Specialised hunting of Iberian ibex during Neanderthal occupation at El Esquilleu Cave, northern Spain

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Traditional views of Neanderthal hunting strategies envisage them preying on herd species such as bison and deer, rather than the sophisticated tracking of solitary animals. Analysis of faunal remains from El Esquilleu Cave in northern Spain, however, demonstrates that during certain periods of the Middle Palaeolithic occupation, Neanderthals focused on the hunting of ibex and chamois, small solitary species that inhabited the mountainous terrain around the site. These results indicate that Neanderthal hunting practices may have had more similarity to those of their Upper Palaeolithic relatives than is usually assumed.

Keywords: Spain, El Esquilleu Cave, Middle Palaeolithic, Mousterian, Neanderthal, Iberian ibex, chamois, hunting, faunal analysis

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Introduction

One of the most controversial issues to arise in the understanding of human evolution in recent decades is the debate on Neanderthal subsistence strategies and the nature of their diet (Ready 2010), as this has extensive implications for early human cognition. Early analyses of Neanderthal dietary habits were based on dentition studies that gave contradictory results. Boule (1923) argued for a vegetarian diet, whilst Hrdlička (1927) argued for a meat-based diet similar to that of modern humans. This established the schism that would dominate

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the field. Were Neanderthals primarily gatherers with limited hunting strategies (Howell 1952), or carnivores hunting large ungulates (Nougier 1954)? The idea of 'Man the Hunter' continued to prevail (Lee & De Vore 1968; Pfeiffer 1969) until the New Archaeology of the 1960s interpreted Neanderthal subsistence as an adaptive environmental response (Binford & Binford 1966; Geist 1978). Subsequently, processual archaeologists, supporting an evolutionary paradigm, hypothesised that Neanderthals had no organisational ability and were only able to implement opportunistic scavenging strategies, in contrast to anatomically modern humans (hereafter AMH), who were supposed to be more foresighted, organised and cooperative (Mellars 1973; Gamble 1986; Stiner 1994). This general belief was questioned by those who advocated more complex, effective and organised hunting strategies among Neanderthals (Chase 1989; Grayson & Delpech 2002).

In recent decades, the emergence of new methodologies has enabled better approaches to the examination of the Neanderthal diet. Stable isotopes (Bocherens *et al.* 1991; Richards & Trinkaus 2009) and the combination of palaeobotanical (Boaz *et al.* 1982), zooarchaeological and taphonomic studies (Gaudzinski & Kindler 2011) have brought us closer to a resolution of the hunting/scavenging debate. The Neanderthal diet was versatile, including plant foods, marine resources and a large assortment of animals that varied widely in size (Scott 1986; Madella *et al.* 2002; Blasco 2008; Stringer *et al.* 2008; Blasco & Fernández-Peris 2009; Hardy & Moncel 2011).

Current debate focuses on establishing the subsistence differences between Neanderthals and AMH. Patterns observed at several archaeological sites suggest similar strategies for both hominins (Chase 1989; Grayson & Delpech 2002; Yravedra 2013). However, there are some outstanding issues that have still to be addressed. Hunting specialisation, and hunting strategies which focus on solitary animals rather than herds, are generally considered to be characteristics of the Upper Palaeolithic, and so are traditionally associated with modern humans: they are poorly documented in the Middle Palaeolithic (Straus 1987; Gamble 1995). Our aim in this paper is to present the Neanderthal subsistence strategy at El Esquilleu Cave, a site where specialised hunting patterns focusing on Iberian ibex and chamois are proved throughout the late Middle Palaeolithic (135–40 kya) in Oxygen Isotope Stage 3 (57–29 kya).

