). This suggests that the upper canines discovered at Spy are mainly from large, male animals (Figure 7), so the Spy cave was probably mostly used by male cave bears. At Spy, especially isolated teeth and paw elements occur. As in Goyet (Germonpré & Hämäläinen, 2007), there is some evidence of human interference with cave bears: one claw displays red ochre stains and a bear bone was used to make a spear point. The AMS age of c. 32,800 BP of this point makes it one of the oldest dated witnesses of the Aurignacian in Belgium (Flas, 2008; Semal *et al.*, 2009; but see also Flas *et al.*, this volume: chapter XII).

The brown bear is also represented by teeth and paw elements. Two incisors were ma-

nipulated by prehistoric people. A third upper incisor is perforated (Figure 6). Interesting to note is the old age of a second upper incisor with ochre traces which is partly perforated through scraping. An AMS date on this specimen resulted in an age of c. 34,600 BP (Semal *et al.*, 2009). Among the carnivores only bears and canids (foxes and wolf) are regularly present with modified teeth in Upper Paleolithic sites. Perforated canines and incisors from both cave bear and brown bear occur regularly from the Aurignacian on (Pacher, 2005; Vanhaeren & d'Errico, 2006). However, perforated bear teeth in Belgium are quite rare. Many of those figured in the literature are in fact misidentified wolf teeth (Otte, 1979). The occurrence at Spy of two perforated brown bear incisors is thus exceptional.

The most important carnivore at Spy is the cave hyena. According to de Loë & Rahir (1911), cave hyena remains were especially plentiful in the third (lowest) level. They are practically absent in the Gravettian level (Figure 19). The youngest dated cave hyena in Belgium was found at the Goyet cave and dates from about 27,200 BP (Germonpré, 1997). All dated British hyenas are older than 27,000 BP. Probably the cave hyena populations were in decline before they became extinct in Europe during the Gravettian, around 26,000 BP (Stuart & Lister, 2007). The cave hyenas occupied most likely the Spy cave intermittently during the Mousterian (AMS date of c. 42,800 BP), the Aurignacian and maybe the beginning of the Gravettian. Their MNI is very high with the remains of at least 126 individuals. The presence of remains of cubs indicates that the hyenas used the cave as a communal den site. A number of cubs died at the age of around six months, others died when they were younger than 12 months, or at an age of more or less one year. Recent spotted hyenas are weaned when they are about 12 months old. The first months after weaning are a difficult period for young spotted hyenas, and possibly they are at that time vulnerable to starvation (Binder & Van Valkenburgh, 2000). This period could also have been difficult for the cave hyenas. De Puydt & Lohest (1886) discovered a perforated canine of a young hyena; this specimen was not seen by us.

As expected, the measurements of the dentition agree with the fact that the hyena material dates from the Last Glacial (Table 6). The P_2 is relatively small compared with the P_3, which is typical for Weichselian cave hyenas (Kurtén, 1963). The length of the lower carnassial is more than 32 mm indicating a glacial climate (Klein & Scott, 1989). Also, the width of this tooth is comparable with that of British Last Glacial hyenas (Kurtén, 1963).

The cave hyenas gnawed several bones from their conspecifics. But gnawing traces occur on a whole range of animals. The antlers of cervids, the metapodials of bovids and horse, and the long bones of rhinoceros and mammoth were particularly attractive to hyenas. In Southern Africa, Skinner *et al.* (1986) observed recent spotted hyenas, especially dams with cubs, which carried ungulate remains to their den. Generally, these remains consist of complete fleshy legs from the shoulder blade or humerus to the hoof, or from the femur to the hoof. The dams fed on these, and bones could accumulate at the den sites. The assemblages in recent hyena dens are dominated by long bones, while vertebrae are rare, since usually they were not brought inside the dens.

