



# Neanderthal megafaunal exploitation in Western Europe and its dietary implications: A contextual reassessment of La Cotte de St Brelade (Jersey)



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## ABSTRACT

The recurrent presence at Middle Palaeolithic sites of megafaunal remains, such as mammoth, elephant and rhinoceros, together with isotope analyses signalling meat as a prominent protein source, have been used to argue that these species played a central role in Neanderthal diet. Key to this model are the bone heap horizons from La Cotte de St Brelade (Jersey), which were previously interpreted as game drive debris resulting from systematic Neanderthal hunting. However, this hypothesis has never been rigorously tested, neither at a site-scale, incorporating taphonomic and contextual data, nor at a wider European scale. First, this paper provides a contextual reassessment of the faunal remains from La Cotte to fully understand Neanderthal behaviour at the site. Second, a comparative database of 30 well-published Middle Palaeolithic sites with megafauna permits a data-driven, broader spatial (European) and diachronic assessment of the role of megafauna in Neanderthal subsistence behaviour. Results suggest initial Neanderthal occupation at La Cotte was intensive although through time site visits became more infrequent, as highlighted by a reduction in cultural debris concurrent with a rise in carnivore presence. While mammoths, just as other large mammals and occasionally carnivores, were clearly butchered at this locality, their acquisition and role in Neanderthal diet remains ambiguous. Broader comparisons across Western Europe indicate a main focus on a range of large herbivores, with only a minor, opportunistic, role for megafauna. Whilst stable isotope analysis suggests that Neanderthal diet was meat-oriented, zooarchaeological data do not support the inference that megafauna were the major contributor of meat.

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## Introduction

Current archaeological evidence suggests that Neanderthals successfully hunted and butchered a wide range of large ungulates including bovines, equids and cervids (Tuffreau and Somme, 1988; Farizy et al., 1994; Gaudzinski, 1995, 1996; Conard and Prindiville, 2000; Gaudzinski and Roebroeks, 2000; Grayson and Delpech, 2003; Hublin and Richards, 2009; Rendu, 2010; Discamps et al., 2011; Gaudzinski-Windheuser and Kindler, 2013; Kindler, 2012; Niven et al., 2012; Kindler et al., 2014). Such behaviour has been documented across a broad geographic area and throughout warm and cold phases between ca. 300,000 to 35,000 years ago (Stiner, 1994; Turner and Gaudzinski, 1999; Gaudzinski and Roebroeks, 2000; Burke, 2004; Gaudzinski, 2004; Valensi and Psathi, 2004; Gaudzinski-Windheuser et al., 2014; Kuhn, 2013; Stiner, 2013;

Gaudzinski-Windheuser and Roebroeks, 2014). The Neanderthal diet appears to have been supplemented, occasionally and where available, with both faster and slower moving small game, such as leporids and tortoises (Barton et al., 1999; Richards et al., 2001; Stiner, 2002; Blasco, 2008; Blasco and Fernández-Peris, 2009, 2012). Moreover, recent studies have increasingly identified the use of plant and marine dietary resources by Neanderthals (Stiner et al., 2000; Stringer et al., 2008; Hardy, 2010; Henry et al., 2010; Hardy et al., 2012; Kuhn, 2013; Salazar-García et al., 2013; Buck and Stringer, 2014; Henry et al., 2014; Sistiaga et al., 2014).

Alongside zooarchaeological analyses, much of the recent work on the Neanderthal dietary niche has been driven by stable isotope analyses (Richards et al., 2000; Bocherens et al., 2005; Balter and Simon, 2006; Bocherens, 2009; Salazar-García et al., 2013; Bocherens et al., 2014; Guil-Guerrero et al., 2014). Stable isotopes, such as  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  from bulk bone collagen, predominantly reflect which types of protein sources were consumed by an organism over the last few years (e.g., Saint Césaire; Bocherens et al.,

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2005; Balter and Simon, 2006). Studies of various Neanderthal skeletal remains continually characterise the diet of this species as heavily meat oriented, with enriched  $\delta^{15}\text{N}$  isotope values relative to other established carnivores, such as hyena and cave lion (Richards et al., 2000, 2001; Bocherens et al., 2001, 2005; Richards et al., 2008; Richards and Schmitz, 2008; Bocherens, 2009; Richards and Trinkhaus, 2009; Dusseldorp, 2013). It has been suggested that such high isotope values could only have been achieved through a systematic and habitual dependence on terrestrial megafaunal<sup>1</sup> meat resources (Bocherens, 2009; Guil-Guerrero et al., 2014; but see also; Hardy et al., 2012; Henry et al., 2014). This link to megafauna is related to the obvious large quantities of meat one of these animals would have provided. In this context, the predominance of, or continued presence of, megafauna in Middle Palaeolithic assemblages has been interpreted as evidence that Neanderthals focussed on these largest animals (see for example Bratlund, 2000; Louguet-Lefebvre, 2005; Schreve, 2006; Auguste, 2008; Gemonpré et al., 2014).

Middle Palaeolithic sites that contain megafaunal and cultural material are relatively common in Western Europe (e.g., Biache St Vaast, Mont Dol, Taubach, Gröben, Lehringen; Thieme and Veil, 1985; Tuffreau and Somme, 1988; Mania et al., 1990; Bratlund, 2000; Gaudzinski, 2004; Louguet-Lefebvre, 2005). In addition, unique finds like the wooden spear embedded in an elephant carcass at Lehringen (Movius, 1950; Thieme and Veil, 1985; Gaudzinski, 2004) have been cited as clear, direct evidence for the proficient and habitual hunting of megafauna by Neanderthals. Although a greater focus on site taphonomy has identified some sites as non-anthropogenic accumulations (Binford, 1985, 1987; Villa, 1990; Villa et al., 2005), new sites with single (Conard and Niven, 2001; Mussi and Villa, 2008) and multiple megafaunal carcasses are still being identified (Schreve, 2006; Boschian and Saccà, 2010; Schreve, 2012; Smith, 2012; Yravedra et al., 2012; Panera et al., 2014). However, the role and importance of megafauna in Neanderthal subsistence is still poorly understood and isotope data have not been tested against the rich Middle Palaeolithic archaeological record. Current studies of megafaunal remains mainly focus on the method of acquisition (Conard and Niven, 2001; Schreve, 2006; Mussi and Villa, 2008; Gamble and Boisnier, 2012; Schreve, 2012; Smith, 2012; Gemonpré et al., 2014). There is little debate about the wider role of megafauna in Neanderthal diet and whether the procurement of these species was coherent and systematically organised or more ad hoc and opportunistic. Therefore, in this paper data on megafauna are situated within a broader diachronic perspective of Neanderthal subsistence across a frequently varied spatial, climatic and environmental context.

Very few sites possess sufficient data to explore such patterns of Neanderthal subsistence behaviour through time. La Cotte de St Brelade (CSB, Jersey), located at the north-western extent of the Neanderthal range (Fig. 1a), is a major exception. This site has been used to suggest a systematic, socially organised focus on megafaunal species, mainly mammoth, expressed through at least two separate game drive events (Scott, 1980, 1986a,b). Since its original formulation, this hypothesis of systematic mammoth exploitation has neither been truly tested nor contextualised with other evidence of Neanderthal subsistence behaviour. The present study aims to understand the role and importance of megafaunal species

in the Neanderthal diet. Therefore, new primary data from the CSB faunal material were collected and compared with a large database of published Middle Palaeolithic sites containing megafauna. This allowed for a unique data-driven analysis of Neanderthal megafaunal exploitation both at CSB and across a broad spatial (Western Europe) and temporal range (Middle Palaeolithic). Moreover, understanding Neanderthal megafaunal exploitation could help contextualise the potential role of these largest mammals throughout hominin evolutionary history.

#### *La Cotte de St Brelade: site background*

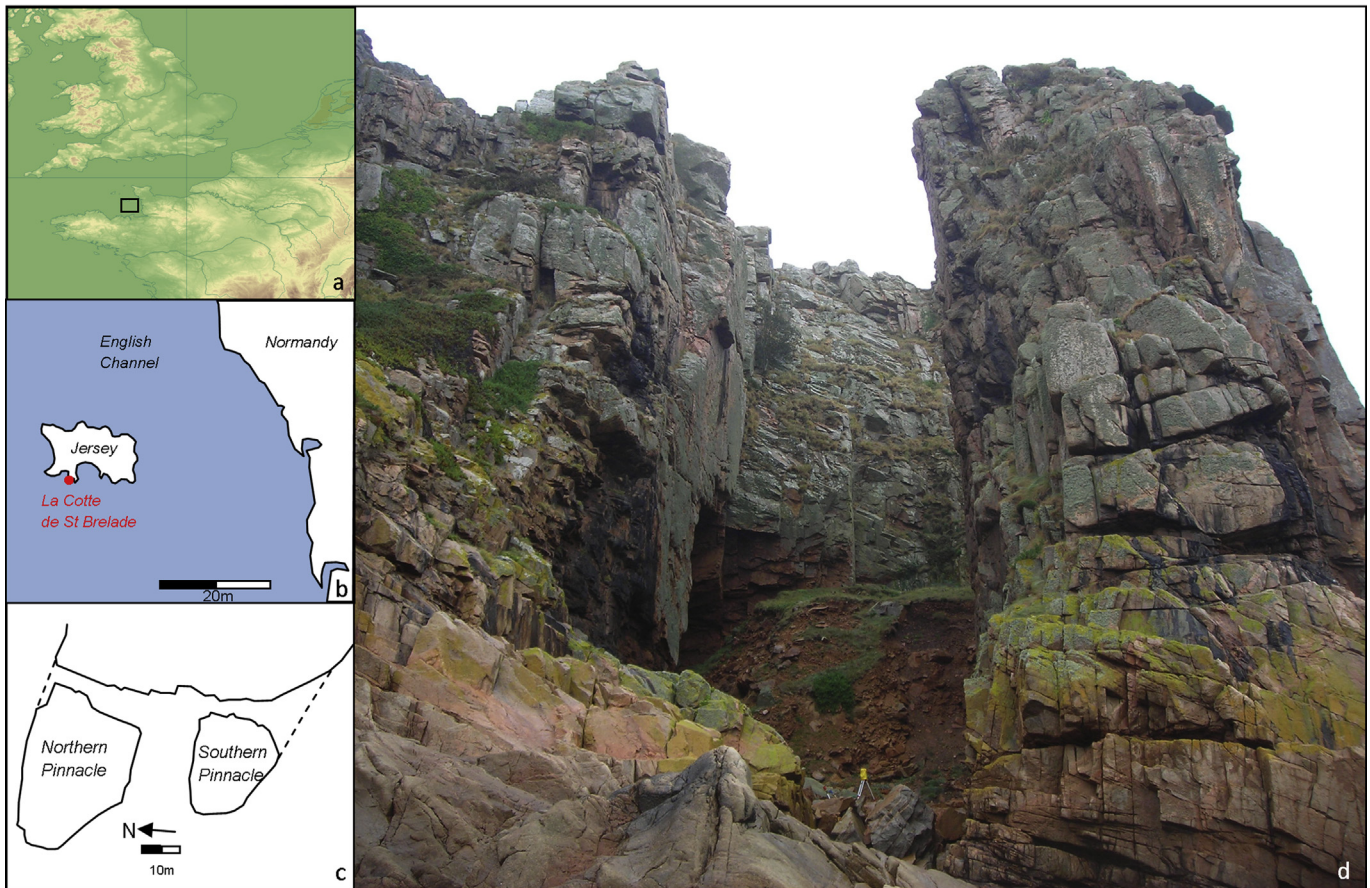
The Channel Islands are situated off the north-west coast of France (Fig. 1b), with Jersey the largest of this archipelago at 118 km<sup>2</sup>. This English Channel region was an area of rapidly changing landscapes and environments throughout the Pleistocene (Callow and Cornford, 1986; Pope et al., 2012; Scott et al., 2014). During warm phases with higher sea-levels, Jersey was geographically isolated from the continental European landmass and largely inaccessible to human populations. During colder phases, and lower global sea-levels, the northern European continental shelf was exposed and connected Jersey to the continent. During these periods, the Channel region represented the most northward extension of the European Plain.

The Jersey bedrock is composed of heavily jointed granite, systematically weathered and eroded through marine and sub-aerial processes (Keen, 1986; Renouf, 1986). These processes initially produced fissures within the bedrock that at their most extreme were widened into steep-sided valleys or ravines (Renouf, 1986). Over time, this produced a unique topographic landscape of parallel, steep sided valley systems and fissures, some often acting as cave systems (Figs. 1d and 2), and many currently submerged offshore (Scott et al., 2014). Pleistocene sediments accumulated within some of these fissures, often in large quantities, preserving a unique record of Neanderthal occupation and behaviour.

