



Neandertal foraging during the late Mousterian in the Pyrenees: new insights based on faunal remains from Gatzarria Cave

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ABSTRACT

This article presents the initial results of a new study of faunal remains from Gatzarria Cave, a Middle-to-Upper Palaeolithic transition site the Pyrenees of southwestern France (department of the Pyrénées Atlantiques). This study attempts to document diet breadth during the late Mousterian, while paying due attention to recently identified problems regarding the stratigraphic context of the assemblages. The faunal analysis focuses on a subset of late Mousterian faunal remains from layer Cj at the site. Taphonomic analysis suggests that humans were the primary bone accumulators. The assemblage is dominated by a single large-bodied species, red deer; smaller-bodied ungulates are poorly represented. Skeletal part representation indicates that within-bone nutrients contained in marrow were probably a key resource for these foragers. The overall pattern of remains is interpreted as evidence of narrow-spectrum foraging, a pattern which appears to be repeated at other Mousterian sites in the Pyrenees region. This may mean that local Neandertal populations existed at relatively low densities. However, this suggestion must be tempered by the fact that settlement patterns, including occupation seasonalities and site functions, are not yet well understood for this region.

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1. Introduction

Gatzarria is a karstic cave site in the French Basque country (Fig. 1), located at an elevation of 290 m on Mont Hargagne, a mountain rising to 855 m above sea level in the eastern part of the Arbailles massif (Laplace and Sáenz de Buruaga, 2003). The site contains an archaeological sequence spanning the Middle to Upper Palaeolithic transition (Table 1), which has been the focus of various studies (Laplace, 1966; Sáenz de Buruaga, 1991; Lévêque and Miskovsky, 1996; Laplace and Sáenz de Buruaga, 2003), including a palaeontological analysis of the faunal remains (Lavaud, 1980). Gatzarria was excavated under the direction of Georges Laplace, beginning in the late 1950s through to 1976. Lithic tools and large or highly diagnostic animal remains were piece-plotted during excavation, and both these and smaller, less diagnostic faunal remains (such as long bone shaft fragments) were systematically collected.

This article examines foraging behaviours during the late Middle Palaeolithic at Gatzarria, and discusses their potential implications for regional patterns of resource exploitation and late Neandertal

demography in the western Pyrenees. This study will provide a baseline for assessing changes in foraging behaviours during the Middle to Upper Palaeolithic transition in the Atlantic Pyrenees, one of many regions where, until recently, faunal remains have been generally under-studied and, more often, under-published (Jaubert and Bismuth, 1996). The paper begins with a re-evaluation of the stratigraphy of the Middle to Upper Palaeolithic transition at Gatzarria, followed by a discussion of the assemblage taphonomy. Analysis of the faunal assemblage focuses first on patch use and diet breadth, then on the foraging currencies guiding transport decisions, and, finally, on the field-processing strategies of the Mousterian occupants of the cave.

2. Stratigraphy and sample selection

The published stratigraphic sequence for Gatzarria is based on both sedimentary and archaeological evidence (Laplace, 1966; Sáenz de Buruaga, 1991). A synthetic stratigraphic profile is shown in Fig. 2. However, during initial sorting of the faunal remains for this study, it was discovered that the majority of remains from the Middle Ensemble (Ej) had been assigned during excavations to a single sedimentary layer (Cj), despite the fact that this ensemble contains Mousterian, Châtelperronian, and Proto-Aurignacian materials. A subsequent analysis of the site notebooks confirmed

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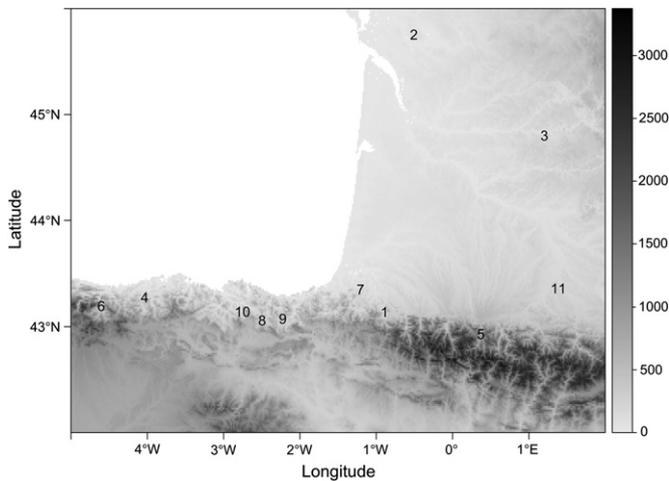


Fig. 1. Location of Gatzarria Cave and other sites mentioned in the text. 1. Gatzarria; 2. Saint-Césaire; 3. Grotte XVI; 4. El Castillo; 5. Le Noisetier; 6. Esquilleu; 7. Isturitz; 8. Labeko Koba; 9. Lezetxiki; 10. Axlor; 11. Abri Olha.

that the Proto-Aurignacian, Châtelperronian, and Mousterian archaeological units in the Middle Ensemble (Cjn-2, Cjn-3, and the Cj Mousterian, respectively) were not discrete archaeostratigraphic levels throughout the site and were rarely differentiated during excavation (see Table 1). Rather, lithic artifacts from the lower part of the Middle Ensemble were divided into the Cjn-2, Cjn-3, and Cj Mousterian assemblages largely through *a posteriori* sorting of lithic artifacts. This sorting procedure was based on raw material and technological criteria defined by Laplace (Sáenz de Buruaga, 1991), some of which are now known to be imperfectly diagnostic. This means that the various archaeological materials in the Middle Ensemble may not represent distinct *in situ* cultural deposits, and that *décapages*—the basic unit by which faunal remains and screened materials were collected—may contain remains associated with more than one cultural period.

To gain a better understanding of the stratigraphic distribution of the lithic complexes in the Middle Ensemble, and to determine if a sample of Mousterian faunal remains could be isolated from Upper Palaeolithic materials, a sample of piece-plotted stone tools from the Middle Ensemble was analysed in collaboration with André Morala and Eugène Morin. Diagnostic tools in this sample were re-attributed to Mousterian, Châtelperronian, or Proto-Aurignacian complexes, based on criteria used in recent analyses of these industries (e.g., Pelegrin, 1995; Bon, 2002). The distribution of these re-attributed artifacts was then plotted in three

Table 1
Sedimentary and archaeological units at Gatzarria. Industries after Sáenz de Buruaga (1991:97).