In the Bohemian caves, the main animal preyed upon or scavenged by cave hyena was *Equus ferus* (Diedrich & Zăk, 2006). The relative thin horse skulls and lower jaws were easily destroyed, leaving a large amount of isolated teeth, like at Spy. Analysis of the Pleniglacial fauna from Bois Roche in Charente, France, demonstrated that the main prey for the cave hyena were bison and horse (Villa *et al.*, 2010). Stable isotope analysis from cave hyena remains from Southwestern France, Belgium and Great-Britain dating from around 36,000 BP, indicate that horse was the most important prey species for this carnivore (Bocherens *et al.*, 2005). According to Diedrich & Zăk (2006), also in the Bohemian caves, antlers with chewing marks were found in cave hyena dens. As at Spy, only the basal parts remain (Figure 5). The diet of cave hyenas has been assessed by stable isotopes. A recent study (Bocherens *et al.*, 2011) showed that cave hyenas in the Ardennes showed a smaller range of $\delta^{13}C$ and $\delta^{15}N$ with a smaller standard-deviation than for cave lions. This could indicate that the hyenas had a more homogeneous prey choice than the cave lions. Their usual prey comprised woolly rhinoceros, bovids and horse (Bocherens *et al.*,

2011; Diedrich, 2012a, 2012b; Bocherens *et al.*, this volume: chapter XVII). However, we know that the cave hyenas did interact with mammoth material due to the gnawing marks found on mammoth bones at Spy (see below). It is not possible, based solely on an analysis of diet, to eliminate the activity of cave hyenas as a possible factor accounting for the accumulation of mammoth bones at Spy.

We wish to determine (a) whether the large number of mammoth remains present at Spy is the result of activity on the part of the prehistoric humans or large carnivores, and (b) if prehistoric humans, whether these were Neandertals or AMH. Therefore, we analysed the frequency distribution of the skeletal elements of the mammoth remains and the age distribution of the mammoth molars. Furthermore, we considered information on the diet of prehistoric humans and Pleistocene carnivores from Spy obtained through analyses of the stable isotopes of their skeletal remains. The results of these analyses are discussed in detail in Germonpré *et al.* (2012).

Germonpré *et al.* (2012) propose that the large number of mammoth remains at Spy was accumulated by prehistoric humans. They hunted the mammoth to have access to the meat and fat. This conclusion is based on following arguments: (i) the frequency distribution of the skeletal elements of the mammoth, (ii) the age distribution of the mammoth molars, and (iii) the diet of the large carnivores and of the prehistoric humans. On the basis of AMS dates, the stratigraphic position of a number of mammoth molars and the absence of red ochre on the mammoth molars and postcranial bones, it was concluded that these prehistoric humans were Neandertals and not AMH. The AMS dates on the mammoth molars suggest that Neandertals visited Spy several times during the Pleniglacial: one period of visits probably happened around 42,000 – 43,000 BP, another period took place around 36,000 – 37,000 BP. During the latter period, two adult Neandertals died and their skeletons were deposited/buried on the terrace of the cave. The analyses of the stable isotopes from the skeletal remains of the Neandertals from Spy showed that their diet included an important amount of mammoth meat (Bocherens *et al.*, this volume: chapter XVII); while the diet of the large carnivores from Spy (Bocherens *et al.*, this volume: chapter XVII) and adjacent sites (Germonpré *et al.*, 2009; Bocherens, 2011; Bocherens *et al.*, 2011) did not contain large quantities of mammoth meat. The frequency distribution of the skeletal elements from the mammoth is dominated by a high number of molars and milk molars; this suggests that mammoth heads were transported to the cave. Therefore we propose that the Neandertals from Spy hunted the mammoth for food. The high frequency of very young animals in the Spy age profiles indicates selective hunting. The consumption of mammoth brains by the Neandertals was likely a very efficient way to obtain the LC-PUFAs that were essential for the neural developments and to balance the large amount of protein in the diet of the Neandertals (Germonpré *et al.*, 2012).