The site of La Cotte de St Brelade is situated at the head of one of these valley systems and was partially covered by a roof during the Pleistocene. The site is positioned on the south-west of the island with the overall site architecture approximating a south-facing 'T-shape' (Fig. 1c). At this locality the granite fissure system preserved a vast sequence of Pleistocene deposits that have been excavated on and off since the beginning of the twentieth century (Nicolle and Sinel, 1911, 1912; Zeuner, 1940; Burdo, 1956; Rybot, 1956; Mourant and Callow, 1986). Early excavations were relatively unsystematic and focused on removal and recovery of material without strict stratigraphic control and recording. Detailed recording and excavations did not begin until fieldwork by Charles McBurney (1961–1978), which exposed a c. 7 m deep sedimentary sequence with deposits that tracked fluctuations between glacial and interglacial conditions (Fig. 2; Table 1). In total an area of c. 100 m<sup>2</sup> was excavated and subdivided into c. 20 stratigraphic horizons and six phases of accumulation.

This paper focuses on the faunal material from layers H through 6.1, relating to accumulation Phases II and III (Table 1). Only layer C/D has been radiometrically dated, with an averaged thermoluminescence age of 238,000 ± 35,000 years BP (before present) (Huxtable, 1986). Therefore, cultural deposits within the overlying accumulation Phases II and III, incorporating layers C–6.1, are post Marine Isotope Stage (MIS) 7/8 in age. Detailed sedimentological and micromorphological analyses allowed for further correlation to specific glacial/interglacial phases (see Table 1; Callow, 1986a). Brief warming events and soil formation, particularly within Phase II and IV, could represent interstadial events. Recent work on surviving deposits produced an MIS 5 age and is thus congruent to the Phase IV formation (Bates et al., 2013). This serves to bracket the CSB

<sup>1</sup> Megafauna is a general term, loosely applied to various large mammal species. Numerous subdivisions and body size cut off points have been used in the past. Throughout this paper the scheme from Rabinovich and Briton (2011; see also Rabinovich et al., 2012) will be applied. This scheme divided animals up into Body Size Groups (BSG). The major focus of this paper will be on BSG A (>1000 kg) and B (c. 1000 kg) including elephants (mammoths, straight-tusked), rhinos (woolly rhino) and hippopotamus.



**Figure 1.** Geographic setting of Jersey and La Cotte de St Brelade. a. Location of Jersey within Northwest Europe; b. Position of Jersey in the English Channel region, off the French coast; c. Schematic plan of the CSB T-shaped ravine system (modified from Callow and Cornford, 1986: Figure 1.8); d. Modern day setting of La Cotte de St Brelade (looking east) with Southern Pinnacle on the right and Northern Pinnacle on the left.

sequence, correlating the Phase II accumulation (layers H–C) to the colder phases of stage 7 and the subsequent Phase III horizons (C–6.1) to the cold stage of MIS 6.

### Materials and methods

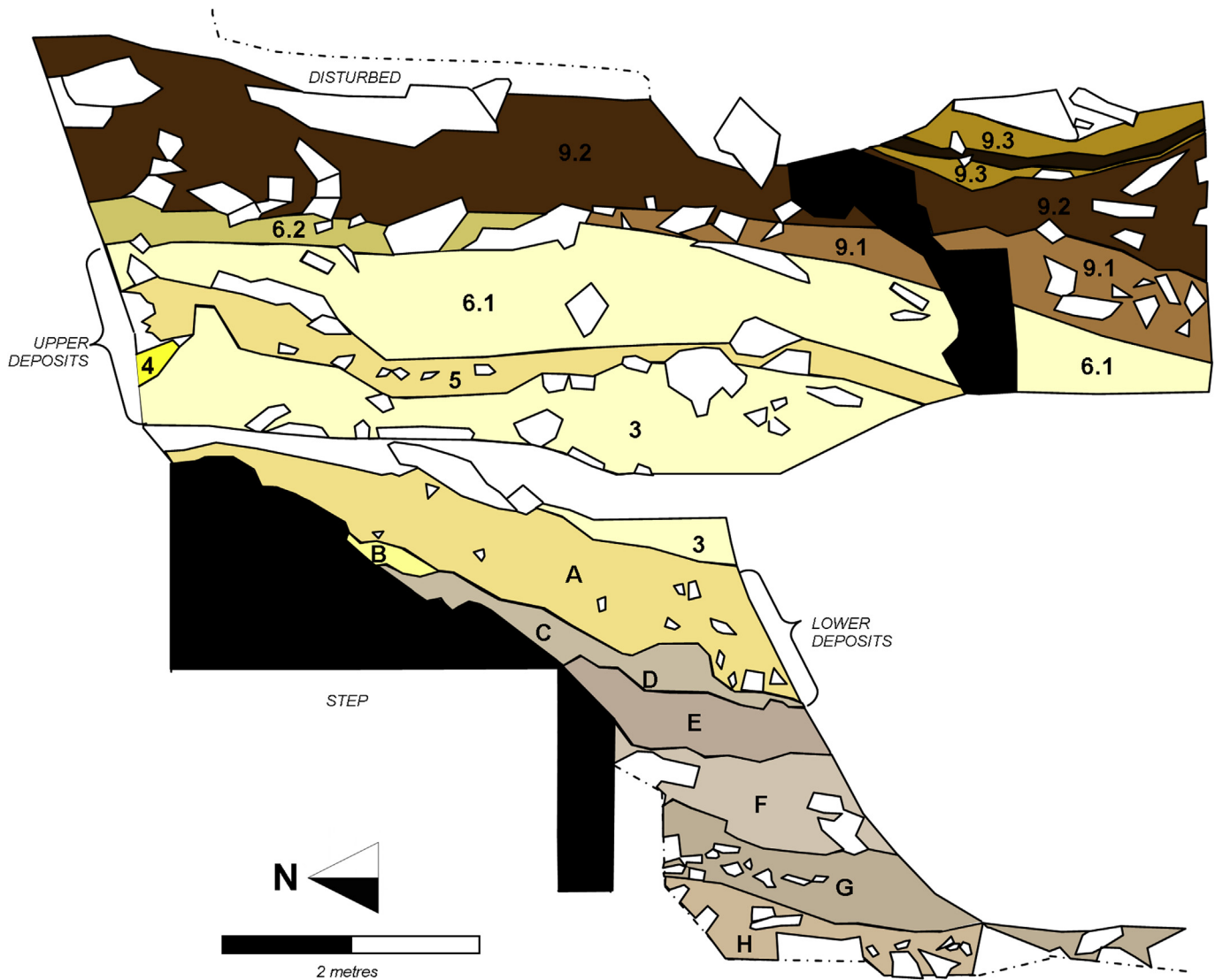
The first section of this paper presents a new analysis of all of the faunal material recovered during excavations at CSB by Charles McBurney (1961–1978). In total 1494 faunal remains were individually recorded from all levels (H–6.1), and include large (e.g., mammoth, rhino) and small (e.g., fox) animals. Faunal material was recorded using a modified zonal system (Dobney and Rielly, 1988), which divides each element into a varying number of zones allowing for a more detailed and precise recording of element and portion preservation. This provides a more comprehensive quantification of the Number of Identified Specimens (NISF) from which a Minimum Number of Individuals (MNI) was calculated. To further understand the specific site formation processes at CSB, zooarchaeological data, such as species and body part identification, were allied with a variety of taphonomic attributes.

Behrensmeier's (1978) weathering stages were used to provide a more qualitative figure for exposure (short/long duration). Root etching provides information about the incorporation of faunal material within the root horizon and, when combined with weathering data, can help to determine the duration of bone exposure. The scheme ranges from 'none' through to 'extreme' (bone surface completely destroyed) (based on Smith,

2010). Burnt bone was recorded using the specific colour change of bone at certain temperatures (Shipman, 1988; Stiner and Kuhn, 1995). Recording the intensity and distribution of natural taphonomic agents provided a detailed site formation framework to contextualise Neanderthal and carnivore behaviour.

All faunal material was studied under magnification (20x) using an oblique light source, which allowed for a detailed assessment of both bone surface condition and modifications. Differentiating human (cut marks, deliberate marrow fractures) from other natural (carnivores, trampling) bone surface modifications has generated considerable debate (Bunn, 1981; Gifford-Gonzalez, 1989, 1991; Fisher, 1995; Dominguez-Rodrigo, 1999, 2003a,b; Dominguez-Rodrigo et al., 2009, 2010, 2012; Galan et al., 2009). More recently, this problem has been approached through high resolution microscopy (Bello et al., 2009, 2011), though blind tests illustrate that even at low magnification differentiation between human and natural signatures is possible (Blumenschine et al., 1996). Therefore, for this study modifications were identified at low magnification and recorded using high resolution digital photographs. Cut, carnivore tooth, and trampling marks were categorised using the definitions proposed by Fisher (1995). To fully understand Neanderthal behaviour at CSB, faunal data were further contextualised with published information on the sedimentology, vegetation, lithics and the wider landscape (Callow and Cornford, 1986; Scott et al., 2014).

The second section of this paper focuses on disentangling the wider European record of Neanderthal megafaunal exploitation. An



**Figure 2.** La Cotte de St Brelade composite section (west facing) with upper and lower deposits highlighted (modified from Callow and Cornford, 1986: Figure 6.6).

extensive literature review provides contextual data from 30 well published Middle Palaeolithic sites containing megafauna. These data were drawn from across Western Europe (Spain, Italy, France, Belgium, Germany, United Kingdom) and situated across different environmental conditions during the period from MIS 8 to MIS 3. This literature review highlighted considerable variation in the reporting of zooarchaeological data, often with megafauna recorded as either present or absent without exact numbers on faunal composition. Thus, this study focussed on well-published sites where exact NISP and MNI values were provided. Further data extracted included site age, type (open/cave), environment, percentage of megafauna in faunal assemblage (%MF), other species and MNI, carnivore modification of megafauna, and human modification of megafauna. The collation of this large Europe-wide, comparative database of Middle Palaeolithic megafaunal sites provides a unique, broader structure to compare and contextualise the primary data from the CSB case study site. This twofold methodology not only allows a wider reassessment of Neanderthal subsistence and site use at CSB, but also provides the first systematic, wide ranging and diachronic comparison of the role and importance of megafauna in the Western European Neanderthal diet.

### Results and preliminary discussion: re-assessing megafaunal exploitation at La Cotte de St Brelade

At CSB, recovery and preservation vary throughout the stratigraphic sequence with the majority of faunal remains present in layers C to 6.1 (NISP = 1395; 93.4%; Table 2). Bone material from underlying deposits (D–H) is very poorly represented (NISP = 99; 6.6%), often with only ephemeral bone traces preserved (Scott, 1986a,b). The faunal assemblage throughout layers C–6.1 is indicative of a cold stage deposit due to a dominance of mammoth (45.0%), woolly rhino (11.8%) and horse (7.1%). The remainder of the faunal material could only be assigned to the genus level or general body size categories (30.8%).

#### *Faunal representation throughout depositional phases II and III*

Mammoth occurs throughout the CSB sequence but the quantity of material varies between specific horizons (Table 2). Whilst dominant within levels 3 (69.5%) and 6.1 (84.0%), mammoth represents a smaller component of the assemblages from underlying deposits and is often overshadowed by other herbivore species. Woolly rhino and horse remains, in particular, are common within

**Table 1**La Cotte de St Brelade stratigraphy and phases of accumulation; modified from Table 6.3 [Callow and Cornford, 1986](#).