Sedimentary Ensemble	Sedimentary layers	Archaeological level	Cultural period
Eb (Upper Ensemble)	Cbn–Cbr	Cbn–Cbr	Historic
	Cbcs	Cbcs	Gravettian
	Cb	Cb	Evolved Aurignacian
Ej (Middle Ensemble)	Cbci–Cbf	Cbci–Cbf	Early Aurignacian
	Cj, Cjf	Cjn-1	Proto-Aurignacian
	Cj	Cjn-2	Proto-Aurignacian
	Cj	Cjn-3	Châtelperronian
	Cj, Cjm/Cjmg	Cj	Mousterian
Ejr (Lower Ensemble)	Cjr, Cjrm	Cjr	Mousterian
	Cgr, Cgrm		(Vasconian)
	Cr, Crm, Crmo	Cr	Mousterian/ Tayacian?

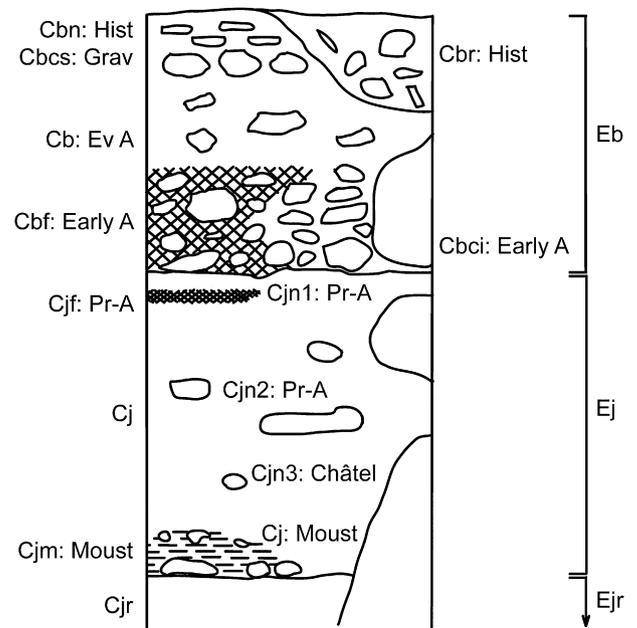


Fig. 2. Theoretical stratigraphic profile at Gatzarria, modified from Laplace (1966:119, Fig. 2). Lower layers in Ejr (the lower ensemble) are not shown in this figure. Cultural periods as follows: Hist = Historic, Grav = Gravettian, Ev A = Evolved Aurignacian, Early A = Early Aurignacian, Pr-A = Proto-Aurignacian, Châtel = Châtelperronian, Moust = Mousterian. Note that this division breaks down for Cj, as this abbreviation was used for both the Mousterian component of Ej and for parts of the sedimentary deposit containing the Cjn-1, Cjn-2, Cjn-3, and Cj Mousterian assemblages.

dimensions, along with additional data on Proto-Aurignacian tools provided by Laura Eizenberg (total $n = 424$; Fig. 3). Using this plot, the lower limit of Châtelperronian and Proto-Aurignacian lithic artifacts was identified in each one-by-one-metre unit, and only *décapages* (5–10 cm excavation spits) lying below these lower limits were included in the Mousterian sample (Fig. 4). Several units had to be eliminated from consideration due to apparent mixing or a lack of data. In the remaining sample, the highest concentration of remains occurs in units along the cave wall (3G, 4F, and 4G) at depths of 100–120 cm below datum. The high concentration of faunal remains in this area suggests a relatively intensive occupation (unit 3G contains 682 bone specimens in 0.033 m²); however, as shown in Fig. 4, the sample covers only a limited area of the cave. Based on the faunal remains, no clear evidence of hearths is present in the Cj Mousterian sample.

By removing upper *décapages* containing unambiguously Upper Palaeolithic artifacts, this strategy should have isolated a predominantly Mousterian sample in the retained *décapages*. Given that ivory and antler working are rare in the Middle Palaeolithic (Villa and d'Errico, 2001), a low representation of ivory and antler and an absence of worked antler or ivory pieces in the sample would support the integrity of the Mousterian sample. All but one fragment of antler, and 80% of mammoth ivory NISP, including the only incised ivory fragment in the assemblage, were removed from the Mousterian sample by the selection procedure outlined above. No refits were found between faunal specimens from the retained Cj Mousterian sample and the eliminated portion. Finally, a set of consistent radiocarbon dates would provide strong support for the temporal and stratigraphic attribution of the assemblage. One bone specimen from the Cj Mousterian sample has been radiocarbon dated to 44,300 ± 1900 BP (OxA-25717) and additional samples from other specimens are consistent with this result (Eugène Morin, pers. comm), confirming a late Mousterian date for the assemblage. Unfortunately, because of the problems identified in the stratigraphic attributions

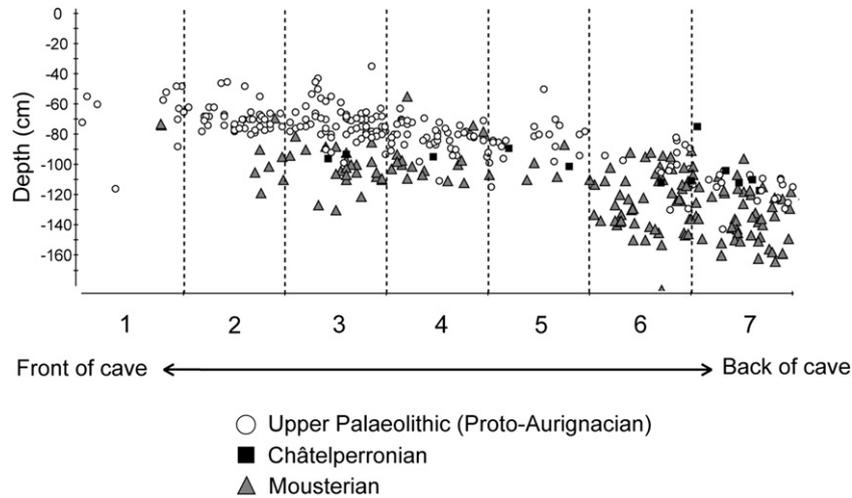


Fig. 3. Stratigraphic distribution of diagnostic artifacts in the Middle Ensemble. Numbers on the x-axis specify 1 m units starting from the front of the cave. All units with available data are included in this cross-section.

used in prior analyses, a discussion of Neandertal technical behaviours at the site must await a formal reanalysis of the lithic assemblages.

