Journal of Archaeological Science 30 (2003) 1633–1648

Journal of Archaeological SCIENCE

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Ungulates and the Middle-to-Upper Paleolithic transition at Grotte XVI (Dordogne, France)

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Received 15 January 2003; received in revised form 10 April 2003; accepted 16 April 2003

Abstract

Grotte XVI (Dordogne, France) contains a rich archaeological sequence that begins during the Mousterian and continues through the Magdalenian and includes Châtelperronian and early Aurignacian assemblages. Analyses of the ungulates from this site show no significant change in skeletal part representation, butchering intensity (as measured by cut mark numbers and placement), degree of bone fragmentation, and intensity of carnivore damage across the Middle-to-Upper Paleolithic transition. Relative taxonomic abundances of ungulates change significantly from the Mousterian to the early Aurignacian, but these changes are consistent with climatic forcing and continue throughout the sequence. Only the Magdalenian ungulate assemblage is clearly distinct from all others when examined in terms of these variables, perhaps because of altered predator/prey ratios on the local landscape. Cave bear relative abundances decline precipitously across the Middle-to-Upper Paleolithic transition; this decline may reflect increased human residence times and/or group sizes during this interval, just as Kurtén observed many years ago.

Keywords: Neanderthals; Middle Paleolithic; Upper Paleolithic; Cave bears; Magdalenian; Grotte XVI; France

1. Introduction

The debate over the hunting capabilities of Neanderthals has clearly entered a new phase. This debate had been fueled by Binford's argument that prior to the Upper Paleolithic in Europe and the Later Stone Age in Africa, human hunters were unable to kill a broad variety of large and often dangerous animals and that a significant part of their meat diet was necessarily derived from scavenged carcasses (e.g., Refs [2,4–6]). Although others had suggested the possibility that Middle Pleistocene humans had scavenged kills left behind by carnivores (e.g., Refs [47,48]), Binford argued that "systematic hunting of moderate to large [sized] animals appears to be part of our modern condition, not its cause" [4, p. 321].

Binford's statements concerning the evolution of human hunting abilities quickly led to insightful research meant to test those statements. As a result, we now know that the two detailed empirical analyses he presented to support his position, of Grotte Vaufrey in France [5] and Klasies River Mouth in South Africa [3], contained significant factual errors ([34,63]; see also Ref. [1]; the third example routinely cited by Binford, Combe Grenal, has never been published); that at least some contemporary hunter–gatherers obtain significant amounts of their meat diet from scavenging [42,65–67]; and that some of the criteria he used to detect scavenging have equivocal meaning (e.g., Ref. [55]). While important work by Stiner [76,77] suggests that Italian sites document significantly more scavenging by Neanderthals prior to 50,000 years ago (see also Refs [56,57,59]), there is also impressive evidence for hunting by Neanderthals prior to this time from a broad variety of sites in western Eurasia [10,17,26,28–31,43,44,59,68,75]. As Burke [11, p. 281] has observed, the issue today is not whether Neanderthals had the ability to kill those animals they wished to kill, but instead "when and how they chose to hunt."

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doi:10.1016/S0305-4403(03)00064-5

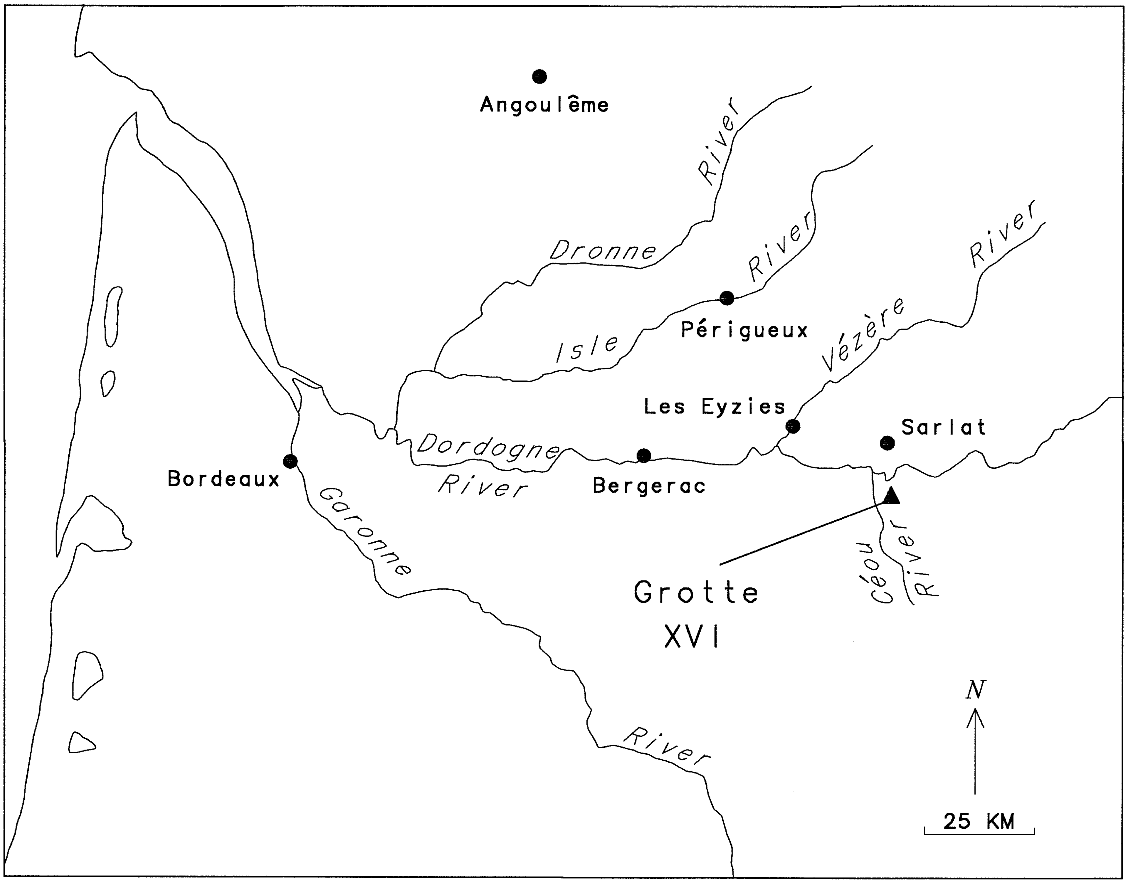

Fig. 1. The location of Grotte XVI.

Indeed, many recent analyses have joined earlier studies in concluding that there is little evidence for significant change in mammal utilization across the Middle-to-Upper Paleolithic "transition" (MUPT) in Europe (e.g., Refs [13–16,22,70,83]). This is the case whether the analyses have focused on the hunting/scavenging debate, on the degree to which the early Upper Paleolithic saw the advent of specialized hunting [37], on the demographic characteristics of the hunted animals themselves (e.g., Refs [29],[31]; see also Ref. [64]), or on isotopic evidence for Neanderthal carnivory (e.g., Refs [8,9,69]). In addition, Clark, Freeman, Straus and others have frequently observed that significant changes in human hunting patterns appear not with the MUPT but instead much later, with the Solutrean and/or Magdalenian [14–16,27,79–83].

Here, we add to this growing body of work by presenting a detailed examination of large mammal use across the MUPT at the archaeological site of Grotte XVI (Dordogne, France). We ask six basic empirical questions about the Grotte XVI ungulate faunas across this transition: (1) do the taxa represented change?; (2) do the skeletal parts represented change?; (3) does the intensity of butchering as represented by cut mark numbers and placement change?; (4) does the intensity of faunal utilization as measured by the degree of bone fragmentation change? (5) does the degree of carnivore damage differ?; (6), and, are there indications from the non-ungulate fraction of the vertebrate faunas that "something important" happened?