El Esquilleu Cave

El Esquilleu Cave is located in the Hermida Gorge in northern Spain (X: 371520, Y: 4790700, pg. MTN: 1:50000 Carreña-Cabrales; Martínez & Rodríguez 1984). It is 68m above the Deva River, 350m above sea level, and 26km from the Cantabrian coast (Baena Preysler *et al.* 2005) (Figure 1). The site was excavated between 1997 and 2006 (Baena [Preysler] *et al.* 2012): 41 archaeological layers covering the end of the Middle Palaeolithic were identified (see Table S1 in the online supplementary material), representing a series of Mousterian occupations. Levels 3 to 5 contain ephemeral occupation evidence with little Mousterian lithic technology using local raw materials. Levels 6 to 14 show dense Neanderthal occupation with Quina Mousterian technology, utilising a greater diversity of raw materials. Levels 15 to 30 comprise more specialised occupation with Levallois, discoid and Quina technology (Baena Preysler *et al.* 2005). Levels 30 to 36 are currently under

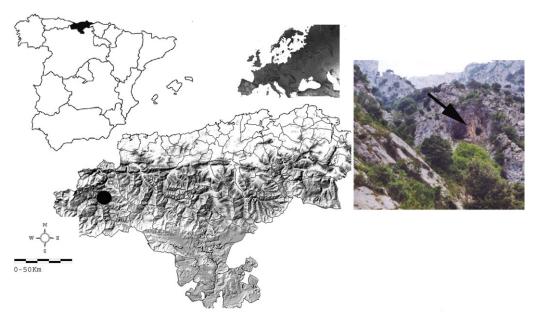


Figure 1. Location of El Esquilleu Cave within the Hermida Gorge.

study and are not discussed in this paper, and levels 37 to 41 are sterile deposits formed by low-energy processes (Jordá Pardo *et al.* 2008).

Sources for 99.2% of the lithic materials used throughout the site are found within 200m of the cave. Even materials from levels 3 to 5 come from the river zone. Nevertheless, material from levels 7 to 20 shows a greater variability and a wider geographical range, extending to the coastline (Baena [Preysler] *et al.* 2012). The topography of the gorge may have affected the mobility of Neanderthal groups, as faunal analyses of this and other nearby sites have demonstrated (Yravedra & Domínguez-Rodrigo 2009); mobility did not appear to extend far beyond the Deva River (Baena Preysler *et al.* 2005, 2012), staying within approximately 5km of the site.

Materials and methods

Archaeological layers 3 to 30 provided 70 717 faunal remains. The results from levels 7, 8, 9, 11, 11f, 12, 13, 17 and 22 will be discussed, but it must be noted that levels 11f and 13 are the most characteristic of Neanderthal activity at the site, and are therefore given the most attention. Greater intensity of activity was observed in these levels, as well as a higher proportion of faunal remains with optimal preservation. 23 450 remains were found in level 11f, and 7470 remains in level 13. Levels 3 to 5 are not considered in this work; taphonomic analyses demonstrated that carnivores were largely responsible for the faunal accumulation of ungulate remains in those layers (Yravedra 2006). Neither are layers 21 to 23 considered; those were analysed in Yravedra and Uzquiano (2013).

Our study presents the results of taxonomic identification, mortality and anatomical profiles, and taphonomic features (see online supplementary material). Taxonomic

identification was conducted with the help of a reference collection. When exact taxonomic identification was difficult (e.g. with shaft fragments), fauna were assigned to two categories of animals based on their size and weight: 'small taxa' refers here to animals <150kg (e.g. *Capral*ibex, *Rupicapral* chamois), and 'large taxa' include animals >150kg (e.g. *Cervus*/deer).

The representation of species is supported by the Number of Identified Specimens (NISP) and the Minimum Number of Individuals (MNI). NISP estimation is based on Lyman's (1994) work and MNI estimation on Brain's (1969). Thanks to the estimates of NISP and MNI we can calculate the representativeness of taxa and so assess whether specialised hunting behaviour was practised (Phoca-Cosmetatou 2009).