Phase	Layer	Principal formation events	Environment	Archaeology	Climate	Dating	MIS
VI	14	Modern soil			Temperate		1
V	13–10	Large quantity of granitic blocks embedded in a loessic head deposit at base; the middle deposits are a sandy head overlain by pure aeolian sand	Poor pollen preservation but presence of arctic lemming suggests extreme cold.	None	Cold		2–4
IV	6.2–9	Large quantities of granitic blocks embedded in a granitic sandy matrix, though occasionally in reworked loessic material; this stage tracks cooling of environment with formation of several ranker soils and intermittent ponding; formation of interglacial soil deposit towards the base affecting underlying sediments [including layer 3] and marine transgression eroding deposits from west ravine.	Poor pollen preservation.	Reworked; charcoal lens in layer H is assumed human visit after fall in sea-level.	Mainly temperate		5
III	B-6.1	Granite blocks embedded within a loessic matrix; occasional episodes of solifluction and mudflow recorded	Arctic lemming and high herbaceous pollen quantity suggest extreme cold.	Frequent cultural deposits including bone heap horizons (layers 3 and 6); slightly disturbed.	Cold	TL date: Levels C and D 238,000 ± 35 kya (OXX-TL 222) (Av)	6
II	H–C	Frequent ponding and rock falls recorded towards base with interglacial soil formation followed by climate deterioration leading into Phase III	Some temperate pollen recovered including <i>Hedera</i> .	Frequent cultural deposits some disturbed but others more in situ (layer E).	Mainly temperate		7
I		No deposits found in situ			Presumed cold		?

the lowermost levels (C–A), though the frequency of these specimens within the upper deposits (3–6.1) is much reduced ([Table 2](#)). Whilst carnivore remains are sparse in the lower horizons (C–A; 0.3%), these species increase in frequency within the upper units (3–6; 0.3–10.3%), alongside a decrease in the quantity of other herbivore species. Other herbivore species, such as bovids, and cervids, are present throughout levels C-6.1 and form a relatively stable percentage of material from all horizons, though in level 5 these species reach their highest values (11.8%). The variation between horizons is also evident when examining MNIs ([Table 2](#)). Mammoth dominates layers 3 (MNI = 7) and 6 (MNI = 11) with other species often represented by only a single individual

([Table 2](#)). Contrastingly, in the lower deposits mammoth have fewer individuals (layer C: MNI = 1; layer B: MNI = 2; layer A: MNI = 3) whilst other more prevalent species include woolly rhino (MNI = 3), horse (MNI = 3) and other herbivores (MNI = 5).

The change in the proportion of NISP values for these major species (mammoth, woolly rhino, horse) throughout the CSB stratigraphy was statistically tested through the calculation of composite chi-square values and adjusted residuals ([Table 3](#)). These residuals refer to the level to the left of the residuals column and should be read as standard normal deviates (see [Grayson and Delpech, 2003](#); [VanPool and Leonard, 2011](#)). Absolute values over 1.96 indicate a significant change between levels. [Table 3](#) illustrates

**Table 2**

La Cotte de St Brelade: number of identified specimens (NISP) and minimum number of individuals (MNI) of species by stratigraphic unit.

Layer	Phase III																		Phase II			Totals
	6.1			5			4			3			A			B			C			
	NISP			NISP			NISP			NISP			NISP			NISP			NISP			
Species	#	%	MNI	#	%	MNI	#	%	MNI	#	%	MNI	#	%	MNI	#	%	MNI	#	%	MNI	
Aves sp.													1	0.3	1	2	1.1					3
<i>Canis lupus</i>	1	0.4	1							1	0.2	1										2
<i>Vulpes lagopus</i>										3	0.7	1										3
<i>Ursus</i> sp.	1	0.4	1	7	10.3	1	1	7.7	1	2	0.5	1	1	0.3	1							12
<i>Mammuthus primigenius</i>	194	84.0	11	27	39.7	1	1	7.7	1	282	69.5	7	85	25.2	3	28	15.1	2	6	3.9	1	623
<i>Coelodonta antiquitatis</i>	12	5.2	2	7	10.3	1				30	7.4	2	48	14.2	3	47	25.4	3	17	11.0	1	161
<i>Equus ferus</i>	1	0.4	1	1	1.5	1				17	4.2	2	56	16.6	7	13	7.0	2	16	10.3	1	104
<i>Megaloceros giganteus</i>										1	0.2	1	3	0.9	1							4
<i>Cervus elaphus</i>				2	2.9	1				2	0.5	1	4	1.2	1	3	1.6	1	1	0.6	1	12
<i>Rangifer tarandus</i>				4	5.9	1							1	0.3	1	1	0.5	1	1	0.6	1	7
<i>Rupicapra rupicapra</i>													3	0.9	1	5	2.7	2				8
<i>Bos primigenius</i>	1	0.4	1							1	0.2	1										2
<i>Bos</i> sp.										10	2.5		1	0.3	1				1	0.6		12
Cervid sp.				2	2.9					1	0.2		6	1.8		4	2.2		1	0.6		14
Large mammal	19	8.2		11	16.2					41	10.1		90	26.7		33	17.8		8	5.2		202
Medium mammal	1	0.4		3	4.4					8	2.0		10	3.0		8	4.3		26	16.8		56
Small mammal																1	0.5					1
Indeterminate	1	0.4		4	5.9		11	84.6		7	1.7		28	8.3		40	21.6		78	50.3		169
<b>Totals</b>	<b>231</b>	<b>100</b>		<b>68</b>	<b>100</b>		<b>13</b>	<b>100</b>		<b>406</b>	<b>100</b>		<b>337</b>	<b>100</b>		<b>185</b>	<b>100</b>		<b>155</b>	<b>100</b>		<b>1395</b>

**Table 3**  
La Cotte de St Brelade: number of identified specimens (NISP) by stratigraphic unit and three major taxa.

Species	Context										Total	
	Unit 6		Unit 5		Unit 3		Unit A		Unit B			Unit C
	NISP	AR	NISP	AR	NISP	AR	NISP	AR	NISP	AR		NISP
<i>Mammuthus primigenius</i>	194	<b>3.2</b>	27	-1.4	275	<b>9.7</b>	92	<b>2.3</b>	28	1.0	6	622
<i>Coelodonta antiquitatis</i>	12	<b>-2.9</b>	7	1.9	30	<b>-4.6</b>	48	<b>-4.9</b>	47	<b>-3.3</b>	17	161
<i>Equus ferus</i>	1	-1.4	1	-0.4	14	<b>-8.0</b>	59	<b>2.7</b>	13	1.9	16	104
Total	207		35		319		199		88		39	
$\chi^2$		<b>10.64</b>		3.87		<b>100.75</b>		<b>24.23</b>		<b>11.40</b>		

Adjusted residuals (AR) and composite  $\chi^2$  values.  
Significant values in bold.

that the relative abundance of species within the lower levels changes substantially. This is driven by a significant decrease of rhino within these levels and, between layers B and A, a significant increase in proportions of both mammoth and horse. The relative abundance of species in layer A differs significantly from those in layer 3 ( $\chi^2 = 100.75$ ,  $p < 0.0001$ ). This results from a substantial increase in mammoth along with a significant decrease in woolly rhino and horse. A similar pattern can also be demonstrated between layers 5 and 6 ( $\chi^2 = 10.64$ ,  $p = 0.005$ ) with the relative abundance of mammoth increasing significantly alongside a reduction in rhino remains. These statistics illustrate a major break between the lower and upper deposits at CSB, highlighted by variation in %NISP and MNI values. Therefore, it is important to test whether such variation resulted from a change in Neanderthal or carnivore behaviour, natural diagenetic processes or a combination.

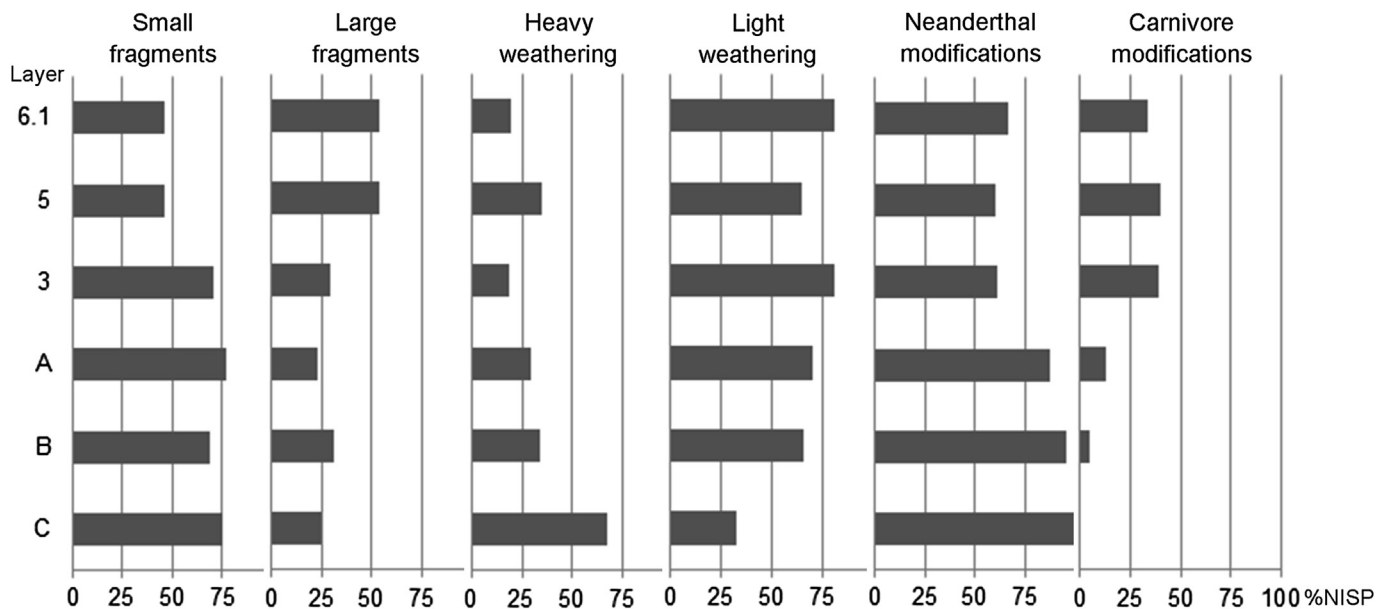
#### Weathering and other natural site formation processes

Bone weathering throughout the CSB sequence appears moderate (Stages 2–3; 55.1%) (Fig. 3), which is encouraging given the geological and sedimentological setting of CSB and the poor survival of specimens from the lowermost levels (Scott, 1986a). However, separating faunal material by context highlights a similar

break between the upper and lower levels. Within the lower deposits (particularly layers C and B) material appears more heavily/moderately weathered (85.7% and 72.5%, respectively). Contrastingly, moving upwards through the sequence material appears better preserved and more lightly weathered, suggesting a shorter duration of exposure (Fig. 3). In particular, within layers 3 and 6.1 the majority of faunal material is only lightly weathered (51.2% and 58.0%, respectively).

The chi-square values show that the relative abundance of weathered bone differs significantly between layer A and layer 3 ( $\chi^2 = 63.40$ ,  $p = <0.00001$ ) (Table 4). This results from an increase of lightly weathered material (stages 0 and 1) and a decrease in bone material from weathering stages 2 and 3. Similar changes in abundance were recorded between layers 5 and 6 ( $\chi^2 = 113.63$ ,  $p = < 0.00001$ ). These statistics illustrate a break between the lower and upper deposits at CSB.

Climatic fluctuations and reduced vegetation cover would have resulted in increased loess deposition throughout the upper levels and in particular within layers 3 and 6. Such increased sedimentation would have rapidly covered any faunal material and prevented substantial sub-aerial destruction. In addition, Scott (1986b) observed that this increased loess deposition provided a more alkaline matrix that helped to preserve faunal remains. Therefore,



**Figure 3.** La Cotte de St Brelade: Panel graph illustrating the relative proportions (%NISP) of fragment size, weathering, Neanderthal and carnivore modifications (including indeterminate specimens) throughout upper (6.1–3) and lower (A–C) deposits. Large and small fragments represent the %NISP above and below average length within each deposit; Average lengths are: layer C = 59.1 mm; layer B = 62.0 mm; layer A = 88.2 mm; layer 3 = 136.5 mm; layer 5 = 82.7 mm; layer 6.1 = 208.6 mm. Weathering based on Behrensmeier (1978); Light weathering: Stages 0–2; Heavy weathering: Stages 3–5.

**Table 4**

La Cotte de St Brelade: number of identified specimens (NISP) by stratigraphic unit and within each weathering stage; based on Behrensmeier (1978).

Weathering	Context											Total
	Unit 6		Unit 5		Unit 3		Unit A		Unit B		Unit C	
	NISP	AR	NISP	AR	NISP	AR	NISP	AR	NISP	AR	NISP	
0	3	1.0	0	-1.5	11	<b>3.2</b>	0		0		0	14
1	129	<b>4.9</b>	19	-3.9	192	<b>6.9</b>	89	-0.9	53	<b>3.4</b>	21	503
2	53	-1.8	26	0.8	114	<b>-4.4</b>	161	1.6	70	<b>3.3</b>	33	457
3	34	-1.9	19	2.9	47	<b>-3.4</b>	76	-2.2	55	<b>-2.2</b>	64	295
4	4	<b>-4.7</b>	12	3.1	22	-1.3	29	1.9	7	<b>-5.4</b>	36	110
5	0		0	-0.4	1	-0.1	1	0.7	0		0	2
Total	223		76		387		356		185		155	1382
$\chi^2$		<b>113.63</b>		27.47		<b>63.40</b>		9.71		<b>49.65</b>		

Adjusted residuals (AR) and composite  $\chi^2$  values.  
Significant values in bold.

an absence of loess in the lower deposits resulted in the selective destruction of mammoth and other faunal material within these horizons (see Scott, 1986b). An increase in more heavily weathered material in layer 5 perhaps suggests a reduction in loess deposition, which is supported by sedimentary and micromorphological analyses that highlight stabilisation events within layer 5 (Callow, 1986a). Bone material from the base of layer 6 was reportedly embedded within the surface of layer 5 (Scott, 1986b). Therefore, bone material from layer 5 could represent the lowermost, more heavily weathered portions of layer 6.