The age profile of the Spy rhinoceros assemblage is based on isolated teeth of which most were not attributed to a level. The profile is thus a combination of several subassemblages with a different origin, but could be dominated by one subgroup. A rhinoceros premolar from the *Niveau supérieur* has an AMS age of about 25,700 BP (Semal *et al.*, 2009), attributing this sample to the Gravettian. A premolar with ochre traces from unit *Intérieur de la grotte* has an AMS age of c. 32,900 BP (Table 1; Semal *et al.*, 2009, this volume: chapter XVI). Notably, the AMS date of this ochre-stained tooth does not differ significantly from the AMS date of the Aurignacian bone point dated at c. 32,800 BP (Semal *et al.*, 2009). A third rhinoceros tooth has an AMS age of c. 44,000 BP (Table 1; Semal *et al.*, 2009, this volume: chapter XVI). According to de Loë & Rahir (1911), just as with the mammoth, rhinoceros material was very frequent in the Middle Palaeolithic level. The Spy rhinoceros profile differs from those of Hofstade I and Tsavo (Figure 13), whereas the Tsavo and Hofstade I distributions are comparable. The Tsavo assemblage contained animals that died from 1958 to 1968. This profile is largely influenced by a severe drought occurring in Kenya in 1961 causing the death of 300 black rhinoceros (Foster, 1965; Goddard, 1970). It is characterised by a peak of subadult (4 b.r.y.) and prime adult animals (12 - 14 b.r.y.). The profile of the woolly rhinoceros from assemblage Hofstade I suggests that the animals died as a result of single or regularly re-

curring catastrophic events. Maybe a combination of harsh winter conditions preceded or followed by a prolonged drought period, was fatal to many rhinoceros of Hofstade I (Germonpré, 2003). The Spy rhinoceros are mainly young adults around eight years old, also calves of one year are rather well represented. Recent African rhinoceros calves are weaned at an age of about two years and are driven away by their mother around the time of birth of the next offspring when they are about two - three years old. Females calve for the first time when they are between six and twelve years old (Owen-Smith, 1992). The main question again is if the Spy rhinoceros calves were killed by prehistoric people or by cave hyenas. Some 43 % of the remains, excluding the dental material, display gnawing traces. Interestingly, two upper milk teeth (dp2) show traces of gastric acids. They are from two rhinoceros with an age of around one year and two years. It is likely that these calves were hunted by cave hyenas. Prehistoric people manipulated at least part of the material as shown by the ochre traces and a cut mark (ST8). The cut mark is made on a humerus of an adult or subadult animal. Interestingly, ochre occurs on teeth of two young rhinoceros with an age of two and four b.r.y., thus older than the rhinoceros calves with carnivore modifications. One of the teeth with ochre stains was found inside the cave and has an AMS age of c. 32,900 BP. The peaks at Spy of young adults and infants can, in our opinion, be explained by the hunting by prehistoric people of young, inexperienced rhinoceros mothers with their calves. This could be confirmed by the AMS date of c. 25,700 BP on a premolar from a young adult rhinoceros (6 b.r.y.). At that time cave hyenas were probably already extinct in Belgium, so prehistoric people were most likely responsible for its death. Interestingly, also at Biache-Saint-Vaast, a Neandertal site in Northern France dating from the Saalian, the *Dicerorhinus mercki* age profile is dominated by animals between six and nine years old. According to Louguet (2006), the rhinoceros were killed by Neandertals. At Taubach, another Neandertal open air site, the rhinoceros age profile is dominated by calves of around 1.5 years and is regarded as the result of a selective hunting by Neandertals (Bratlund, 2000). At the Vogelherd cave site in Germany, two rhinoceros age profiles were reconstructed. One dates from the Middle Palaeolithic; here the largest frequency is reached by calves under three years old, while the Aurignacian profile is dominated by remains from animals 4 - 11 years old (Niven, 2006). According to the latter author, the rhinoceros and mammoth remains at Vogelherd reflect a combination of human procurement and contributions of large carnivores. At the open air site of Zwolen, Poland, three cultural levels correspond to three phases of intensive utilisation of the site by Neandertals. During winter, they hunted nursery herds of horses (Gautier, 2005). During summer, the hunters tracked other species, such as the rhinoceros, as shown by cut marks on the bones of a juvenile (Bratlund, 2005). At the Middle Palaeolithic site of La Cotte de St. Brelade, rhinoceros remains are dominated by young animals (Scott, 1986a, 1986b). Cave hyenas scavenged at least a part of the material from Spy as testified by the gnawing marks on the long bones. Cave hyena is a typical scavenger of woolly rhinoceros carcasses. Bones of this pachyderm with hyena gnawing marks were found in fluvial deposits of the Flemish Valley (Germonpré, 1993), in Trou de l'Hyène at Walzin (Dupont, unpublished notes), in Scladina cave (Bonjean, pers. comm.), in open air hyena prey deposits in Germany (Diedrich, 2006a) and in numerous caves of the Czech Republic (Diedrich, 2006b) and Germany (Diedrich, 2008). Also, in recent African spotted hyena dens, gnawed remains of adult rhinoceros have been found (Diedrich, 2006b). At Spy, the hyenas scavenged rhinoceros material killed by humans, as suggested by gnawing marks on a humerus fragment with cut marks. However, cave hyenas did kill some calves (*cf.* Diedrich, 2006b). Black rhinoceros calves under four months old, with a body weight of less than 250 kg, can be the victim to spotted hyena attacks (Owen-Smith, 1992). However, woolly rhinoceros calves older than two years certainly had a body weight above 250 kg and were probably safe from cave hyena attacks. Interestingly, the two teeth that were swallowed by cave hyenas are from rhinoceros calves of two years or younger, while the rhinoceros calves with ochre-marked teeth were two years or older.