2. The Grotte XVI ungulate faunal assemblages

Grotte XVI is one of a series of caves and rock-shelters that mark the limestone cliffs overlooking the Céou River near its confluence with the Dordogne (Fig. 1). Excavated under the direction of J.-Ph. Rigaud and J. F. Simek between 1983 and 2001, the site provided a Paleolithic sequence that begins during the Mousterian and continues through the Magdalenian (Table 1). Rigaud, Simek, and Ge [71] provided a description of the stratigraphy as well as a discussion of the thick ash layer that characterizes Mousterian Stratum C; Karkanas et al. [46] provided a more detailed discussion of these ash deposits, as well as of those found higher in the site. Grayson et al. [38] described the Upper Paleolithic ungulate faunas (strata B through 0) as they were then known. The analyses we present here

Table 1
A summary of the stratigraphy and chronology of Grotte XVI (from Ref. [38])

Stratum		
0	Magdalenian	12,285 ± 100 (AA-6843)
		12,530 ± 105 (AA-6842)
As	Solutrean	20,070 ± 330 (AA-2668)
		20,230 ± 270 (AA-2669)
		20,280 ± 220 (AA-2992)
		20,410 ± 380 (AA-2991)
		20,460 ± 260 (AA-2993)
Abc	Gravettian	26,430 ± 470 (AA-2670)
Abb	Aurignacian	28,140 ± 405 (AA-6840)
		29,285 ± 420 (AA-6841)
		29,710 ± 510 (GifA-94201)
Aib	Aurignacian	Undated
B	Châtelperronian	35,000 ± 1200 (GifA-95581)
		38,100 ± 1670 (AA-2997)
		>39,800 (AA-2674)
C	Mousterian	64,600 ± 3100*
D–K	Mousterian	Undated

*Average of six TL dates.

are based on larger sample sizes than those used in our earlier paper and, for the first time, incorporate data on the ungulate assemblage from Mousterian Stratum C. Since identifications of the Grotte XVI mammals are now complete, the raw data we present here will not change. Although the sample sizes for the Upper Paleolithic assemblages have changed from those used in our previous assessment [38], the conclusions presented in that paper are not affected in any way.

Although our focus here is on the MUPT, represented at Grotte XVI by Mousterian Stratum C, Châtelperronian Stratum B, and Aurignacian Stratum Aib, we analyze all Grotte XVI ungulate assemblages except for Mousterian strata D through K (the Grotte XVI birds and fishes have not been identified). We include Aurignacian Stratum Abb, Gravettian Stratum Abc, Solutrean Stratum As, and Magdalenian Stratum 0 to provide the more general context for our analysis of the transitional units. Unfortunately, for no stratum do we currently have adequate control over the season or seasons during which the ungulate assemblage accumulated [38]. We do not examine strata D through K because these strata provided a total of only 329 identifiable ungulate specimens.

2.1. A note on laboratory protocol

The laboratory procedures that we have used for analyzing the Grotte XVI fauna are the same that we have used for Grotte Vaufrey [34] and Le Flageolet I [20,35]. Each specimen is initially examined by one of us (FD), who identifies it anatomically and taxonomically (if possible), conducts a preliminary scan for taphonomically relevant information, and enters the results into an electronic database. Each specimen, identified or not, is then reexamined by the other (DKG). In cases of disagreement over a particular identification, the specimen in question is examined by both of us together. The examination for taphonomically relevant information uses procedures very similar to those discussed by Blumenschine et al. [7]. Specimens are initially examined with the naked eye, followed by inspection under a 10× hand lens. To resolve questions about particular specimens, a binocular zoom microscope, with magnification up to 40×, is used. Particularly perplexing specimens are examined jointly by both of us. In this approach, every specimen, identifiable or not, is examined at least twice by two experienced investigators.

Marean and his colleagues [56,58,59] have amply documented that failure to identify long bone shaft fragments can introduce significant observer bias into skeletal element patterning in archaeological and paleontological contexts. Accordingly, we observe that while we do not attempt to refit all shaft fragments as Marean does (e.g., Ref. [61]), we do place significant emphasis on identifying shaft fragments on morphological grounds. Compared to African contexts, our task is greatly eased by the fact that we are not dealing with a bewildering variety of often similarly-sized ungulates, but instead with a relatively small set of ungulates that are well-graded in terms of size (Delpech in Ref. [59]). By including size as a criterion for identification, we are able to identify many shaft fragments to the genus level. Refitting would certainly allow us to identify a greater number of such specimens, but our approach does provide us with significant numbers of shafts identified to at least the genus level.

2.2. Do the abundances of ungulate taxa change significantly?

Table 2 presents the number of identified specimens (NISP) per ungulate taxon by stratum at Grotte XVI. These counts do not include 25 specimens of *Mammuthus* ivory, nearly all of which were modified for tool use. Specimens that were referred to a particular taxon (e.g., cf. *Rangifer*) have been included in the counts for that taxon; one specimen of *Bison* from Stratum Abc has been included in *Bos*/*Bison* and two of *Equus hydruntinus* (from strata Abc and C) have been included in *Equus* spp.

As this table shows, ungulate assemblage richness does not change across the MUPT—that is, from Mousterian Stratum C to Aurignacian Stratum Aib. In fact, ungulate assemblage richness does not change in any meaningful way throughout the entire sequence; all assemblages, regardless of the size of the sample involved, contain 8 or 9 ungulate taxa. Thus, these

Table 2
Grotte XVI: number of identified specimens (NISP) by stratigraphic unit and taxon (*Mammuthus* tusk specimens excluded)

Taxon	Stratum														
	0		As		Abc		Abb		Aib		B		C		
	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	Σ
Bos/*Bison*	2	0.09	4	0.80	26	1.83	38	2.49	17	3.79	26	4.41	44	8.15	157
Equus spp.	30	1.38	23	4.57	58	4.08	114	7.46	25	5.57	26	4.41	37	6.85	313
C. capreolus	10	0.46	14	2.78	99	6.97	141	9.23	58	12.92	103	17.49	77	14.26	502
C. elaphus	24	1.10	22	4.37	173	12.18	260	17.02	79	17.59	122	20.71	183	33.89	863
Capra sp.	2	0.09	5	0.99	6	0.42	12	0.79	1	0.22	11	1.87	12	2.22	49
Megaceros giganteus	0		0		0		1	0.07	0		0		0		1
R. tarandus	2049	94.34	409	81.31	1011	71.20	887	58.05	235	52.34	248	42.11	142	26.30	4981
(Rhinoceros)	0		0		0		0		0		2	0.34	0		2
Rupicapra rupicapra	27	1.24	18	3.58	35	2.46	54	3.53	23	5.12	37	6.28	34	6.30	228
Saiga tatarica	26	1.20	3	0.60	0		0		0		0		0		29
Sus scrofa	2	0.09	5	0.99	12	0.85	21	1.37	11	2.45	14	2.38	11	2.04	76
Σ	2172		503		1420		1528		449		589		540		7201

Table 3
Grotte XVI: number of identified specimens (NISP) by stratigraphic unit and taxon: adjusted residuals (AR) and composite χ^2 values; significant values in bold