Furthermore, the average length and width of the specimens illustrates that bone fragments are smaller in the lower horizons (C–A), increasing in size within the upper horizons, especially in layers 3 and 6.1 (Fig. 3). The variation in faunal fragment size and preservation could also result from the spatial distribution of material particularly within layers 3 and 6.1. Within these levels faunal material was recovered next to and abutting the CSB western wall, and away from the drip line, which could have protected bone remains from more extensive sub-aerial destruction (Scott, 1986b). Scott (1986b) also discusses the possibility that these deposits originally extended further beyond the drip line at CSB, and that these elements suffered substantially more sub-aerial weathering and were destroyed. A lower percentage of other natural bone surface modifications (1.2%) (e.g., root etching and fluvial modifications) suggests minimal re-exposure, movement or natural wash

into the site itself. During excavation, numerous elements, including ribs and scapulae, were identified resting against other elements in a vertical position (Scott, 1986b). Scott (1986b) suggests that these elements would not have remained in these positions had they been exposed and deposits accumulated for a long period of time.

The weathering of bone material at CSB illustrates a similar statistically significant pattern of variation between lower and upper horizons. Some of this variation probably relates to increased alkaline loess deposition in the upper deposits. In addition, the spatial distribution of faunal remains near to and abutting the site walls, and crucially away from the drip line, may also have helped improve faunal preservation within layers 3 and 6.1 (Scott, 1986b). Therefore, it is important to assess the degree to which bone weathering affected body part representation at CSB.

#### Megafaunal body part representation (BPR)

This discussion will focus on those levels that contained most of the faunal, and especially megafaunal, material (levels A, 3, 5 and 6.1; Table 5). There appear to be considerable differences in the representation of mammoth skeletal elements between both layers 3 and 6.1 and their underlying deposits (A and 5). Levels 3 and A are dominated by cranial remains (74.8% and 87.1%, respectively), including tusks (38.8%) and dental fragments (46.3%). Whilst layers

**Table 5**

La Cotte de St Brelade: number and percentage of identified specimens (NISP; %NISP) for mammoth throughout major stratigraphic units.

Element	Context															Total	
	Unit 6.1			Unit 5			Unit 3			Unit A			Unit B				Unit C
	#	%	AR	#	%	AR	#	%	AR	#	%	AR	#	%	AR		#
cranium <sup>a</sup>	23	13.7	0.2	3	12.5	<b>-6.8</b>	187	77.6	-1.0	46	83.6	-0.9	22	91.7	-0.7	6	287
vertebrae	0		<b>-5.3</b>	4	16.7	<b>2.4</b>	11	4.6	0.9	1	1.8	0.7	0			0	16
rib	15	8.9	<b>-6.8</b>	15	62.5	<b>7.8</b>	18	7.5	-0.8	6	10.9	1.7	0			0	54
scapula	75	44.6	<b>3.8</b>	1	4.2	-0.1	11	4.6	0.9	1	1.8	0.7	0			0	88
humerus	8	4.8	1.1	0		-0.5	3	1.2	-0.8	0			0			0	11
radioulna	2	1.2	0.5	0		-0.3	1	0.4	-0.5	0			0			0	3
pelvis	24	14.3	<b>2.0</b>	0		-1.0	9	3.7	1.5	0		-1.5	1	4.2	0.5	0	34
femur	12	7.1	1.4	0			0			0			0			0	12
tibia	4	2.4	0.8	0			0		-2.1	1	1.8	0.6	1	4.2	0.5	0	6
tarsals	1	0.6	-1.6	1	4.2	<b>2.0</b>	1	0.4	0.5	0			0			0	3
metapodial	2	1.2	0.5	0			0			0			0			0	2
phalanges	2	1.2	0.5	0			0			0			0			0	2
Total	168			24			241			55			24			6	518
$\chi^2$			<b>85.57</b>			<b>76.99</b>		10.10			6.27			0.54			

Adjusted residuals (AR) and composite  $\chi^2$  values.  
Significant values in bold.

<sup>a</sup> Tusk fragments excluded

**Table 6**  
La Cotte de St Brelade: number of identified specimens (NISP) with Neanderthal and carnivore modifications throughout layers C-6.1; indeterminate specimens not included; indetlb = indeterminate long bone.

Species	Element	Context											
		6.1		5		3		A		B		C	
		Neand	Carniv	Neand	Carniv	Neand	Carniv	Neand	Carniv	Neand	Carniv	Neand	
<i>Canis lupus</i>	radius	1											
<i>Ursus sp.</i>	femur			2	1								
<i>Mammuthus primigenius</i>	cranial	1				3							1
	rib					1							
	scapula	3				1							
	humerus	1	2			1							
	ulna	1	1				1						
	pelvis		2			1							
	femur	3	1										
	tibia		1					1		1	1		
	indetlb	3								1			
<i>Coelodonta antiquitatis</i>	cranial									1			4
	humerus									1			
	radius					1	1						
	ulna					1	1						
	pelvis						1		2				
	femur	4								1			
	metapodial									1			
	carpal/tarsal										1		
	indetlb									1			
<i>Equus ferus</i>	teeth					1		4					
	femur							1					
<i>Bos sp.</i>	horncore						1						
<i>Megaloceros giganteus</i>	phalanx 1							1					
<i>Cervus elaphus</i>	humerus			1		1	1						
	radius					1							
<i>Rangifer tarandus</i>	phalanx 1				2								
<i>Cervid sp.</i>	humerus									1			
	metapodial												
	<b>Total</b>	17	7	3	3	12	6	8	2	8	2	5	73

5 and 6.1 contain a relatively high proportion of cranial specimens (18.5% and 20.2%, respectively), these horizons are dominated by axial elements (Unit 5: 70.4%) and within layer 6.1 long bone fragments (64.8%). Chi-square values with adjusted residuals illustrate significant differences in mammoth body parts within the upper deposits (see Table 5). Between levels 3 to 5 the variation results from a decrease in cranial portions and an increase in axial fragments (vertebra, ribs). The variation in body parts between layers 5 and 6 results from both a significant increase in scapulae and pelvis and also a decrease in vertebrae and ribs. Mammoth body part representation within the lower deposits showed no statistically significant changes, perhaps in part due to the small assemblage sizes.

The woolly rhino body part representation (BPR) illustrates a similar pattern to that observed for mammoth. The percentage of cranial fragments is high within both of the 'bone heaps' (layer 3: 55.3%; layer 6.1: 51.7%) and in the deposits that immediately underlie them (Unit A: 85.4%; Unit 5: 66.7%). However, a comparison of the axial and appendicular elements illustrates that appendicular body parts are more prevalent within layer 6.1 (37.9%) and the level that underlies it (layer 5: 29.2%). This is in contrast to the lower values obtained for these skeletal portions in layer 3 (23.4%) and layer A (2.1%). Statistical tests, using chi square with adjusted residuals, only highlight a significant change between layer A to 3 ( $\chi^2 = 21.12$ ,  $p = 0.006835$ ) resulting from a decrease in the proportion of cranial fragments. The absence of further statistically significant variation between deposits undoubtedly results from the small assemblage size in some levels. Nevertheless, variation in the abundance of specific body parts for both mammoth and woolly rhino suggests a distinction between the upper and lower deposits at CSB. Some variation probably relates to the spatial distribution and more rapid burial of faunal material within these upper

horizons and/or changes in bone transport and duration of occupation by carnivores and hominins, which is explored in the next section.

#### Neanderthal and carnivore bone surface modifications

This study identified bone surface modifications by both Neanderthal and carnivore agents on faunal specimens throughout layers C-6.1 (NISP = 155; 11.1%) and across numerous species and skeletal elements (Fig. 3; Table 6). Neanderthal modifications are always dominant, representing over 90% of the bone surface modifications in the lower deposits (C-A) (Fig. 3) (see Table 6). However, it is clear that both Neanderthal and carnivore bone surface modifications occur more frequently at CSB than previously attested (Jones and Vincent, 1986).

**Carnivore modifications** Despite limited skeletal evidence, the intermittent use of CSB by carnivores is highlighted by bone surface modifications. These modifications are limited but are nonetheless present across a range of species. Carnivore modifications of the CSB megafauna (mammoth and woolly rhino) include the gnawing of long bone epiphyses, dense podials and metapodials and around the pelvis (see Fig. 4). The deliberate acquisition of marrow from long bone cavities and more dense lower limb bones occurred presumably when bones were relatively fresh. Such behaviour has been well documented amongst modern populations of wild carnivore species and during experiments with captive animals (Crader, 1974; Haynes, 1980; Fisher, 1995; Blumenschine et al., 1996; Dominguez-Rodrigo, 2001; Lupo and O'Connell, 2002). The extreme size and density of both mammoth and woolly rhino remains perhaps suggests that these modifications were caused by larger, bone-cracking hyaenas (Brain, 1981), though obviously





**Figure 4.** Woolly rhino pelvis (CSB77 676) from layer A with carnivore gnawing and crelation on the ilium.

other carnivore species, such as wolf and arctic fox, cannot be excluded.

Carnivore processing has also been identified across smaller species including bovids, cervids (red deer, reindeer) and even bear (Figs. 5 and 6). Most modifications are related to the extraction of marrow from long bone cavities and more dense autopodium and are similar to modifications identified at other Middle Palaeolithic sites (Smith, 2012). The gnawing of a bovid horncore is an interesting and, apparently, isolated occurrence. The composition of horn is entirely bone with a keratinous covering with very little nutritional value. Therefore, such modification is similar to carnivores gnawing skeletal elements whilst bored or resting (Haynes, 1980; Brain, 1981), further suggesting a repeated carnivore presence in the CSB fissure system.

**Neanderthal butchery and carcass processing** Neanderthal bone surface modifications were recorded across a range of species from various horizons (Fig. 3 and Table 6). In the lower deposits (C–A),

most modifications are isolated cut marks and marrow fractured elements (see Table 6). Some cut marks relate to meat removal but the location of others suggests the disarticulation of some elements. Within these levels, bone specimens from species such as mammoth, rhino, and bovid display evidence of having been burnt by Neanderthals, perhaps either for fuel or waste management and disposal (Callow, 1986b). Alongside larger fragments of charred bone, a smaller fraction of burnt material was also identified, often contained within sediment still adhering to faunal specimens (Fig. 7). These findings are all consistent with observations made during the excavations and subsequently during both micromorphological and zooarchaeological analysis (van Vliet-Lan e, 1986; Scott, 1986a).