Based on the stable isotopes, the diet of the Neandertals was based mainly on mammoth, rhinoceros and bison (Bocherens *et al.*, 2005; Balter, 2007). At Spy, the woolly rhinoceros seems to have been hunted by Neandertals, Upper Palaeolithic people and cave hyenas alike.

The Spy horses had a mean shoulder height of 140 cm typical of the Belgian Pleniglacial horses (Germonpré *et al.*, 1993). This height is comparable to the one of the Przewalski horse which ranges between 120 and 146 cm. The body mass of the latter species lies between 200 and 300 kg (Heptner *et al.*, 1966), a weight that most probably can be applied to the Spy horse as well. The historical Przewalski horses lived in harem groups of 10 - 15 individuals (females and their offspring) led by a stallion (Heptner *et al.*, 1966). The horse remains show only few evidence of human involvement. At Spy, two postcranial bones display cut marks and three have ochre stains, on a total of 149 postcranial bones. The frequency of anthropogenic traces on the horse bones is much lower than on the horse bones of the Goyet cave and the differences are significant (Fisher exact test, results not shown). In Goyet level A1, postcranial horse bones have a NISP of 151; 14 % and 10 % display resp. cut marks and ochre traces (Germonpré, unpublished data). In Goyet level A2, the NISP of the postcranial horse bones is 193; 10 and 11 % of the postcranial horse bones show resp. cut marks and ochre traces (Soenen, 2005-2006). Most of the Goyet material from A1 and A2 dates from the Magdalenian. However, a certain mixture with the remains from lower lying levels has occurred (Stevens *et al.*, 2009). At the Magdalenian cave of Trou de Chaleux, horse is the most frequent species hunted. Extensive evidence for butchery exists, with cut marks on 27 % of the horse bones (Charles, 1998), again much more than at Spy.