Taxon	Stratum													
	0		As		Abc		Abb		Aib		B		C	
	NISP	AR	NISP	AR	NISP	AR	NISP	AR	NISP	AR	NISP	AR	NISP	Σ
Bos/*Bison*	2	**−3.00**[1]	4	−1.61	26	−1.22	38	−1.47	17	−0.50	26	**−2.59**[1]	44	157
Equus spp.	30	**−4.63**[2]	23	+0.47	58	**−3.90**[2]	114	+1.38	25	+0.85	26	−1.78	37	313
C. capreolus	10	**−4.98**[2]	14	**−3.43**[2]	99	**−2.24**[3]	141	**−2.28**[3]	58	**−2.01**[3]	103	+1.48	77	502
C. elaphus	24	**−5.08**[2]	22	**−4.49**[2]	173	**−3.70**[2]	260	−0.29	79	−1.26	122	**−4.98**[2]	183	863
Capra sp.	2	**−3.57**[2]	5	+1.46	6	−1.26	12	+1.30	1	**−2.46**[3]	11	−0.42	12	49
M. giganteus	0	–	0	–	0	−0.96	1	+0.54	0	–	0	–	0	1
R. tarandus	2049	**+9.64**[2]	409	**+4.44**[2]	1011	**+7.45**[2]	887	**+2.15**[3]	235	**+3.27**[1]	248	**+5.58**[2]	142	4981
(Rhinoceros)	0	–	0	–	0	–	0	–	0	−1.24	2	+1.35	0	2
R. rupicapra	27	**−3.67**[2]	18	+1.31	35	−1.70	54	−1.53	23	−0.79	37	−0.01	34	228
S. tatarica	26	+1.17	3	**+2.91**[1]	0	–	0	–	0	–	0	–	0	29
S. scrofa	2	**−3.57**[2]	5	+0.31	12	−1.36	21	−1.58	11	+0.08	14	+0.38	11	76
Σ	2172		503		1420		1528		449		589		540	7201
χ^2		**127.47**[2]		**53.69**[2]		**59.05**[2]		**17.32**[3]		**19.46**[3]		**51.82**[2]		

[1] *P*<0.01.

[2] *P*<0.001.

[3] *P*<0.05.

assemblages provide no suggestion that the ungulate component of diet breadth changed across the MPUPT at Grotte XVI (see Refs [35,36,38]).

On the other hand, taxonomic relative abundances do change significantly across the MUPT here. In Stratum C, reindeer (*Rangifer tarandus*) contribute 26.3% of the ungulate fauna; in Stratum Aib, they contribute 52.3%. Likewise, red deer (*Cervus elaphus*) contribute 33.9% of the Stratum C ungulate fauna, but only 17.6% of the Aib assemblage. In both cases, Châtelperronian Stratum B reindeer and red deer abundances are intermediate between those of strata C and Aib.

Composite chi-square values and adjusted residuals for adjacent Grotte XVI strata are provided in Table 3. The residuals are to be read as standard normal deviates [25]; the signs of those residuals refer to the stratum to the left of the residuals column. For example, the increase in abundance of reindeer from Stratum As to Stratum 0 is associated with an adjusted residual of +9.64 (*P*<0.001). The corresponding value in the other direction can be obtained by changing the sign of the residual (−9.64 for the decrease in reindeer abundance from Stratum 0 to Stratum As).

The statistics provided in Table 3 show that the relative abundances of ungulates in Stratum C differ significantly from those in Stratum B (χ^2=51.82, *P*<0.001), with this relationship driven by the changing abundances of *Bos*/*Bison* and red deer, which decrease

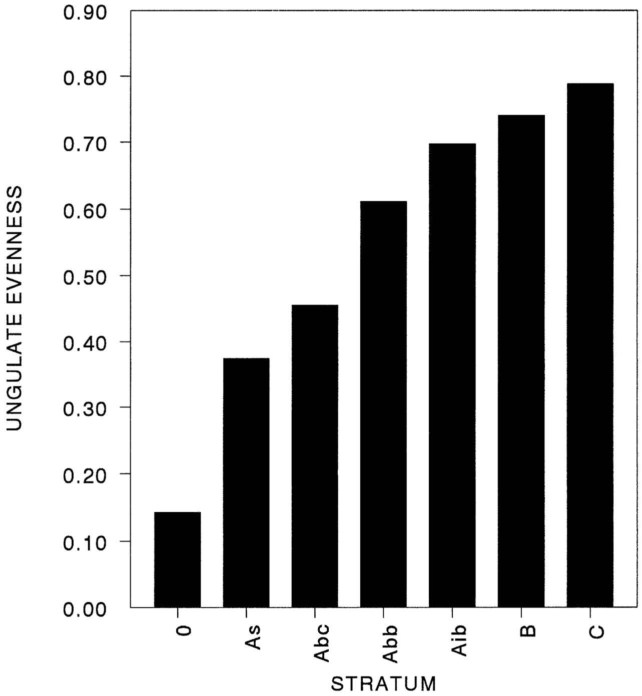

Fig. 2. Grotte XVI ungulate evenness.

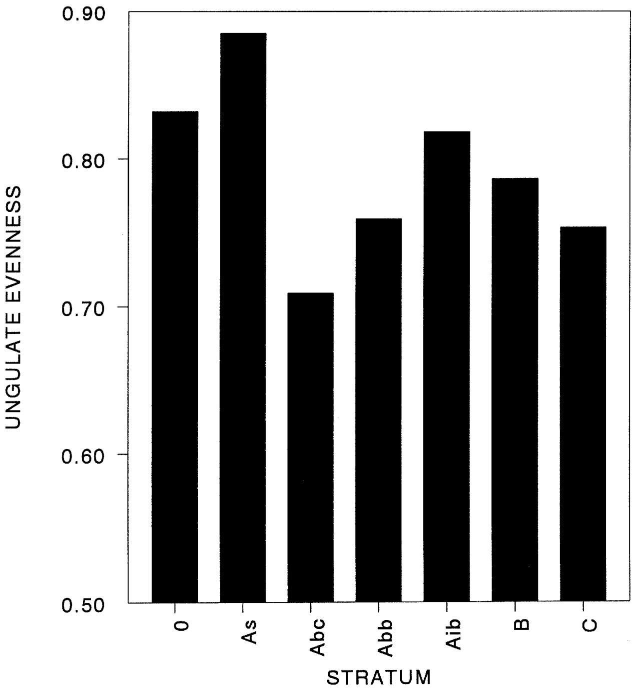

Fig. 3. Grotte XVI ungulate evenness with reindeer excluded.

significantly from Stratum C to Stratum B, and of reindeer, which increases significantly. Likewise, Stratum B differs significantly from Aib (χ^2=19.46, P<0.05), with this difference driven by a significant decrease in roe deer (*Capreolus capreolus*) and *Capra* sp. coupled with a significant increase in reindeer. From this perspective, there is a very significant change in the relative abundances of ungulate taxa across the MUPT at Grotte XVI.

Elsewhere [38], we have observed that the evenness of the Grotte XVI ungulate faunas declines steadily from Stratum B to Stratum 0. Fig. 2 shows this decline, using the final ungulate tallies presented here, and shows that Stratum C, previously unpublished, falls into this pattern as well. It is easy to show that these changes are due to the numerical behavior of reindeer in the Grotte XVI assemblages: removing reindeer from the analysis removes the pattern (Fig. 3).

We have also shown that the steady increase in reindeer relative abundances from Stratum B to Stratum 0 at Grotte XVI is correlated with decreasing summer temperatures, and have suggested that this relationship is a causal one ([38]; because of the large variance associated with the chronometric dates for Stratum C [see Table 1], we do not attempt to incorporate this stratum into the argument). If this pattern is caused by the climate-driven relative abundance behavior of reindeer, then the significant differences between strata C, B, and Aib are most likely caused by climate change as well.

Table 4 removes reindeer from the comparison and presents the relevant statistical measures. Couches C and B remain significantly different (χ^2=20.76, P<0.01), the difference now driven by the behavior of roe deer and red deer. Couches B and Aib do not differ significantly, even though the abundance of *Capra* sp. does decline significantly from Stratum B to Stratum Aib.