Seasonality profiles for individuals under three years of age have been established on the basis of dental eruption, and mortality patterns according to dental crown wear and dental eruption, from the work of Pérez-Ripoll (1988). Pérez-Ripoll's (1988) study was chosen for reference as it is founded on observations of *Capra pyrenaica* (the Iberian ibex), whereas other researchers, such as Couturier (1962), analysed *Capra ibex* (from the Alps). Our observations focus on the crown height and wear of molars and upper and lower P4. Mortality profiles are classified into four categories: elderly (i.e. over eight years), adult (i.e. over four years), juvenile and infant.

Skeletal profiles have been divided into 4 groups: cranial, trunk (i.e. axial), upper limb bones and lower limb bones, after the methodology of Yravedra and Domínguez-Rodrigo (2009). Skeletal profile quantification is based on the Minimum Number of Elements (MNE), including shafts (Barba & Domínguez-Rodrigo 2005).

Analysis of the bone surface was performed with hand magnifiers according to Blumenschine (1995). Cut-mark identification used Binford's (1981) guidelines, as well as Blumenschine and Selvaggio's (1988) and Blumenschine's (1995) work for the identification of percussion marks. The counts and distributions of marks were calculated on the basis of the NISP according to the bones and bone section as published by Domínguez-Rodrigo (1997). These were compared to the experimental work conducted by Capaldo (1997) and Blumenschine (1995), and studies by Lupo and O'Connell (2002) and Domínguez-Rodrigo and Barba (2005) to determine the likelihood of human access to bones before carnivore intervention. The prevalence of tooth marks on the bone assemblage provided additional information on this topic (based largely on the work of Blumenschine (1995), Capaldo (1997), Domínguez-Rodrigo (1997), Domínguez-Rodrigo *et al.* (2007) and Yravedra *et al.* (2011, in press)).

Bone fragmentation is examined from two different perspectives. The first measures the maximum length of every bone fragment, grouping them into: 1) fragments <30mm; 2) fragments between 31 and 50mm; and 3) fragments >51mm. The second analyses the circumference of the shaft according to Bunn (1982), who differentiates between: 1) where <25% of the circumference of the bone survives; 2) where the bone retains 25–75% of the original circumference; and 3) where >75% of the circumference is complete. This analysis allows estimations of whether bone accumulation is the result of human activity, or is actually a result of some other agent, such as carnivores. Human-produced accumulations have very high fracture rates where less than 25% of the degree of circumference remains, as humans

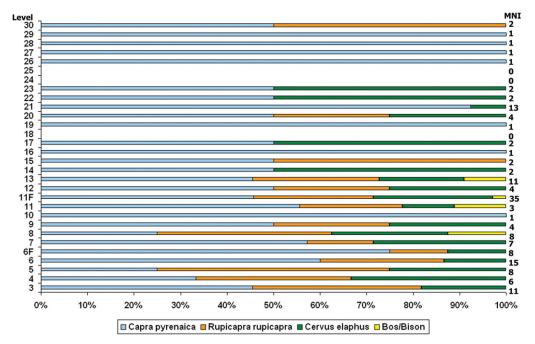


Figure 2. Percentage MNI representation of principal prey species by level at El Esquilleu; numbers to the right give total MNI.

are assumed to be shattering the bones to access the marrow, whereas carnivore-produced assemblages tend to contain bones where more than 50% of the shaft circumference remains.

Results

Taxonomic profiles

Iberian ibex and chamois are the most abundant animals at El Esquilleu (Figure 2; Tables S2 & S3 in online supplementary material). These two species make up more than 85% of the assemblage of each level with the exception of levels 7, 9 and 12. Deer are the third most common taxon, followed by sporadic *Bos/Bison* (Figure 2; Tables S2 & S3). This is consistent with the taxonomically indeterminate remains that have been assigned to size groups: small animals under 150kg form over 98% of the total sample (Table S2). The other levels of the sequence comprise few individuals or fewer than 600 determinable bone fragments (except for level 21, studied by Yravedra & Uzquiano 2013, and level 20). The MNI results are similar, although deer appears to be as common as other small ungulates in some levels with only 2–3 individuals including deer, chamois and ibex (Figure 2; Table S2). For example, in levels 15 and 30 there are only one ibex, one chamois and one deer, and levels 17, 22 and 23 have only one ibex and one deer.