The selection procedure described above removed 56% of the faunal remains from the sample. The remaining Cj Mousterian

sample consists of 376 identified and 4907 unidentified faunal specimens. The taxonomic composition of the sample is presented in Table 2, and detailed skeletal part representation for the most abundant species in the sample, red deer (*Cervus elaphus*), is provided in Table 3.

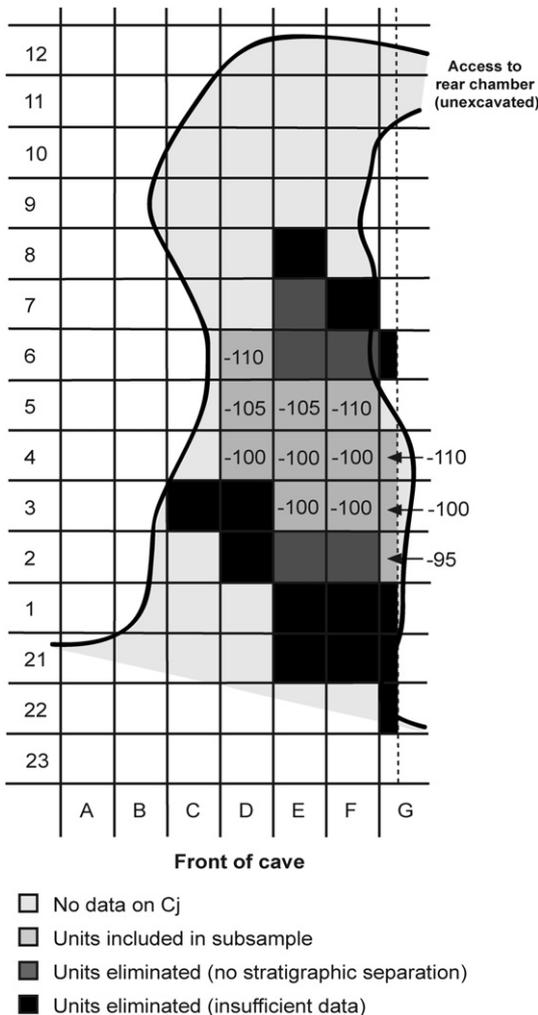


Fig. 4. Plan of the cave showing spatial extent and upper limits of décapages included in the Cj Mousterian sample.

3. Methods

The analysis of the Gatzarria faunal remains was carried out at the Musée National de Préhistoire, les Eyzies-de-Tayac, France. Identifications were made using the museum’s zooarchaeological reference collection. Elements or taxa for which modern reference materials were not available were identified using archaeological specimens in the museum collections, or with photographs and illustrated anatomical guides (e.g., Pales and Garcia, 1981). All specimens were examined under a 10× magnification hand lens to observe surface modifications.

Refitting was carried out on all long bone shaft fragments, rib fragments, and taxonomically identified specimens (NISP) in the sample. All of these were refitted with other specimens from the same décapage, and identified specimens were also tested for refits with all specimens belonging to the same element and taxon. MNE/MNI were not calculated because, for such a fragmented assemblage, it was decided that only an MNE/MNI calculated in the lab, using refits and overlaps, would be sufficiently accurate. This was impossible due to time limitations caused by the need to address

Table 2
Taxonomic composition of the Cj Mousterian sample.

Species	Common name	NISP	%
<i>Cervus elaphus</i>	Red deer	268	71.3
<i>Bos primigenius/Bison priscus</i>	Aurochs or bison	28	7.4
<i>Mammuthus primigenius</i>	Mammoth	10	2.7
<i>Rupicapra pyrenaica</i>	Pyrenean chamois	26	6.9
<i>Equus caballus</i>	Horse	11	2.9
<i>Vulpes vulpes/Alopex lagopus</i>	Red or arctic fox	2	0.5
<i>Capreolus capreolus</i>	Roe deer	12	3.2
<i>Capra sp.</i>	Pyrenean ibex	8	2.1
<i>Megaloceros giganteus</i>	Giant deer	2	0.5
<i>Rangifer tarandus</i>	Reindeer	3	0.8
<i>Ursus spelaeus</i>	Cave bear	3	0.8
<i>Crocuta crocuta</i>	Hyaena	1	0.3
<i>Coelodonta antiquitatis</i>	Woolly rhinoceros	1	0.3
<i>Panthera leo</i>	Lion	1	0.3
Total		376	100.0

a correlation with density does not identify the attritional agent responsible for bone destruction (Lyman, 1994; Cleghorn and Marean, 2004).

4.2. Human versus carnivore action

Carnivores are common agents of density-mediated destruction and also of bone accumulation in Palaeolithic assemblages. To what degree has the Gatzarria assemblage been accumulated and/or transformed by non-human animals? Evidence of human and carnivore action in the Cj Mousterian assemblage is summarized in Table 4, and some examples are shown in Fig. 6. Anthropogenic marks affect 11.3% of the Cj Mousterian assemblage. When teeth and antler are excluded from the tally, evidence of human action increases to 14.1% of NISP (42/297), or 14.3% of ungulate remains (42/293). The percentage of human-marked ungulate remains is highly comparable to other primarily anthropic French Palaeolithic deposits, such as Saint-Césaire (Morin, 2004), Combe Saunière, Castanet, and Cuzoul de Vers (Villa et al., 2004).

Carnivore remains constitute roughly 2% of the Cj Mousterian sample ($n = 7$; Table 2). No carnivore remains bear anthropic traces, and none of the carnivore specimens are juveniles. Carnivore damage, including gnawing and digestion, affects 5.6% of NISP, or, if only ungulate remains are considered, 4.9%. This level is higher than carnivore mark frequencies at Middle Palaeolithic sites such as Level 22 at Jonzac, Charente-Maritime, France (0.4% of ungulate NISP; Villa et al., 2004), and the Denticulate Mousterian at Saint-Césaire (0.1% of total NISP; Morin, 2004). The frequency of carnivore damage at Gatzarria is more comparable to the Solutrean levels (Unit IV) at Combe Saunière (Dordogne, France), where gnawing affected 3.4% of ungulates (Villa et al., 2004). These authors suggested that, because carnivore marks were rare on shaft fragments at Combe Saunière, carnivores had secondary access to human-deposited remains and probably did not contribute a significant amount of bone to the assemblage. Less than 1% of ungulate long bone shafts are carnivore-marked at Combe Saunière. At Gatzarria, 2.6% (5/189 ungulate diaphyses) show carnivore marks.