With reindeer included in the comparison (Table 3), the largest number of significant changes in ungulate relative abundances occurs between Solutrean Stratum As and Magdalenian Stratum 0. In this sense, the transition from the Solutrean to the Magdalenian at Grotte XVI is far more pronounced than is the transition from the Mousterian to the Châtelperronian, or from the latter to the Aurignacian. With reindeer excluded (Table 4), the largest number of significant differences occurs between Gravettian Stratum Abc and Solutrean Stratum As.

In short, there is nothing in the Grotte XVI fauna to suggest that the kinds and abundances of ungulate taxa taken differed more substantially across the MUPT than they differed during the Upper Paleolithic itself. The most substantial change in ungulate relative abundances recorded at Grotte XVI—the increasing frequencies of reindeer (and presumably the decreases in red deer)—are rather clearly attributable to climate change.

2.3. Do the abundances of body parts change significantly?

Of the ungulates represented at Grotte XVI, only reindeer and red deer are sufficiently abundant to

Table 4
Grotte XVI: number of identified specimens (NISP) by stratigraphic unit and taxon: adjusted residuals (AR) with reindeer excluded; significant values in bold

Taxon	Stratum													
	0		As		Abc		Abb		Aib		B		C	
	NISP	AR	NISP	AR	NISP	AR	NISP	AR	NISP	AR	NISP	AR	NISP	Σ
Bos/*Bison*	2	−1.17	4	−0.78	26	+0.28	38	−1.04	17	+0.14	26	−1.59	44	157
Equus spp.	30	−0.01	23	**+2.45**[1]	58	−1.54	114	**+2.09**[1]	25	+1.61	26	−0.81	37	313
C. capreolus	10	−1.57	14	−1.95	99	+0.83	141	−1.53	58	−0.78	103	**+3.43**[2]	77	502
C. elaphus	24	−0.70	22	**−3.39**[2]	173	+0.56	260	+0.94	79	+0.27	122	**−2.81**[3]	183	863
Capra sp.	2	−1.53	5	**+2.30**[1]	6	−0.49	12	+1.45	1	**−2.17**[1]	11	+0.16	12	49
M. giganteus	0	–	0	–	0	−0.80	1	+0.58	0	–	0	–	0	1
(Rhinoceros)	0	–	0	–	0	–	0	–	0	−1.12	2	+1.53	0	2
R. rupicapra	27	+0.50	18	**+3.02**[3]	35	−0.08	54	−1.03	23	−0.04	37	+1.06	34	228
S. tatarica	26	**+3.85**[2]	3	**+3.62**[2]	0	–	0	–	0	–	0	–	0	29
S. scrofa	2	−1.53	5	+1.15	12	−0.31	21	−1.24	11	+0.57	14	+1.01	11	76
Σ	123		94		409		641		214		341		398	2220
χ^2		**21.47**[3]		**43.24**[2]		3.75		11.89		9.05		**20.76**[3]		

[1] *P*<0.05.
[2] *P*<0.001.
[3] *P*<0.01.

Table 5
Grotte XVI: number of identified specimens (NISP) and associated adjusted residuals (AR) for selected reindeer body parts; significant values in bold

Element	Stratum												
	0		As		Abc		Abb		Aib		B		C
	NISP	AR	NISP	AR	NISP	AR	NISP	AR	NISP	AR	NISP	AR	NISP
Carpals	21	+1.71	1	−1.56	11	+1.91	3	−0.18	1	−0.82	3	−1.27	4
Cranium	363	**−2.49**[1]	105	+0.98	238	−0.48	217	+1.64	47	+0.05	56	**+3.25**[2]	12
Femur	60	−0.56	16	−0.50	46	+0.05	40	+1.40	6	−1.42	14	+0.11	7
Humerus	57	−0.25	14	+1.39	22	−0.90	25	+1.00	4	−0.06	5	−1.42	6
Innominate	11	+0.92	1	+0.18	2	−1.61	6	−1.45	4	−0.06	5	−0.18	3
Metapodials	298	−0.96	76	−0.93	211	+0.39	179	−1.25	57	−0.14	70	−1.13	44
Phalanges	133	+1.84	20	−0.46	56	+1.64	35	+1.39	5	−0.74	9	−1.42	9
Radioulna	96	−0.41	24	+1.08	46	−0.64	46	−1.63	19	+0.76	18	−1.63	16
Ribs	238	**+2.96**[3]	33	+1.16	65	+0.11	56	−1.12	20	+1.11	17	+1.53	4
Scapula	15	+1.28	1	−1.31	9	−0.52	10	−0.67	4	+0.63	3	+1.26	0
Tarsals	10	−0.96	4	−0.17	11	**+2.28**[1]	2	**−2.12**[1]	3	−0.45	5	+0.33	2
Tibia	90	+0.33	19	−0.72	57	−1.69	67	+0.69	15	−0.32	20	−0.38	12
Vertebrae	34	−1.32	12	−0.82	39	+0.83	28	−0.14	8	+0.63	7	+0.30	3
Σ	1426		326		813		714		193		232		122
χ^2		**24.30**[1]		11.24		18.85		18.85		5.85		**21.40**[1]	

[1] *P*<0.05.
[2] *P*<0.001.
[3] *P*<0.01.

support an analysis of changing body part representation across strata. Table 5 provides NISP values by major skeletal element for reindeer, the most abundant Grotte XVI ungulate. We have excluded such elements as the fibula, sesamoids, and sternum, as well as specimens for which anatomical part could not be determined with certainty; NISP values for the "skull" included the skull per se, as well as mandible, teeth, and antler specimens. Table 5 also provides composite chi-square and adjusted residual values for adjacent strata (see the discussion of Table 3, above).

As the chi-square values in this table show, two sets of adjacent strata differ significantly in terms of skeletal element abundances as we have measured them here: strata 0 and As (χ^2=24.30, $P<0.05$) and strata B and C (χ^2=21.40, $P<0.05$). As the adjusted residuals show, the

Table 6
Grotte XVI: number of identified specimens (NISP) and associated adjusted residuals (AR) for selected red deer body parts; significant values in bold

Element	Stratum												
	0		As		Abc		Abb		Aib		B		C
	NISP	AR	NISP	AR	NISP	AR	NISP	AR	NISP	AR	NISP	AR	NISP
Carpals	1	−0.07	1	+0.61	4	+0.61	4	+1.14	0	−0.81	1	+0.27	1
Cranium	14	+1.53	8	−0.02	62	−0.58	102	−0.84	37	+1.17	47	−1.84	87
Femur	0	–	0	−0.51	2	−1.28	8	−0.74	4	+0.63	4	−0.30	7
Humerus	1	+0.97	0	−0.82	5	−0.29	9	+1.08	1	−0.22	2	+0.92	1
Innominate	0	–	0	−0.63	3	−0.12	5	+0.44	1	+0.31	1	+1.21	0
Metapodials	4	+0.28	3	+0.25	20	−0.28	33	+0.18	10	−0.10	16	+1.30	15
Phalanges	1	**−2.21**[1]	6	+1.34	27	**+2.54**[1]	21	−0.43	8	−0.97	18	+0.74	21
Radioulna	0	−1.06	1	+0.40	5	−0.29	9	+1.73	0	**−2.62**[2]	10	−1.16	22
Ribs	0	−1.06	1	−0.15	9	−1.75	26	+0.45	7	+0.60	8	+1.87	4
Scapula	0	–	0	−0.51	2	+0.97	1	+0.57	0	–	0	−1.17	2
Tarsals	0	–	0	−0.36	1	−0.22	2	−0.36	1	−0.22	2	+0.92	1
Tibia	1	+0.97	0	−0.73	4	−0.65	9	−0.55	4	−0.44	8	+1.02	7
Vertebrae	0	–	0	−1.17	10	+1.67	7	−0.42	3	**+2.17**[1]	0	−1.18	2
	22		20		154		236		76		117		170
χ^2		9.28		5.55		14.87		7.69		14.43		15.32	

[1] $P<0.05$.