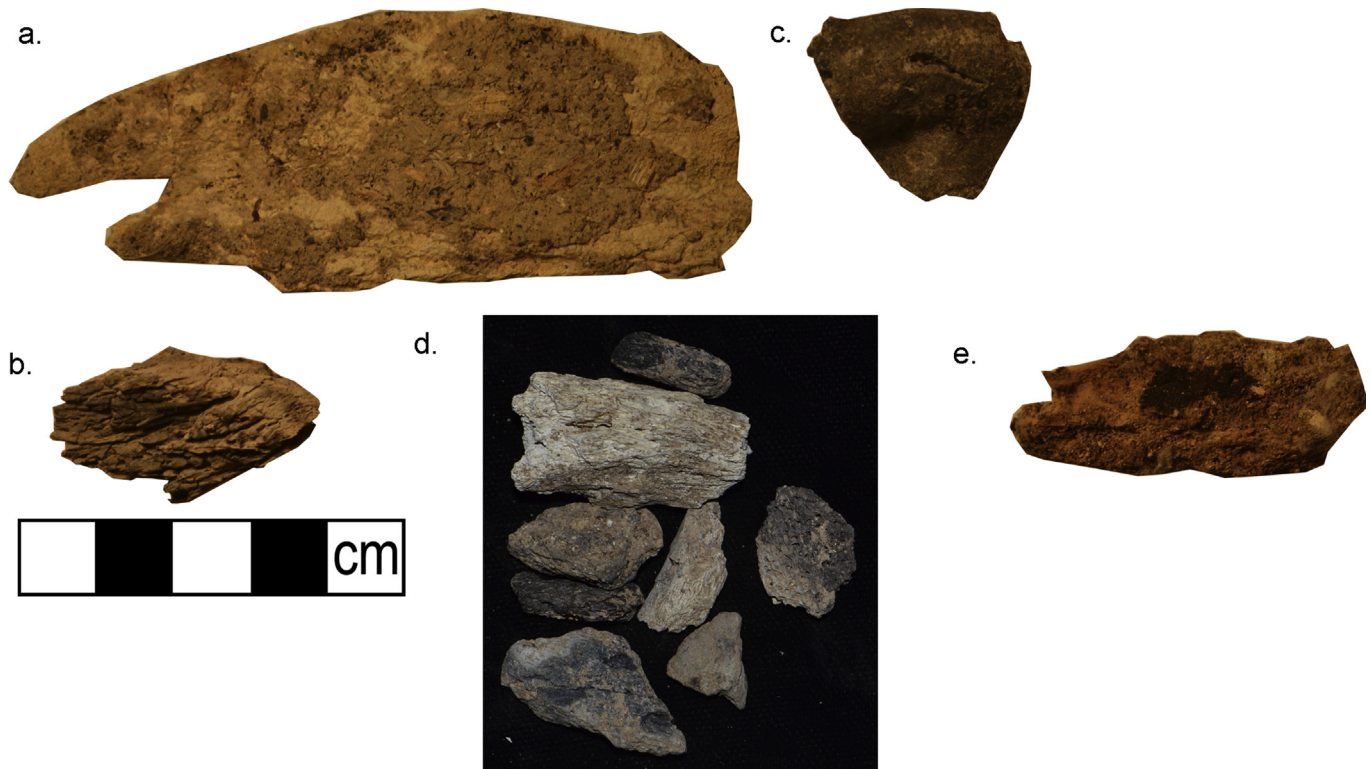
Conversely, no burnt faunal material has been identified within the upper horizons (3–6.1), whilst other Neanderthal butchery signatures are more frequent (see Table 6). The majority of these signatures are concentrated within layers 3 and 6.1 and are



**Figure 5.** Red deer humerus (CSB76 299) from layer 3 with carnivore gnawing of the distal shaft on both caudal (black arrow) and lateral views (white arrow).



**Figure 6.** Reindeer phalanges from layer 5 with carnivore tooth puncture (top; CSB61 7) and gnawed proximal epiphysis (bottom; CSB61 8).



**Figure 7.** Bone fragments recovered throughout the lower deposits with indications of burning; a. Mammoth lamella (CSB77 701) from layer A with sediment still adhering with numerous microscopic charcoal fragments and small mammal remains; b. Bone fragment from layer H; c. Bovid astragalus (CSB78 928) from layer C; d. Various large mammal bone fragments (CSB78 949) from layer A; e. Indeterminate long bone fragment (CSB76 275) from layer A with burnt material visible within sediment adhering to specimen.

present across a range of species including mammoth, woolly rhino, horse and cervids. Cut marks, chop marks and marrow fracturing suggest that Neanderthals used this location to butcher and process large herbivore carcasses (Fig. 8). Bone surface modifications on mammoth remains indicate that the brain and other non-muscle meat products were also exploited. Indeed, one mammoth skull from layer 3 appears to have had a rib driven into it from the parietal to squamosal region, perhaps to help extract portions of the brain (Fig. 9). Scott (1986b) also identified other ribs driven into the ground surrounding other mammoth skulls in layer 6 (see Fig. 18.8, Callow and Cornford, 1986: 167). This suggests that mammoth carcass portions were differentially distributed, and potentially butchered, at various locations within CSB (Scott, 1986b). The movement of bone material away from the protective cover of the site walls and beyond the drip line could have resulted in the destruction of specific elements and may account for the absence of specific portions within levels 3 and 6.1 (Scott, 1986b).

Interestingly, within the CSB upper horizons, new evidence was identified for the limited exploitation of carnivore species by Neanderthals. This includes chop marks on a wolf long bone and cut marks on a bear femur, possibly indicating disarticulation (Figs. 10 and 11). The exploitation of carnivores appears restricted to these upper levels (Fig. 3), which would be consistent with a rise in carnivore presence around CSB as indicated by higher levels of both their remains and bone surface modifications they created.

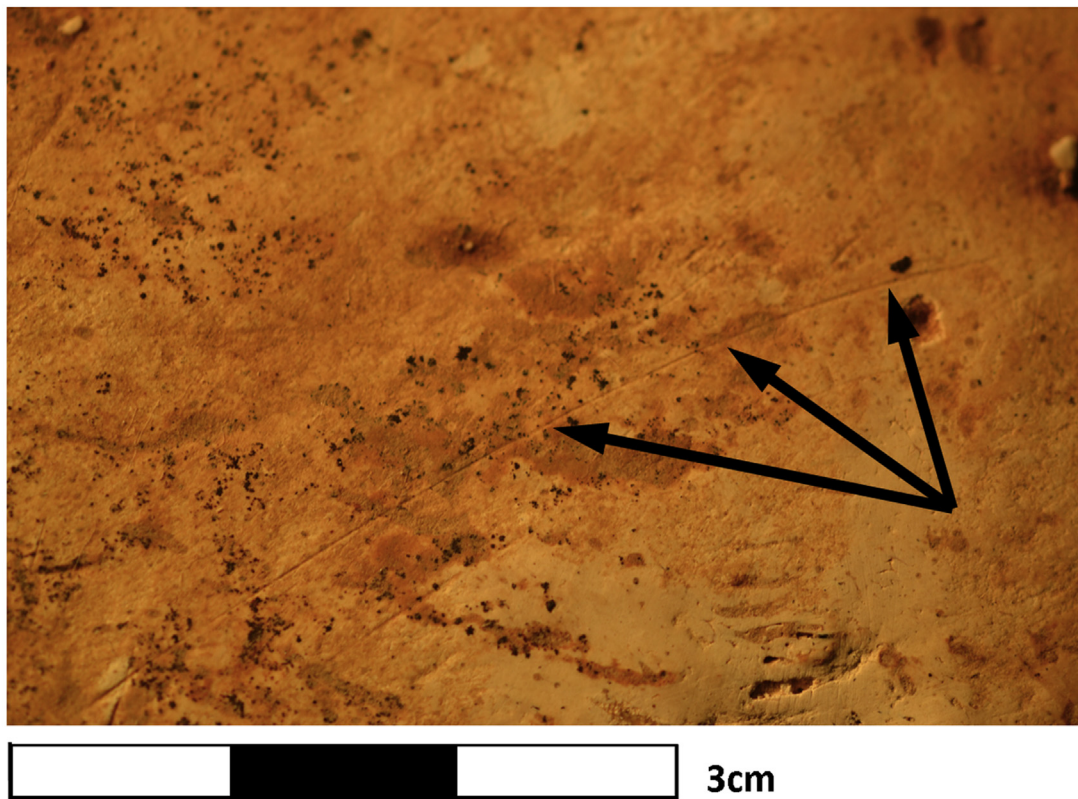
These new analyses of the CSB fauna indicate the recurrent exploitation of megafauna at this locality, but also a more complex signature of both site use and behaviour by Neanderthal and carnivore species. These data can now be further contextualised, first in relation to other aspects of the CSB archaeological record, and secondly within a broader, comparative Western European framework.

### Discussion: megafaunal accumulation and exploitation across the Western European Middle Palaeolithic and its importance and role in Neanderthal diet

#### *Megafaunal accumulation and exploitation at La Cotte de St Brelade*

The data from this new study suggest that whilst megafaunal species were undoubtedly exploited at CSB, these formed part of a broader subsistence framework that included other herbivores and (sporadically) carnivores. Furthermore, deterioration in climate, illustrated by changes in the sedimentology and pollen records (Cartwright, 1986; Jones, 1986; Callow, 1986a; Scott, 1986a), may have necessitated a change in Neanderthal site use. This perhaps resulted in a more infrequent or seasonal use of the site within the upper horizons and may also have triggered modifications of Neanderthal subsistence behaviour. A more prolonged Neanderthal presence at CSB is suggested throughout layers C-A by burnt material and higher lithic density (Table 7). Reduced sedimentation rate in the lower horizons may also have produced a palimpsest effect that, whilst presenting the appearance of increased lithic density, could have accumulated at a comparable rate and therefore represents similar duration of Neanderthal site use. However, an increased presence of carnivore skeletal remains and modifications within the upper deposits nonetheless suggests less frequent or sustained use of CSB by Neanderthals. In the light of the probable weight of mammoth skulls containing flesh and grease, it is unlikely they were transported far.

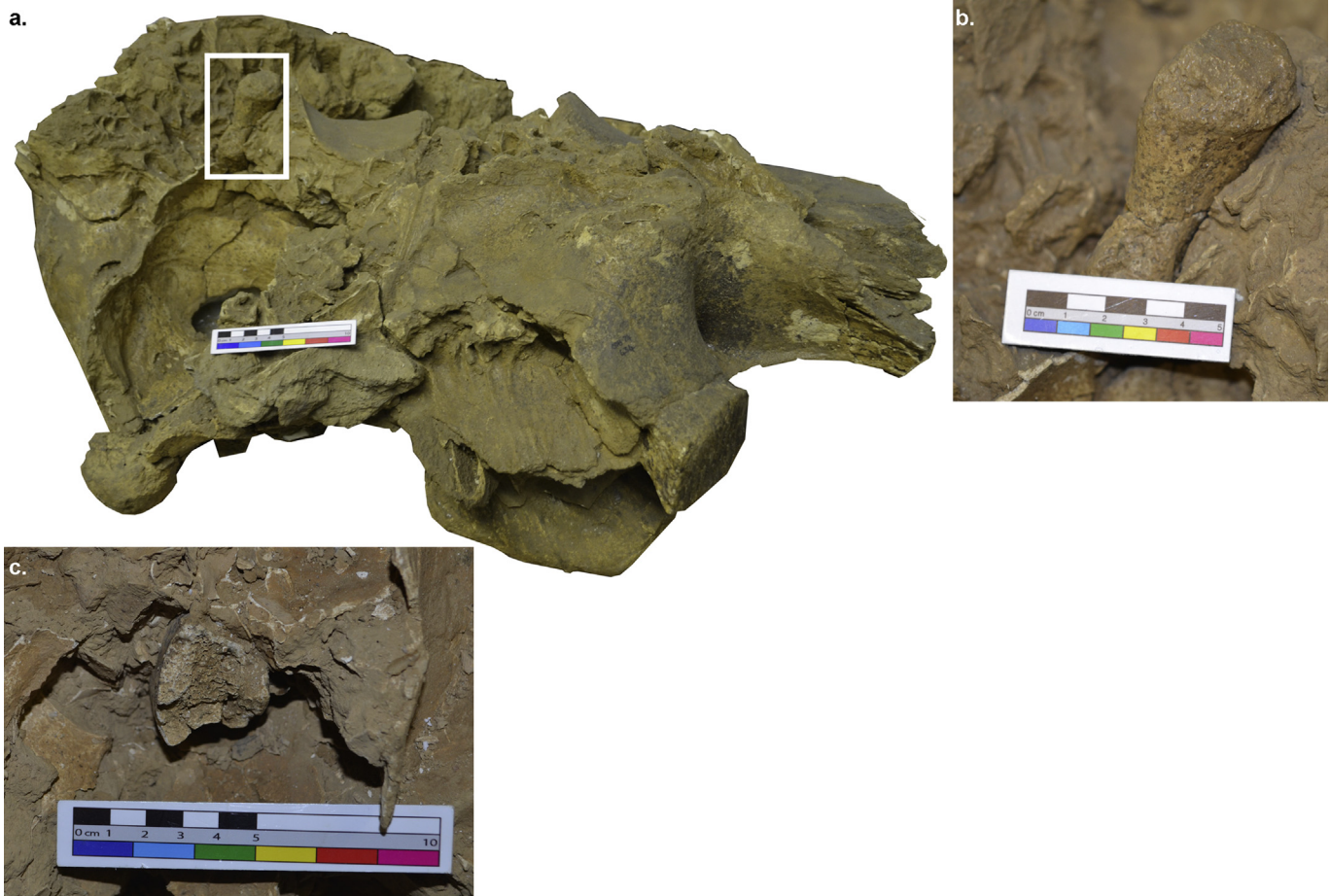
Evidence presented throughout this paper could support several interpretive models for Neanderthal acquisition of the megafaunal remains, including hunting and opportunistic exploitation at both a wider landscape scale or at the site itself. Whilst megafaunal species (mammoth and woolly rhino) were exploited throughout the sequence, the predominance of these species in layers 3 and 6.1



**Figure 8.** Mammoth scapula (CSB70 18) from layer 6 with cut marks clearly visible on the medial surface.

could represent, rather than a single catastrophic event, a more opportunistic exploitation of these resources concurrent with site visits of a shorter duration. This new faunal analysis supports the latest topographic data, which suggest that the physical geography of the La Cotte headland may not have provided the most suitable conditions for repeated, systematic game drives by Neanderthals (Scott et al., 2014). Furthermore, recent bathymetric survey identified the presence of a dissected landscape submerged offshore,

with CSB sitting at the top of a dead-end valley (Scott et al., 2014). Thus, the geographic positioning of the site could perhaps have been utilised as a barrier/boundary to both track and hunt various large mammal species during both shorter and longer term occupation of the site (Scott et al., 2014). Thus, the wider topographic landscape could have facilitated Neanderthal hunting, whilst CSB provided a close, safe location to transport a range of faunal materials for further butchery and processing. However, to fully



**Figure 9.** Mammoth skull (CSB74 434) from layer 3 with mammoth rib driven into parietal region; rib proximal epiphysis clearly visible (a. and b.) and continues through the skull emerging in the squamosal region (c.).

understand the role and importance of megafauna in Neanderthal diet, both at CSB and across their broader European range, requires further detailed contextualisation of these data at a wider spatial and temporal scale.