The analysis of levels 11f and 13 supports these results. Level 11f includes 23 450 remains, of which 12.2% (2865) could be assigned to a total of 35 individuals. 7470 remains were found in level 13, including 1167 identifiable bones (15.7%) that could be from at least 11

individuals. Iberian ibex and chamois are the most abundant species in both levels, making up 70% of the total MNI (Figure 2; Table S2).

Mortality profiles and seasonality

Individual mortality profiles of all kinds of taxa in levels with a MNI >6 individuals are dominated by adults (see Table S3 in online supplementary material). Equal representation of juveniles and adults occurs only in levels with fewer than 5 adults. Of levels 6, 7, 8, 11 and 13, only level 6 could be precisely assigned to a particular season. It is difficult to determine the time of death from adult remains: these dominate the assemblage and hence it is hard to establish when in the year the site was occupied. Seasonal hunting patterns could only be estimated on the basis of tooth eruption and wear studies on a few individuals from levels 3 to 13 (see Table S4 and comments in the online supplementary material). Iberian ibex and chamois were both exploited during the same seasons. Most individuals were brought to the site during autumn or summer, or occasionally at the end of the spring (see Table S4 and comments). This suggests that the site was occupied during the warmer seasons, when a higher proportion of young animals would normally be expected. However, in levels 11f and 13 it is adult and elderly ibex, chamois and deer that make up more than 60% of the individuals in the assemblage. This indicates an intentional focus on adults at this site. The results should nonetheless be treated with caution as the analysis does not include all of the individuals recorded at El Esquilleu: the site could have been occupied at other times of year.

Skeletal profiles

Skeletal profiles from El Esquilleu were grouped into two categories; small animals (<150kg) and animals of medium or large size (>150kg). Representation differs between levels: small animals exceed 100 MNE in levels 3, 6, 11f, 13 and 21. Cranial and lower limb sections are the most common, and trunk bones the least (Table S5 in online supplementary material). Appendages are represented by both upper and lower limb bones, suggesting that complete legs were transported to the site. In levels 11f and 13 parts of the entire skeleton were found, hinting at the transport of complete ibex and chamois (Table S5).

Level 11f also has a high number of large animals (>150kg): deer exceed 100 MNE. Deer in the other levels are characterised by a predominance of limb bones compared to cranial and trunk specimens. Even in level 11f, the deficit of cranial elements is noticeable due to the lack of teeth recorded in the assemblage. This may result from the size difference between deer and ibex, leading to the transport of only parts of deer and other larger carcasses, or because the surface excavated varies from level to level with different kinds of activity area in each. Skeletal profiles of *Bos/Bison* are represented by shaft fragments of limb bones, suggesting only appendages of these species were transported to the site.

Bone alteration patterns

As already noted, carnivores were responsible for the accumulation of fauna in levels 3 to 5 (Yravedra 2006), but from level 6 a series of changes can be recognised that suggest greater

human involvement. The frequency of bones with cut and percussion marks increase, as does the frequency of bones showing traces of thermal action (Table S6 in online supplementary material). An increase in bone fragmentation was also observed. From level 8 onwards, over 88% of the remains measure less than 30mm in length, and approximately 99% of the long bones have less than 25% of their circumference preserved. This matches fracture patterns from human activities observed by Bunn (1982) when humans produce bone assemblages. The preservation of the bones in these levels is good: weathering damage is low, dry fractures are few, and bone surfaces show good preservation. The main factor affecting the assemblage in levels 6 to 13 is the high incidence of fracture: a large percentage of specimens could not be attributed to species.