The Spy horse age profile (Figure 14) does not, just as the ones of the mammoth and rhinoceros, take into account the stratigraphic position of the teeth. It is dominated by prime adult horses. Juveniles are underrepresented, probably because of preservation and collecting biases. Older horses (> 12 years) are not well represented. The profile is very similar to the ones at Neandertal, Solutrean and Magdalenian hunting sites and also to the profile found in hyena den sites. In the Magdalenian assemblage of the Solutré site, the assemblage is dominated by horses aged between 6 to 10 years (Turner, 2002). In the Magdalenian profile of the Tureau des Gardes site, the best represented classes range between 5 and 15 years (Bignon, 2008). Also Fernandez *et al.* (2006) observed that the predation by hyenas is comparable to the one applied by Neandertals. Based on the age profile, it is not possible to decide if the main predator of the Spy horses were humans or hyenas. Canines are usually found only in male horses, although occasionally canine teeth erupt in female horses (Pence, 2002). The low frequency of canines suggests that only few male horses were killed (MNI: 10, i.e. 7 % of the total MNI) and that especially female horses, living in harem groups, were slain. Their body weight falls more or less in the supposed range of preferred prey of the cave hyena (Germonpré *et al.*, 2012). So this animal was most probably regularly hunted by cave hyenas. Horse remains are typically found in cave hyena dens (Diedrich & Žák, 2006). As mentioned above, stable isotope analyses of cave hyena remains from Western Europe dating from around 36,000 BP suggests that horse was an important prey species for this carnivore (Bocherens *et al.*, 2005). The few cut and ochre traces at Spy indicate that the horse was also occasionally killed by Palaeolithic people.

Rucquoy (1886-1887: Fig. 1) discovered a pile of antlers from reindeer, and also from red deer, some of which were still attached to the skull, on a precise spot inside the cave near the cave wall of the second gallery. Recent European reindeer cows cast their antler in spring (April-May), after the birth of the calves. Older males shed their antler in November or December, after the rut, and young males at the end of the winter (January-March; Bouchud, 1959; Herre, 1986). At Spy, the cast male antler indicates that reindeer were present in the area during winter. The occurrence of several shed antlers of calves and/or cows is more problematic. If belonging to young males, the reindeer were in the area during late winter. In the other case cows visited the area during spring. A number of antlers display carnivore gnawing traces.

According to Miller (1974, cited in Morrison & Whitridge, 1997) the first molar is the first permanent tooth to erupt at an age from three to five months. At Spy, two calves died at an age younger than three – five months, since their first molar was not yet erupted. They died thus during summer. About 28 % of the reindeer remains are teeth. The most frequent skeletal

elements are the phalanges that together account for about 29 % of the NISP and for almost 51 % of the postcranial remains. Differential preservation cannot be invoked to explain the large number of these bones, since the bone mineral densities of these bones are not the highest of the deer bones (Lyman, 1994: table 7.6). Other distal elements such as carpals, tarsals and metapodials are also well represented. The postcranial material is highly fragmented. Likely, this fragmentation is related to marrow procurement. Cut marks are present on several postcranial elements but occur mostly on distal elements (Table 11). A dismembering mark on a distal humerus is shown in Figure 6. Cut marks present at the posterior face of the metatarsus above the distal epiphysis can be related to the removal of tendons (Figure 17a-17b). Cut marks on the first phalanx can be associated with skinning (Figure 17c). Comparable cut marks are described in Binford (1987) based on his ethnoarchaeological observations among the Nunamiut Inuit. According to Binford (1987), cut marks on phalanges suggest that they were made during careful skinning of the reindeer foot done in order to obtain skins from which skin socks and skin boots can be assembled. The distribution of ochre traces on the skeletal elements follows a similar pattern. Red pigment traces can be found especially on the metapodials and phalanges (Figure 18). Reindeer is the species which contains the highest NISP with ochre traces for the total Spy assemblage. The high frequency of reindeer phalanges and teeth at Spy could be related to the fact that the phalanges and heads were brought to the camp attached to the skins. The carcasses were probably partly butchered on the kill site and only a selection of body parts was taken back to the camp by the human hunters. The leg skins were likely used for the fabrication of footwear.