#### *Megafauna at Middle Palaeolithic sites: a spatial and temporal review*

Of the hundreds of Middle Palaeolithic sites and find spots from across Western Europe, only 30 well-published sites contain significant evidence for megafaunal material, including mammoth, elephant, woolly rhino, and other interglacial rhinoceros species (see Table 8). These sites are distributed across a wide geographic area from Spain through Germany (Fig. 12) and include both cave and open-air localities. At a temporal scale, these sites reflect the entire Middle Palaeolithic, from MIS 8 through MIS 3, with a larger number of sites dating to the late Middle Palaeolithic (MIS 5d–3). At this broader geographic and temporal scale, sites containing megafauna, such as La Cotte de St Brelade, appear as the exception, not the rule.

From the 30 sites documented, eight have faunal assemblages dominated by more than 10 megafaunal individuals, whilst at six locations a single individual is represented (Table 8). A total of 18 sites remain once single carcass locations and sites with limited data are excluded, which indicates the rarity of faunal assemblages containing megafauna during the Middle Palaeolithic (Fig. 13). Of these 18 sites, 13 (72.2%) have faunal assemblages with over 50.0%

of material (NISP) assigned to Body Size Group C, including Salzgitter-Lebenstedt, Scladina, Spy and Biache-Saint-Vaast, with only a small megafaunal component. At only three sites, including the upper levels from CSB, megafaunal species compose over 70%. The remaining locations, whilst containing a significant proportion of megafaunal remains, include comparatively large proportions (20–30%) of species from BSG C.

Overall, sites dominated by megafauna do not appear to be correlated with a particular species, geography, or site type (Table 8). Closer examination of these sites highlights inconsistencies in both the accumulation factors and available information. At many open-air localities, such as Neumark Nord 1, Taubach, Mont Dol and Biache St Vaast (Table 8; Tuffreau and Somme, 1988; Bratlund, 2000; Gaudzinski, 2004; Louguet-Lefebvre, 2005; Mania, 2010), megafaunal remains accumulated around lake margins and, at some sites, were subsequently scavenged by carnivores (Diedrich, 2014).

At Biache St Vaast and Mont Dol, the overall density of megafaunal material is low: 4.2/m<sup>2</sup> and 1.5/m<sup>2</sup>, respectively. At Taubach, the value is substantially greater (24.3/m<sup>2</sup>) though the excavated area is considerably less (200 m<sup>2</sup>) compared with both Biache (1000 m<sup>2</sup>) and Mont Dol (1300 m<sup>2</sup>). Calculating the lithic density in proportion to the megafaunal MNI (MFMNI) for these sites produces similar values for all three sites (Biache: 11.8 lithics/MFMNI; Mont Dol: 15.0 lithics/MFMNI and Taubach: 11.8 lithics/MFMNI). These values are quite low particularly considering the overall large assemblage sizes/MNIs produced at these sites, and in particular



**Figure 10.** Wolf radius (CSB72 201) from Layer 6 with chop marks on the distal shaft.

considering the small excavation area at Taubach. Whilst megafaunal butchery may require only a small quantity of lithic tools, the low density recorded at all of these locations could indicate shorter visits focussed on the hunting of larger animals (bovids, equids, cervids) and opportunistic exploitation of megafaunal species.

Interestingly, these area and density values are considerably lower when compared with both the overall excavated area at CSB (c.100 m<sup>2</sup>) and megafaunal density (14.9/m<sup>2</sup>). At CSB, density values of lithic/MFMNI ratio are especially low within bone heap horizon 6.1 (7.3 lithics/MFMNI; Table 7). Even the value of 131.7 lithics/MFMNI for layer 3 is considerably lower than the ratios in the underlying deposits, ranging from 1940 to 6552. At all of these sites, including CSB, the lithic density suggests either a shorter duration of site use and/or a more opportunistic exploitation of megafaunal species. There is always an element of uncertainty about comparing open-air and cave localities in terms of variation in both horizontal distribution and vertical time depth (e.g., palimpsests). Nevertheless, at all locations with evidence for megafaunal exploitation, Neanderthal presence appears rather opportunistic in nature. A focus on medium-sized species (bovids, cervids, equids) is noted, with megafaunal elements representing a smaller, supplementary element of Neanderthal diet. This leads to questions about identifying the exploitation of megafauna by Neanderthals.



**Figure 11.** *Ursus* sp. femur (CSB73 245) from layer 5 with cut marks on distal epiphysis perhaps related to disarticulation.

#### *Identifying megafaunal exploitation: direct versus indirect evidence*

A wide variety of interpretive criteria have been applied to the study of megafauna and used to argue for a specific Neanderthal exploitation strategy (Table 9). Across the sampled sites there is considerable variation in the amount of evidence for direct modification, both by humans (cut marks, marrow fractures) and carnivores (gnawing). This could have resulted from this information not being reported, or perhaps not recognised if the material was studied before the advent of modern taphonomic methodologies.

However, at many localities (Lynford, Spy), carnivore modification is substantially more significant, in terms of overall bone surface modifications, than that resulting from Neanderthal butchery behaviour (Smith, 2012; Gemonpré et al., 2014). For example, on the 11 mammoth individuals at Lynford no single trace of human modification has been recorded (Smith, 2012). Where direct evidence for Neanderthal modifications appears, this often seems to be mainly related to the exploitation of marrow (e.g., at Biache St Vaast, Mont Dol and Caours). The rare occurrence of burnt megafaunal remains (e.g., CSB and Taubach) may indicate the use of these remains for fuel. This has been suggested especially for colder glacial/interstadial periods where other sources of fuel were either lacking or sparse (see White, 2006).

**Table 7**  
Lithic and faunal density by context at La Cotte de St Brelade; area estimated from stratigraphic sections from Callow and Cornford (1986), Figure 6.4. MF (includes mammoth and woolly rhino) – megafauna.

Layer	Approximate excavated area (m <sup>2</sup> )	Total lithics	Lithic density	Total fauna (NISP)	Faunal density	Lithic/Fauna density	MF NISP	MF MNI	Lithic/MF MNI density
6.1	30	95	3.2	231	7.7	0.4	206	13	7.3
5	42	3378	80.4	68	1.6	49.7	34	2	1689.0
4	4	0	0.0	13	3.3	0.0	1	0	
3	35	1185	33.9	406	11.6	2.9	312	9	131.7
A	32	39312	1228.5	336	10.5	117.0	133	6	6552.0
B	24	5821	242.5	183	7.6	31.8	75	3	1940.3
C	27	9623	356.4	147	5.4	65.5	23	2	4811.5

The absence of, or inability to identify, direct processing marks has often required researchers to search for more indirect evidence to support megafaunal accumulation and exploitation by Neanderthals. These include body part profiles (Haynes, 1988a, 1991), mortality profiles (Haynes, 1985, 1987, 1988b), pathology (Schreve, 2006), proximity to lithic tools (Mussi and Villa, 2008), isotopes (Bocherens, 2009), and hunting equipment (fractured lithic points, wooden spears) (Movius, 1950; Mussi and Villa, 2008). However, interpretations of many of these indirect lines of evidence remain ambiguous. For example, various agents can produce similar skeletal part and age profiles, and especially in cave sites various accumulation features can overlap or even mask each other in these palimpsest settings. The presence of lithic tools, either surrounding megafaunal carcasses or within the same deposits, suggest a hominin presence. However, numerous case studies have identified lithic tools at cave and open-air sites without any evidence for direct human exploitation or accumulation of the faunal material present (Villa and Soressi, 2000; Boschian and Saccá, 2010). In addition, some authors have argued for megafaunal exploitation based on the presence of ‘projectile’ points and even a single broken point (Mussi and Villa, 2008). However, such fracture patterns are still keenly debated and discussed, and can result from numerous processes or agents (Iovita et al., 2014; Rots and Plisson, 2014). Overall, the use of indirect evidence for megafaunal exploitation is not, in itself, invalid. However, these approaches are reliant on a comprehensive understanding of the specific taphonomic and deposit formation processes that operated at each site; none of them should be used in isolation.

Actualistic work throughout the 1980s investigated the cull patterns and bone surface modifications caused during the natural thinning of African elephant herds (Haynes, 1988b, 1991). Butchery of these animals left very few cut marks due to the quick removal of large muscle packages (but see Haynes and Klimowicz, *in press*, for recent review). Therefore, the recurrent absence of cut marks on megafauna from Middle Palaeolithic sites has been interpreted by some authors as evidence for a similarly quick butchery of these animals by Neanderthal groups (see for example Spy; Lynford; Schreve, 2012; Gemonpré et al., 2014). However, an absence of cut marks may not be related to the skill of the individual butcher, but either to specific site formation and faunal accumulation or the actual resources these groups exploited. Most of the sites with clear bone surface modifications indicate a focus on marrow and other non-muscle meat resources (brain, offal) (Conard, 1992; Turner, 1998; Louguet-Lefebvre, 2005) although at some sites, including CSB, muscle meat removal can also be attested. This suggests that Neanderthals exploited and utilised different resources from the megafaunal carcass. Indeed, the degree and intensity of butchery of a wide range of animals at other Middle Palaeolithic sites (Neumark-Nord 2, Salzgitter Lebenstedt) and the common presence of cut marks and other butchery signatures at these localities, suggests that Neanderthals were efficient and skilled butchers that exploited the maximum amount of resources from each carcass

(Gaudzinski and Roebroeks, 2000; Gaudzinski-Windheuser et al., 2014; Kindler et al., 2014). However, this leaves open the question of how frequently megafaunal species were exploited by Neanderthals and hence what role they actually played in the Neanderthal diet.

#### *The role of megafauna in Neanderthal diet*

Scenarios of megafaunal exploitation based on interpretation of the stable isotope data are at odds with the zooarchaeological evidence, especially when considered together with the complexities of site taphonomy and accumulation, as reviewed in the previous sections. The Neanderthal isotopic signature is linked specifically to mammoth protein sources based on a shared high  $\delta^{15}\text{N}$  value, which relates to the specific plant foods mammoths consumed (Fox-Dobbs et al., 2008). It is argued that the high  $\delta^{15}\text{N}$  values could not be achieved without a significant contribution of mammoth to the Neanderthal diet and even that mammoth must have been their most important protein source (Drucker and Bocherens, 2004). However, further insight is required in order to understand how these signatures are related to other prey species with regard to how carbon isotopes, specifically  $\delta^{13}\text{C}$ , are consumed by herbivorous species with different diets (Lee-Thorp and Sponheimer, 2006). It is important to understand the variation in isotope signatures amongst herbivores in order to fully understand the values obtained for both Neanderthals and other carnivores (Bocherens et al., 2014; Willerslev et al., 2014). A one to one relationship between these high  $\delta^{15}\text{N}$  values and a mammoth protein resource therefore seems preliminary, especially when taking into account the zooarchaeological evidence for Neanderthal mammoth exploitation.