Levels 14 to 18 and 23 to 30 comprise highly fractured, poorly preserved bones: this made it impossible to recognise traces of anthropogenic exploitation on bone surfaces. However, between levels 19 and 22, skinning, disarticulation and defleshing marks were found, as well as evidence suggesting the use of the bones as fuel (Yravedra & Uzquiano 2013).

Taphonomic evidence from the most representative levels (11f and 13) shows a significant anthropogenic contribution. Bones with cut marks and percussion marks are abundant, fragmentation is very high and less than 25% of the circumference of the shaft is preserved in 98–100% of the large bones (Table S7 in online supplementary material). This pattern is the same as that observed in the human-produced assemblages in the experimental reference data and in the archaeological sites (Bunn 1982; Domínguez-Rodrigo 1997; Domínguez-Rodrigo & Barba 2005).

Fewer than 10% of large bones in levels 11f and 13 have percussion marks, and these frequencies are slightly lower than those recorded in the reference studies (Figure 3). Cut-mark frequencies suggest human access to meat before carnivore intervention, as the frequencies are not dissimilar to the patterns observed when humans have primary access to carcasses (points 1–4 in Figure 4). Finally, there are few teeth marks on the carcasses, and these do not resemble those left by wolves, foxes, felids or hyenas. The frequency of tooth marks on all bones, even in the levels under discussion, is very small (Figure 5). All of this evidence—percussion marks, cut marks and tooth marks—indicate that carnivores only intervened as scavengers and did not create the assemblage.

The distribution of cut marks on limb bones of small and large animals at El Esquilleu also coincides with the variability described in experiments where humans are the main taphonomic agent (Figure 6). Data recorded on the foot bones (metapodia) concurs with the results obtained in those experiments. Marks on upper limb bones also support the case for primary human access to the carcasses (Figure 6). Tibia and radius specimens show no diagnostic results: when compared to the reference collection, cut-mark frequencies at El Esquilleu are equally likely to have been from humans acting as scavengers as from hunting. The frequency of teeth marks on these bones matches the frequencies seen elsewhere when carnivores scavenge animal carcasses after humans (Figure 7).

Humans were hence the main agents of bone accumulation in levels 11f and 13. Level 11f includes ibex and chamois carcasses on which skinning marks could be recognised. These appear mainly on the bases of horns and on phalanges, while defleshing marks were observed on various long-bone shafts, and on bones of the trunk such as ribs, scapulae and pelves. Evisceration marks stand out on the ventral faces of ribs; dismembering marks were observed

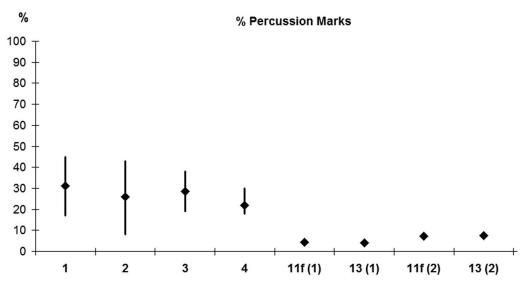


Figure 3. Percentage of percussion marks (PM) relating to: 1) animals <150kg (experimental data from Blumenchine 1995); 2) animals >150kg (experimental data from Blumenschine 1995); 3) animals <150kg (experimental data from Blumenschine 1995); 3) animals <150kg (experimental data from Capaldo 1997); compared to %PM for small animals from El Esquilleu levels 11f and 13, where '1' refers to animals <150kg and '2' to animals >150kg. Vertical lines show range of results from different experiments; diamonds show mean values.