[2] $P<0.01$.

significant difference between strata 0 and As is caused by a significant decrease in the number of skull specimens, and an increase in rib fragments, in Stratum 0. The difference between strata B and C is driven entirely by an increase in the number of skull fragments in Stratum B. Strata B and Aib do not differ significantly in body part representation (χ^2=5.85, P>0.50).

We do not pursue the Magdalenian/Solutrean contrast here. We do observe that the increase in skull specimens from Stratum C to Stratum B is not confined to one of the four elements (skull per se, mandible, teeth, antler) that comprise this category: there is no significant difference in the relative abundances of these four elements between the two strata (4, 17, 32, 3 specimens, respectively, in Stratum B, and 0, 2, 10, and 0 specimens in Stratum C; χ^2=3.26, P<0.30). Perhaps most importantly, the difference between observed and expected values for skull specimens in strata B and C is 11.44 specimens. That is, the only significant difference to found in the distribution of reindeer specimens by major skeletal elements across the MUPT at Grotte XVI involves fewer than a dozen specimens from a single skeletal component.

The second most-abundant ungulate at Grotte XVI is red deer. As the chi-square values in Table 6 show, there are no significant between-stratum differences in NISP-based skeletal part distributions for this ungulate, although there are scattered single-cell comparisons whose values are significant.

In sum, there are few well-marked differences in skeletal element abundance across strata C, B, and Aib for reindeer and red deer when these elements are examined in terms of NISP values. Those differences that do exist are comparable to those that occur between Upper Paleolithic assemblages higher in the sequence.

2.4. Do the relative abundances of cut marks differ?

Table 7 provides the number of specimens with cut marks in the Grotte XVI ungulate assemblages, and shows that there are no significant differences in the relative abundances of cut-marked specimens across the strata that mark the MUPT. Indeed, excluding Magdalenian Stratum 0, the percentage of specimens within a given assemblage that is cut-marked is fairly stable, varying from 6.21% in Stratum Abc to 8.89% in Stratum As. It is Stratum 0 that stands out in this regard, with 19.50% of ungulate specimens showing cut marks. The degree to which Stratum 0 specimens are cut-marked is significantly higher than for any other Grotte XVI assemblage (χ^2 ranges from 22.79 to 101.50, P<0.001). This, of course, is not the first Magdalenian ungulate assemblage known to have been intensively cut-marked (e.g., Refs [18,21]). We return to this issue below.

2.5. Does the distribution of cut marks across skeletal parts differ?

Of the 678 Grotte XVI ungulate specimens with cut marks, the vast majority (559, or 82.4%) are of reindeer, and our analysis of cut marks across skeletal elements focuses on this taxon. Table 8 provides the number of

Table 7
The distribution of cut marks across the Grotte XVI strata; significant values in bold (uncut specimens excludes teeth)

Stratum	0		As		Abc		Abb		Aib		B		C
NISP cut	388		36		70		102		26		27		29
NISP uncut	1602		369		1058		1065		286		372		330
% cut	19.50		8.89		6.21		8.74		8.33		6.77		8.08
χ^2		**25.99**[1]		3.33		**5.32**[2]		0.05		0.62		0.47	

[1] $P<0.001$.
[2] $P<0.05$.

Table 8
The distribution of cut marks across Grotte XVI reindeer skeletal elements and strata: NISP Cut/Total NISP

	Stratum						
	0	As	Abc	Abb	Aib	B	C
Carpals	5/21	0/1	0/11	0/3	0/1	0/3	0/4
Cranium	14/53	1/13	0/25	1/22	0/3	0/4	0/0
Femur	25/60	2/16	2/46	8/40	1/6	3/14	0/7
Humerus	27/57	1/14	4/22	8/25	0/4	2/5	1/6
Innominate	6/11	0/1	1/2	0/6	1/4	0/5	2/3
Mandible	41/96	2/25	1/68	1/51	0/10	0/17	0/2
Metapodials	59/298	6/76	13/211	16/179	5/57	4/70	2/44
Phalanges	40/133	0/20	3/56	2/35	0/5	1/9	1/9
Radioulna	24/96	4/24	4/46	0/46	3/19	0/18	0/16
Ribs	53/238	6/33	3/65	6/56	1/20	1/17	0/4
Scapula	6/15	0/1	0/9	1/10	0/4	0/3	0/0
Tarsals	1/10	1/4	0/11	0/2	1/3	1/5	0/2
Tibia	21/90	1/19	7/57	12/67	0/15	2/20	3/12
Vertebrae	15/34	0/12	0/39	2/28	0/8	0/7	0/3

cut-marked reindeer specimens across the same skeletal elements used in Table 5, except that we have excluded teeth and antler and have entered the mandible separately. Rather than comparing adjacent ungulate assemblages according to this full set of elements, we have created four major body part classes meant to contrast parts of the skeleton that differ substantially in terms of attached muscle masses—the feet (carpals, tarsals, metapodials, and phalanges), skull (skull and mandible), forelimb (humerus and radioulna) and hindlimb (femur and tibia). The distribution of specimens with and without cut marks across these categories is provided in Table 9. We now ask whether the proportion of cut-marked specimens across body classes changes significantly between adjacent strata.

We have used Mantel–Haenszel chi-square analysis [74] to answer this question. For any given comparison between adjacent strata (for instance, strata 0 and As), we first determine whether the log-odds ratios across the four body part categories differ significantly from one another. The test statistic for this determination, given in the homogeneity column of Table 10, is distributed as chi-square with three degrees of freedom (the homogeneity value for the 0–As comparison is 0.79, which is not significant at $P=0.05$). If these ratios do not differ significantly from one another, we calculate a composite estimate of the odds ratios across all four body part classes for the two-stratum comparison; this is provided in column three of Table 10 (and is 4.33 for the 0–As comparison). Finally, we calculate the Mantel–Haenszel chi-square value to determine whether this odds ratio differs significantly from unity (in the 0–As case, the value is 36.08, significant at $P<0.001$).

As Table 10 shows, neither strata C and B, nor strata B and Aib, differ significantly from one another in the distribution of cut marks across these body classes, or in the number of specimens per body class that are cut-marked. The strong difference that emerges from this analysis again involves Magdalenian Stratum 0. Not only are all four body part classes heavily cut-marked in Stratum 0, but the odds of a Magdalenian specimen in one of these classes being cut-marked are 4.3 times the odds that a Solutrean specimen would be cut, a difference that is extremely significant. Finally, and similar to the results we obtained from our analysis of the percentages of cut-marked specimens across all taxa as a whole, there is no trend in odds ratios from Stratum C to Stratum As (Table 10, column 3). The similarity in these ratios is not surprising, given that most cut-marked specimens in the Grotte XVI ungulate assemblages are reindeer (559/678), and that our examination here has included 387 of those 559.

Tables 11 and 12 present the equivalent results for the comparison of strata C and B, respectively, with all other strata. As these tables show, these assemblages differ significantly in this regard only from Stratum 0. We also observe that Stratum 0 differs significantly from all other assemblages, but we do not pursue this issue here.