Gnawing damage (tooth pits, scooping, etc.) affects 1.3% of NISP, but only 0.8% when ungulates are considered alone (Table 4). Consequently, 29% (2/7) of carnivore remains are carnivore gnawed. Although carnivore remains are infrequent, this suggests that they are more likely than ungulate specimens to be modified by carnivores. Digestion marks are more common than gnawing, affecting 4.3% of total NISP and 4.1% of ungulates in the Mousterian sample. Although the sample size is small, 39% (7/18) of digested ungulate specimens are phalanges, another three (17%) are teeth, and one additional specimen is an antler fragment. Because teeth, phalanges, and antler are only of marginal nutritional utility to humans, this pattern suggests secondary access by carnivores to a previously accumulated deposit. It should be noted that phalanges and teeth may be easier to identify after digestion than

Table 4
Frequencies of carnivore and anthropic marks in the Cj Mousterian sample. Tooth and percussion notches are excluded. The categories of anthropic marks do not sum to the total because some specimens show more than one type of mark.

Mark type	NISP	%	Ungulate NISP	%
Anthropic	42	11.3	42	11.5
Cut marks	33	8.8	33	9.0
Scrape marks	5	1.3	5	1.4
Retouchers	6	1.6	6	1.6
Burning	1	0.3	1	0.3
Carnivore	21	5.6	18	4.9
Gnawing	5	1.3	3	0.8
Digestion	16	4.3	15	4.1
Total NISP	373		366	

other skeletal parts; however, traces of digestion were found on only 2.5% of unidentified specimens. Overall, the frequency of carnivore damage at Gatzarria is somewhat high for a presumably anthropogenic assemblage, but it remains much closer in line with anthropic deposits than with hyaena dens such as Bois Roche (Charente, France) where 81.7% of ungulate remains show carnivore damage (Villa et al., 2004).

Finally, the lengths and shaft circumferences of long bone specimens in the assemblage are another diagnostic measure of carnivore versus human accumulated assemblages (Villa et al., 2004). Table 5 shows that long bone shafts in the Cj Mousterian sample are highly fragmented, with most specimens belonging to the smallest size category (shaft circumference $<1/2$; shaft length $<1/4$), with very few specimens longer than half the total element length. There are also very few bone cylinders. This is consistent with fragmentation patterns from other anthropic sites, and contrasts Gatzarria with carnivore sites, such as Bois Roche (Villa et al., 2004:723, Fig. 7), which has a high proportion of long fragments and bone cylinders.

Together, the data on anthropic marks, carnivore marks, and fragmentation patterns demonstrate that, although the level of carnivore damage is slightly higher in the Gatzarria Cj Mousterian sample than at some other Palaeolithic assemblages, the material closely resembles other primarily anthropic sites. The data suggest that most of the remains at Gatzarria were brought to the site and fragmented by humans. Visits to the site by carnivores undoubtedly occurred between human occupations at Gatzarria, although these visits do not appear to have included denning. The frequency and patterning of carnivore marks suggest that many of the animal marks on ungulate specimens may represent secondary access to the remains. Yet, it remains likely that at least some ungulate remains in the assemblage were accumulated by carnivores. Many Mousterian deposits in the Pyrenees demonstrate high levels of carnivore activity—for example, Amalda and Esquilieu (Yravedra Sainz de los Terreros, 2006), Le Noisetier (Costamagno et al., 2008), Les Abeilles (Altuna, 2006), as well as Isturitz, Abri Olha, and Lezetxiki (Straus, 1982; Altuna, 1990). Notably, at Amalda (Yravedra Sainz de los Terreros, 2006) and Le Noisetier (Costamagno et al., 2008), smaller ungulates (ibex and chamois) may have been largely accumulated by non-human animals, while red deer and larger ungulates appear to have been accumulated by humans. For instance, at Le Noisetier, nearly 75% of chamois specimens show evidence of digestion while only 2% show cut marks (Costamagno et al., 2008). The frequency of human-induced marks (cut marks, scrape marks, retouchers, burning) and carnivore marks (gnawing and digestion) on small ungulate remains at Gatzarria are compared to red deer in Table 6. While there is a minor difference—which may indeed suggest a slightly greater role for carnivores in the accumulation of small ungulates—clearly the pattern differs vastly from Le Noisetier (~75% digestion of chamois) and non-human agents cannot be implicated as the primary accumulators of small ungulates at Gatzarria. Overall, despite some involvement of carnivores as accumulators and/or ravagers, the faunal remains at Gatzarria may have been more exclusively accumulated by hominin foragers relative to many other Mousterian sites in the Pyrenees.

4.3. Burning

The use of bone as combustible is another important density-mediated taphonomic filter at many Palaeolithic sites in France, such as Combe Saunière and Cuzoul de Vers (Castel, 1999) and Saint-Césaire (Morin, 2004). Although the overall abundance of burnt bone in the Cj Mousterian assemblage is low (3.3% of the total sample, 0.3% of NISP), bone burning may have had an impact on the