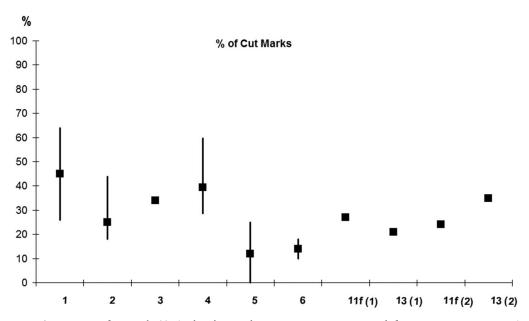


Figure 4. Percentage of cut marks (CM) where humans have primary access to carcasses before carnivore intervention: 1) after Domínguez-Rodrigo 1997; 2) after Capaldo 1997; 3) after Lupo & O'Connell 2002 for animals > 150kg; 4) after Domínguez-Rodrigo & Barba 2005 for animals < 150kg. Frequencies of cut marks when carnivores have primary access to the carcasses before human intervention: 5) after Domínguez-Rodrigo 1997; 6) after Capaldo 1997 for animals > 150kg; compared with percentage of cut marks from El Esquilleu levels 11f and 13, where '1' refers to animals < 150kg and '2' to animals < 150kg. Vertical lines show range of results from different experiments; squares show mean values.

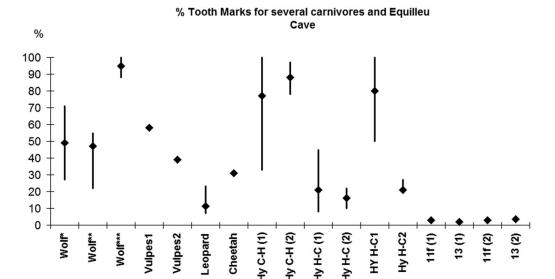


Figure 5. Percentages of tooth marks (TM) when carnivores have primary access to carcasses: wolf (Yravedra et al. 2011; wolf* for animals = 100–150kg, consumption in one event; wolf** for animals > 150kg and wolf*** for animals = 100–150kg, consumption in several events); fox (Vulpes) for animals <150kg (Yravedra et al. in press; Vulpes 1 = Spain, Vulpes 2 = France); leopard and cheetah for animals <150kg (Domínguez-Rodrigo et al. 2007). Hyenas show different patterns when they have primary access to animals <150kg (Hy C-H (1)) and >150kg (Hy C-H (2)), and when humans have first access to animals <150kg (Hy H-C (1)) and >150kg (Hy H-C (2)) (all Blumenschine 1995); also Hy H-C1 (Domínguez-Rodrigo 1997) and Hy H-C2 (Capaldo 1997) when humans have first access to animals >150kg, compared with %TM from El Esquilleu levels 11f and 13, where '1' refers to animals <150kg and '2' to animals >150kg. Vertical lines show range of results from different experiments; diamonds show mean values.

on the articular areas of long bones, on the mandibular condyle and on compact bones, e.g. carpals and tarsals (Figure 8a). The same processes were also observed on deer carcasses; flaying marks on phalanges, dismembering marks on the epiphyses and metadiaphyses of long bones, and defleshing marks on long-bone shafts and bones of the trunk (Figure 8b).

These processes were also observed to a lesser extent in level 13 (Figure 9a). Flaying marks were only found on ibex phalanges, and some dismembering marks were seen on the metadiaphyses and epiphyses of long bones. Chamois, ibex and deer exploitation is mainly represented by filleting and defleshing marks on both limb and trunk bones (Figure 9b).