Other analyses of the distribution of cut-marked specimens across skeletal elements and strata are, of course, possible. For instance, a comparison of adjacent strata in terms of the distribution of reindeer specimens with and without cut marks on the feet versus the limbs reveals significant differences between strata Aib and Abb ($\chi^2_{\mathrm{MH}}=3.85$, $P<0.05$), Abb and Abc ($\chi^2_{\mathrm{MH}}=7.81$ $P<0.01$), and As and 0 ($\chi^2_{\mathrm{MH}}=8.50$, $P<0.01$). There are,

Table 9
The distribution of reindeer specimens with and without cut marks across major body classes and strata

	Foot			Skull			Forelimb			Hindlimb		
	Cut	Uncut	Σ	Cut	Uncut	Σ	Cut	Uncut	Σ	Cut	Uncut	Σ
0	105	357	462	55	94	149	51	102	153	46	104	150
As	7	94	101	3	35	38	5	33	38	3	32	35
Abc	16	273	289	1	92	93	8	60	68	9	94	103
Abb	18	201	219	2	71	73	8	63	71	20	87	107
Aib	6	60	66	0	13	13	3	20	23	1	20	21
B	6	81	87	0	21	21	2	21	23	5	29	34
C	3	56	59	0	2	2	1	21	22	3	16	19

Table 10
Mantel–Haenszel analyses of reindeer specimens with and without cut marks across body part classes and adjacent strata (see Table 9 for raw data); significant values in bold

Comparison	Homogeneity of log-odds ratio	Odds Ratio Estimator	Mantel–Haenszel Chi-square
0–As	0.79	4.33	**36.08**[1]
As–Abc	2.45	1.37	0.79
Abc–Abb	1.91	0.61	**4.33**[2]
Abb–Aib	1.97	1.29	1.07
Aib–B	1.40	1.01	0.87
B–C	1.42	1.26	0.12

[1] $P<0.001$.

[2] $P<0.05$.

Table 11
Mantel–Haenszel analyses of reindeer specimens with and without cut marks across body part classes: Stratum C comparisons (see Table 9 for raw data); significant values in bold

Comparison	Homogeneity of log-odds ratio	Odds Ratio Estimator	Mantel–Haenszel Chi-square
C–0	1.67	5.02	**18.45**[1]
C–As	1.80	0.78	1.21
C–Abc	3.40	0.94	0.78
C–Abb	1.71	0.61	0.94
C–Aib	3.01	0.75	1.99
C–B	1.42	1.26	0.12

[1] $P<0.001$.

Table 12
Mantel–Haenszel analyses of reindeer specimens with and without cut marks across body part classes: Stratum B comparisons (see Table 9 for raw data); significant values in bold

Comparison	Homogeneity of log-odds ratio	Odds Ratio Estimator	Mantel–Haenszel Chi-square
B–0	2.59	4.52	**28.86**[1]
B–As	1.63	0.91	0.75
B–Abc	0.72	1.23	0.89
B–Abb	0.04	0.75	0.49
B–Aib	1.40	1.01	0.87
B–C	1.42	1.26	0.12

[1] $P<0.001$.

however, no significant differences across the strata that mark the MUPT.

Finally, as a potential measure of changing degrees of emphasis placed on flesh removal, periosteum removal and disarticulation [21,57,59,60], we have compared the degree to which cut marks are located on the diaphyseal and epiphyseal portions of reindeer metacarpals, metatarsals, femur, humerus, radioulna, and tibia. We found no significant differences in the degree to which cut marks are located on shafts or articular ends between any adjacent strata (χ^2 ranges from 0.03 to 2.23, $P>0.10$). We obtained similar results when we restricted the analysis to the femur, tibia, humerus, and radioulna (χ^2 ranges from 0.01 to 2.21, $P>0.10$).

When examined in this fashion, there is no suggestion that the Grotte XVI ungulate assemblages that span the MUPT at Grotte XVI differ from one another in any meaningful way. Once again, the unit that emerges as significantly different is the Magdalenian.

2.6. Does the degree of bone fragmentation differ?

In an earlier paper [38], we examined the degree of bone fragmentation in the Grotte XVI ungulate assemblages to determine whether differential fragmentation across taxa and assemblages could have altered specimen counts in such a way as to have determined the numerical structure of taxonomic abundances that characterizes these assemblages. We were particularly interested in knowing whether differential fragmentation could have caused the steady increase in reindeer abundance, and associated decrease in ungulate assemblage evenness, that marks the site. We found it could not.

The measure of bone fragmentation we used was straightforward: the ratio of diaphysis to epiphysis specimens among a subset of skeletal elements (humerus, femur, metaphodials, radioulna, ribs). In that analysis, the cause of the fragmentation was not of

Table 13
Diaphysis/epiphysis ratios for the Grotte XVI Upper Paleolithic ungulate taxa, ribs included; significant values in bold

	Stratum						
	0	As	Abc	Abb	Aib	B	C
Reindeer							
Diaphysis NISP	664	138	358	347	108	121	72
Epiphysis NISP	150	41	85	61	12	22	17
Ratio	4.43	3.37	4.21	5.69	9.00	5.50	4.24
Shaft Adjusted Residual	−0.72	−1.92	−0.94	+1.59	**+2.27**[1]	+0.74	−0.36
$\chi^2=11.95$, $0.10>P>0.05$							
Other ungulates							
Diaphysis NISP	22	12	57	154	38	57	84
Epiphysis NISP	13	10	28	56	11	22	34
Ratio	1.69	1.20	2.04	2.75	3.45	2.59	2.47
Shaft Adjusted Residual	−1.08	−1.72	−0.84	+0.96	+1.07	+0.26	+0.08
$\chi^2=6.28$, $P>0.30$							

[1] $P<0.02$.

concern to us. It mattered only that the degree of fragmentation did not correlate with taxonomic abundances. In the current context, however, we are primarily interested in knowing whether the degree of human-induced bone fragmentation changed across the MUPT. Unfortunately, the number of Grotte XVI ungulate specimens showing attributes diagnostic of human-induced fractures is insufficient to allow us to focus our analysis on these specimens alone. As a result, we first duplicate the analysis presented in Grayson et al. [38], using the sample now available to us and extending it to include Stratum C. Then, we rerun the analysis excluding ribs, which are easily fragmented by a much wider variety of processes than can fragment other, more massive, bones. We recognize that not all bone fragmentation at Grotte XVI, even among the more massive specimens, was caused by human hands. To the extent that this was the case, our analyses here are misguided. We also note that, as Marean and his colleagues have discussed [60], epiphysis/diaphysis ratios can be strongly influenced by the differential removal of epiphyses by carnivores. However, as we discuss in the following section, very few Grotte XVI ungulate specimens show carnivore damage, and it is extremely unlikely that our measure of bone fragmentation has been significantly influenced by carnivore activity.

Table 13, directly comparable to the analysis presented in Grayson et al. [38, Table 3], presents diaphysis/epiphysis ratios for reindeer, on the one hand, and for all other ungulates, on the other. Only for reindeer in Stratum Aib does the fragmentation ratio differ significantly from that which would be expected from the entire set of assemblages. In no case do epiphysis and diaphysis relative abundances change significantly between adjacent strata, either for reindeer (χ^2 ranges from 0.54 to 2.68, $P>0.05$), or for all other ungulates combined (χ^2 ranges from 0.02 to 1.19, $P>0.20$). If we examine red deer from strata C through Abc in the same way (red deer abundances in more recent strata are too low to support this analysis meaningfully), we obtain the same results: epiphysis and diaphysis ratios do not differ significantly between adjacent strata (χ^2 ranges from 0.07 to 1.91, $P>0.10$). Finally, we note that while some of the absolute values have changed from those presented in Grayson et al. [38], the interpretive meaning of the results have not: fragmentation does not correlate with reindeer abundance.