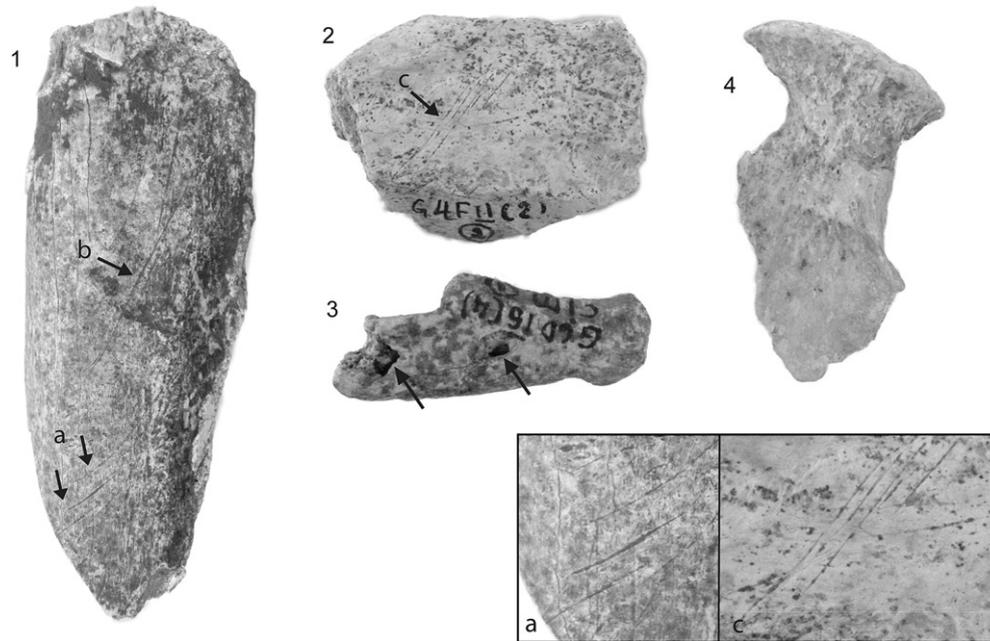


Fig. 6. 1. Red deer long bone fragment with (a) cut marks and (b) scrape marks; 2. Red deer long bone fragment with (c) cut marks; 3. Fox calcaneum with carnivore tooth punctures; 4. Digested fragment of a *Bos/Bison* phalanx. Inset shows close-up of cut marked areas (a) and (c).

assemblage composition by destroying spongy bone portions such as long bone epiphyses and vertebral bodies, which are under-represented in the sample. Wet sieving did take place during the excavations, but the smallest sieve size used varied between 3.8 mm, 3.3 mm, and 2 mm depending on the year, and collection of small unidentifiable bone fragments (<1 cm) may have been incomplete. This problem may be partially responsible for the low frequency of burnt bone fragments at Gatzarria. The limited spatial extent of the sample may also be a factor in the poor representation of burnt bones. For example, 59% of fragments from layer Cj in unit 22G at Gatzarria are burnt. Although this unit was eliminated from the Cj Mousterian sample because of insufficient lithic data (see Fig. 4), it may indicate that the frequency of burning varies substantially throughout the site.

4.4. Summary of the taphonomic analysis

The Gatzarria assemblage appears to have been predominantly accumulated by humans. The poor representation of low-density portions is likely due to a combination of factors, including carnivore action, burning, and some post-depositional breakage. To circumvent this problem, the analysis of skeletal part profiles in subsequent sections focuses on high-density bone portions, notably long bone shafts, which are more resistant to density-mediated attrition and are more likely to accurately represent the original abundances of bone portions (Marean and Kim, 1998; Pickering et al., 2003). Long bone shaft fragments were not subject to selective discard at Gatzarria, and constitute over 45% of NISP in the Cj Mousterian sample.

Table 5

Long bone fragmentation at Gatzarria, measured using relative proportions of shaft lengths (<1/4, <1/2, <3/4, >3/4) and shaft circumferences (<1/2, >1/2 or complete).

	<1/4	<1/2	<3/4	>3/4	Total
<1/2	135	34	3	0	172
>1/2	9	21	3	0	33
Complete	5	1	1	0	7
Total	149	56	7	0	212

5. Zooarchaeological analysis

5.1. Seasonality and mortality profiles

The presence of two small fetal ungulate specimens, as well as a lightly-worn red deer dP₄ suggest a possible occupation during the fall and/or winter. Due to the small sample size, however, the possibility that the site was occupied during other seasons cannot be excluded. Although tooth-wear data suggest a focus on prime-aged and older sub-adult individuals, due to small sample size, the different susceptibility of juvenile and adult remains to density-mediated attrition (Munson, 2000; Munson and Garniewicz, 2003; Munson and Marean, 2003), and the possible impact of predator-prey dynamics on ungulate demography (e.g., Wolverton, 2008), it is not possible to conclude that hunters from Gatzarria focused only on these age groups.

5.2. Patch use and diet breadth

Because different prey types may have occurred in different habitats (or patches), search time for all prey types during foraging near Gatzarria was probably not shared, and the foraging time of the site occupants may have been unevenly divided between patches. Consequently, for analytical purposes, the ungulate species in the assemblage are assumed to have occurred in two patch types according to their ecological characteristics (Fig. 7): a lowlands patch, which includes species that would have been found at lower elevations in valleys, grasslands, wetlands, and forests; and a mountain patch, which includes prey types that would be located

Table 6

Rates of bone modifications for size 1–2 ungulates (chamois, ibex, roe deer) and red deer at Gatzarria. Bone modifications as described in Table 4.

Modifications	Size 1–2	%	Red deer	%
Anthropic marks	4	8.7	37	13.8
Carnivore marks	3	6.5	7	2.6
Total NISP	46	100.0	268	100.0

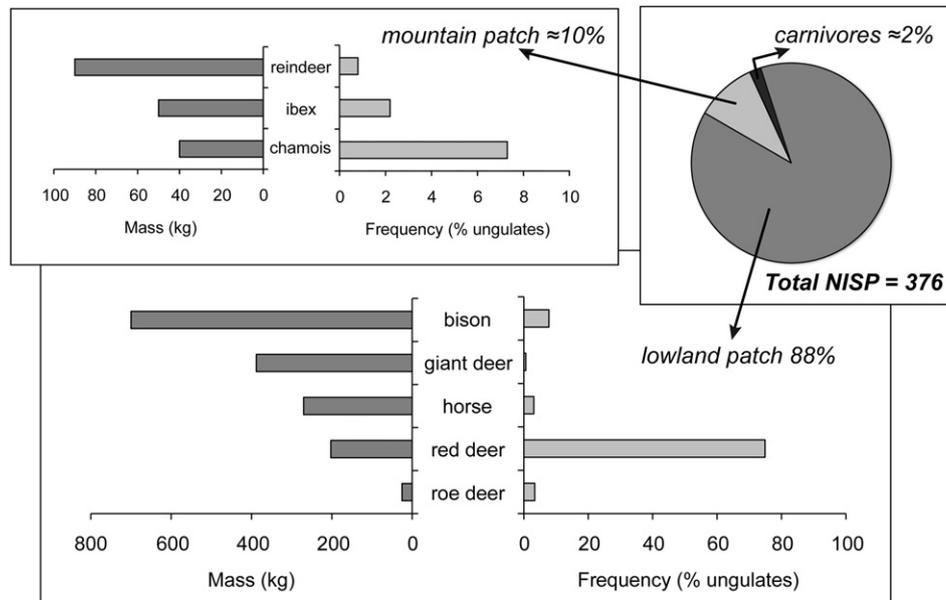


Fig. 7. Patch divisions, prey rankings, and prey abundances at Gatzarria. Body mass estimates from MacDonald and Barrett (2001), except for giant deer, estimated from Pushkina and Raia (2008:773).

at higher elevations or in rocky habitats. Following modern analogues (Miller, 2003), reindeer could have occupied either lowland or mountain habitats. Given the association of reindeer with colder habitats, and their limited ecological overlap with warmer-adapted species such as red deer (Mysterud, 2000), reindeer are tentatively placed in the mountain patch. The coarse grain of these patches means that encounters with prey types within them may not have been entirely random; however, this approach is a necessary compromise between the requirements of patch choice models (the fine-grained search assumption; MacArthur and Pianka, 1966; Smith, 1991), and our imprecise knowledge of ungulate community ecology during the time period under consideration.