In addition, there are several interpretive problems that still need to be resolved when using data from dietary stable isotopes. Much of this work has been undertaken on Neanderthal fossils located within the northern area of their range (Bocherens, 2009), with recent additions from more southern (Spain) and western regions indicating a more varied diet (Salazar-García et al., 2013). Although southern Neanderthals had a substantial terrestrial-meat component, their diet appears to have been supplemented by plant and occasionally marine resources. Of course, this could simply represent regional variation in diet amongst different Neanderthal groups. Moreover, new non-zooarchaeological studies have questioned the more simplistic view of a single Neanderthal diet that was largely based on animal protein (Henry et al., 2014; Sistiaga et al., 2014). The detrimental nature of such a monolithic diet to the health of individuals has been discussed (Hardy, 2010; Hockett, 2012) and the recovery of larger and more varied plant and marine data suggests a broader subsistence pattern (Henry et al., 2010; Hardy et al., 2012; Buck and Stringer, 2014). Henry et al. (2014) have also discussed the inherent problems with a sole focus on  $\delta^{15}\text{N}$  values, particularly related to the non-linear relationship between food source and consumer. This approach does not permit

**Table 8**

Comparative database of Middle Palaeolithic sites across Western Europe and throughout MIS 8–3.

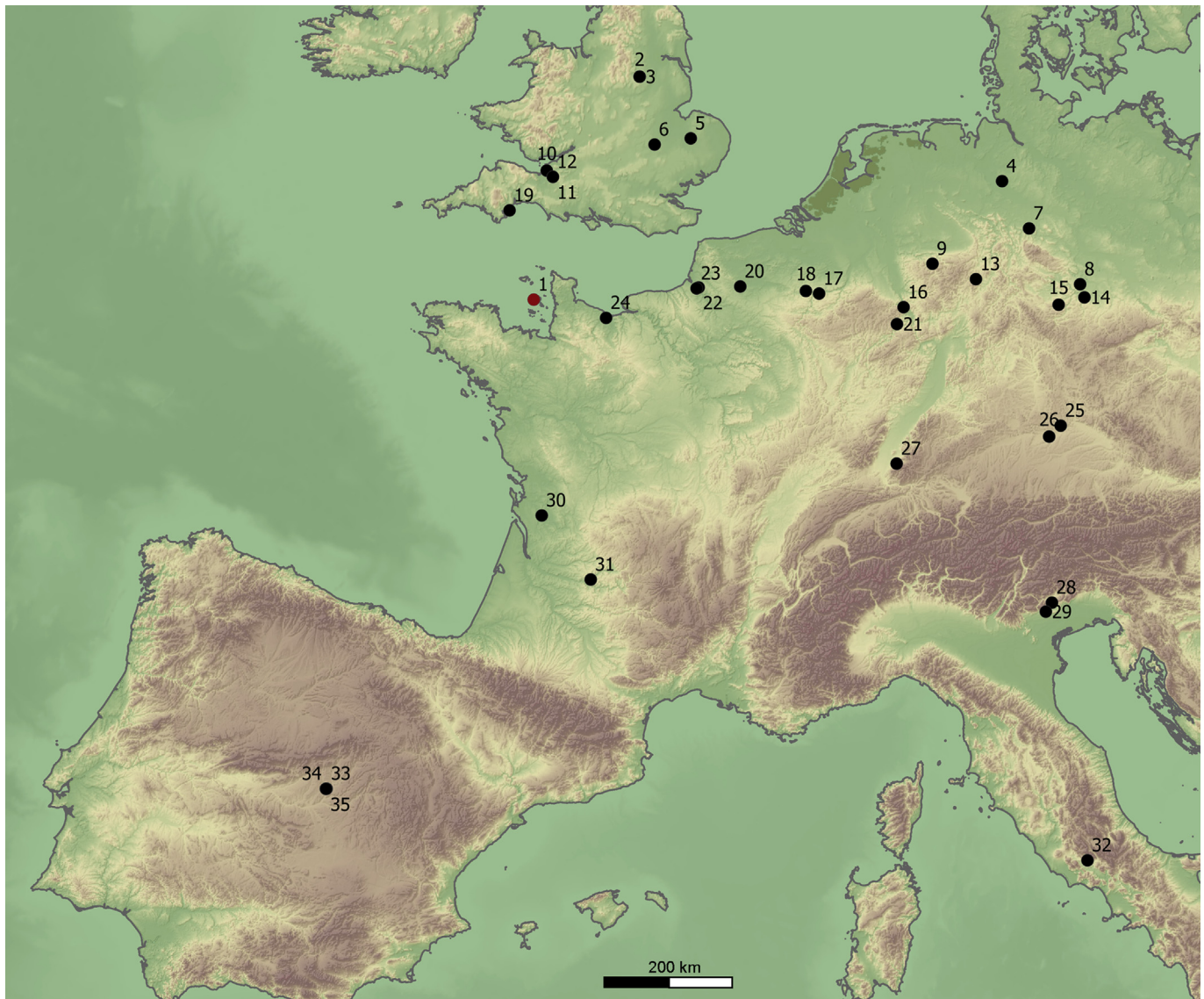
MIS	Site	Region	Level	Climate	Location	Type	NISP	MF	MF NISP	%NISP	MF MNI	Age	Other species	OtherMNI	References
8	Ariendorf 2	Ge	Bed I & II	cold	open	single	336	MA, WR	202	60.1	4	unknown	BO, RD, H, W	RD (2), BO (2), H (3)	Turner et al., 1997; Turner, 1998.
7	Biache St Vaast Ila	Fr	Ila & IIb	warm	open	multi	ca. 20000	STE; RH	1500	7.5	61	juvenile	BO, RD, GD, RoD	BI (NISP = 13780)	Auguste, 1995a,b; Louguet-Lefebvre, 2005.
6	CSB Ranville	UK	A-C	warm	cave	single	667	MA; WR	231	34.6	13	unknown	BO, RD, ReD, H	1	Scott, 1980,1986a,b.
		Fr		warm	open/cave	single	698	STE, RH	125	17.9	2	adult	BOV, H, RD, W	RD (9); H (4)	Auguste, 2008.
6	Tönchesberg CSB	Ge	1A	cold	open	single	766 <sup>c</sup>	WR	5	0.6	1/2	unknown	BO, RD, ReD, H	RD (4), H (3)	Conard, 1992.
		UK	3 & 6	cold	cave	multi	586	MA; WR	501	85.5	7; 11	prime	BO, RD, ReD,H, BE, AF	2	Scott, 1980,1986a,b
5e	Caours	Fr	4a & 6b	warm	open	single	892	STE, RH	9	1	2	unknown	BO, RD, FD, Rod	RD (8), FD (4), BO (4)	Antoine et al., 2006.
	Mont Dol	Fr	6 & 8	warm	open	multi	4159	MA; WR	1538	37.9	58	natural	BO, RD, FD, ReD, RoD, GD, H	ReD (15)	Louguet-Lefebvre, 2005.
	Tönchesberg Taubach	Ge	2B	warm	open	single	921	RH	9	1	1	unknown	BO, RD, FD, H	RD (55), BO (4)	Conard, 1992.
		Ge	"bone sand"	warm	open	multi	4864	STE; RH	1505	36.2	76	juvenile	BO, BE, RD, RoD, H, BE	BE (30)	Bratlund, 2000; Gaudzinski, 2004.
	Gröben Lehringen	Ge	unknown	warm	open	single	unknown	STE; RH	unknown	unknown	1	adult	RD, FD	unknown	Gaudzinski, 2004.
		Ge	unknown	warm	open	single	unknown	STE; RH	unknown	unknown	1	adult	BO, RD, FD, RoD, GD, H	unknown	Thieme and Veil, 1985; Gaudzinski, 2004.
	Neumark Nord 1	Ge	unknown	warm	open	multi	unknown	STE; RH	unknown	unknown	24	adult	BO, RD, FD, RoD, GD, H	unknown	Mania et al., 1990; Mania, 2010; Gaudzinski, 2004.
5a–5d	EDAR Culebro 1 Balve	Sp	2 & 3	warm	open	single	45	MA	35	77.7	1	adult	unknown	unknown	Yravedra et al., 2012.
		Ge	AHII	cool	cave	multi	22093	MA	416 <sup>b</sup>	1.9	unknown	unknown	CB, W, H	NISP = 5894	Kindler, 2012.
4	Scladina	Be	5	cold	cave	multi	1871	MA, WR	62	3.3	8	unknown	RD, FD, RoD, I, H, CB	CB (34)	Abrams et al., 2013.
		It	all	cold	cave	single	50	MA	50	100	1	adult	unknown	no	Mussi and Villa, 2008.
4	Bollschweil Balve	Ge	unknown	cold	cave	multi	423	MA; WR	243	57.4	6	adult	BO, RD, H, BE	unknown	Conard and Niven, 2001.
		Ge	AHIII	cool	cave	multi	22093	MA; WR	416 <sup>b</sup>	1.9	unknown	unknown	CB, W, CH, H, ReD	(NISP = 5894)	Kindler, 2012.
3	Saint-Césaire	Fr	10, 11, 12	cold	cave	multi	1682	MA, WR	33	2	6	unknown	BI, RD, ReD, HY, B, CL	BI (60); H (46)	Morin, 2012
	Spy Pin Hole	Be	Multi <sup>a</sup>	cold	cave/open	multi	10000	MA; WR	1178	11.8	unknown	juvenile	H	(H NISP = 3900)	Gemonpré et al., In press.
		UK	lower cave earth	cold	cave	unknown	unknown	MA, WR	unknown	unknown	unknown	unknown	BO, ReD, GD, H, W, HY	unknown	Jenkinson, 1984; Wragg-Sykes, 2010.
	Robin Hood Cave	UK	cave earth	cold	cave	unknown	unknown	MA, WR	unknown	unknown	unknown	unknown	BO, ReD, H, HY, W	unknown	Jenkinson, 1984; Wragg-Sykes, 2010.
	Rhinoceros Hole	UK	B	cold	cave	unknown	unknown	MA, WR	unknown	unknown	unknown	unknown	BO, ReD, H, HY, W	unknown	Proctor et al., 1996; Wragg-Sykes, 2010.
	Kent's Cavern	UK	loamy cave earth	cold	cave	unknown	853	MA, WR	148	17.4	unknown	unknown	BO, ReD, H, B, W, HY	H (NISP = 309); HY (NISP = 228)	Campbell and Sampson, 1971; Wragg-Sykes, 2010.
	Hyaena Den	UK	cave earth	cold	cave	multi	1586	MA, WR	473	30	unknown	unknown	BO, RD, ReD, H, HY, W, B	HY (NISP = 477)	Currant and Jacobi, 2004.
	Little Paxton Lynford	UK	unknown	cold	open	unknown	unknown	MA, WR	unknown	unknown	unknown	unknown	H, ReD	unknown	Wragg-Sykes, 2010.
		UK	all	cold	open	multi	3498	MA; WR	2341	66.1	11	adult	B, H, ReD	1	Schreve, 2006, 2012; Smith, 2012.
	Salzgitter-Lebenstedt	Ge		cold	open	multi	2860	MA; WR	418	14.3	17	unknown	ReD	ReD (86)	Gaudzinski and Roebroeks, 2000.

Abbreviations: MF – megafauna; MA – mammoth; WR – woolly rhino; STE – straight tusked elephant; RH – rhino; BI – bison; BO – bovid; RD – red deer; FD – fallow deer; RoD – roe deer; GD – giant deer; H – horse; ReD – reindeer; BE – bear; AF – arctic fox; CB – cave bear; W – wolf; CH – cave hyaena; H – hyaena.

<sup>a</sup> Note that faunal material from cave and terrace deposits 84% (NISP = 1926).

<sup>b</sup> This is overall site total.

<sup>c</sup> But over 1000 additional pieces not recorded in three dimensions.