Discussion and conclusion

El Esquilleu Cave is of major significance to the study of Neanderthal hunting patterns, and Neanderthal behaviour more generally. Occupation during the end of the Middle Palaeolithic reflects their great adaptability, in particular the ability to successfully exploit the mountain environments of the Hermida Gorge and Picos de Europa, overturning formerly held assumptions. Evidence of seasonal practices is inconclusive, but there are indications that the main activity at the site occurred during the milder seasons, when crossing the Deva River was easier. The presence of several sites on the river banks (El Habario, El Arteu, Ivan Cave, Fuentepara and El Esquilleu) shows that settlement in this region was constant and

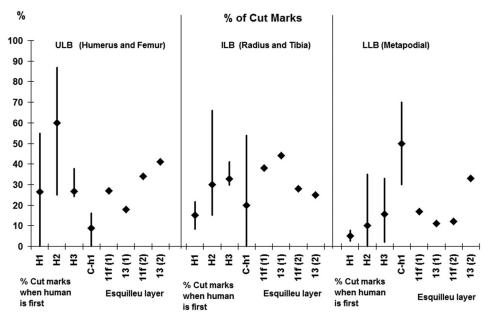


Figure 6. Percentages of cut marks on different limb bones from El Esquilleu levels 11f and 13, where '1' refers to animals <150kg and '2' to animals > 150kg, compared to experimental data based on primary access to small prey (H1, data from Domínguez-Rodrigo & Barba 2005) and to large animals (H2, data from Domínguez-Rodrigo 1997; and H3, data from Lupo & O'Connell 2002). C-h1 shows data for primary access of carnivores to carcasses, i.e. carnivores first with human access second after carnivore activity (after Domínguez-Rodrigo 1997). Vertical lines show range of results from different experiments; diamonds show mean values.

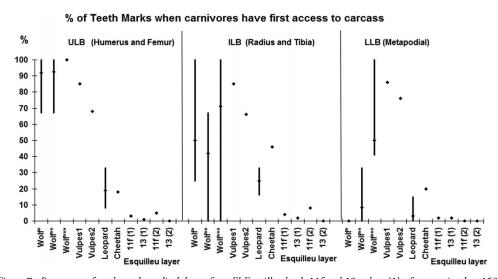


Figure 7. Percentage of tooth marks on limb bones from El Esquilleu levels 11f and 13, where '1' refers to animals <150kg and '2' to animals >150kg, compared to tooth mark patterns seen in wolf samples in Figure 5 (Yravedra et al. 2011); fox (Yravedra et al. in press); leopard and cheetah (Domínguez-Rodrigo et al. 2007). Vertical lines show range of results; diamonds show mean values.

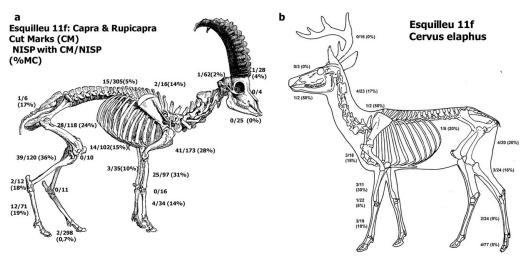


Figure 8. Representation of cut marks: a) on small animals (Iberian ibex and chamois) at El Esquilleu layer 11f, b) on mid-sized animals. The percentage of bones with cut marks was calculated from those bones with well-preserved surfaces.

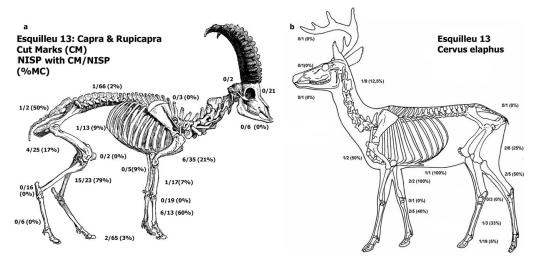


Figure 9. Representation of cut marks: a) on small animals (Iberian ibex and chamois) at El Esquilleu layer 13; b) on mid-sized animals. The percentage of bones with cut marks was calculated from those bones with well-preserved surfaces.

that the river was the leading artery between the valleys of the Picos de Europa and the Cantabrian coast (Baena Preysler *et al.* 2005, 2012).