In order to consider how Neandertals at Gatzarria used the patches identified above, the prey types within each patch are ranked using the body size rule (Bayham, 1979; Broughton, 2002). This rule assumes that the post-encounter return rates of prey increase with body size (i.e., that a larger animal provides more calories per unit of foraging time). This rule has often been criticized (Madsen and Schmitt, 1998; Stiner et al., 2000; Bird et al., 2009) and cannot be applied across prey types with widely differing mobility strategies. For instance, sessile or slow prey types such as tortoises may have high return rates for their size due to low search and handling times (Stiner et al., 2000; Stiner, 2001). However, it is likely that the body size rule is valid within the ensemble of large mammals in the Gatzarria assemblage, possibly excepting megaherbivores (Owen-Smith, 1988) such as mammoth and rhinoceros. Mobility patterns among mid- to large-sized artiodactyls—in particular, a pattern of decreasing maximal velocity with increasing body mass—suggest that the body size rule may be relatively strong for this group (Morin, 2012). Prey ranking scales which privilege total fat content of a carcass over body mass generally reproduce the body size rankings for species common in Middle and Upper Palaeolithic assemblages in France, with only minor changes (Morin, 2012).

The breakdown of the Gatzarria ungulates (excluding mammoth and rhinoceros) by patch and by species is illustrated in Fig. 7, in which average body masses are arrayed next to the frequency of each species. The greater diversity and the larger size of prey in the

lowlands patch suggest that this patch would have been higher-ranked. The mountain patch may also have been costlier to exploit than lowland habitats, due to difficult vertical travel or rocky terrain. The taxonomic data indicate that indeed the majority of remains brought back to the site were from prey types in the lowlands patch, particularly one moderately-ranked prey type, red deer. Larger prey types that are relatively infrequent in the assemblage (horse, bison/aurochs, and giant deer) may have had lower encounter rates than red deer, but might also have been passed over on occasion if hunters' success rates for these prey were lower than for smaller prey types (Bird et al., 2009). Related to this last suggestion is the possibility that even if larger ungulates were moderately abundant and always pursued upon encounter, pursuit success rates for these larger prey types may have been so low that few bouts were successful, resulting in low abundances of these animals in the assemblage (Coddington et al., 2010). Roe deer, the smallest ungulate in either of the patches, were occasionally brought back to the site.

Species from the mountain patch constitute less than 10% of the total assemblage. This may suggest that higher elevation or rocky habitats were infrequently utilized. This is consistent with the predictions of the patch choice model, because this was likely a lower-ranked patch, and also may have been less abundant around Gatzarria. Considering that a fall/winter occupation is signalled for the deposit, it is also possible to envisage that mountain species descended to lower elevations, below the snow line, to forage. This behaviour is particularly characteristic of chamois (García-González and Cuartas, 1996; Herrero et al., 1996; Lovari et al., 2006), which is the mountain prey type most abundant in the assemblage. In this case, foraging activities undertaken during the Mousterian occupation(s) may have been restricted to lowland patches.

Despite the relatively small sample size, nearly all the ungulate species that were likely present in the local environment are sampled in the Cj Mousterian assemblage. Evidence of hominin intervention (i.e., cut marks) on chamois and roe deer remains suggests that these animals were not deposited by carnivores alone. Thus, the available data suggest that *maximum diet breadth* (Grayson and Delpech, 1998) at Gatzarria during the time period

sampled included the lowest-ranked ungulate species in the local environment. Nevertheless, the rarity of small species in the assemblage, compared to the numerical dominance of red deer, suggests that diet breadth at Gatzarria was, on average, relatively narrow.

Several alternative explanations for this pattern can be suggested. First, small ungulates (roe deer, chamois, female ibex) may have always been taken upon encounter, but were simply infrequently encountered relative to red deer. Mountain patches may simply not have been very abundant near Gatzarria. In addition, roe deer are cryptic, territorial, and tend to live alone or in pairs (Geist, 1998), and roe deer and chamois may be mutually exclusive (Herrero et al., 1996)—characteristics that might cause lower encounter rates for both species. Indeed, larger, more gregarious species that tend to feed in open areas, such as red deer, bison, and horse, may have been relatively easier to locate. The patchiness in the distributions of different ungulate prey, and encounter rates within patches, the latter being conditioned not only by prey abundance but also by the nature of the topography and vegetative cover, may have been important in determining the opportunity costs of different hunting areas. Scavenging is a second possible explanation for the low representation of small ungulates. Even if these species were generally excluded from the diet breadth, occasional carcass finds would be different prey types with low handling costs and potentially high returns. Finally, another possibility is that smaller ungulates were generally excluded from the diet, but that these prey types were a fallback resource at times when higher-ranked prey (such as red deer) were less abundant.

Overall, patch use and diet breadth at Gatzarria appear to have been narrow, with only limited inputs of mountain prey types and smaller ungulates. For the moment, the patch use and diet breadth patterns outlined here apply only to the late Mousterian occupations at Gatzarria, and cannot be generalized temporally, geographically, or even seasonally. Gatzarria may have been used as a campsite during certain seasons (fall/winter) to take advantage of high local abundances of red deer, and as such may not be representative of the Neandertals' annual round in the region.

5.3. Foraging currencies

In this section, the foraging (or more accurately, transport) goals of Neandertals at Gatzarria are examined using correlations between patterns of skeletal representation and relevant utility indices. Only red deer is considered in this section, as it is the only species in the assemblage with a sufficient sample size ($n = 268$). As mentioned in the discussion of taphonomy, low-density bone portions are under-represented at Gatzarria, and may have been subject to density-mediated destruction. For this reason, only high-density elements (Lam et al., 1999), are considered in the analysis of skeletal part representation. These parts include teeth and mandibular bone, limb bone shafts, and the glenoid portion of the scapula (Table 3). First phalanges are also included due to their relatively high density and their potential importance when considering the transport of low-utility parts. Because this analysis concentrates only on a subset of skeletal parts, primarily long bones, the currency identified in this section may apply only to this subset. It is possible that transport decisions for parts excluded from the analysis (i.e., most of the axial skeleton) were based on a different set of criteria.