The results are similar when ribs are excluded from the comparisons. Only Stratum Aib has a fragmentation ratio that differs significantly from that which would be expected from the entire set of assemblages, and no adjacent strata differ significantly from one another (for reindeer, χ^2 ranges from 0.55 to 2.83, $P>0.05$; for all other ungulates, from 0.00 to 1.92, $P>0.10$; for red deer in strata C through Abc, from 0.71 to 1.44, $P>0.20$).

We conclude that there is no evidence that the degree of skeletal element fragmentation changes across the MUPT at Grotte GXVI.

2.7. Does the degree of carnivore damage differ?

Very few Grotte XVI ungulate specimens (102/7201, or 1.42%) show carnivore damage (Table 14). These specimens are not randomly distributed across strata ($\chi^2=14.61$, $P<0.05$), but this is due to Stratum Abb, which has more damaged specimens than would be expected by chance, and Stratum 0, which has fewer. There are no significant increases or decreases in carnivore damaged specimens across the MUPT, or between any other adjacent strata (χ^2 ranges from 0.01 to 2.91, $P>0.05$).

Table 14
Carnivore-damaged ungulate specimens by stratum; the signs of the adjusted residuals (AR) refer to the values for carnivore-damaged specimens; significant values in bold

	No. damaged	Σ NISP	AR	% damaged
0	18	2172	**−2.77**[1]	0.83
As	3	503	−1.61	0.60
Abc	23	1420	+0.72	1.62
Abb	32	1528	**+2.53**[2]	2.09
Aib	9	449	+1.09	2.00
B	8	589	−0.12	1.36
C	9	540	+0.51	1.67
Σ	102	7201		1.42
χ^2=**14.61**, $P<0.05$				

[1] $P<0.05$.
[2] $P<0.01$.

Table 15
Grotte XVI cave bear NISP values and the cave bear/ungulate ratio

	Cave bear NISP	Ungulate NISP	Ratio
0	0	2172	0.00
As	0	503	0.00
Abc	14	1420	0.01
Abb	47	1528	0.03
Aib	54	449	0.12
B	426	589	0.72
C	585	540	1.08
Σ	1126	7201	

3. Cave bears and the Middle-to-Upper Paleolithic transition

That we have been unable to detect significant changes in the nature of the ungulate assemblages across the MUPT at Grotte XVI does not mean that no such changes occurred; it means only that if such differences exist, we have not looked for them appropriately.

However, there is one very pronounced change that does mark these assemblages. Compared to the frequency of ungulate specimens, the frequency of cave bear (*Ursus spelaeus*) specimens declines dramatically from Stratum C to Stratum Aib (see Table 15 and Fig. 4), a decline that is extremely significant (for the Stratum C–Stratum Aib comparison, χ^2=248.21, $P<0.001$).

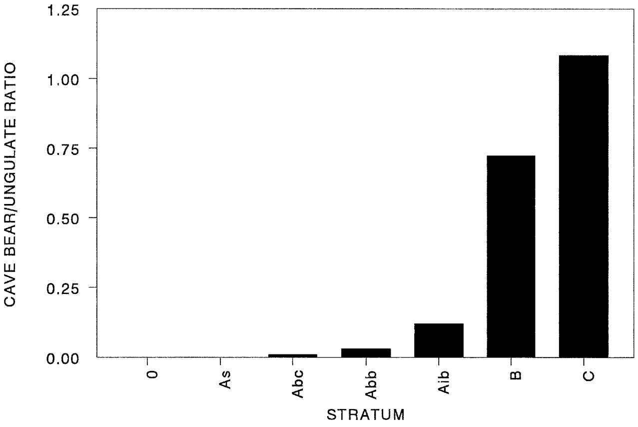

Fig. 4. The ratio of cave bear to ungulate specimens at Grotte XVI.

Elsewhere [36], we have referred to this decline as the Kurtén Response. This we have done in honor of Bjorn Kurtén who, in 1958, observed that the abundance of cave bear remains in European sites declined significantly at the same time as morphologically modern peoples entered the archaeological record. Neanderthals, he suggested, did not have any dramatic impact on cave bear populations, but "the incursion of Aurignac Man and the subsequent increase in human populations" [50, p. 48] led to the exclusion of cave bears from their winter denning sites. Cave bear populations dwindled, with extinction the end result. Kurtén [51] later abandoned this argument in the face of the observation that cave bears also declined in areas that seemed to lack human occupation [52]. We suggest that the heart of this hypothesis—that cave bears declined in response to changing human demographics—should be resurrected.

Others, of course, have shown that there is a negative correlation between the intensity of human occupation of European Pleistocene caves and the degree to which these caves contain the remains of cave bears and other carnivores (e.g., Refs [14,15,54,78,80]). In the Grotte XVI setting, we have suggested that the plummeting cave bear/ungulate ratios that mark the transition from the Mousterian to the Aurignacian reflect the result of competition between people and bears for shelter, just as Kurtén argued [36]. In addition, we observed that some combination of increased human group sizes and residence times could readily account for the Kurtén Response.

Simek [72] has questioned this interpretation, observing that the decline in cave bear relative abundance at Grotte XVI is evident in the Châtelperronian, attributed by most archaeologists to Neanderthals. This, he concludes, implicates Neanderthals, not modern humans. He also notes that he sees "no strong evidence for increased population during the Aurignacian" [72, p. 201].

These are valuable observations and we will not skirt them by questioning the assumption that all Châtelperronian assemblages were deposited by Neanderthals and all Aurignacian ones by morphologically modern peoples. Instead, we return to the two variables that we suggested might have caused the cave bear decline: increased human population densities and/or increased human residence times.

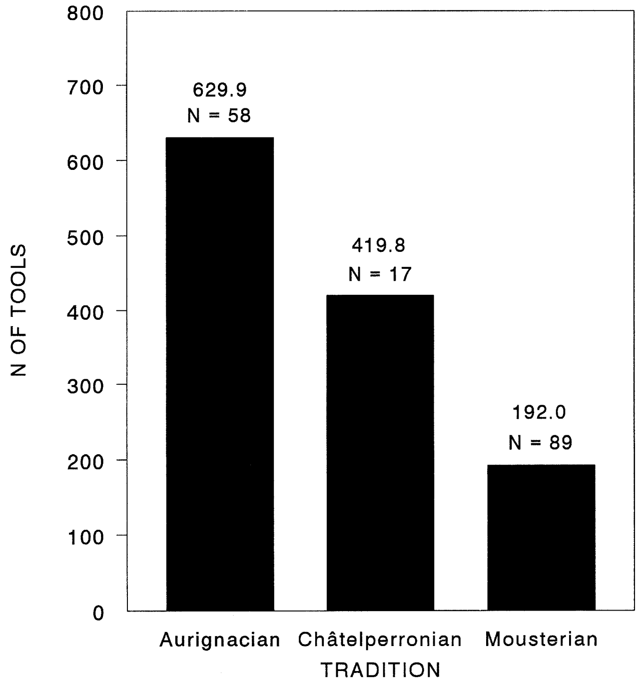

Fig. 5. Average Mousterian, Châtelperronian, and Aurignacian lithic assemblage sizes in France (data from Ref. [33]).