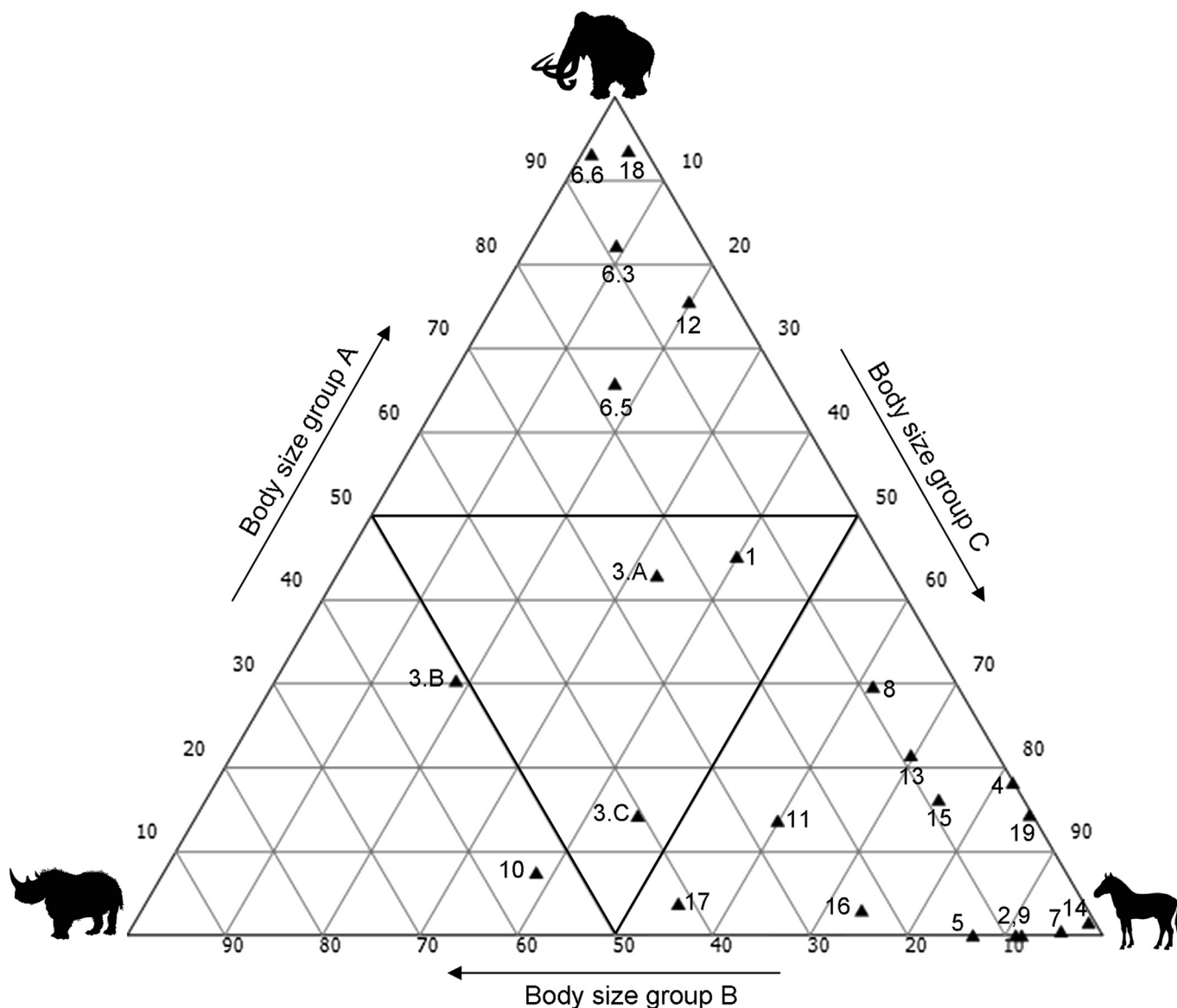
**Figure 12.** Location of major Middle Palaeolithic sites (MIS 8–3) containing megafaunal remains and discussed in the text; 1. La Cotte de St Brelade; 2. Pin Hole Cave; 3. Robin Hood Cave; 4. Lehringen; 5. Lynford; 6. Little Paxton; 7. Salzgitter-Lebenstedt; 8. Neumark-Nord; 9. Balve; 10. Picken's Hole; 11. Hyaena Den; 12. Rhinoceros Hole; 13. Buhlen; 14. Gröben; 15. Taubach; 16. Ariendorf; 17. Scladina; 18. Spy; 19. Kent's Cavern; 20. Biache-St-Vaast; 21. Tönchesberg; 22. Caours; 23. Abbeville; 24. Ranville; 25. Sesselfelsgrötze; 26. Königsau; 27. Bollschweil; 28. Vidor; 29. Asolo; 30. Saint Cesaire; 31. Abri du Musée; 32. Veroli; 33. Arenero de Arriaga; 34. Arenero de Rojas; 35. EDAR Culebro 1.

the estimation of proportion of meat versus plant foods in diets since changes in meat are indicated by only small increases in  $\delta^{15}\text{N}$  values (Henry et al., 2014). Finally, the human focus on starch and sugar (e.g., seeds) from plant resources that may have higher nitrogen value, but account for a smaller proportion of dietary protein, are thus masked by the meat protein signature (Henry et al., 2014). The potential for equifinality in isotope signatures must be made more explicit and requires detailed comparative studies in order to provide more distinction and to differentiate both the carnivore and, perhaps more importantly, herbivore signals and also to differentiate the meat versus plant signal from human skeletal remains (Bocherens, 2003; Kuitens et al., 2012; Buck and Stringer, 2014; Henry et al., 2014).

This wider, data-driven review and discussion of megafaunal exploitation during the European Middle Palaeolithic has highlighted considerable variation in both the type and quality of evidence used. It has demonstrated that whilst megafaunal species appear to represent a recurrent component of Middle Palaeolithic

faunal assemblages, they are most frequently outnumbered by other prey species. Recent excavations, combined with the re-evaluation of older collections, are continuing to identify evidence for Neanderthal exploitation of various megafaunal species, but this appears to represent more opportunistic subsistence behaviour and is of secondary importance compared with other prey species. Sites dominated by megafaunal remains, such as CSB, are rare throughout the Western European Middle Palaeolithic and in general the Neanderthal diet seems to have a stronger focus on medium-sized ungulates such as bovids, equids and cervids. Therefore, at present, the zooarchaeological data do not support claims, based on isotope evidence alone, for systematic exploitation of megafaunal species by Neanderthals (see for example Dusseldorp, 2013). At the vast majority of Neanderthal sites, evidence for megafaunal exploitation is absent, indicating that their diet could not have been solely dependent on mammoth protein sources. Furthermore, this calls into question the role and importance of megafauna in the hominin diet during earlier Palaeolithic





**Figure 13.** Ternary graph of European sites with megafauna and the percentage of specimens (%NISP) within different herbivore Body Size Groups (BSG); BSG A: mammoth and elephants, BSG B: rhino, BSG C: bovids (*Bos*, *Bison*), equids, cervids (*Cervus elaphus*, *Megaloceros* sp.); single carcass sites excluded; 1. Ariendorf 2; 2. Biache St Vaast IIa; 3.C. CSB (layer C); 3.B. CSB (layer B); 3.A. CSB (layer A); 4. Ranville; 5. Tönchesberg 1A; 6.3. CSB (layer 3); 6.5. CSB (layer 5); 6.6. CSB (layer 6); 7. Caours; 8. Mont Dol; 9. Tönchesberg 2B; 10. Taubach; 11. Scladina; 12. Bollschweil; 13. Balve; 14. Saint Cesaire; 15. Spy; 16. Kent's Cavern; 17. Hyaena Den; 18. Lynford; 19. Salzgitter-Lebenstedt.

periods and highlights a need for the re-evaluation of wider megafauna-related theories based on anecdotal archaeological evidence (Conard and Niven, 2001; Mussi and Villa, 2008; Ben-Dor et al., 2011; Gemonpré et al., 2014). Wider perspectives incorporating evidence from a series of sites, alongside taphonomic studies, isotope analysis and detailed zooarchaeological analyses, are needed before the real importance of megafaunal species in any hominin diet can be assessed.

## Conclusion

La Cotte de St Brelade remains a key site for understanding changing subsistence behaviour and the exploitation and importance of megafauna in the Neanderthal diet. New analyses confirm Neanderthals occasionally exploited megafaunal species (mammoth, woolly rhino) at this site. However, detailed taphonomic analyses have challenged the previous interpretation of CSB

as a game drive locality (Scott, 1980, 1986a,b). Variation in Neanderthal bone surface modifications and behavioural signatures suggest a shift in both the duration and frequency of site visits over time. This is most evident through an increase in carnivores throughout the depositional sequence concurrent with more extensive bone surface modifications, especially within the upper layers 3 and 6. Despite a clear dominance of mammoth, overall site use, assemblage formation and Neanderthal subsistence behaviour at CSB were complex and varied through time.

At a broader scale, megafaunal remains occur sporadically at Middle Palaeolithic sites across Western Europe in a variety of geographic, environmental and topographic settings. However, only a few localities have megafaunal remains in similar concentrations to CSB. Moreover, at nearly all of these sites the exploitation of megafauna appears opportunistic and is allied with a more frequent exploitation of other large animals, especially equids, bovids and cervids. Moreover, the type, quality and appropriateness

**Table 9**  
Evidence for human and carnivore exploitation of megafaunal species and interpretation of major sites.

Site	Modification		Other evidence		References
	Carnivore	Human	Direct	Indirect	
Ariendorf 2	unknown	yes <sup>c</sup>	MF	no	Turner, 1998.
Biache St Vaast IIa	yes	yes	CM, MF	AS, BPR	Louguet-Lefebvre, 2005.
CSB	no	yes	BU		Scott, 1980, 1986a, b.
Ranville	unknown	yes <sup>e</sup>	no	BPR, AS	Auguste, 2008.
Tönchesberg	no	no	no	no	Conard, 1992.
CSB	yes	yes	CM, MF	BPR, AS, LT	Scott, 1980, 1986a, b.
Caours	no	yes?	MF	LT	Antoine et al., 2006.
Mont Dol	yes	yes	MF	BPR, MF	Louguet-Lefebvre, 2005.
Tönchesberg	yes <sup>b</sup>	yes	MF	BPR, LT	Conard, 1992.
Taubach	yes	yes	CM, BU	AS, PA	Bratlund, 2000; Gaudzinski, 2004.
Gröben	yes	no	unknown	BPR, PA, LT	Gaudzinski, 2004.
Lehringen	yes	no <sup>a</sup>	unknown	WS, LT	Thieme and Veil, 1985; Gaudzinski, 2004.
Neumark Nord 1	yes	no	unknown	BPR	Mania et al., 1990; Mania, 2010; Gaudzinski, 2004.
EDAR Culebro 1	no	yes	MF	AS	Yravedra et al., 2012.
Balve	yes	yes	CM, MF		Kindler, 2012.
Scladina	no	yes	CM		Abrams et al., 2013.
Asolo	no	no	no	LT, LIF	Mussi and Villa, 2008.
Bollschweil	no	no			Conard and Niven, 2001.
Balve	yes	yes	CM, MF		Kindler, 2012.
Saint Cesaire	yes	yes <sup>d</sup>	unknown	unknown	Morin, 2012
Spy	no <sup>a</sup>	no	no	BPR, AS, ISO, LT	Gemonpré et al., in press.
Pin Hole	yes	unknown	unknown	unknown	Jenkinson, 1984; Wragg-Sykes, 2010.
Robin Hood Cave	yes	unknown	unknown	unknown	Jenkinson, 1984; Wragg-Sykes, 2010.
Rhinoceros Hole	unknown	unknown	unknown	unknown	Proctor et al., 1996; Wragg-Sykes, 2010.
Kent's Cavern	yes	unknown	unknown	unknown	Campbell and Sampson, 1971; Wragg-Sykes, 2010.
Hyaena Den	yes	no	no	no	Currant and Jacobi, 2004.
Little Paxton	unknown	unknown	unknown	unknown	Wragg-Sykes, 2010.
Lynford	yes	no	no	BPR, PA, AS, LT	Schreve, 2006, 2012; Smith, 2012.
Salzgitter-Lebenstedt	yes	yes	BT	no	Gaudzinski and Roebroeks, 2000.

Abbreviations: BPR – body part representation; PA – pathology; AS – age structure; ISO – isotopes; LT – lithic tools; CM – cut marks; WS – wooden spear; MF – marrow fracture; LIF – lithic impact fracture; BT – bone tools; BU – burning.

<sup>a</sup> Though no exact figures are provided.

<sup>b</sup> Only on non megafaunal species.

<sup>c</sup> Only modifications recorded at Ariendorf 2 but unclear whether on megafauna.

<sup>d</sup> Burning and cut marks but unclear whether on megafauna.

<sup>e</sup> Only recorded on red deer and bovinds.

of the data used to identify megafaunal exploitation varies considerably and needs to take into account specific site formation factors. Therefore, these new data from CSB, in conjunction with a broader review and contextualisation, call into question the central role of megafaunal species in Neanderthal diet.

Although isotope values from Neanderthal fossils have been interpreted as representing a high 'meat signal' resulting from large quantities of terrestrial megafauna, current zooarchaeological data do not support a simple equation of one with the other. This does not preclude that Neanderthals exploited these animals, or even hunted them. However, Neanderthal diet was not necessarily dependent on systematic contributions from megafaunal species such as mammoth, elephant and woolly rhinoceros. Rather, it can be envisaged that a flexible approach with a core focus on large mammals, combined with the circumstantial exploitation of megafaunal species, could have allowed Neanderthals to adapt to constantly fluctuating climates and changing environments. Therefore, this paper represents another step in furthering the debate into the various components of Neanderthal diet and opens up wider questions about the role and importance of megafaunal exploitation by other hominin species throughout the Pleistocene.

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