The high number of reindeer bones with ochre traces suggests that AMH handled the bulk of the reindeer remains. Furthermore, three AMS dates on reindeer bones fall in the Upper Palaeolithic (Table 1): a metatarsal fragment with ochre traces with an AMS age of about 34,600 BP, a phalanx from the *niveau moyen* with an AMS age of about 29,000 BP and a metatarsal fragment with cut marks and ochre traces with an AMS age of about 26,400 BP (Semal *et al.*, 2009). Reindeer at Spy appears to have been hunted mainly by Upper Palaeolithic people, based on the high occurrence of ochre traces on the reindeer remains and the AMS dates. At Spy, this deer was seemingly not a typical prey animal of Neandertals although a metacarpus with cut marks from the unit *niveau moyen* with an AMS age of c. 36,900 BP (Semal *et al.*, this volume: chapter XVI) indicates that this species was occasionally bagged by Middle Palaeolithic people. Also de Loë & Rahir (1911) remarked that reindeer bones were very rare in the middle and lower levels. At Trou Magrite, Aurignacian people mainly hunted reindeer (Gautier, 1995). At Goyet, the third, Pleniglacial level delivered more reindeer remains, many with cut marks and ochre traces, than horse remains (Dupont, 1871; Dekeyzer, 2006-2007). A cut-marked reindeer astragalus from this level has an AMS age of 34,670 +900/-810 BP (KIA-33600).

Cut marks and ochre traces are present on a number of bones of the large bovids, which implies that their remains were manipulated by Palaeolithic people. Upper Palaeolithic people were involved with large bovids, as suggested by the presence of a few bones with ochre traces. However, the frequency of carnivore modified bones is higher, indicating that bovids were scavenged and/or preyed upon by large carnivores, probably cave hyenas. A small number of the large bovids could be identified as either aurochs or steppe bison. In several sites from Southwestern France, remains from large bovids are more frequent in Mousterian levels than in the younger, Upper Palaeolithic levels (Delpech & Grayson, 2007).

CONCLUSION

The cave of Spy yielded around 11,600 remains from Ice Age mammals. The most frequent species present are horse and cave hyena, followed by woolly mammoth, woolly rhinoceros, reindeer and other animals in still lower frequencies. The dentition is the best represented skeletal element. The fact that most of the fossil material was without stratigraphic context and that the skeletal element distribution is partly biased encumbered a detailed interpretation of the faunal remains.

At Spy, it is likely that Neandertals hunted mammoth calves. The data from several Mousterian sites shows that the Neandertals had developed successful hunting techniques, based on adequate strategies and planning adapted to different types of prey. They hunted in a selective and recurrent way different mammal species and did develop butchering methods that permitted to treat large quantities of prey (Gaudzinski & Roebroeks, 2000; Schild, 2005). Based on the dates of the mammoth molars, a cut-marked reindeer bone and the Neandertal skeletons, two phases of Neandertal occupations at Spy can be deduced: between 43,000 and 42,000 BP and between 36,000 and 37,000 BP.

At Spy, Upper Palaeolithic people (AMH) probably preferred reindeer. Furthermore, it is possible that both Neandertals and AMH hunted to a lesser extent horse, large bovids and woolly rhinoceros. Upper Palaeolithic people were also very interested in mammoth ivory and fox teeth for the fabrication of ornaments and/or tools. Based on cut-marked bones, remains with ochre traces and an Aurignacian spear point, it seems that AMH visited Spy at least three times: at around 34,500 BP, 33,000 BP and 26,000 BP.

Cave hyenas heavily utilised the horse, mammoth, rhinoceros, and large bovid material. The remains from these species were brought to the cave by the hyenas themselves and/or by prehistoric humans and were then subsequently scavenged by the carnivores. The large number of individuals and the presence of remains from hyena cubs suggest that the Spy cave was used as a communal den throughout recurrent occupations, mainly at Mousterian and Aurignacian times. This predator became extinct during the Gravettian (Stuart & Lister, 2007).

The bears used Spy cave as a hibernation den as indicated by the remains of cubs, and female and male adult bears that died during dormancy.

The analysis of the Spy bone assemblage indicates that the accumulation of the bone remains was caused by a series of agents over a long period of the Pleniglacial.

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