Correlation with utility indices is one way to identify possible criteria used by foragers to make decisions about what parts of a large carcass to transport (Binford, 1978). Unfortunately, no utility indices have been derived for either red deer or its North American counterpart, the elk or wapiti. However, the anatomical structure of ungulates is strongly consistent between species (Lam et al., 1999),

so utility models constructed for caribou (*Rangifer tarandus*) should provide a reasonable ordinal-scale approximation for red deer. Four indices are considered here: the Food Utility Index or FUI, which measures the total mass of useable tissue (meat, marrow, and grease) in skeletal parts (Metcalf and Jones, 1988); a proxy for the bone grease content of skeletal parts based on an ethnographic episode in which caribou bones were selected for grease rendering by Nunamiut women (Binford, 1978); the Unsaturated Marrow Index or UMI, which measures the total quantity of unsaturated fat in marrow bones (Morin, 2007); and the Meat Drying Index or MDI, which measures the “dryability” of a carcass portion (Friesen, 2001).

The red deer skeletal part abundance data correlate most strongly with the UMI, and the results of the Spearman's rank-order correlation are nearly significant ($p < 0.07$, Table 7). This lack of statistical significance is probably a result of the low number of elements ($n = 7$) included in the correlation, because the phalanges, mandible, and cranium are not considered in this set due to a lack of marrow values. A further reason to consider the correlation with the UMI as meaningful is that the red deer metacarpal is larger in relation to other long bones than the caribou/reindeer metacarpal, and therefore should be higher-ranked for this species. The strong representation of marrow bones at Gatzarria is part of what seems to be a widespread pattern of assemblage composition in natural shelters during the Late Pleistocene in Western Europe (Morin and Ready, in press). This pattern is consistent with the physiological importance of fat consumption among humans with diets heavily dominated by protein (Speth, 1983; Speth and Spielmann, 1983).

Extraction of marrow from red deer long bones appears to have been systematic at Gatzarria. The considerable proportion of fractures typical of fresh bone (67%), which usually show a curved fracture edge and a smooth fracture surface, suggests that most of the fractures occurred around the time of assemblage deposition. Probable percussion notches were documented on 15.8% (26/165) of red deer long bone specimens. However, the degree to which small marrow-bearing bones (mandible, astragalus, calcaneus, phalanges) were cracked for marrow is uncertain due to small sample sizes. The mandible is represented only by a few bone ($n = 6$) as opposed to tooth fragments. However, one fragment bears a probable percussion notch and green fractures. All of the first phalanges in the assemblage ($n = 7$) are fragmentary, except for one almost-complete specimen, and four of the broken specimens bear green bone fracture edges. Therefore, it seems that there may be positive evidence for marrow-extraction from small marrow-bearing elements, but these parts were probably infrequently transported to the site.

5.4. Field-processing and transport

In assemblages deposited by central place foragers, differences in evenness or mean utility of skeletal assemblages may be informative about transport decisions, field-processing, and potentially,

Table 7

Spearman's correlations between the Cj Mousterian red deer assemblage and four utility indices: the caribou FUI (Food Utility Index; Metcalf and Jones, 1988:492, Table 2); the percentage of caribou parts saved for grease rendering in the spring by a Nunamiut woman (Binford, 1978:36, Table 1.13); the caribou UMI (Unsaturated Marrow Index; Morin, 2007:77, Table 4); and the caribou MDI (Meat Drying Index; Friesen, 2001:320, Table 2).

Index	r_s	p -value	n
FUI	0.30	0.40	10
Grease rendering episode	0.64	0.09	8
UMI	0.72	0.07	7
MDI	-0.53	0.11	10

variability in prey encounter rates. Central place foraging field-processing models predict that, as average transport distances increase (with decreasing resource encounter rates), more effort will be allocated to field-processing, in order to increase the utility of transported loads (e.g., Metcalfe and Barlow, 1992; Barlow and Metcalfe, 1996; Bettinger et al., 1997; Cannon, 2003; Lupo, 2006; Faith and Gordon, 2007). For large prey types that exceed the average transport capacity of foraging parties, increased field-processing should result in less even assemblages, as hunters increasingly specialize on the highest utility parts. Measures of assemblage evenness circumvent some problems associated with using mean utility to consider field-processing, because evenness measures make no assumptions about how foragers determine the utility of skeletal parts (Faith, 2007; Faith and Gordon, 2007).

Skeletal element evenness has been used to investigate reindeer skeletal part patterns at Grotte XVI (Faith, 2007). Here, reindeer skeletal part data from the most recent Mousterian assemblage at this site (Layer C) are compared to the red deer assemblage from Gatzarria (Table 8). Again, only high-density bone portions are considered, as chemical diagenesis at Grotte XVI (Karkanas et al., 2002) may have significantly affected the representation of low-density bone portions at this site. Table 8 indicates that Gatzarria Cj assemblage is more even than the Grotte XVI assemblage. At the latter site, the metatarsal heavily dominates the assemblage, while at Gatzarria the representation of the highest-ranking marrow bones (the tibia and both metapodials) is more equal, and lower-ranked parts contribute a relatively greater proportion of the assemblage. These observations are borne out by diversity values (Table 9). The measure of diversity used here is the reciprocal of Simpson's Index ($1/D$; Simpson, 1949). Simpson's Index is preferred for this analysis because of its lesser sensitivity to sample size and richness in comparison to the Shannon Index (Magurran, 2004). Using the Shannon Evenness Index, Faith (2007) argued that the increasing diversity of reindeer parts at Grotte XVI from the Mousterian through to the Magdalenian was a result of increasing encounter rates with reindeer through time. Using a central place foraging model, Faith concluded that, as average search time decreased, foragers became less selective in their transport decisions (i.e., field-processing time decreased). Using the reciprocal of Simpson's Index rather than the Shannon Index to measure evenness does not change the rank order of the Grotte XVI assemblages relative to Faith's (2007) values ($r_s = 1.00$). Faith also demonstrated that the pattern of diversity at Grotte XVI is not a result of sample size effects. In comparison with the Grotte XVI values, the diversity values for the Gatzarria Mousterian indicate moderate selectivity in transport decisions. These data could imply lower field-processing times and lower average search times for the major prey species

Table 8

High-density bone portion frequencies in the Mousterian assemblages from Gatzarria Cj and Grotte XVI layer C. Values are for red deer at Gatzarria and for reindeer at Grotte XVI. For comparability with the data provided by Faith (2007) for Grotte XVI, the numbers of metapodial shaft fragments at Gatzarria were divided by two and added to the NISP of metacarpals and metatarsals before re-calculating NNISP. Teeth are excluded from cranial and mandibular counts.