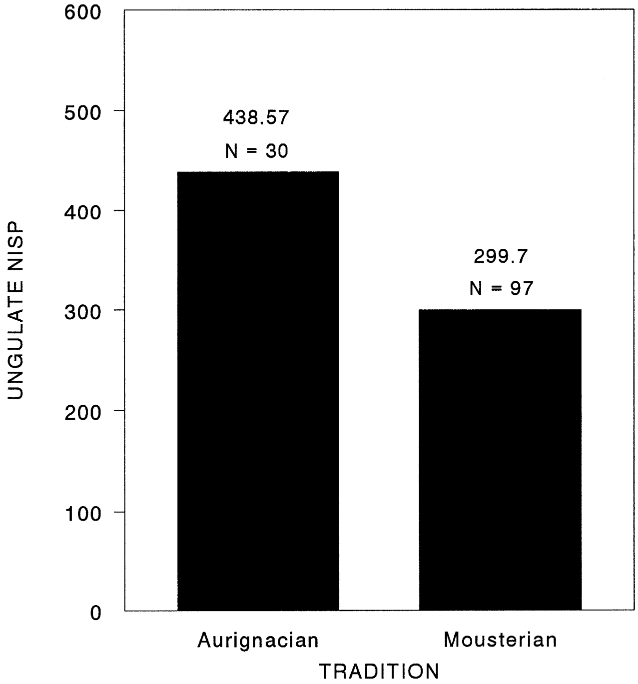

Fig. 6. Average Mousterian and Aurignacian ungulate assemblage sizes in southwestern France (data from Ref. [37]).

With Simek, we see no strong evidence for increased human population densities during Aurignacian times in southwestern France. Current censuses suggest that there are 3.5 times as many Aurignacian sites known from France as there are Châtelperronian ones [23]. However, these two archaeological units are not only of different durations, but we are not even sure what those durations are (e.g., Ref. [88]). Perhaps more importantly, even if there is no strong evidence that Aurignacian population densities were greater than those immediately earlier, we actually have no reliable population density data at all for this period of time.

We do have what appears to be more secure data on lithic and faunal assemblage sizes for the Mousterian and Aurignacian and, to a lesser extinct, for the Châtelperronian. Fig. 5 shows average lithic assemblage sizes for the Mousterian, Châtelperronian, and Aurignacian in southwestern France. These averages were calculated from the data provided by Grayson and Cole [33]; with some exceptions, they reflect average numbers of formed tools in these assemblages. Obviously, average assemblage size increases sharply from the Mousterian to the Aurignacian.

Fig. 6 provides data on average ungulate assemblage sizes for the French Mousterian and Aurignacian, using data from Grayson and Delpech [37]; we do not include data for the Chatelperronian because there are only six such assemblages known to us from this area for which NISP values are available (see the discussion in Ref. [37]). Even though we lack Châtelperronian data, the same upwards trend in assemblage size that is displayed by the lithic assemblages is evident.

We suggest that these increases are consistent with either increased group residence times or increased group size, or both. It is to this increase—and not to anything involving innate Neanderthal behavioral abilities—to which we attribute the decline of cave bear abundances seen at Grotte XVI.

We are not arguing that human residence times necessarily increased at Grotte XVI across the MUPT. We are instead suggesting that this process occurred on a regional basis, and that the cave bear history provided by Grotte XVI provides a glimpse of this process as monitored from a single point on the ground. Indeed, Leney [53] has suggested that by providing increased competition for prey items, expanding human population densities may have played a role in driving morphological changes in European cave bear populations. If this turns out to have been the case, and the heart of Kurtén's hypothesis survives additional tests, we might finally be in a position to confirm an anthropogenic role in the Pleistocene extinction of a large mammal on a Northern Hemisphere continent [39,40].

4. Conclusions

We have been unable to detect any significant change in ungulate utilization by people across the MUPT at Grotte XVI that cannot be accounted for by climate change. This result joins the more general arguments made by others, cited above, that there is no evidence for major changes in the nature of human subsistence in western Europe at this time.

Indeed, the Grotte XVI ungulate assemblage that emerges as distinctly different is neither Mousterian nor Châtelperronian, but Magdalenian. We argue that the extreme focus on a single taxon displayed by this assemblage (95% of which is reindeer) is a direct reflection of what was available on the landscape at that time, in turn a function of cold summer temperatures [38]. However, the degree to which the specimens in this assemblage bear cut marks distinguishes it from every other assemblage in the site. Had it been the Mousterian Couche C assemblage that stood out in this way, one might have argued that this was caused by the inability of Neanderthals to perform precise manipulations of cutting tools (e.g., Refs [12,41,86]). While we do not explore the distinctive nature of the Grotte XVI Magdalenian ungulate assemblage in detail here, we do note that analyses of archaeological site densities by Demars for France [23] and Straus and his colleagues for northern Spain [84,85] strongly indicate that human populations during later Magdalenian times were higher than anything that had come before (see also Ref. [19]). We suggest that the intensive utilization of ungulates during Magdalenian times indicated by the Stratum 0 fauna, as well as by other Magdalenian faunas in France (e.g., Refs [18,21]), may reflect an increase in human predator–prey ratios on the landscape and an attendant increase in the amount of effort taken to extract energy from prey items [32,45,73].

The focus of this paper, however, is the MUPT at Grotte XVI, and here we find no significant differences in ungulate utilization across this transition. Unfortunately, this result may have equivocal meaning for the heated arguments that involve this period, and not simply because we lack adequate control over the season or seasons during which the Grotte XVI ungulate assemblages accumulated. Perhaps most bothersome is the fact that archaeologists do not agree as to the meaning of the differences that exist between the Mousterian and Aurignacian—the presence of complex rock art, for instance, or of bone tools [14,15,62]. If we have no framework within which to interpret such differences, then it follows that we also have no framework in which to interpret similarities.

In addition, that there are no detectable differences in ungulate use across the MUPT at Grotte XVI does not mean that the adaptations that led to the accumulation of these faunas were identical. There is obvious technological change that occurs during this period of time, but we have little secure idea as to the relationship of that change to subsistence pursuits. It could, for instance, be suggested that Middle and early Upper Paleolithic peoples in western Europe pursued exactly the same taxa in exactly the same proportions, but that Middle Paleolithic failure rates were both higher and equally distributed across all taxa pursued. Were that the case, Upper Paleolithic peoples would have had distinctly higher energetic return rates from hunting even though the faunal assemblages that accumulated across the MUPT could not be distinguished in ways other than can be explained by changing climates. That is, similarities in ungulate faunal assemblages may be telling us less about return rates than we might wish, even though differential return rates are assumed to be key in understanding the evolution of subsistence systems.

There are also obvious changes in human morphology that occur across the MUPT. If those changes—decreased energy expenses in walking, for instance [86]—led to greater energetic returns from hunting across the MUPT, then, in this way as well, identical ungulate assemblages may be telling us less than we might hope about the most crucial aspects of human subsistence adaptations that marked this period of time. That is, it is fully possible that structurally identical faunal assemblages across the MUPT were provided by anatomically driven adaptive regimes that provided distinctly different energetic returns. This might be the case whether the shift from Neanderthal to modern morphology in Europe were driven by replacement via migration [49,62] or some form of multiregional evolution [24,87].

Caveats aside, Grotte XVI is the first site from southwestern France to have provided substantial ungulate assemblages from securely stratified, carefully excavated Mousterian, Châtelperronian, and early Aurignacian contexts. Our analyses suggest that there are no detectable, significant differences across these assemblages, other than those that can be accounted for by climate change.

Acknowledgements

Our sincere thanks to Kristine M. Bovy, Richard G. Klein, James F. O'Connell, J.-Ph. Rigaud, John D. Speth, and Lawrence G. Straus for extremely valuable comments on earlier versions of this paper. The analysis of the Grotte XVI fauna was supported by the National Science Foundation (BCS98-04692, BCS02-03278), the Sous Direction de l'Archéologie et Direction des Musées de France (Ministère de la Culture), and the Conseil Général de la Dordogne.

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