Exploitation of this territory might not have been easy: nonetheless, Neanderthals adapted successfully to the environment. Their livelihood strategies focused on specialised hunting of Iberian ibex and chamois and on the exploitation of local resources, as evidenced by the origins of the raw materials used at the site (Baena Preysler *et al.* 2005). Adaptation would have been encouraged by the local conditions: although the rocky, steep terrain would have hindered mobility, it was favourable for ibex and chamois. Transport patterns of ibex and deer did not extend more than 5–7km from the site (Yravedra & Domínguez-Rodrigo

2009), demonstrating an intentional focus on local resources. Additionally, good-quality raw material for stone tools was available on the riverbank. Nevertheless, the remains of large bovids and more distantly obtained raw materials found in levels 11 to 13 suggest that longer-distance movement did occur (Baena Preysler *et al.* 2005, 2012).

The focus on hunting mountain species—ibex and chamois—identified at El Esquilleu reflects a subsistence strategy that is rarely documented among Neanderthals. Although ibex is often present at Mousterian sites, it has traditionally been linked to the action of carnivores (Gamble 1995), rather than to humans. That has been confirmed by taphonomic analyses at sites such as Moros de Gabasa (Blasco 1997), Zafarraya (Geraads 1997), Caldeirão (Davis 2002), Amalda (Yravedra 2010), Hornos de la Peña and El Ruso (both Yravedra 2013): human activity there focused on the exploitation of cervids, large bovids and equids. However, El Esquilleu reflects a different strategy where ibex and chamois were the main species exploited.

The ibex and chamois hunting described at El Esquilleu can be recognised in the NISP and MNI results: they share common characteristics with other Upper Palaeolithic deposits that show specialised hunting (Straus 1987, 1992; Delpech & Villa 1993; Gamble 1995; Tagliacozzo & Fiore 2000; Phoca-Cosmetatou 2009), such as Mezmayeskata (Baryshnikov *et al.* 1996). This hunting strategy is clearly not exclusive to the Upper Palaeolithic, but has earlier origins.

The patterns of mortality, particularly age profiles, and the patterns of seasonality identified at El Esquilleu, show that hunting techniques focused on solitary individuals and not on herds of females and calves, as seen in the Upper Palaeolithic (Bailey 1983; Straus 1987, 1992). Whether all Neanderthals hunted solitary individuals or whether they more usually hunted herds, and the extent to which this was a factor of group size, is a broader research question yet to be resolved. Nonetheless, this new evidence shows the great complexity and versatility of Neanderthal behaviour.

In addition to these specialised strategies (Straus 1987, 1992; Delpech & Villa 1993; Gamble 1995; Tagliacozzo & Fiore 2000; Phoca-Cosmetatou 2009), Neanderthals also exploited a wide spectrum of different taxa at other sites (Scott 1986; Madella *et al.* 2002; Blasco 2008; Stringer *et al.* 2008). Early hunting strategies are now also known to have focused on ibex (Baryshnikov *et al.* 1996), caribou (Gaudzinski & Roebroeks 2000; Rendu *et al.* 2012), deer (Yravedra 2013) and large bovids (Girad & David 1982; Jaubert & Brugal 1990). The next step is to understand the causes that motivated selection strategy. For example, at Pradelles, caribou specialisation was determined by seasonal availability (Rendu *et al.* 2012). At El Esquilleu, it seems to be determined by the topography of the land, but it would be important to analyse the broader geographical framework in order to reconstruct behaviour and mobility patterns between El Esquilleu and the coast.

The findings from El Esquilleu demonstrate Neanderthal adaptation in hilly regions, showing they were able to employ effective hunting strategies on mountain ungulates, notably ibex and chamois. This directly contradicts earlier beliefs about Neanderthal survival strategies, and has direct implications for our understanding of Neanderthal cognition. In particular, the evidence suggests that Neanderthals share more similarities with their Upper Palaeolithic relatives than formerly assumed, implying that Neanderthal diet is another topic of the Middle–Upper Palaeolithic transition which should be reassessed.

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