Bone portion	Gtz Cj Moust		Grotte XVI C	
	NNISP	%NNISP	NNISP	%NNISP
Metatarsal	21.5	100.0	19.0	100.0
Tibia	21.0	97.7	6.0	31.6
Metacarpal	20.0	93.0	2.5	13.2
Humerus	7.5	34.9	3.0	15.8
Femur	7.5	34.9	3.5	18.4
Radius	6.0	27.9	7.5	39.5
Mandible	4.0	18.6	1.0	5.3
Cranium	0.0	0.0	0.0	0.0

Table 9

Simpson's diversity ($1/D$) values for the Gatzarria, and Grotte XVI assemblages. Diversity values calculated using the data in Table 8. The scapula is excluded because this element was not included in Faith's analysis. LB = long bones.

Sample	$1/D$	Σ NISP	$1/D$ (LB only)	Σ NISP
Gtz Cj Moust	5.22	175	4.80	167
Grotte XVI				
Mousterian (C)	3.75	85	3.58	83
Châtelperronian (B)	5.33	141	4.23	121
Aurignacian? (Aib)	4.91	113	4.02	100
Aurignacian (Abb)	6.37	409	4.89	337
Gravettian (Abc)	6.11	462	4.61	370
Solutrean (As)	6.41	177	4.72	139
Magdalenian (0)	6.88	722	5.15	573

during the Gatzarria Cj occupations relative to layer C at Grotte XVI. Moderate to high encounter rates for red deer at Gatzarria would be consistent with the diet breadth patterns observed.

6. Discussion and conclusion

What can the foraging patterns observed at Gatzarria tell us about Neandertal populations in the Pyrenees prior to the arrival of modern humans in the region? On the most basic level, an increase in forager population densities implies an increase in the biomass of utilized food resources (Winterhalder et al., 1988). In addition, the characteristics of regional faunal complements, such as the number of large-bodied prey types, the availability of high-ranked small-bodied prey, and the susceptibility of prey populations to predation-induced depression may have been important factors in the timing of Palaeolithic population expansions (Stiner et al., 2000; Morin, 2012). However, predator population densities are not linked to prey biomass in a linear fashion. Due to fluctuations in population sizes resulting from both human predation and density-independent factors such as climate variability, the "carrying capacities" of different animal resources are not static (Winterhalder et al., 1988). Based on these dynamic relationships, Morin (2004: 377) has argued that the population densities of Palaeolithic hunter-gatherer groups who were highly dependent on ungulate fauna fluctuated in response to climatically induced changes in the diversity and abundance of their prey.

The diet breadth and skeletal part analyses of the Cj Mousterian assemblage may permit a few general inferences about how the adaptive strategies of Neandertals at Gatzarria were linked to fluctuations in the availability of their preferred resources. Red deer heavily dominates the Mousterian faunal assemblage at Gatzarria, suggesting a generally narrow diet breadth. Similarly, although extraction of marrow from long bones was thorough, marginal marrow-bearing elements were only occasionally transported and exploited. This suggests that the Cj Mousterian sample was produced during a period of relative abundance of high-ranked prey in relation to local human population densities. The high cost of potential additional prey items (leporids, birds, fish) relative to the profitability of ungulate prey taxa may have led to substantial inertia to diet breadth change in this region, in comparison to Mediterranean areas which had fewer large-bodied ungulates (Morin, 2012). For this reason, without a significant, threshold-type increase in foraging effort, there may have been little room for a permanent population expansion.

Is the pattern at Gatzarria representative of the overall foraging pattern during the late Mousterian in the Pyrenees? Altuna (1990:233) suggested that the faunal spectra of Mousterian sites in the Pyrenees could be considered to be "strongly linked to the environment surrounding the site" and that hunting during this period was "opportunistic, not selective, and all, or nearly all, of the

species in the local area were exploited.”¹ However, recent taphonomic analyses have undermined this hypothesis, demonstrating that, at some Mousterian sites in the region, ibex and chamois were primarily accumulated by non-human animals (Yravedra Sainz de los Terreros, 2006; Costamagno et al., 2008; Mallye et al., 2010). Red deer appears to have been the predominant prey of humans at these locations, as well as at sites located in less rugged terrain, such as Gatzarria and El Castillo (Level 20) in Cantabria (Dari and Renault-Miskovsky, 2001). Arrizabalaga et al. (2003) have also noted the predominance of large valley-floor ungulates (red deer, bison, horse) in Upper Palaeolithic assemblages from Labeko Koba, in the Spanish Basque Country. Nevertheless, as the Gatzarria data suggest, small mountain ungulates were not completely ignored by Neandertals during the final Mousterian in the Pyrenees. Levels B–C and D at Axlor contain large proportions of ibex (>25% NISP; González Urquijo et al., 2004). Although a detailed taphonomic analysis is not yet available, González Urquijo et al. (2004) suggest that carnivore marks are rare at Axlor and that the fragmentation patterns, notably a high frequency of long bone shaft fragments, is consistent with a primarily anthropic accumulation.

Overall, the pattern of faunal remains in the western Pyrenees suggest narrow-spectrum diets throughout the region during the late Mousterian. Unfortunately, seasonality estimates are not available for the majority of sites, and open-air sites are not well represented. Further work with the Gatzarria material, and additional information on other Mousterian sites in the Atlantic Pyrenees region, will hopefully permit tests of specific predictions regarding how increased competition for preferred resources and/or climatic shifts might have impacted foraging strategies during the Middle to Upper Palaeolithic transition in the region. However, the problems in the stratigraphy at Gatzarria will have to be addressed more thoroughly in future research.

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¹ “El espectro faunístico parece estar mucho más ligado al medio ambiente circundante al yacimiento [...] la caza es oportunista, no selectiva y que se explotan todas o casi todas las especies existentes en el entorno.”

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